Cumulative effects of human landscape change, predators, and natural habitat drive distributions of an invasive ungulate

by

Siobhan Darlington

B.Sc. Dalhousie University, 2014

A Thesis Submitted in Partial Fulfillment of the

Requirements for the Degree of

MASTER OF SCIENCE

in the School of Environmental Studies

Cumulative effects of human landscape change, predators, and natural habitat drive distributions of an invasive ungulate

by

Siobhan Darlington

B.Sc. Dalhousie University, 2014

Supervisory Committee

Dr. Jason T. Fisher, Co-Supervisor

(School of Environmental Studies)

Dr. John P. Volpe, Co-Supervisor

(School of Environmental Studies)

Dr. Cole Burton, Outside Member

(Department of Forest Resources Management, University of British Columbia)

Abstract

Human footprint - in which land is converted for human use - is a leading contributor to global habitat and biodiversity loss. The accelerated rate of human landscape change to meet our growing needs has led to the direct loss of critical habitat and shifts in species distributions, interactions, and behaviour. These altered conditions affect species' ability to adapt to environmental stressors, while some species thrive and others decline. In North America, one ungulate has successfully invaded new habitat in conjunction with human land use – the white-tailed deer. Across the continent, the invasion of white-tailed deer has led to increased competition with other ungulate species including mule deer, moose, and woodland caribou. In regions with abundant apex predators, they have become a source of primary prey as their populations increase. The mechanisms by which deer occupy landscapes in the northern extents of their geographic range are not well studied outside of the winter months, or how deer respond behaviourally to various types of human disturbance in a predator-rich environment.

To address these knowledge gaps, I examined population scale resource selection across seasons and individual movement behaviour in white-tailed deer in northeastern Alberta's intensively developed oil and gas landscape. I used previously developed models of predator frequency to spatially extrapolate wolf and black bear occurrence across my study region as indicators of indirect predation risk. I used two approaches to habitat modeling to examine deer responses to various modes of human landscape change, including roads, seismic lines, and cut blocks in addition to predators and natural habitat. Deer were best described by cumulative effects – or the combination of all of these factors – across all seasons with proximity to linear features explaining the most variation among the parameters tested. Most prominently in winter, deer strongly selected for habitat features expected to contain abundant natural sources of forage, and linear features, despite a potential increased risk of predation by wolves – suggesting that deer make energetic trade-offs between forage availability and predation risk. At the individual level, deer significantly increased their rate of movement when occupying habitat associated with predation risk. I suggest that deer make greater energetic trade-offs during winter when mobility is limited to evade predators and energetic costs are higher.

The continued use of anthropogenic features post-winter, increased rate of movement and spread of landscape occupancy by deer may allude to the importance of human disturbance in maintaining deer in northern climates. Linear corridors may be an important mechanism by which deer are able to successfully colonize new areas at the northern extents of their range. My results shed light on the drivers of deer distributions in human altered landscapes for managing populations where the invasion of deer is complicit in the decline of other ungulate species such as woodland caribou in Alberta's boreal forest.

Table of Contents

List of Tables

List of Figures

Acknowledgements

The past three years have provided me with some of the most challenging and rewarding experiences in my early career. Much of what I have learned would not have been possible without the encouragement, dedication, and support of my supervisor Dr. Jason Fisher who never failed to remind me of the importance of this research and to own my successes as much as the failures. I am forever grateful for his positivity and ability to spin a bug into a feature. I am lucky to have worked alongside my co-supervisor Dr. John Volpe who always challenged me to think about the big picture, and test my understanding of the most fundamental ecological concepts. Joining their team has allowed me to become a better researcher, science communicator, and a slightly better foosball player. Thank you to Dr. Cole Burton for his contribution as my committee member and for providing a kind and critical eye to my research. And thank you to everyone on the InnoTech Alberta and ABMI team that worked on the boreal deer project through its conception, implementation, and completion over the past 7 years.

The surf & turf lab has been a fundamental support system throughout this journey, from challenging one another in lab meetings to sharing papers and R code and taking much needed beer breaks at Smuggler's pub. I would like to thank Frances Stewart for always initiating beer time and for being my role model and big sister in the lab. You have been a much needed source of both brainpower and advice and I am very grateful to you for all of your kindness and your endless step selection puns. Sandra Frey and Gillian Fraser you are my co-conspirators and the best field partners I could have asked for. Thank you for lending your ears when I needed to rant or brainstorm about my project, I hope we get to collar some big cats together someday.

I would like to thank my friends in Geography at UVic for getting me through my first year. Without you I may not have continued down this path and found a home in Environmental Studies. I would like to thank Alexandra Frances for her tremendous support and stats wisdom, and her pup Arlo for being the perfect lab buddy. Thank you to the rest of Team Gin and to everyone in the School of Environmental Studies for making me feel welcome and for all of the food and fun times we've shared. Thank you to Ecology @ UVic for providing a space for ecologists across campus to meet and share their research.

To my family and friends in Nova Scotia thank you for your love, encouragement, and visits to Victoria. I would especially like to thank my granny Christine Darlington for helping me out in any way she can and for checking in with me regularly on Skype. And to my mum Michelle Darlington whose years of hard work and world views have allowed me to pursue my passion in life. I'm grateful to my sister Tonya and brother Cameron for their visits, advice, and support. And finally my adventure partner David Bell for joining me in my love of the outdoors, birding, and for keeping me sane through the roller coaster that is grad school.

Funders

I would like to thank InnoTech Alberta for the opportunity to collaborate on this project and for the funding and resources that supported me through my studies. Thank you to NSERC for awarding me with a Canada Graduate Scholarship and the University of Victoria for numerous Graduate Awards and the President's Research Award. Thank you to the department of Environmental Studies for awarding me the Lorene Kennedy Write-Up Award. Finally, thank you to our project funders for their financial support of Boreal Deer Project including Alberta Environment and Parks, the Petroleum Technology Alliance, and Mitacs Accelerate.

Dedication

I would like to dedicate this work to

M*y mother Michelle, grandparents Christine & David,*

my sister Tonya, and brother Cameron.

CHAPTER 1: An introduction to the causes and implications of white-tailed deer range expansion in Canada's boreal north

Human land-use and global climate change are the leading causes of habitat and biodiversity loss world-wide (Segan *et al*. 2016). As global average temperatures and human development increase, species are faced with accelerated changes in their environment. The impacts of these changes include declines in populations, reduced reproductive success, the spread of invasive species, and altered predator-prey interactions (Segan *et al*. 2016). Furthermore, habitat loss can prevent species' adaptive responses to climate change which include shifts in species distributions and changes in behaviour (Segan *et al*. 2016). The ability to adapt is essential for species in northern climates where rates of warming are greatest and seasonal extremes occur (Parmesan & Yohe, 2003). Migratory animals can travel long distances to evade severe weather and reduced habitat quality while other, non-migratory animals must employ energy-saving strategies to cope with harsh conditions (Runge *et al.* 2014). Converted landscapes from intensive human development in the north can tip the balance in favour of some species by introducing new suitable habitat (Fisher & Burton, 2018). Ultimately, the effects of human land-use compounded by a changing climate can impact how species interact with their environment, and determine which species thrive under new conditions and which fail to adapt.

Few large mammals have been as successful at colonizing new habitat and boosting population size as the white-tailed deer. White-tailed deer (*Odocoileus virginianus*, Zimmermann) are highly adaptable to changing environments and have been expanding the limits of their geographic range across North America over the past sixty years (McCabe & McCabe, 1984; VerCauteren, 2003; Côté *et al.* 2004; DeYoung, 2011; Dawe *et al*. 2014). Their western range expansion across the United States is largely attributed to an affinity to urban and agricultural landscapes and predator control (Vogel, 1989; VerCauteren, 2003). The northern extents of their range have normally been limited by harsh winters, deep snow, and low quality forage offered by conifer stands (Hewitt, 2011). They are now one of the most pervasive ungulates in Canada and maintain the largest range on the continent of any native terrestrial mammal (Pagel *et al*. 1991; Hewitt, 2011).

The invasion of white-tailed deer has resulted in cascading effects of overabundance in areas with limited predation or hunting pressure. Higher densities of deer can lead to overbrowsing, causing reduced forest understorey cover and complexity, accelerated forest succession, and decelerated nutrient cycling (Côté *et al.* 2004). These changes to forest ecosystems indirectly affect birds, small mammals, and invertebrates that depend on understorey canopy (Côté *et al*. 2004). Increasingly, white-tailed deer invasion has led to competition with other ungulates such as mule deer (McClure *et al*. 1997; McClure *et al*. 2015) in the west, and moose (*Alces alces*) and caribou (*Rangifer tarandus caribou*) (DeCesare, *et al.* 2010) in the north.

Recently, the causes attributed to white-tailed deer expansion have been linked to global climate change with warmer average temperatures incurring lower winter snowfall totals (Dawe & Boutin, 2016). Mortality rates in deer increase dramatically during harsh winters (Hewitt, 2011), therefore warmer temperatures may be allowing deer to occupy formerly inhospitable environments, reduce energetic costs, and increase survivorship (Loison, 1999; Hewitt, 2011). Milder winters lead to higher body mass in deer (Mysterud *et al.* 2001) and may contribute to local range expansion by increased occupancy in summer ranges (VerCauteren, 2003). During harsh winter conditions, deer are thought to seek refugia in coniferous stands and yard together due to limited movement, increased energetic costs, and higher susceptibility to predation (Hewitt, 2011). In the summer, deer typically occupy hardwood forests and agricultural areas with greater forage availability (VerCauteren, 2003). Deer preferentially feed on woody stems of deciduous trees, nuts, berries, and grasses which are provided by early successional stages of regeneration (Hewitt, 2011). Increased temperatures play a vital role in the lengthening of the growing season, promoting primary productivity and providing increased forage resources for deer (Jarvis & Linder, 2000, Dawe *et al*. 2014).

Though the effects of climate change are wide-spread, they act at large scales over slower temporal gradients to promote forage availability than the direct conversion of land for human development. Consequently, human land-use has been identified as a second driver of white-tailed deer range expansion (Côté *et al*. 2004; Dawe & Boutin, 2016). The causes of range expansion have been historically linked to the intensification of agriculture, silviculture, and timber harvesting in North America during the 20th century (Alverson *et al*. 1988; Porter & Underwood, 1999; Fuller & Gill, 2001; Côté *et al*. 2004). Deer populations were traditionally

managed by First Nations by hunting and controlled burns to promote deer habitat (VerCauteren, 2003). During the pre-industrial era, populations declined due to intensive market hunting in the United States until the turn of the century when hunting regulations (Brown *et al*. 2000), predator control (Boitini, 1995), and land conversion, lead to population surges (VerCauteren, 2003). The conversion of mature forests to grassy meadows and early successional stages of regenerating aspen and hardwoods has resulted in large expanses of favourable deer habitat (VerCauteren, 2003; Hewitt, 2011). In northern regions, agriculture is less prominent on the landscape prompting research regarding other potential human land-use changes that promote forage for deer (Fisher & Wilkinson, 2005). In Canada, extensive industrial development in the north for oil and gas extraction has led to vast areas of clear-cut boreal forest in tandem with the invasion of white-tailed deer (Latham *et al*. 2011; Dawe *et al*. 2016).

The northern Alberta boreal forest is a model system for analyzing the effects of human land-use change and seasonality on white-tailed deer distributions and behaviour. Northern Alberta has undergone rapid development in the past thirty years as a hub for multiple extractive industries including timber harvesting and oil and gas exploration on the world's second-largest oil reserve (Wasser at al. 2011). Open pit surface mining comprises 19% of energy development with the remaining 81% attributed to in-situ extraction of deep underground reserves (Schneider & Dyer, 2006). In-situ development involves extensive linearization of the landscape in the form of seismic lines, roads, and pipelines, directly causing loss of habitat and creating travel corridors for wildlife (McKenzie *et al*. 2012). Timber harvesting further alters habitat by clear-cutting mature stands and replacing them with patches of early seral vegetation (McKenzie *et al*. 2012).

Industrial development indirectly affects predator-prey interactions by facilitating predation through improved visibility in clear-cut areas and movement through corridors (Mckenzie *et al*. 2012). This effect has been studied most notably in gray wolves (*Canis lupus*), who use seismic lines to travel faster and more efficiently across their territory to predate woodland caribou (Latham *et al*. 2011). The perceived risk of predation associated with these features can elicit a behavioural response in prey with regard to habitat selection. Habitat selection is a behavioural consequence of animals actively selecting where they live, or passively persisting in certain habitats (Boyce & McDonald, 1999). Selection occurs when resources are used

disproportionately to their availability (Manly *et al*. 2002). As such, caribou avoid traveling or foraging along seismic lines (Latham *et al*. 2011).

The continued decline in woodland caribou populations has been largely attributed to increases in wolf densities, encounters, and hunting efficiency (Schneider *et al*. 2010). In turn, gray wolf populations have been artificially increasing in response to primary prey enrichment of moose and invasive white-tailed deer in the boreal forest (Latham *et al*. 2011). The artificial increase in apex predators by prey enrichment leads to increased predation pressure on alternative prey by apparent competition (DeCesare *et al.* 2010). Apparent competition is defined as the indirect interaction between two or more prey species through a shared predator, where the presence or abundance of one prey species is negatively correlated with the other (Holt, 1977; Wittmer *et al.* 2013). Consequently, increases in white-tailed deer indirectly reduce woodland caribou populations.

Research regarding the effect of industrial linear and block features on predator-prey movement behaviour in Alberta has been focused on wolves (Latham *et al.* 2011; Dickie *et al.* 2016), caribou (Latham *et al.* 2011) and elk (Prokopenko *et al.* 2017) with little attention given to the most abundant ungulate – white-tailed deer. Whether deer use linear features as movement corridors to travel more efficiently or access resources similar to wolves, or whether they perceive these features as "risky" (Creel *et al.* 2008) similar to caribou is not well understood. How, when, and why animals move is important for elucidating the mechanisms behind species habitat selection, biotic interactions, and energetic trade-offs. Movement ecology is important for wildlife management (Allen & Singh, 2016) and can help us understand how individual variation in movement can lead to population level shifts in species distributions.

The focus of my thesis is to further our understanding of seasonal changes in white-tailed deer habitat selection and movement with regard to industrial development and predators in the northeastern Alberta boreal forest. Previous research has highlighted the importance of climate change in driving deer range expansion, however industrial sources of forage subsidy may contribute more to deer occupancy at a landscape scale. Gaps in the literature exist regarding the contribution of various modes of industrial disturbance to deer distributions and whether there are differential effects across seasons. In Chapter 2, I focus on identifying the drivers of white-

tailed deer third-order habitat selection across biological seasons. I extrapolate existing predator frequency models derived from camera trap data across our study region and use these estimates as indicators of predation risk. I then model white-tailed deer occurrence in relation to predators and industrial features associated with timber harvesting and in-situ oil and gas extraction. In Chapter 3, I narrow my lens to identify movement patterns of individual white-tailed deer. I employ a newly developed approach to modeling mechanistic movement and measure how the rate in which deer move changes with various landscape features to examine foraging and risk avoidance behaviour at a finer scale.

The northerly expansion of white-tailed deer is an indirect and persistent contributor to woodland caribou decline; therefore the inclusion of white-tailed deer management efforts is paramount to effective caribou recovery plans in Alberta. Understanding the mechanisms by which deer distribute and occupy human-altered landscapes at multiple scales is important for mitigating the effects of overabundance and contributes to the greater literature on energetic trade-offs, linear disturbances, predator-prey interactions, and movement ecology.

Literature Cited

Alverson, W.S., Waller, D.M., & Solheim, S.L. (1988). Forests to deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2:348-58.

Boitani L. 1995. Ecological and cultural diversities in the evolution of wolf-human relationships. In Ecology and Conservation of Wolves in a Changing World, ed. LN Carbyn, SH Fritz, DR Seip, pp. 3-11. Edmonton, Al berta: Can. Circumpolar Inst., Occas. Publ. 35. 642 pp.

Boyce, M. S., & McDonald, L.L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution, 14(*7): 268-272.

Brown, T.L., Decker, D.J., Riley, S.J., Enck, J.W., Lauber, T.B. (2000). The future of hunting as a mechanism to control white-tailed deer populations. *Wildl. Soc. Bull. 28*:797- 807.

Côté, S.D., Rooney, T.R., Tremblay, J.P., Dussault, C., & Waller, D.M. (2004). Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics, 35: 113-147.

Coristine, L.E., & Kerr, J.T. (2011). Habitat loss, climate change, and emerging conservation challenges in Canada. *Canadian Journal of Zoology, 89*(5): 435-451.

Dawe, K.L, & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (Odocoileus virginianus) range expansion at the northern extent of its range; land-use is secondary. *Ecology and Evolution. 6*(18); 6435-6451.

Dawe, K.L., Bayne, E.M., & Boutin, S. (2014). Influence of climate and human land use on the distribution of white-tailed deer (Odocoileus virginianus) in the western boreal forest. *Can. J. Zool. 92*: 353–363.

DeCesare, N. J., Hebblewhite, M., Robinson, H. S., Musiani, M. (2010). Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation, 13*: 353–362.

DeYoung, R. W., Miller, K.V., & Hewitt, D. (2011). White-tailed deer behaviour. Biology and management of white-tailed deer:311-351.

Environment Canada. (2012). Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population in Canada.

Fisher, J.T., & Burton, A.C. (2018). Wildlife winners and losers in an oil sands landscape. *Front Ecol Environ. 16*(6): 323-328.

Fisher, J.T., & Burton, A.C. (2016). Moose and Predator Numerical Responses to Anthropogenic Features in the Alberta Oil Sands Region of Alberta. Alberta Innovates – Technology Futures, Vegreville, AB. 34 pp.

Fisher, J.T., & Wilkinson, L.(2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev 35*: 51–81.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005). Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. *Ecology 86*:1320-1330.

Fuller, R.J. (2001). Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. *Forestry*, 74:289-98.

Government of Alberta. (2016). Setting Alberta on the path to caribou recovery. Retrieved at: http://aep.alberta.ca/fish-wildlife/wildlife-management/caribou-management/caribou-action-range-planning/documents/OnThePathtoCaribouRecovery-May-2016.pdf

Hebblewhite, M., Merrill, E.H., & Mcdonald, T.L.. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos, 111*:101–111.

Hewitt, D. G. (2011). Nutrition. Pages 75-106 Biology and management of white-tailed deer. CRC Press, Taylor & Francis Group, Boca Raton, Florida.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol 12*:197-229.

Kie, J.G. (1999). Optimal Foraging and Risk of Predation: Effects on Behaviour and Social Structure in Ungulates. *Journal of Mammology, 80*(4): 1114-1129.

James, A. R. C., & Stuart-Smith, A.K.. (2000). Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management, 64*: 154-159.

Johnson, C.J., Ehlers, L.P.W., Seip, D.R. (2015). Witnessing extinction – Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biological Conservation, 186:* 176–186.

Johnson, C. J., Nielsen, S. E., Merrill, E.H., Mcdonald, T. L., Boyce, M. S. (2006). Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management 70*:347–357

Latham, A. D. M., Latham, M.C., Boyce, M.S., & Boutin, S. (2011)a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications 21*:2854-2865.

Latham, A. D. M., Latham, M.C., McCutchen, N.A., &. Boutin, S. (2011)b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management 75*:204-212.

Latham, A. D. M., Latham, M.C., & Boyce, M.S. (2011)a. Habitat selection and spatial relationships of black bears (Ursus ameriCanis) with woodland caribou (Rangifer tarandus caribou) in northeastern Alberta. *Canadian Journal of Zoology 89*:267-277.

Latham, A. D. M., Latham ,M.C., Knopff, K.H., Hebblewhite, M., & Boutin, S. (2013). Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography, 36*(12): 1276–1290.

Leblond, M., Dussault, C., & Ouellet, J.P. (2010). What drives fine-scale movements of large herbivores? A case study using moose. *Ecography, 33*: 1102-1112.

Loison, A., Langvatn, R., Solberg, E.J. (1999). Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecog raphy, 22*:20-30.

Losier, C., Couturier, S., St-Laurent, M., Drapeau, P., Dussault, C., Rudolph, T., Brodeur, V., Merkle, J., & Fortin, D . (2015). Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *Journal of Applied Ecology, 52*; 496–50.

Mahat, V., & Tarboton., D.G. (2013). Representation of canopy snow interception, unloading and melt in a parsimonious snowmelt model. *Hydrological processes, 28*(26); 6320–6336.

McCabe, R.E., and T.R. McCabe. 1984. Of slings and arrows: an historical retrospection. Pages 19-72 in L.K. Halls, editor, White-tailed deer: ecology and management. Stackpole Books, Harrisb

McClure, M.F., Bissonette, J.A., Conover, M.R., & Austin, D.D. (1997). Range expansion of White-tailed deer (Odocoileus virginianus) into urban and agricultural areas of Utah. The Great Basin Naturalist, 57(3): 278-280.

Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R., Steinheim, G. (2001). Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature, 410*:1096-99.

Pagel, M.D., May, R.M., & Collie, A.R. (1991). Ecological aspects of the geographyical distribution and diversity of mammalian species. American Naturalist, 137: 791-815.

Parker, K. L., Robbins, C.T., & Hanley, T.A. (1984). Energy expenditures for locomotion by mule deer and elk. *J. Wildl.Manage. 48*: 474-488.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature, 421*;37–42.

Porter, W.F. (1999). Of elephants and blind men: deer management in the U.S. national parks. *Ecol. Appl*. 9:3-9.

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G., Fuller, R.A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment, 12*(7): 395-402.

Schneider, R. R. (2002). Alternative futures: Alberta's boreal forest at the crossroads. Federation of Alberta Naturalalists, Edmonton, Alberta, Canada.

Schneider R.R., & Dyer, S. (2006). Death by a Thousand Cuts: The Impacts of In Situ Oil Sands Development on Alberta's Boreal Forest. Pembina Institute for Appropriate Development.

Schneider R.R., Hauer, G., Adamowicz, W.L., & Boutin S. (2010). Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biol Conserv 143:* 1603-11.

Segan, D.B., Murray, K.A, Watson, J.E.M. (2016). A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. *Global Ecology and Conservation, 5*: 12-21.

VerCauteren, K.C. (2003). The Deer Boom: Discussions on Population Growth and Range Expansion of the White-Tailed Deer. U.S. Department of Agriculture: Animal and Plant Health Inspection Service. Pages 15-20 in G. Hisey and K. Hisey, editors. Bowhunting records of North American white-tail deer. Pope and Young Club, Chatfield, MN, USA.

Vogel, W.O. 1989. Response of deer to density and distri- bution of housing in Montana. *Wildlife Society Bulletin, 17:*406-413

Wasser, S.K., Keim, J.L., Taper, M.L., & Lele, S.R. (2011). The influences of wolf predation, habitat loss, and human activity on caribou and moosein the Alberta oil sands. *Frontiers in Ecology and the Environment, 9*(10); 546-551.

Wittmer, H. U., Serrouya, R., Elbroch, M. L., Marshall, A. J. (2013). Conservation Strategies for Species Affected by Apparent Competition. *Conservation Biology*, *27*(2): 254-260.

CHAPTER 2: Cumulative effects of human land-use, natural habitat & predation risk best predict seasonal resource selection of white-tailed deer in a high disturbance landscape

2.0 Introduction

Habitat loss from the conversion of natural habitats to human-dominated habitats (Pereira *et al*. 2012) is one of the largest drivers of biodiversity loss globally (Segan *et al*. 2016). The demand for resources to satisfy a growing global population has been driving land-use change at an accelerated rate. On average, populations of terrestrial vertebrates around the globe for which trend data are available have declined by 25% since the 16th century (Dirzo *et al*. 2014). The main drivers of this decline are attributed to overexploitation – the harvesting of species from the wild – and agriculture – the production of food, fibre, fuel, and the cultivation of trees (Maxwell *et al*. 2016). Direct habitat loss from the conversion of mature forests for agriculture is often viewed as the most intensive form of disturbance to wildlife (Eisner *et al*. 2016), though habitat fragmentation from road networks and other forms of linear disturbance have more recently received attention (Tilman *et al*. 1994; Fahrig, 2003; Wilting *et al*. 2017). These forms of landscape change can alter biodiversity indirectly by modifying community structure, shifting species distributions (Pereira *et al*. 2012; Fisher & Burton, 2018), and influencing animal behaviour (Latham *et al*. 2011).

Canada's boreal region contains one quarter of the world's remaining original forests (Schneider & Dyer, 2006) and is subject to rapid human development, creating a landscape far outside the range of natural variation (Pickell *et al*. 2015). Alberta's famous oil sands region is the epitome of intensive human land-use change (Rosa *et al*. 2017), with industrial impacts extending far beyond open pit mining. In 2010 over half of the 600,000 km of linear disturbance in Alberta's boreal forest was attributed to timber harvesting and in-situ oil and gas extraction (Pascher *et al*. 2013) with an average of 14, 000 new 1 ha well sites cleared every year for drilling (Alberta Environment and Sustainable Resource Development, 2013; Pickell *et al*. 2015). This mosaic of disturbance creates a fragmented, grid-like landscape of cleared forest over time that is slow to regenerate (Dabros *et al*. 2018), creating a wide-spread source of early seral forage (Fisher & Wilkinson, 2005) and travel corridors for wildlife (Latham *et al*. 2011;

Dickie *et al*. 2017) that directly and indirectly affect species interactions (Fisher & Burton, 2018).

Landscape change in northern environments like the boreal forest occurs against a backdrop of climate change that cumulatively alters species distributions (Dawe & Boutin, 2016; Heim *et al*. 2017). Species that experience seasonal extremes are under pressure to adapt to changing conditions quickly as winters fluctuate in severity, vegetation shifts, and habitat is lost (Parmesan & Yohe, 2003). The most immediate animal response to changing environmental conditions is likely to alter habitat selection in an effort to maintain maximum fitness as the abundance and quality of resources fluctuate (Parmesan, 2006; Lemay *et al*. 2013). Habitat selection – when resources are used disproportionately to their availability (Manly *et al.* 2002) – is influenced by a number of interacting environmental and biological factors, including competition, predation, human land-use, and climate change (Kie, 1999).

The role of human land-use in contemporary invasions or range expansions is crucial and receives less attention than global climate change (González-Moreno *et al.* 2015). Human land-use change often provides nutrient-rich conditions for invasive and regenerating vegetation that support higher trophic levels (Hobbs & Huenneke, 1992; Dietz & Edwards, 2006). Some species, such as invaders, benefit from landscape change and warmer conditions while others are imperiled by the loss of suitable habitat, connectivity, and altered predator-prey dynamics (Fisher & Burton, 2018). Shifting species' distributions and invasions affect the communities they invade, and are a primary focus for conservation biology (Clavero & Garcia-Berthou, 2005). Invasive species negatively impact biodiversity and ecosystem function directly through increased competition and predation, and indirectly through changes in disturbance regimes, nutrient levels, and micro-climate (Parker *et al*. 1999, Pimentel *et al*. 2005; Shackelford *et al*. 2013). Treating the underlying causes of invasion can be an effective management strategy for mediating the impacts of invasive species (Hobbs 2000; Shackelford *et al*. 2013). The nearctic boreal forest is a special case of this global problem, where intensive landscape change has affected the entire mammal community (Fisher and Burton 2018) but one species in particular– white-tailed deer – is thriving.

White-tailed deer (*Odocoileus virginianus*, Zimmerman, 1780) have been expanding the limits of their northern range for the past fifty years, with populations occurring today as far north as the southern Yukon Territory and increasing in abundance in areas of high human disturbance (Webb, 1967; McCabe & McCabe, 1984; DeYoung *et al*. 2011; Dawe & Boutin, 2016). Previously limited by deep snow, poor quality forage, and cold temperatures, white-tailed deer are now one of the most pervasive ungulates in western Canada's boreal forest (Fisher & Burton, 2018). They are complicit in declines of native subspecies of caribou (*Rangifer tarandus caribou*) (DeCesare *et al*. 2010; DeYoung *et al*. 2011) as apparent competitors (Holt, 1977) through the shared predator, wolves (Latham *et al*. 2011). Woodland caribou are federally listed as threatened under SARA Schedule 1and threatened under the Alberta Wildlife Act (Alberta Environment and Parks, 2018; Environment Canada, 2012) Thus, any effective caribou recovery strategy requires mitigation measures that address the underlying causes of white-tailed deer expansion. Moreover, deer expansion allows us to better understand the ecological processes behind species range expansion into new biomes.

White-tailed deer range expansion at provincial scales has been attributed to human land use and reduced snowfall due to climate change (Dawe *et al*. 2014). The role of human disturbance in maintaining deer populations has not been examined beyond the winter months, and may be an important factor in determining deer occupancy year-round (Fisher & Burton, 2016). Previous studies have hypothesized that the role of human land-use in sustaining deer populations is attributed to early seral vegetation from cut blocks and other polygonal forms of deforestation (Fisher & Wilkinson, 2005; Fisher & Burton, 2018), though few have included linear features (roads, seismic lines, etc.) as indicators of risk, sources of forage subsidy, or travel corridors for prey species (DeCesare *et al*. 2010; Dawe *et al*. 2014). The effect of landscape linearization on large carnivores has been documented in the boreal forest of Alberta primarily in the last decade (Latham *et al*. 2011; Dickie *et al*. 2016), with some studies examining the effects on ungulate habitat selection (Kittle *et al*. 2008; Dawe *et al*. 2014; Prokopenko *et al*. 2017) though only during the winter months. Deer are considered poorly adapted to northern climates and face increased energetic requirements during winter when foraging is significantly hampered by snow and movement is limited (Moen, 1976; Mech *et al*.1987; Schmidt, 1993). Inability to move quickly, and weakened body condition, make deer more susceptible to starvation and

predation by wolves during winter (Kunkel and Pletscher 2001; Mech and Boitani 2003; Kittle *et al*. 2008).

Figure 2.1. Current range map white-tailed deer in the Americas (Patterson *et al*. 2003) White-tailed deer have been expanding the limits of their northern range over the past 50 years and are now present across northern Alberta and into the Yukon Territory (Dawe & Boutin, 2016).

Few studies have examined the response of white-tailed deer to landscape features and predators across biological seasons, where life history traits such as mating and calving play a role in behaviour and habitat selection (Hewitt, 2011; Cherry *et al*. 2015). For example, female ungulates face greater energetic demands from reproduction and a greater risk of predation to their calves from parturition through summer (Oftedal, 1985; Kilgo *et al*. 2012). In ungulates, anti-predator behaviour is an energetic trade-off with foraging behaviour; as vigilance levels

increase less time is a spent gathering resources in the presence of a perceived threat (Kie, 1999; Hebblewhite & Merrill, 2009; Cherry *et al*. 2015). Predation risk is a function of perceived risk and results in anti-predator behaviour both temporally and spatially (Brown *et al*. 1999; Kittle *et al*. 2008). Indirect predation risk is defined as landscape features associated with a higher risk of predation that elicits anti-predator responses (Kittle *et al*. 2008). Direct and indirect predation risk have been previously examined in white-tailed deer during the winter in central Ontario where deer selected areas associated with forage and with wolves, demonstrating a trade-off with forage acquisition and predator avoidance (Kittle *et al*. 2008). The strength of energetic trade-offs by deer are likely to fluctuate with predator abundance, resource availability, and consequently the degree of landscape disturbance.

To examine the seasonal drivers of white-tailed deer habitat selection, we sampled deer in the northeastern Alberta boreal forest, a globally unique mosaic of intensive human disturbance that experiences seasonal extremes and maintains substantial white-tailed deer and large carnivore populations (Fisher & Burton, 2018). A hub for in-situ oil and gas extraction (Rosa *et al*. 2017) and timber harvesting, this landscape is subject to large-scale linearization and clear-cutting of mature forest (Pickell *et al*. 2015; Fisher & Burton 2018) that provide travel corridors and primary prey enrichment for wolves (Latham *et al*. 2011; Hervieux *et al*. 2013). We tested, for the first time, whether industrial disturbance, predation risk, and/or natural habitat best explain white-tailed deer distributions. We weighed support for six hypotheses whereby deer habitat selection is best predicted by 1) proximity to polygonal "block" resource subsidies 2) Proximity to linear features 3) indirect predation risk 4) natural habitat 5) total human footprint from industrial linear and block features and 5) cumulative effects - the combined effects of multiple environmental and anthropogenic variables on deer distributions. We predicted that indirect anthropogenic sources of forage subsidies act as key drivers of white-tailed deer habitat selection, and that this effect is strongest during the winter when natural forage is scarce and energetic costs are high.

2.1 Methods

2.11 Study area

Our study area encompasses 3000 km^2 of mixedwood boreal forest in northeast Alberta, Canada, and intersecting the ranges of the Cold Lake and the Eastside Athabasca River caribou herds (Appendix I, Figure 1) (Schneider *et al.* 2010, Alberta Environment & Parks, 2017). The landscape is a heterogeneous mosaic of boreal forest, bog, lakes and rivers, and extensive human disturbance arising from oil and gas development to the south and forestry in the north. Petroleum extraction, timber harvesting, and industrial camps in particular have superimposed a mosaic of disturbance across the study region (Pickell *et al*. 2013, Pickell *et al*. 2015). These anthropogenic disturbances include linear features such as road and trail networks, pipelines, and seismic lines as well as block features such as cut blocks, well pads, industrial camps and facilities (Pickell *et al*. 2013, Pickell *et al*. 2015).

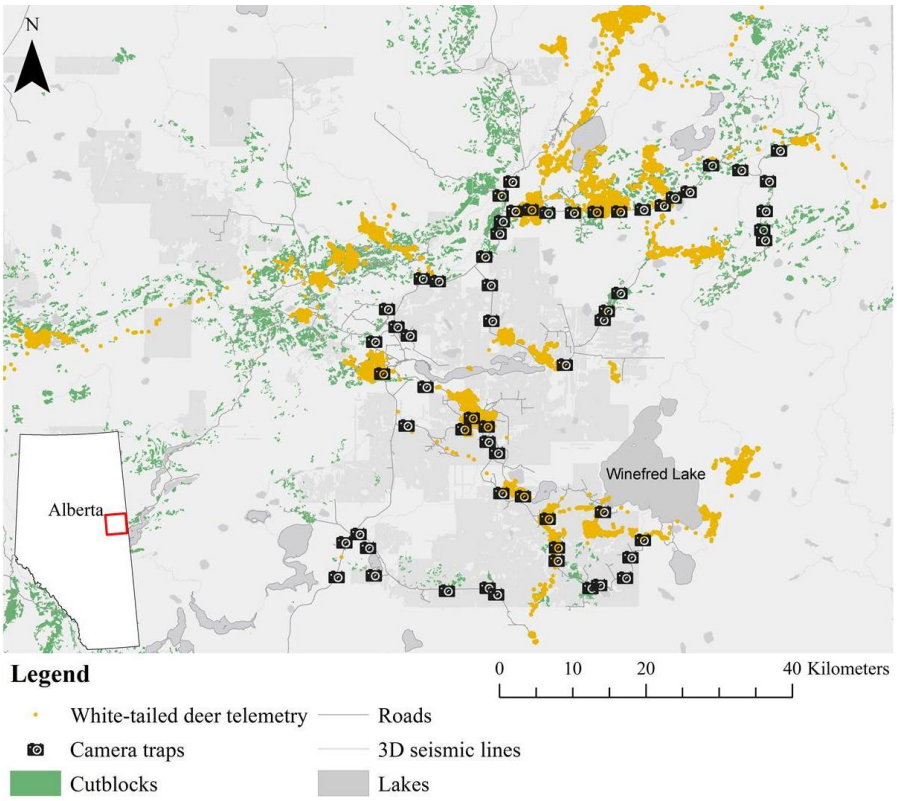


Figure 2.2. Study area and distribution of telemetry detections and camera traps
Telemetry locations for 38 female white-tailed deer collared from October 2011-2014 and 62 cameras array in a stratified random design in relation to trails, 3D seismic lines, large lakes and cut blocks across the 3000km^2 study area in northeastern Alberta.

2.12 White-tailed deer Telemetry

Thirty-eight white-tailed does were captured and collared from 2012-2014 throughout the study area in accordance with animal care protocols by Innotech Alberta's Animal Care Committee, and permitted by Alberta Environment and Parks (Permits 49365 and 48602). Does were captured using clover traps (Clover 1956) which minimize stress to deer relative to other modes of capture (DelGiudice *et al*. 1990a, DelGiudice *et al*. 2001, Haulton *et al*. 2001). Individuals were fitted with LOTEK Iridium Track M 3D telemetry collars programmed to record locations at 2-hour fixed intervals (Figure 2.2). A total of 111,978 telemetry locations were obtained over the three-year period with a mean of 2,946 locations per individual. The data were further reduced to 100, 117 locations after removing erroneous fixes. To analyze resource selection across seasons, we defined seasons for deer according to their life history stages. Winter occurs from January 1st-April 30th, parturition from May 1st to June 30th, summer from July 1st to September 30th and rut from October 1st to December 31st (DeYoung *et al*. 2011; William *et al*. 2012). Telemetry data were subset by season with 47,038 locations in winter, 27,772 in parturition, 10,253 in summer, and 15,054 in rut.

2.13 Mapping indirect predation risk

In their northern range, white-tailed deer fawns are predominantly predated by black bears in the summer, where adults are predated by wolves year-round (Kunkel & Metch, 1994; Fuller, 2004; DeYoung *et al*. 2011, Kilgo *et al*. 2012, Latham *et al*. 2013). While we did not have a direct measure of predation risk for the sampled collared deer (e.g. mortalities attributed to predation, concurrently collared predators) we used an indirect measure derived from a concurrent camera trap study by Fisher & Burton (2018) within the same study region. The camera array of unbaited infra-red Reconyx PC900 Hyperfire remote digital camera traps (Burton *et al*. 2015) was deployed using a stratified random design at 62 sites from October 2011 to 2014 to quantify frequency of carnivore occurrence (Figure 1). Species were identified from a total of 141,140 images captured including 2,508 gray wolf (*Canis lupus*), and 2,657 black bear (*Ursus americanus*) and were related to natural and anthropogenic landscape features using generalized linear models (proportional binomial; Fisher & Burton, 2016).

These models were then projected across the landscape, and we assumed that the projections represented variation in the likelihood of collared deer encountering predators which we considered to be a measure of indirect predation risk (Kittle *et al*. 2008). Extrapolation requires consistency in the environmental conditions under which the models were created (Gove & Merriam Webster, 1986) and we contend we met these assumptions as we extrapolated across the same landscape from which the models were derived.

To create our extrapolated maps we measured habitat covariates (Table 2.1) in ArcGIS 10.5 using vector data converted to raster data with 12m resolutions projected to Transverse Mercator (UTM Zone 11) and datum NAD 1983. Each raster covariate was run with a focal statistic with a search radius reflecting the best predicted scale for each species (Fisher & Burton, 2018). The resulting relative occurrence frequency distributions were generated by using the top GLM model beta coefficients as model weights and rescaled from 0 to 1 using a linear equation to extrapolate species-habitat relationships across the study area. We validated the predation risk maps by relating relative predicted occurrence frequency against camera detection rates for each species using linear regression in R (Appendix A). Predator occurrence frequency values were extracted to the telemetry data points as a measure of predation risk and included as covariates in the modelling process (Figure 2.3; Appendix A). Black bears were considered biologically irrelevant as predictors of perceived risk during their winter hibernation period, so we excluded them from the winter analysis.

2.14 Landscape covariates

We included natural and anthropogenic land cover characteristics quantified in ArcGIS 10.5. Forest cover - percent cover of overstorey species - were obtained from the Alberta Vegetation Index (AVI) (Government of Alberta, 2017) and extracted from telemetry point locations. We measured the distance between telemetry locations and all other covariates including industrial linear and polygonal features obtained from the ABMI Caribou Monitoring Unit at the University of Alberta (U of A) linear features mapping project and the Alberta Biodiversity Monitoring Institute (ABMI) human footprint project (Table 2.1).

Table 2.1. Core hypotheses and land cover covariates

Landscape variables used to quantify natural landscape features from the Alberta Vegetation Inventory (AVI), and anthropogenic landscape features from two sources: industrial linear features from the University of Alberta (U of A) updated to 2012, and industrial block features from the Alberta Biodiversity Monitoring Institute (ABMI) human footprint project updated from 2010.

Hypothesis	Variable Name	Description	Source
Resource subsidy	DistCutblock	Distance to (m) forest harvesting areas with mature trees removed and saplings regrowing	ABMI 2010
	DistWellSites	Distance to (m) well pads deforested for in-situ oil extraction	
Linear Features	DistSeismic	Distance to (m) traditional seismic petroleum exploration line *ca.* 7-10 m wide	U of A 2012
	Dist3DSeismic	Distance to (m) seismic petroleum exploration line *ca.* 1-3 m wide	U of A 2012
	DistPipe	Distance to (m) petroleum pipeline and grassy right of way	U of A 2012
	DistRail	Distance to (m) railway line and associated vegetated right of way	
	DistRoad	Distance to (m) hard surface road, Roads including vegetated verge, Unimproved (gravel) roads, truck trails, winter roads	U of A 2012
	DistTrail	Distance to (m) unimproved dirt track ca. 5-10 m wide navigable by off-highway vehicle or foot	U of A 2012
Natural Features	DistWetland	Distance to (m) open wetland including lakes, streams, and bogs	AVI
	PCT Aw*	Trembling aspen *Populus tremulodies*	AVI
	PCT Bw	White birch *Betula papyrifera*	AVI
	PCT Fb	Balsam fir *Abies balsamea*	AVI
	PCT Lt	Tamarack *Larix laricina*	AVI
	PCT Pb	Balsam poplar *Populus balsamifera*	AVI
	PCT Pj	Jack pine *Pinus banksiana*	AVI
	PCT Sb	Black spruce *Picea mariana*	AVI
	PCT Sw	White spruce *Picea glauca*	AVI
Indirect Predation Risk	Wolf GLM	Gray wolf predicted relative occurrence frequency scaled from 0-1	Fisher & Burton 2018
	Bear GLM	Black bear relative occurrence frequency scaled from 0-1	Fisher & Burton 2018

All distance-to metrics are measured in metres (m) ✦These are composite variables; we measured the distance to the closest of any of these features. .*PCT refers to the *percent* of the forest canopy overstorey dominated by this leading tree species. We also included variable denoted uPCT, referring to the percent of the forest understorey dominated by each of these tree species. AVI data were created and provided by Alberta Environment and Parks 2010 Provincial Human Footprint layers and 2012 linear features were provided by ABMI and University of Alberta, Integrated Landscape Management Lab

2.15 Seasonal Resource Selection Functions

Resource selection functions (RSFs) are habitat suitability models that are statistically estimated directly from used/available resource data (Boyce, 2002) and are common in ecological studies for quantifying the spatial and temporal changes in animal distribution and abundance (Manly, 1985, Boyce & McDonald, 1999, Manly *et al*. 2002). RSFs characterize the probability of a resource unit being selected by an organism, where each resource unit consists of a point or shape in space comprising of any number of covariates of categorical or continuous data (Manly *et al.* 2002). RSFs can be used to model species interactions in space such as mapping predator and prey encounters on a shared landscape (Hebblewhite *et al.* 2005).

We generated four seasonal RSF models according to biological season to examine the drivers of population-scale deer resource selection.We used logistic regression in a General Linear Mixed-Effects Model (GLMM; binomial errors, logit link) with used locations (1) and randomly selected available but unused points (0) regressed against landscape covariates and predation risk. The number of random points generated in a RSF depends on the sample size and the domain of availability (Boyce *et al.* 2002) however a minimum sample of 10,000 random points is generally considered to be adequate for logistic regression models (Manly *et al*. 2002, Baasch *et al.* 2010). We generated one random point for every used point, for a total of 200, 234 locations. Used locations were defined as the telemetry locations within each season's time frame; available but unused locations were randomly generated within the seasonal distribution's 100% minimum convex polygon (MCP) (Burgman & Fox, 2003; Losier *et al.* 2015).

We standardized all model covariates (mean = 0, sd = 1) (R Core team, 2016). We tested for multicollinearity following the Zuur (2013) protocol to remove shared variance and reduce type II errors across model covariates using Spearman Rank correlation coefficient (r^2) matrices for non-normal data in multi-panel scatterplots and a step-wise approach for evaluating variance inflation (Graham, 2003; Zuur *et al*. 2013). We used a Spearman Rank tolerance of $r^2 > 0.5$ and a variance inflation factor (VIF) tolerance of < 3 for all covariates (Craney & Surles, 2002). Landscape features that occurred sparsely or at distances completely outside of the species' immediate surroundings were excluded from the analysis.

We included individuals as a random effect in our GLMM models to account for pseudo-replication arising from the dependent nature of telemetry data (Gillies *et al.* 2006). The top models for each season were ranked using an information-theoretic approach using a step-wise Akaike Information Criteria (AIC) correction where the lowest AIC score reflects the most parsimonious model with the most deviance explained (Akaike, 1973, Burnham & Anderson, 2016) . We used k-fold cross validation with k=10 folds to validate each candidate model (Boyce, 2002). The top candidate GLMM equations were extrapolated in ArcGIS 10.3 for each season to obtain predicted seasonal distributions across the study region.

Table 2.2 White-tailed deer population scale RSF models

White-tailed deer hypotheses and corresponding model sets and variables for population-scale species-habitat relationships in northeastern Alberta. Each model set was tested across four seasons: winter, parturition, rut and summer to detect seasonal variation in selection. Further model combinations were generated to assess the relative importance of each model set (See candidate model tables by season in Appendix B).

Model set	**Model variables**	**Hypotheses:** Deer resource selection is best predicted by
Resource subsidy	DistCutBlock + DistWellSite	Distance to industrial block features as sources of early seral forage
Linear features	DistRoad + DistSeismic + DistSeismic3D + DistPipe + DistTrail	Distance to industrial linear features as an indirect measures of risk
(Indirect) Predation risk	WolfGLM + BearGLM	Relative predator occurrence frequency, or increased likelihood of encounters
Natural resource	PCTAw + PCTSb + PCTBw + PCTSw + PCTPb + PCTLt + PCTPj + PCTFb + DistWetland	Naturally occurring forage and canopy cover
Total Human Footprint	DistCutBlock + DistWellSite + DistRoad + DistSeismic + DistSeismic3D + DistPipe + DistTrail	The cumulative effects of all polygonal and linear industrial landuse
Cumulative effects	DistCutBlock + DistWellSite + DistRoad + DistSeismic + DistSeismic3D + DistPipe + DistTrail + WolfGLM + BearGLM + PCTAw + PCTSb + PCTBw + PCTSw + PCTPb + PCTLt + PCTPj + PCTFb + DistWetland	The cumulative effects of human footprint, natural habitat, and predation risk

2.2 Results

The white-tailed deer population distribution was best predicted by a combination of human footprint and natural landscape features across all seasons. Linear features carried the most weight within the cumulative models and were the best supported models of the four core hypotheses tested. Deer consistently selected greater aspen cover, areas with higher predicted wolf frequency, and proximity to roads, cut blocks, and trails throughout the year with seasonal variation in the relative strength of selection.

2.21 Indirect predation risk

The extrapolated wolf predator occurrence frequency estimates derived from camera trap data overlapped spatially with our deer telemetry data (Figure 2.3). Areas frequented by black bear largely excluded 3D seismic lines and spatial overlap with deer was less prominent (Figure 2.3). Consequently, deer used habitat with higher wolf predation risk than other available habitat across all seasons, and lower black bear predation risk than available during non-hibernating seasons (Figure 2.4).

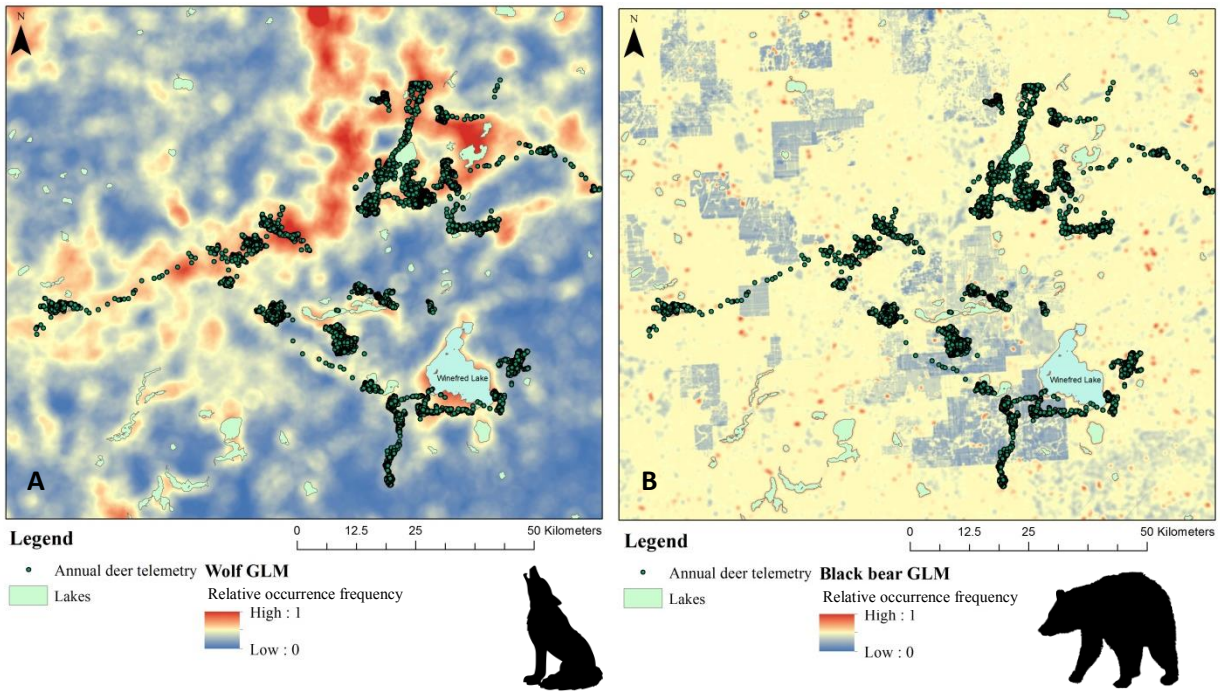


Figure 2.3. Predator distribution maps derived from Fisher & Burton (2018)
Extrapolated predator relative occurrence frequency and deer telemetry detections for A) Gray wolf B) Black bear.

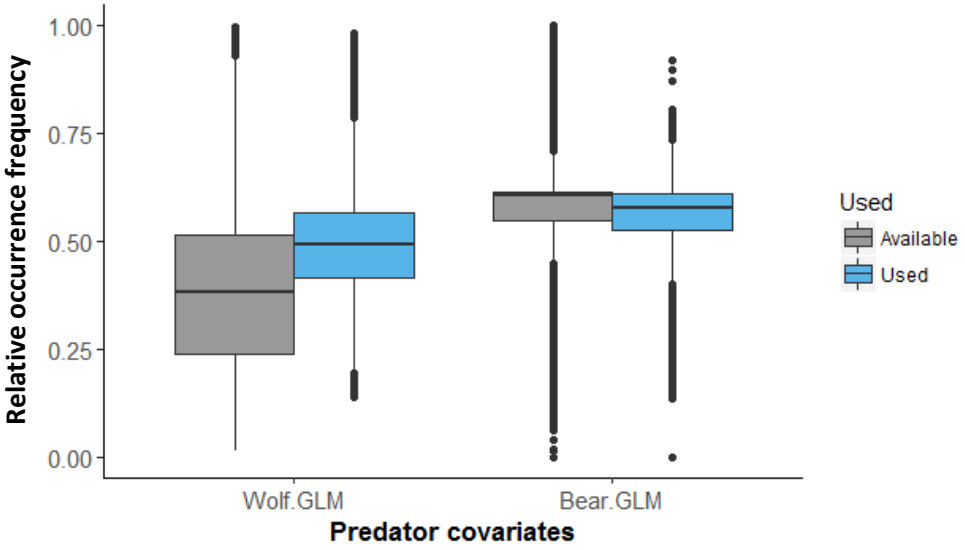


Figure 2.4. Relative predator occurrence habitat use by white-tailed deer.
Median used and available relative predator occurrence frequency index values for white-tailed deer habitat selection.

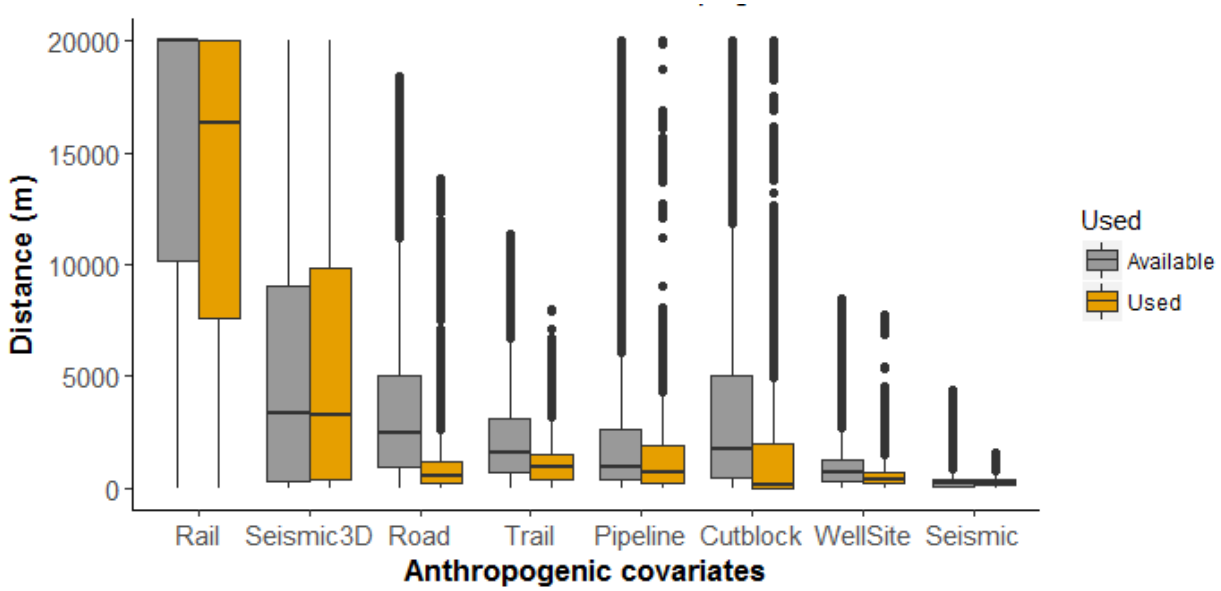


Figure 2.5. Median distances of white-tailed deer to used and available habitat
Distance to anthropogenic features (m) including industrial linear and block features between October 2011-2014.

2.22 Seasonal drivers of white-tailed deer occurrence

The cumulative effects – or global - models including predictors from all core hypotheses were the best-supported models explaining deer habitat selection during winter, parturition, and rut. Linear features, predation risk, and natural habitat best explained white-tailed deer summer distributions (Table 2.3). Candidate models including distance to linear features had consistently lower AIC scores across all seasons (Figure 2.6, Appendix B). The total human footprint model outranked linear features during winter and marginally during parturition (Figure 2.6, Appendix B). Selection of block features outranked predator distributions and natural resources during winter, though explained distributions during other seasons the least (Figure 2.6).

Table 2.3. Cumulative effects best explain seasonal deer distribution
Top models that best explain white-tailed deer resource selection by season with K parameters, candidate model set, AIC score, Log Likelihood (LL), k-fold cross validation Spearman Rank coefficient (r_s) and corresponding p-value.

Season	K	Model	AIC	LL	r_s	p-value
Winter	12	Cumulative	107433.3	-53704.7	0.98457	< 0.001
Parturition	12	Cumulative	53154.81	-26566.4	0.9851	< 0.001
Summer	9	Linear + Natural + Predator	19524.16	-9753.08	0.9779	< 0.001
Rut	11	Cumulative	26298.69	-13137.34	0.9959	< 0.001

Global = cumulative effects parameters from each core hypothesis
Linear = distance-to industrial linear features
Natural = %understorey species & distance-to wetlands
Predator = apex predator

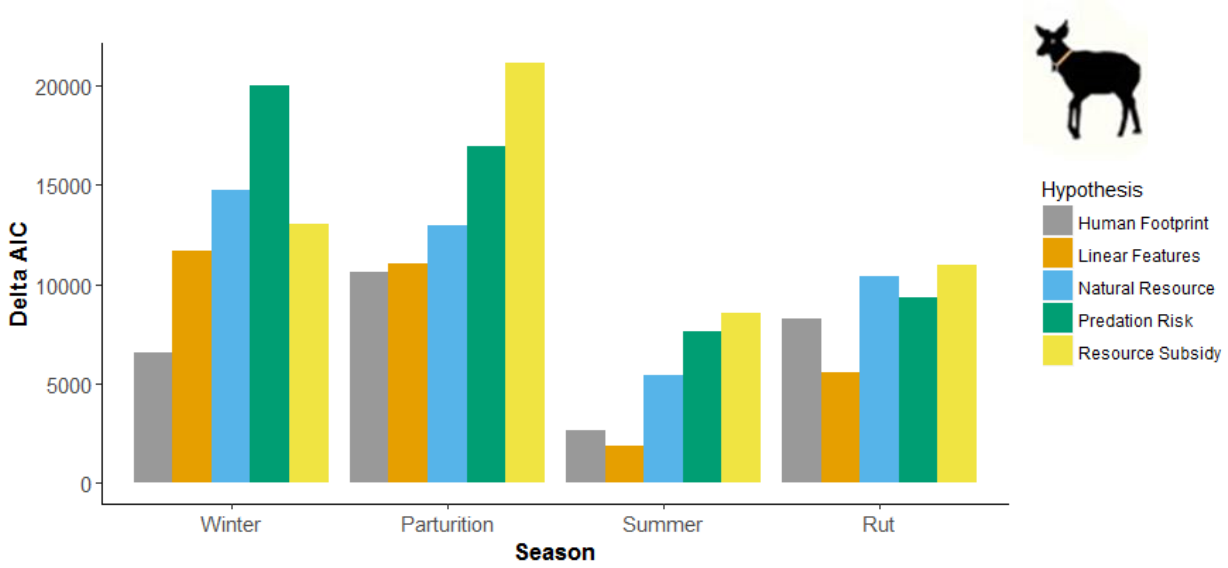


Figure 2.6. Human footprint outperforms other core hypotheses predicting seasonal deer distribution based on AIC

Difference in model ranking by delta AIC for core hypotheses against the top seasonal cumulative effects models.

The strength of white-tailed deer' selection and avoidance of landscape features varied across seasons, though deer continuously selected resource subsidies. Selection of industrial block features was strongest in winter where selection of industrial linear features was strongest during the rut and summer (Figure 2.7). Deer selected aspen stands across all seasons, most strongly in summer (β=0.679, p= 2e-16) (Figure 2.8; Appendix C). Behaviour associated with risk such as selection for roads and high predator occurrence frequency occurred most strongly during the rut where avoidance of bear abundant areas and neutral responses to wolf abundance occurred most strongly during parturition (Figure 2.8). Avoidance of open wetland (β=0.494, p=2e-16) and black spruce stands (β= -0.704, p=2e-16) were also strong predictors of deer occurrence during parturition (Appendix C).

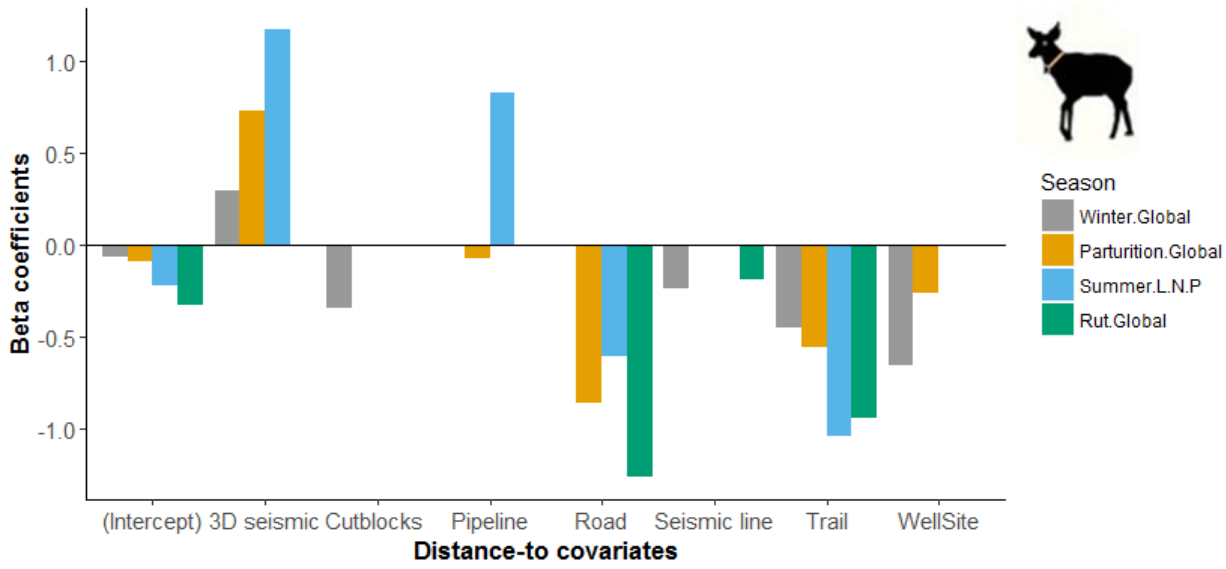


Figure 2.7. Direction & selection strength (β) for white-tailed deer probability of use of anthropogenic landscape co-variates across seasonal top models.

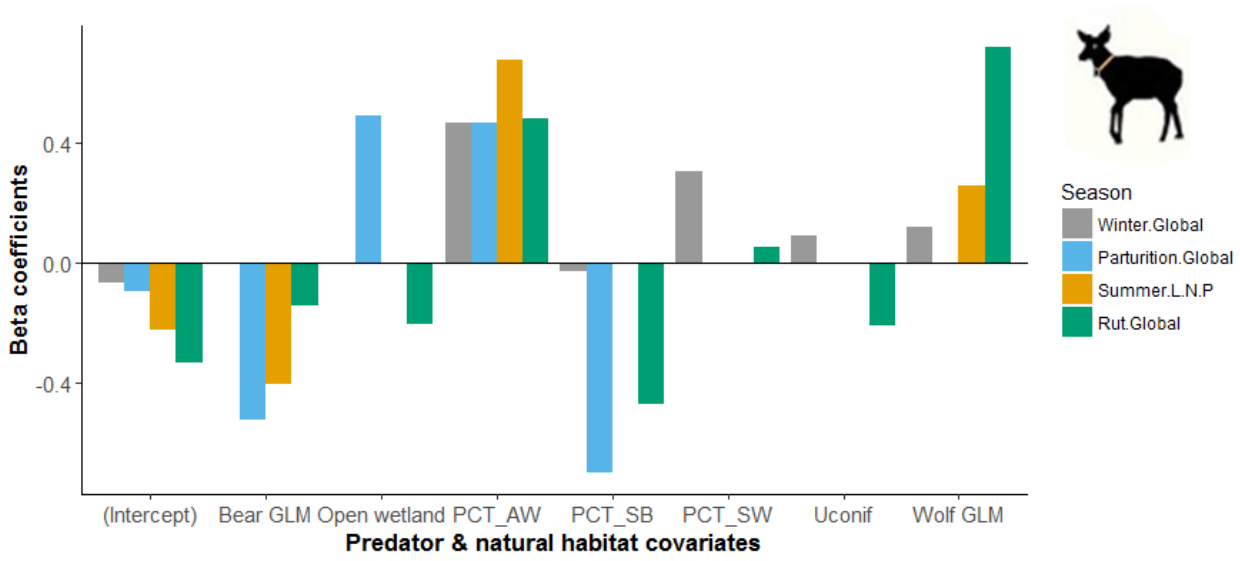


Figure 2.8. Direction & selection strength (β) for white-tailed deer probability of use of predator habitat and natural landscape co-variates across seasonal top models.

2.23 Seasonal white-tailed deer distributions

The predicted spatial distributions of white-tailed deer across seasons show consistency of the locations of "hot spots" – areas of high predicted probability of white-tailed deer occurrence – within the study region, with the exception of rut. Predicted and unsampled hot spots for the winter model are again predicted and occupied by deer during parturition and summer (Figure 2.9). In general, hot spots are located near the larger lakes and in upland deciduous and lowland deciduous habitat (Figure 2.9). During rut, the top model predicted strong selection of roads above other landscape features (Appendix C) and therefore manifests as a response to roads in the extrapolated spatial distribution (Figure 2.9).

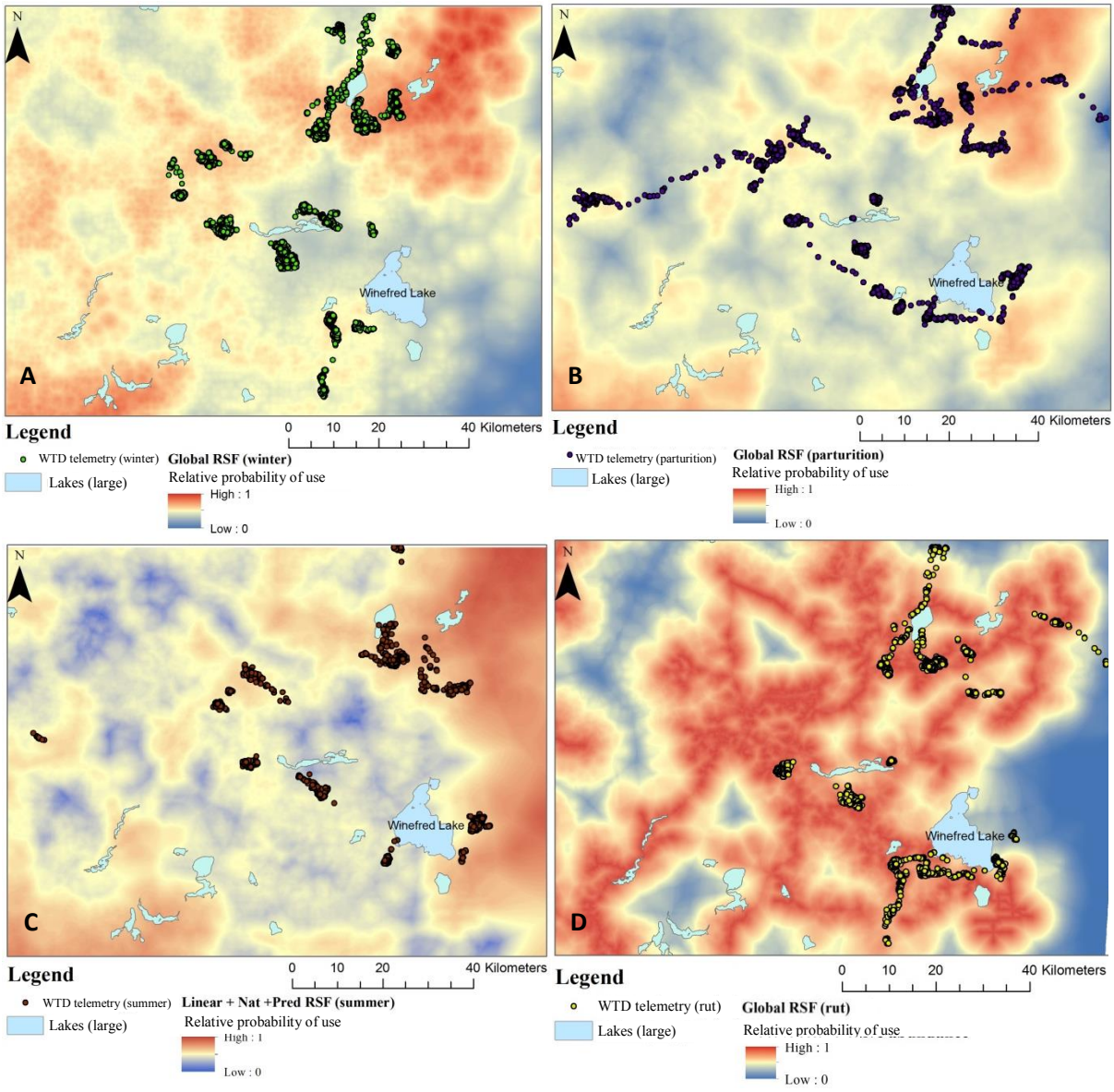


Figure 2.9. Predicted white-tailed deer distribution by season.
Distribution of white-tailed deer extrapolated from top cumulative effects models by season from 2011-2014 with 12 m resolution for A) Winter B) Parturition C) Summer and D) Rut.

2.3 Discussion

Cumulative effects of human footprint, natural vegetation, and predation risk best predicted white-tailed deer distributions across seasons, with linear features as the most important predictor variables. Industrial linear features are pervasive in the boreal landscape (Hebblewhite, 2017); we hypothesized that deer would perceive these features as risky due to their association with apex predators (Latham *et al.* 2011, Dickie *et al.* 2016). However our models indicate that, at a population scale of analysis, deer select some linear features including roads, trails, and conventional seismic lines rather than avoiding them. Deer strongly avoided 3-dimensional seismic lines, as do black bears (Fisher & Burton, 2018). We contend that some linear features are selected by deer as they provide forage subsidies as is hypothesized with block features (Finnegan *et al.* 2018). We hypothesized that block features would best explain deer distributions; though this hypothesis was not well supported, the combination of block features and linear features - total human footprint - better explained deer distributions than natural habitat and predation risk on the landscape. With a rate of 2875 km of industrial disturbance created each year in Alberta (Komers & Stanojevic, 2013) the continuation of deforestation for seismic exploration and timber harvesting may facilitate the northerly expansion of deer in the boreal as they search and select for forage opportunities.

Optimal foraging theory predicts that animals will attempt to maximize energy gain per unit cost; hence white-tailed deer must balance their need to forage while minimizing their exposure to temperature extremes, predators, and other threats (Kie, 1999). Energetic trade-offs between forage acquisition and predation risk have been observed in other ungulate studies (Kittle *et al.* 2008, Hebblewhite & Merrill, 2009; Seamans *et al*. 2016) and examined in the context of oil and gas development (Northrup *et al.* 2015). We found that deer consistently selected habitat features regardless of higher predation risk by gray wolves, and showed varying strength of selection responses based on seasonality. Generally, frequency of gray wolf occurrence, percent aspen cover, and distance to cutblocks, trails, roads, and seismic lines were all significantly selected for by deer. Our models suggest that deer do not prioritize risk avoidance at the habitat level and select for features that offer quality resources despite the increased likelihood of an encounter with wolves. Alternatively, deer may select human footprint as a means of refuge to evade predators (Berger, 2007); however, our human footprint

parameters comprised primarily of abandoned well sites, seismic lines, and cut blocks and industrial camps which high human activity were eliminated from analyses due to low sample size.

Deer in our study exhibited some seasonal differences in selection and in the strength of selection of some parameters. Deer more strongly selected for roads and high-frequency predator habitat during the rut and least during parturition when they are highly vulnerable (Hewitt, 2011). During winter, summer, and rut, deer significantly selected habitat that provided abundant forage but also had greater wolf frequencies, with a neutral response during parturition. The selection of early seral vegetation within human footprint as well as aspen stands suggests that deer prioritize foraging over predator avoidance. In contrast, deer exhibited the strongest avoidance to predators during parturition, suggesting deer change their behaviour to reduce access to forage subsidies in favour of avoiding encounters with predators. Deer exhibited the weakest predator avoidance behaviour during the rut, when mating occurs (DeYoung *et al*. 2011). A reduction in vigilance behaviour during the rut was expected, due to deer prioritizing mating and forage acquisition over energetic requirements associated with reproduction and withstanding forage-limiting winter conditions (Moen, 1976; Mech *et al*.1987; Schmidt, 1993). Deer avoided habitat associated with bears during all seasons when bears are active on the landscape with the strongest response during parturition, suggesting some spatial anti-predator response. Black bears are known to predate fawns of white-tailed deer and other neonates of boreal Cervidae (Kunkel & Mech, 1994, Latham *et al*. 2011). Alternatively, some habitat features avoided by bears are highly selected for by deer, such as upland and lowland deciduous forest. Therefore, this relationship may arise due to an incompatibility of resource quality rather than being an example of avoidance behaviour.

2.31 Caveats & Future Directions

We use coarse-scale measures of human land use and indirect proxies for resource subsidies and predation risk examining seasonal deer distributions at the population scale. One of the factors we did not include in our analysis that can tip the scale in favour of foraging in "risky" places is group size (Clark & Mangel, 1986; Childress & Lung, 2003; Lashley *et al*. 2014). Increases in group size in ungulates allow individuals to maximize forage intake and

minimize vigilance behaviour while simultaneously reducing their risk of immediate predation (Clark & Mangel, 1986; Hebblewhite & Pletscher, 2002; Lashley *et al.* 2014). Therefore, if deer are grouping together while foraging then the risk of starvation may outweigh their risk of predation, particularly during the winter when resources are scarce and movement is limited (Clark & Mangel, 1986; Schmidt, 1993). We could not account for group size as a possible explanation for foraging in areas with high relative wolf abundance though future work could include camera detections of deer as a proxy for group size. Future research regarding selection of linear features and predation risk should include group size to examine the energetic trade-offs individual deer make when they are most susceptible to predation and starvation. Furthermore, the inclusion of direct measures of forage availability and browsing by vegetation sampling, regeneration rate or clear-cut age, and cause of mortality in deer would allow more fine-scale and robust analyses of energetic trade-offs.

The inclusion of biotic interactions in species distribution models is still a relatively new concept (Fisher *et al.* 2012), with few practical examples in ungulate studies (Guisan *et al*. 2006; Elith & Leathwick, 2009; Godsoe & Harmon, 2012). We used extrapolation of raw camera detections to obtain a distribution surface for deer predators as a measure of predation risk. Distribution maps represent estimates of species occurrence and are rarely validated by ground-truthing due to the constraints associated with scale such as additional time and cost (Elith & Leathwick, 2009). We validated our predator distribution maps using linear regression and so contend that they are reasonable predictions of predator-habitat associations on the boreal landscape. We used scale-specific, best-supported, statistically validated species distribution models by Fisher & Burton (2018) based on three years of camera data and extrapolated these estimates of predator occurrence frequency as a measure of predation risk for the duration of the study. Our estimates were extrapolated no farther than 50 km from the camera sites, and covariates were parameterized at the same spatial scale as the best-fit models. We meet the assumption of continuity in the environment for reasonable extrapolation and therefore do not expect the coefficients of the species-habitat relationships to change in the immediate surroundings of the camera sites (Gove and Merriam Webster, 1986). Due to limitations with sample size, we were unable to account for changes in predator distributions with deer biological seasons. These estimates are based on the space use of predators within our study region for the

duration of the deer telemetry data collection. Future research may endeavor to include temporal variation of both direct and predation risk to better understand the extent to which deer make energetic trade-offs in the presence of predators (Creel *et al.* 2008).

2.32 Management implications

Our research shows strong associations between white-tailed deer occurrence and linear disturbance at the population scale, providing additional corroborating evidence that human footprint is a leading driver of seasonal white-tailed deer habitat selection. Expanding white-tailed deer ranges in the Alberta boreal forest contributes to numerous ecological implications on native fauna and flora. Deer are apparent competitors with declining woodland caribou (DeCesare, 2010) – where the presence of one species leads to a reduced population density for another by a shared a predator (Holt, 1977). The recovery of woodland caribou is dependent on the reduction of habitat loss within their ranges and predation pressure by gray wolves (Hebblewhite, 2017). However, the continued removal of gray wolves from the boreal landscape reduces predation pressure on caribou as well as white-tailed deer. Local increases in deer populations can alter ecosystems by spreading zoonotic diseases and over browsing, which reduces plant growth, forest understorey diversity, and consequently animal diversity (Côté *et al*. 2004, Hewitt *et al*. 2011). Mitigating the variety of sources of anthropogenic resource subsidies for deer in the boreal may reduce their ability to persist in harsh winter conditions and lessen their impact on woodland caribou and vegetative communities. Some mitigation measures that are currently in place include seismic line restoration where slow natural regeneration rates and rapid development of new seismic lines call for drastic remediation measures (Dabros *et al*. 2018). The current caribou recovery plan for Alberta lists 10,000 km of restored seismic lines as a primary objective in the recovery of declining herds (Government of Alberta, 2016).

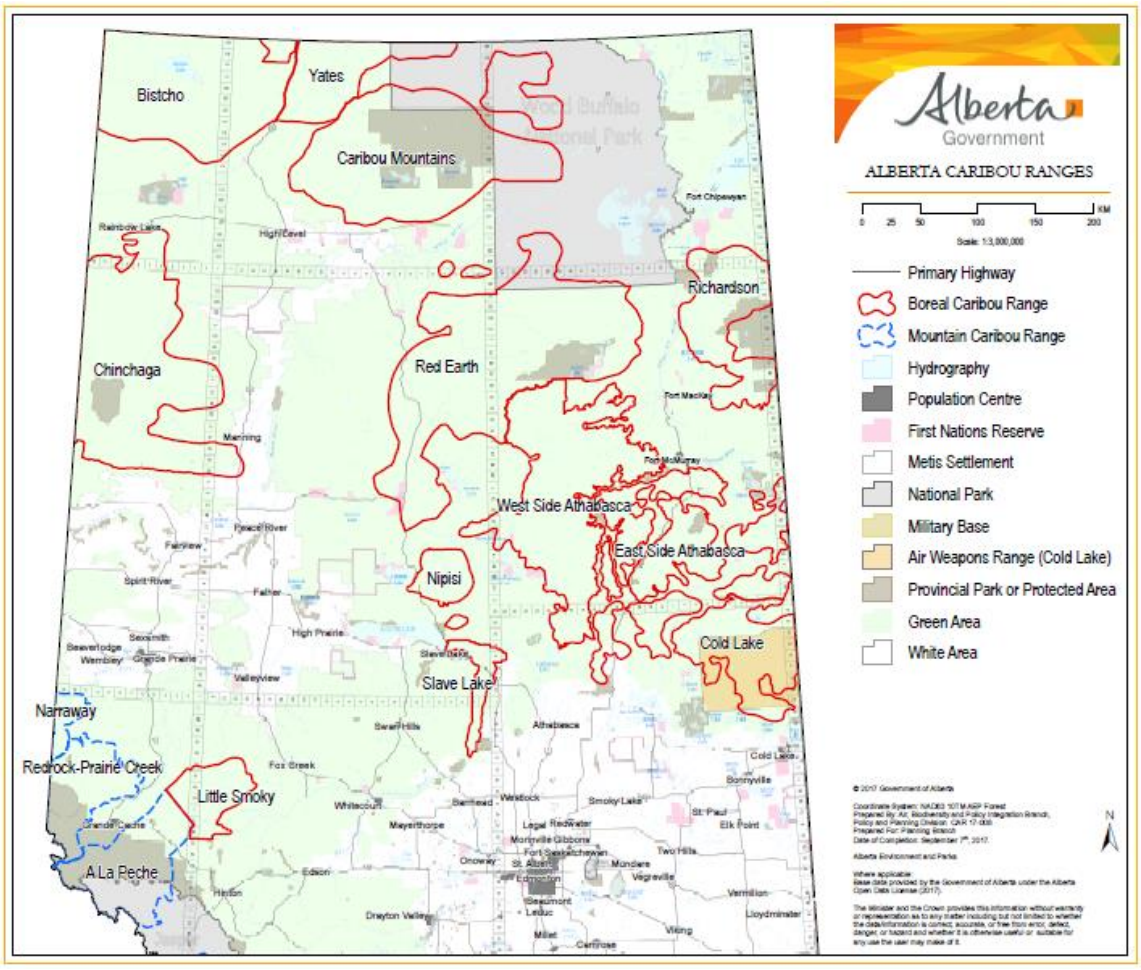
As deer continue to invade Canada's northwest, it is important to consider the mechanisms for initial colonization and persistence on the landscape. Though winter severity may act as a driver in deer expansion at large scales (Dawe *et al*. 2016), land-use change provides the short-term, local forage subsidies that deer require to survive winter conditions. Furthermore, our results indicate that human footprint is important for deer beyond the winter months when movement is less restricted and when winter severity is not a limiting factor.

Future research regarding the mechanisms underlying deer expansion should examine fine-scale deer distribution during the summer months when forage is abundant and occupancy is more widespread on the landscape. Our results support the conclusion that female deer make energetic trade-offs between access to resource subsidies and predator avoidance dependent on biological season (Kittle *et al*. 2008) and energetic requirements to survive and reproduce in northern climates appear to be strongly dependent on the availability of early successional vegetation provided by human land-use change. Access to these resource subsidies is likely more vital to deer than avoiding predation. Wildlife management plans in the boreal north must address these subsidies to control deer populations.

Appendix A

Caribou ranges of northern Alberta, Canada

Distribution and range extents of boreal woodland caribou ranges in Alberta. Notably, the East Side Athabasca and Cold Lake herds intersect our study region in surrounding Christina Lake, ALTA.



Appendix B

Candidate models by season

Model selection for winter deer RSF

Candidate models for white-tailed deer winter resource selection with K parameters weighed by AIC score, delta AIC (ΔAIC), AIC weight (AICwt), Log Likelihood (LL), and model validation coefficients by k-fold cross validation procedure with Spearman Rank value (rs) and significance value (p).

Model	K	AIC	ΔAIC	AIC_{Wt}	LL	r_s	p-value
Global	12	107433.3	0	1	-53704.7	0.98457	< 0.001
Human footprint + Natural	9	109293.1	1859.73	0	-54637.5	0.9780	< 0.001
Human footprint + predators	8	112747.8	5314.45	0	-56365.9	0.8814	< 0.001
Block + Natural + predators	7	113206	5772.66	0	-56596	0.97933	< 0.001
Linear + Natural + predators	9	113718.4	6285.03	0	-56850.2	0.99267	< 0.001
Linear + Natural	8	113838.1	6404.8	0	-56911.1	0.957088	< 0.001
Human Footprint	7	113979.9	6546.55	0	-56982.9	0.84379	< 0.001
Block + Natural	6	114265.9	6832.52	0	-57126.9	0.9318	< 0.001
Block + predators	5	117365	9931.69	0	-58677.5	0.85948	< 0.001
Linear + predators	7	118216	10782.62	0	-59101	0.87453	< 0.001
Linear Features	7	119130	11696.63	0	-59558	0.9155	< 0.001
Resource subsidy	4	120483.4	13050.04	0	-60237.7	0.82855	< 0.001
Natural + predators	5	121339.9	13906.53	0	-60664.9	0.90388	< 0.001
Natural Resources	4	122174.6	14741.24	0	-61083.3	0.73266	< 0.001
Predators	3	127442.8	20009.45	0	-63718.4	0.5322	< 0.001

Linear = roads, seismic, 3D seismic, trails, pipelines.
Block = Cut blocks, well sites
Natural = aspen and deciduous understorey percent cover
Predators = gray wolf relative occurrence frequenc
Global = all variables
Human footprint = Linear + Block features

Model selection for parturition deer RSF

Candidate models for white-tailed deer parturition resource selection with K parameters weighed by AIC score, delta AIC (ΔAIC), AIC weight (AICwt), Log Likelihood (LL), and model validation coefficients by k-fold cross validation procedure with Spearman Rank value (rs) and significance value (p).

Model	K	AIC	ΔAIC	AIC_{Wt}	LL	r_s	p-value
Global	11	53154.81	0	1	-26566.4	0.9851	< 0.001
Human footprint + Natural	8	57723.48	4568.67	0	-28853.7	0.9464	< 0.001
Linear + Natural	7	57901.25	4746.44	0	-28943.6	0.8744	< 0.001
Linear + Natural + predators	8	58434.61	5279.8	0	-29209.3	0.9649	< 0.001
Human footprint + predators	9	61905.78	8750.98	0	-30943.9	0.9069	< 0.001
Linear + predators	9	62146.45	8991.64	0	-31064.2	0.9194	< 0.001
Block + Natural + predators	7	62850.96	9696.15	0	-31418.5	0.9165	< 0.001
Natural + predators	6	63704.43	10549.62	0	-31846.2	0.9827	< 0.001
Human Footprint	7	63792.16	10637.35	0	-31889.1	0.7393	< 0.001
Linear Features	7	64203.82	11049.01	0	-32094.9	0.7783	< 0.001
Block + Natural	5	64404.25	11249.44	0	-32197.1	0.7338	< 0.001
Natural Resources	4	66127.84	12973.03	0	-33059.9	0.6306	< 0.001
Block + predators	5	69095.16	15940.35	0	-34542.6	0.8595	< 0.001
Predators	4	70065.28	16910.47	0	-35028.6	0.9361	< 0.001
Resource subsidy	4	74248.13	21093.32	0	-37120.1	0.8892	< 0.001

Linear = roads, seismic, 3D seismic, trails, pipelines.
Block = Cut blocks, well sites
Natural = aspen and deciduous understorey percent cover
Predators = gray wolf relative occurrence frequency

Model selection for rut deer RSF

Candidate models for white-tailed deer rut resource selection with K parameters weighed by AIC score, delta AIC (ΔAIC), AIC weight (AICwt), Log Likelihood (LL), and model validation coefficients by k-fold cross validation procedure with Spearman Rank value (rs) and significance value (p).

Model	K	AIC	ΔAIC	AICwt	LL	rs	p-value
Global	12	26298.69	0	1	-13137.34	0.9959	< 0.001
Linear + Natural + predators	9	27186.12	810.46	0	-13584.06	0.9897	< 0.001
Linear + predators	7	28635.47	2259.81	0	-14310.74	0.9844	< 0.001
Linear + Natural	7	28884.51	2508.85	0	-14435.25	0.9837	< 0.001
Human footprint + Natural	7	30021.86	3646.2	0	-15003.93	0.9287	< 0.001
Human footprint + predators	7	30570.59	4194.93	0	-15278.29	0.8913	< 0.001
Block + Natural + predators	8	30789.41	4413.75	0	-15386.71	0.9716	< 0.001
Linear Features	5	31969.27	5593.6	0	-15979.63	0.9407	< 0.001
Block + predators	6	32860.36	6484.7	0	-16424.18	0.8837	< 0.001
Block + Natural	6	33087.94	6712.28	0	-16537.97	0.7570	< 0.001
Natural + predators	5	33657.27	7281.61	0	-16823.63	0.8278	< 0.001
Human Footprint	5	34620.01	8244.35	0	-17305	0.9714	< 0.001
Predators	4	35741.64	9365.98	0	-17866.82	0.9307	< 0.001
Natural Resource	4	36757.95	10382.29	0	-18374.97	0.7177	< 0.001
Resource subsidy	4	37378.54	11002.88	0	-18685.27	0.6782	< 0.001

Linear = roads, seismic, 3D seismic, trails, pipelines.
Block = Cut blocks, well sites
Natural = aspen and deciduous understorey percent cover
Predators = gray wolf relative occurrence frequency

Model selection for summer deer RSF

Candidate models for white-tailed deer summer resource selection with K parameters weighed by AIC score, delta AIC (ΔAIC), AIC weight (AICwt), Log Likelihood (LL), and model validation coefficients by k-fold cross validation procedure with Spearman Rank value (rs) and significance value (p).

Model	K	AIC	ΔAIC	AIC_{wt}	LL	r_s	p-value
Linear + Natural + predators	9	19524.16	0	1	-9753.08	0.9779	< 0.001
Linear + Natural	7	19864.75	340.6	0	-9925.38	0.9832	< 0.001
Global	10	20180.86	656.7	0	-10080.43	0.9873	< 0.001
Linear + predators	8	20642.31	1118.15	0	-10313.15	0.9537	< 0.001
Human footprint + Natural	8	20700.61	1176.46	0	-10342.31	0.9508	< 0.001
Linear Features	6	21384.85	1860.69	0	-10686.43	0.7764	< 0.001
Human footprint + predators	8	21700.45	2176.3	0	-10842.23	0.8783	< 0.001
Human Footprint	6	22167.31	2643.15	0	-11077.65	0.8503	< 0.001
Block + Natural + predators	8	24455.5	4931.35	0	-12219.75	0.9482	< 0.001
Natural + predators	6	24655.08	5130.93	0	-12321.54	0.9247	< 0.001
Block + Natural	6	24759.12	5234.96	0	-12373.56	0.9586	< 0.001
Natural Resource	4	24986.51	5462.35	0	-12489.25	0.6006	< 0.001
Block + predators	6	26957.75	7433.59	0	-13472.88	0.9325	< 0.001
Predators	4	27175.69	7651.54	0	-13583.85	0.844	< 0.001
Resource subsidy	4	28092.82	8568.66	0	-14042.41	0.5111	< 0.001

Linear = roads, seismic, 3D seismic, trails, pipelines.
Block = Cut blocks, well sites
Natural = aspen and deciduous understorey percent cover
Predators = gray wolf relative occurrence frequency

Appendix C

Top model specifications

Global model best predicts winter resource selection by deer

Binomial GLM global model parameter estimates (β), standard error (Std. Error), z-value, and significance (pr(>|z|)) for winter resource selection by white-tailed deer.

	β Coefficient	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.067492	0.089202	-0.76	0.44928
Wolf.GLM.std	0.119211	0.009818	12.14	< 2e-16
Trail.std	-0.452034	0.009187	-49.21	< 2e-16
CutBlocks.std	-0.343671	0.009651	-35.61	< 2e-16
Cutline3D.std	0.292954	0.011068	26.47	< 2e-16
WellSite.std	-0.654962	0.010984	-59.63	< 2e-16
Cutline.std	-0.240644	0.01157	-20.8	< 2e-16
PCT_AW.std	0.467	0.008999	51.9	< 2e-16
PCT_SB.std	-0.028656	0.008765	-3.27	0.00108
PCT_SW.std	0.304358	0.008412	36.18	< 2e-16
UConif.std	0.090662	0.00815	11.12	< 2e-16

Global model best predicts parturition resource selection by deer

Binomial GLM global model parameter estimates (β), standard error (Std. Error), z-value, and significance (pr(>|z|)) for parturition resource selection by white-tailed deer.

	β Coefficient	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.09629	0.11709	-0.82	0.41088
Bear.GLM.std	-0.52666	0.01461	-36.05	< 2e-16
Road.std	-0.86187	0.01928	-44.71	< 2e-16
Trail.std	-0.55701	0.01596	-34.9	< 2e-16
Pipeline.std	-0.07574	0.02489	-3.04	0.00235
Cutline3D.std	0.73222	0.0167	43.85	< 2e-16
WellSite.std	-0.26901	0.02133	-12.61	< 2e-16
PCT_AW.std	0.46936	0.01268	37.01	< 2e-16
PCT_SB.std	-0.70428	0.01426	-49.4	< 2e-16
OpenWet.std	0.49427	0.01307	37.82	< 2e-16

Global model best predicts rut resource selection by deer

Binomial GLM global model parameter estimates (β), standard error (Std. Error), z-value, and significance (pr(>|z|)) for rut resource selection by white-tailed deer.

	β Coefficient	Std. Error	z-value	Pr(>|z|)
(Intercept)	-0.3328	0.10814	-3.08	0.002087
Wolf.GLM.std	0.72488	0.02119	34.22	< 2e-16
Bear.GLM.std	-0.14441	0.01926	-7.5	6.45E-14
Cutline.std	-0.19013	0.02509	-7.58	3.55E-14
Trail.std	-0.94877	0.02441	-38.87	< 2e-16
Road.std	-1.27009	0.02882	-44.07	< 2e-16
PCT_AW.std	0.4811	0.01903	25.29	< 2e-16
UConif.std	-0.2104	0.01655	-12.71	< 2e-16
PCT_SB.std	-0.47291	0.01879	-25.17	< 2e-16
PCT_SW.std	0.05433	0.01447	3.76	0.000173
OpenWet.std	-0.20498	0.02325	-8.82	< 2e-16

Linear + Natural + Predation risk model best predicts summer resource selection by deer

Binomial GLM linear, natural feature, and predator model parameter estimates (β), standard error (Std. Error), z-value, and significance (pr(>|z|)) for winter resource selection by white-tailed deer.

	β Coefficient	Std. Error	z-value	Pr(>|z|)
(Intercept)	-0.22241	0.25044	-0.89	0.375
Road.std	-0.60698	0.0268	-22.65	<2e-16
Trail.std	-1.04628	0.03099	-33.76	<2e-16
Cutline3D.std	1.16804	0.0285	40.99	<2e-16
Pipeline.std	0.82458	0.02634	31.31	<2e-16
PCT_AW.std	0.67953	0.02106	32.27	<2e-16
Wolf.GLM.std	0.25731	0.02477	10.39	<2e-16
Bear.GLM.std	-0.40619	0.02395	-16.96	<2e-16

Literature Cited

Alberta Environment & Parks. (2017). Alberta Caribou Ranges Map. Retrieved from: http://aep.alberta.ca/fish-wildlife/wildlife-management/caribou-range-planning/caribou-range-maps.aspx

Alberta Environment & Parks (2018). Species at risk public registry. Retrieved at: http://aep.alberta.ca/fish-wildlife/species-at-risk/default.aspx

Alberta Environment and Sustainable Resource Development (ESRD). 2013. Oil and gas reclamation. Available from http://environment.alberta.ca/02862.html.

Akaike, H. (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, **60**, 255–265.

Andrewartha, H.G. (1961) Introduction to the Study of Animal Populations, University of Chicago Press. City?

Avgar, T., Potts, J. R., Boyce, M.S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution,7*: 619–630

Baasch, D.M., Tyrea, A.J., Millspaughb, J.J., Hygnstroma, S.E., Vercauterenc, K.C. (2010). An evaluation of three statistical methods used to model resource selection *Ecological Modelling* 221: 565–574.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters, 3*: 620–623.

Bergerud, A.T., Butler, H.E., & Miller, D.R. (1984). Antipredator tactics of calving caribou: dispersion in mountains. C*anadian Journal of Zoology 62*:1566–1575.

Boyce, M. S., & McDonald, L.L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution, 14(*7): 268-272.

Boyce, M. S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K. (2002). Evaluating resource selection functions. *Ecological Modelling 157*:281-300.

Boyce, M. S., Mao, J.S., Merrill, E.H., Fortin, D., & Turner, M.G. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience 10*:421–431.

Bronson, F. H. (1989). Mammalian Reproductive Biology. University of Chicago Press, Chicago.

Burgman, M.A. & Fox, J.C. (2003) Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation,6*;19– 28.

Burnham, K. P., & Anderson, D. R. (2016). Multimodel Inference. *Sociological Methods & Research, 33*(2), 261-304.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference. *Sociological Methods & Research, 33(*2), 261-304.

Burnham, K.P., & Anderson, D.R. (2002). Model selection and inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Burton, A.C., Neilson, E., Moreira, D., *et al*. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J Appl Ecol 52*: 675–85.

Cherry, M.J., Conner, L.M., Warren, R.J. (2015). Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. *Behavioral Ecology, 26*(4): 1091–1099.

Childress, M.J., Lung, M.A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behavior of conspecifics? *Anim Behav. 66*:389–398.

Clark, C.W., Mangel, M. (1986). The evolutionary advantages of group foraging. *Theor Popul Biol. 30*:45–75.

Clavero, M., & Garcia-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution, 20*(3): 110-117.

Coristine, L.E., & Kerr, J.T. (2011). Habitat loss, climate change, and emerging conservation challenges in Canada. *Canadian Journal of Zoology, 89*(5): 435-451.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst. 35*:113-47.

Creel, S., Winnie, J.A, Christianson, D., & Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour 76*:1139-1146.

Craiu, R. V., Duchesne, T., & Fortin, D. (2008). Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal, 50*:97–109.

Dabros, A., Pyper, M., & Castilla, G. (2018). Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. *Environmental Reviews, 26*(2), 214-229.

Dawe, K.L, & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (Odocoileus virginianus) range expansion at the northern extent of its range; land-use is secondary. *Ecology and Evolution. 6*(18); 6435-6451.

Dawe, K.L., Bayne, E.M., & Boutin, S.(2014). Influence of climate and human land use on the distribution of white-tailed deer (Odocoileus virginianus) in the western boreal forest. *Can. J. Zool. 92*: 353–363.

DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. (2014). Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology, 83*:343–352.

Delgiudice, G. D., B. A. Mangipane, B. A. Sampson, and C. O. Kochanny. 2001. Chemical immobilization, body temperature, and post-release mortality of white-tailed deer captured by Clover trap and net-gun. Wildlife Society Bulletin:1147-1157.

Delgiudice, G. D., K. E. Kunkel, Mech, L.D., Seal, U.S. (1990a) Minimizing capture-related stress on white-tailed deer with a capture collar. *The Journal of Wildlife Management*:299-303.

DeYoung, R. W., Miller, K.V., & Hewitt, D. (2011). White-tailed deer behaviour. Biology and management of white-tailed deer:311-351.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**; 1359–1367.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B. (2014). Defaunation in the Anthropocene, Science 345(6195): 401-406.

Elith, J. & Leathwick, J. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu. Rev. Ecol. Evol. Syst, 40*: 677–97.

Environment Canada. (2012). Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population in Canada. Species at Risk Act Recovery Strategy Series (p. ix+138pp. Environment Canada, Ottawa).

Festa-Bianchet, M. (1988). Seasonal Range Selection in Bighorn Sheep: Conflicts between Forage Quality, Forage Quantity, and Predator Avoidance. *Oecologia*, *75*(4);580-586.

Finnegan, L., MacNearney, D., & Pigeon, K. E. (2018). Divergent patterns of understory forage growth after seismic line exploration: Implications for caribou habitat restoration. *Forest Ecology and Management, 409*.

Fisher, J.T., & Burton, A.C. (2018). Wildlife winners and losers in an oil sands landscape. *Front Ecol Environ. 16*(6): 323-328.

Fisher, J.T., & Burton, A.C. (2016). Moose and Predator Numerical Responses to Anthropogenic Features in the Alberta Oil Sands Region of Alberta. Alberta Innovates – Technology Futures, Vegreville, AB. 34 pp.

Fisher, J.T., M.T. Wheatley, S. Bradbury, B. Anholt, Volpe, J.P. (2012). Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes. *Ecography 36*(2): 240-248.

Fisher, J.T., & Wilkinson, L.(2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev 35*: 51–81.

Forester, J., Im, H., Rathouz, P. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology, 90* (12): 3554-3565.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005). Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. *Ecology 86*:1320-1330.

Fuller, K.A. (2004). Canada lynx predation on white-tailed deer. *Northeastern naturalist*, 11(4): 395-398.

Fuller, T.K., Mech, L.D. & Cochrane, J.F. (2003) Wolf population dynamics. Wolves: Behaviour, Ecology, and Conservation (eds L.D. Mech & L. Boitani), pp. 161–191. University of Chicago Press, Chicago, USA.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., . . . Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, *75*(4), 887-898.

Godsoe, W., & Harmon, L. J. (2012). How do species interactions affect species distribution models? *Ecography*, *35*(9), 811-820.

González-Moreno, P., Diez, J. M., Richardson, D. M., & Vilà, M. (2015). Beyond climate: disturbance niche shifts in invasive species. *Global Ecology and Biogeography, 24*(3), 360-370.

Government of Alberta (2017). The Alberta Vegetation Inventory (AVI) Crown. Forest Management Branch, Forestry Division, Alberta Agriculture and Forestry. Retrieved from: https://extranet.gov.ab.ca/srd/geodiscover/srd_pub/biota/Vegetation/AlbertaVegetationInventoryCrownIndex.zip

Government of Alberta. (2016). Setting Alberta on the path to caribou recovery. Retrieved at: http://aep.alberta.ca/fish-wildlife/wildlife-management/caribou-management/caribou-action-range-planning/documents/OnThePathtoCaribouRecovery-May-2016.pdf

Hall, L. S., Krausman, P.L., &. Morrison, M.L. (1997). The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin 25*:173–182.

Haulton, S. M., Porter, W. F., Rudolph, B.A. (2001). Evaluating 4 methods to capture white-tailed deer. *Wildlife Society Bulletin:* 255-264.

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation, 206*: 102-111.

Hebblewhite, M., Merrill, E.H., & Mcdonald, T.L. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos, 111*:101–111.

Hebblewhite, M., & Merrill, E.H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology, 90*(12): 3445–3454.

Hebblewhite, M., & Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology, 80*(5), 800-809.

Hervieux, D., Hebblewhite, M., DeCesare, N. J., Russell, M., Smith, K., Robertson, S., &Boutin, S. (2013). Widespread declines in woodland caribou (Rangifertaranduscaribou) continue in Alberta. *Canadian Journal of Zoology, 91*(12), 872-882.

Hewitt, D. G. (2011). Nutrition. Pages 75-106 Biology and management of white-tailed deer. CRC Press, Taylor & Francis Group, Boca Raton, Florida.

Hobbs, R. J., and L. F. Huenneke. (1992). Disturbance, diversity, and invasion—implications for conservation. *Conservation Biology*, 6:324–337.

Hobbs, R. 2000. Ecological repair following biotic invasions.Pages 181–188 in G. Preston, G. Brown, and E. Van Wyk,editors. Best management practices for preven ting andcontrolling invasive alien species. The Working for Water Program, Kirstenbosch Botanical Gardens, Cape Town,South Africa.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol 12*:197-229.

Kie, J.G. (1999). Optimal Foraging and Risk of Predation: Effects on Behaviour and Social Structure in Ungulates. *Journal of Mammology*, *80*(4): 1114-1129.

Kilgo JC, Ray HS, Vukovich M, Goode MJ, Ruth C. (2012). Predation by coyotes on white-tailed deer neonates in South Carolina. *J Wildl Manage*.76:1420–1430.

Kittle, A.M., Fryxell, J.M., Desy, G.E., Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia, (157)*:163–175.

Komers, P.E., Stanojevic, A. (2013). Rates of disturbance vary by data resolution: implications for conservation schedules using the Alberta Boreal Forest as a case study. *Glob. Change Biol. 19;* 2916–2928.

Kunkel, K.E., and Mech, L.D. (1994). Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Can. J. Zool.72*(9): 1557–1565.

Kunkel, K.E., Pletscher, D.H. (2001). Winter hunting patterns of wolves in and near Glacier National Park, Montana. *J Wildl* Manage 65:520–530.

James, A. R. C., & Stuart-Smith, A.K.. (2000). Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management, 64*: 154-159.

Johnson, C.J., Ehlers, L.P.W., Seip, D.R. (2015). Witnessing extinction – Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biological Conservation, 186:* 176–186.

Johnson, C. J., Nielsen, S. E., Merrill, E.H., Mcdonald, T. L., Boyce, M. S. (2006). Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management 70*:347–357

Lashley, M. A., Chitwood, M. C., Biggerstaff, M. T., Morina, D. L., Moorman, C. E., & DePerno, C. S. (2014). White-tailed deer vigilance: the influence of social and environmental factors. *PLoS One, 9*(3).

Latham, A. D. M., Latham, M.C., Boyce, M.S., & Boutin, S. (2011)a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications 21*:2854-2865.

Latham, A. D. M., Latham, M.C., McCutchen, N.A., &. Boutin, S. (2011)b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management 75*:204-212.

Latham, A. D. M., Latham, M.C., & Boyce, M.S. (2011)a. Habitat selection and spatial relationships of black bears (Ursus ameriCanis) with woodland caribou (Rangifer tarandus caribou) in northeastern Alberta. *Canadian Journal of Zoology 89*:267-277.

Latham, A. D. M., Latham ,M.C., Knopff, K.H., Hebblewhite, M., & Boutin, S. (2013). Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography, 36*(12): 1276–1290.

Leblond, M., Dussault, C., & Ouellet, J.P. (2010). What drives fine-scale movements of large herbivores? A case study using moose. *Ecography, 33*: 1102-1112.

Lele, S.R., & Keim, J.L. (2006). Weighted distributions and estimation of resource selection probability functions. *Ecology, 87*(12): 3021-302.

Lemay, M.A., Henry, P., Lamb, C.T., Robson, K.M, Rusesello, M.A. (2013). Novel genomic resources for a climate change sensitive mammal: characterization of the American pika transcriptome. BMC Genomics, 14(311), 1-11.

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640

Losier, C., Couturier, S., St-Laurent, M., Drapeau, P., Dussault, C., Rudolph, T., Brodeur, V., Merkle, J., & Fortin, D . (2015). Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *Journal of Applied Ecology, 52*; 496–50.

Manly, B. F. J. (1985). The Statistics of Natural Selection, Chapman & Hall.

Manly, B. F., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P. (2002). Resource selection by animals: statistical design and analysis for field studies. Page 221. Kluwer Academic Publishers. Dordrecht, The Netherlands.

Maxwell, S., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). The ravages of guns, nets and bulldozers. Nature, 536, 143–145.

Mech, L.D., and Boitani, L. (Editors). 2003. Wolf social ecology. In Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Ill. pp. 1–30.

Moen, A. N. (1976). Energy conservation by white tailed deer in the winter. *Ecology* 57:192-198.

Nielsen, S. E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M.L., & Jevons, S. (2004). Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation, 120*:101-113.

Northrup, J.M., Anderson, C.R., and Wittemeyer, G. (2015). Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology, 21*: 3961–3970.

O'Connell, A. F., Nichols, J.D., & Karanth, K.U. (2011). Camera traps in animal ecology: methods and analyses.Springer Tokyo.

Oftedal OT. 1985. Pregnancy and lactation. In: Hudson R, White RG, editors, Bioenergetics of wild herbivores. Boca Raton (FL): CRC Press. p.215–238.

Ozoga, J.J., Verme, L.J., and Bienz, C.S. 1982. Parturition Behaviour and Territoriality in White-Tailed Deer: Impact on Neonatal Mortality. The Journal of Wildlife Management, 46(1); 1-11.

Pascher, J., Seed, E., and Duffe, J. (2013). Development of boreal ecosystem anthropogenic disturbance layers for Canada based on 2008 to 2010 Landsat imagery. *Can. J. Remote Sens. 39*: 1–17.

Parker, K. L., Robbins, C.T., & Hanley, T.A. (1984). Energy expenditures for locomotion by mule deer and elk. *J. Wildl.Manage. 48*: 474-488.

Parker, I. M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H.,Von Holle B., Moyle, P.B., Byers, J.E., Goldwasser, L.(1999). Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1:3–19.

Parmesan C. (2006). Ecological and evolutionary responses to recent climate change. Annu Rev Ecol, Evol Syst, 37: 637–669.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature, 421*;37–42.

Patterson, B.D., G. Ceballos, W. Sechrest, M.F. Tognelli, T. Brooks, L. Luna, P. Ortega, I. Salazar, and B.E. Young. (2003). Digital Distribution Maps of the Mammals of the Western Hemisphere, version 1.0. NatureServe, Arlington, Virginia, USA.

Pearson, R.G., Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecol. Biogeog. 12*:361–71

Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. Annual Review of Environment and Resources, 37, 25–50.

Pickell, P. D., D. W. Andison, and N. C. Coops. (2013). Characterizations of anthropogenic disturbance patterns in the mixedwood boreal forest of Alberta, Canada. *Forest Ecology and Management 304*:243-253.

Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. (2015). The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. *Canadian Journal of Forest Research 45*:732-743

Pimentel, D., Zuniga, R., Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics, 52*(3): 273-288.

Seamans, T.W., Blackwell, B.F., Linnell, K.E. (2016). Use of predator hair to enhance perceived risk to white-tailed deer in a foraging context. *Human–Wildlife Interactions* 10(2): 300–311.

Schmidt, K. (1993). Winter ecology of nonmigratory alpine red deer. *Oecologia, 95:* 226–233.

Schneider, R. R. (2002). Alternative futures: Alberta's boreal forest at the crossroads. Federation of Alberta Naturalalists, Edmonton, Alberta, Canada.

Schneider R.R., & Dyer, S. (2006). Death by a Thousand Cuts: The Impacts of In Situ Oil Sands Development on Alberta's Boreal Forest. Pembina Institute for Appropriate Development.

Schneider R.R., Hauer, G., Adamowicz, W.L., & Boutin S. (2010). Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biol Conserv 143:* 1603-11.

Segan, D.B., Murray, K.A, Watson, J.E.M. (2016). A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. *Global Ecology and Conservation, 5*: 12-21.

Thurfjell, H., Ciuti, S., & Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology 2*:4.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature, 371*: 65–66.

Turchin, P. (1998). Quantitative analysis of movement. Sinuaer Associates, Sunderland, Massachussetts, USA.

Van Rensen, C.K., Nielsen, S.E., White, B., Vinge, T., Lieffers, V.J. (2015). Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. *Biol. Conserv. 184*, 127–135.

Wasser, S.K., Keim, J.L., Taper, M.L., & Lele, S.R. (2011). The influences of wolf predation, habitat loss, and human activity on caribou and moosein the Alberta oil sands. *Frontiers in Ecology and the Environment, 9*(10); 546-551.

Zerbe, P., Clauss, M., Codron, D., Bingaman Lackey, L., Rensch, E., Streich, J. W., Muller, D. W. (2012). Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. *Biol Rev Camb Philos Soc, 87*(4), 965-990.

Zuur, A.F., Hilbe, J. Leno, E.N. 2013. A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists. Highland Statistics.

Zuur, A. F., Leno, E. N., Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

Zuur, A.F., Leno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.H., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer-Verlag (New York, USA).

CHAPTER 3: A greater stride to their step: White-tailed deer increase movement rate in the predator-rich and human-altered oil sands landscape of northeastern Alberta

3.0. Introduction

Moving is one of the ways animals respond to environmental stressors. Analyzing movement is critical for understanding species invasion, dispersal, migration, resource acquisition, predator-prey interactions, and adaptation (Greenwood & Swingland, 1983; Dingle, 2015). At large scales, seasonal migration or shifts in geographic range characterize population movement as animals follow resource opportunities (Dingle, 2015). At small scales, species movement is often characterized by behavioural responses to the local environment, such as avoiding threats or pursuing resources (Fahrig, 2007).

In an era of fast-paced human development and climate change that are altering landscapes around the globe species are increasingly confronted with environmental stressors at an unprecedented rate. Habitat loss arising from land conversion for agriculture is one of the greatest threats to biodiversity globally (Maxwell *et al*. 2016) with increasing rates of urbanization and energy extraction further altering landscapes. Human land-use change and habitat fragmentation – in which habitat is broken apart (Fahrig, 2003) – are expected to constrain animal migration in response to climate change in the coming century (Lawler *et al.* 2013; Heard, 2013; *McGuire et al.* 2016). On a behavioural level, human-altered landscapes can change how animals move in relation to their surroundings (James & Stuart-Smith, 2000), alter predator-prey interactions (Rogala *et al.* 2011) and ultimately affect their reproductive fitness and survivorship (Losier *et al.* 2015; Cattarino *et al*. 2016).

The role of human land use in changing animal activity is evident in areas with a history of continuous development within habitats used by large mammals. Alberta's oil sands region is a hub for in-situ oil and gas exploration and timber harvesting in which the size, shape, and distribution of early seral vegetation – replacing mature forest – is without historical analogs (Pickell, 2015). The cumulative effects of resource extraction have been shown to affect the entire mammal community. Increases in disturbance alter activity patterns (Frey *et al.* 2017) of multiple species. Distribution and abundance is also affected, wherein some species such as gray

wolves (*Canis lupus*) and white-tailed deer (*Odocoileus virginianus*) benefit and others such as black bears (*Ursus americanus*) and woodland caribou (*Rangifer tarandus caribou*) are negatively impacted (Fisher & Burton, 2018). Gray wolves use linear features – petroleum-exploration "seismic" lines, roads, and trails – to increase hunting efficiency (Latham, 2011) due to their ability to travel faster and farther through the boreal forest (Dickie *et al*. 2017). The effect of linear anthropogenic landscape features on the rate of animal movement is less understood for prey species, as is how prey respond to corridors used by predators.

In prey species, individuals' decisions about movement and habitat selection result from energetic trade-offs between avoiding perceived risks and searching for quality resources (Kie, 1999; Creel *et al*. 2008). In the context of predation risk, avoidance behaviour is a decision made by prey to compromise their rate of resource acquisition to reduce the probability of death (Frid & Dill, 2002). The recognition of predation risk by prey is spatio-temporal, where prey associate risk with certain times and habitat characteristics (Fortin *et al*. 2005; Creel *et al*. 2008). Prey adjust their movement patterns in response to risk by increasing their movement rate and spending less time in risky places (Frair *et al*. 2005; Prokopenko *et al*. 2017). For example, Prokopenko *et al*. (2017) found that elk avoided habitat near roads at all times of day and increased their rate of movement when in the vicinity of roads. Increased human activity along roads, as well as their use by predators, may induce avoidance of roads by prey (Latham *et al*. 2011; Leblond *et al*. 2013). The movement responses of prey in landscapes with multiple forms of linear disturbance and large numbers of predators are not well understood and may differ according to seasonal differences in energetic requirements (McGreer *et al*. 2015). We can hypothesize that prey species alter movement behaviour based on energetic trade-offs between avoiding risks and searching for quality resources (Creel *et al.* 2008).

We tested some of these hypotheses by examining fine-scale movement responses and habitat selection by invasive white-tailed deer in a highly disturbed and predator-rich region of northeastern Alberta, Canada. White-tailed deer have been expanding their northern range over the past fifty years (DeYoung, 2011) and pose a threat to native woodland caribou herds in Alberta (Dawe *et al*. 2016) by apparent competition – the decrease in one species population by another through a shared predator rather than competition for resources (Holt, 1977; DeCesare *et al*. 2010). Climate change and human land-use have been linked to the northward shift in deer

distribution at provincial spatial scales (Dawe *et al*. 2016). However; the role of local habitats and landscapes in affecting movements of individual white-tailed deer movement remains unknown. We modeled white-tailed deer movement using a form of Species Distribution Models (SDMs), which are increasingly evolving beyond the traditional practice of using solely abiotic features to predict species-habitat relationships by incorporating more dynamic parameters such as biotic interactions and species movement (Elith & Leathwick, 2009; Miller, 2015). Technological advances in satellite GPS collars allow us to analyze fine-scale individual movement (Hebblewhite & Haydon, 2010). Recent developments in SDMs derived from telemetry data allow simultaneous analysis of movement with habitat selection (Avgar *et al*. 2016) for behavioural studies.

Introduced by Fortin *et al*. (2005) in a study of wolf influences on elk movement, Step Selection Functions (SSFs) use the straight line distance linking successive animal locations, called "steps", as the sampling unit in fine-scale habitat selection (Turchin 1998, Fortin *et al*. 2005; Thurfjell *et al*. 2014). SSFs address issues of scale within the domain of availability in Resource Selection Function (RSF) analysis by using conditional logistic regression (Forester *et al*. 2009). Each step for a given individual is paired with a set of *n* random steps of differing lengths and directions to estimate an animals' selection for habitat features at the end of a step or between successive telemetry fixes (Fortin *et al*. 2005). SSFs have been used to analyze ungulate avoidance behaviour to predators and human disturbance across North America with studies on caribou and moose (Latombe *et al*. 2014). Integrated Step Selection Analysis (iSSA) is an extension of SSF that relaxes the assumption that observed movement attributes such as velocities and their temporal autocorrelations are independent of resource selection (Avgar *et al*. 2016). It allows the effects of environmental variables on the movement and selection processes to be distinguished (Avgar *et al*. 2016). The iSSA is useful for testing whether animals travel faster in certain times or through certain habitats such as those associated with predation risk (Prokopenko *et al*. 2017; Stewart *et al*. 2019, *in review*).

We used iSSA to examine the extent to which individual deer alter movement near landscape features that are expected to be associated with perceived risk of predation and forage acquisition. We tested four principal hypotheses and a cumulative effects hypothesis to determine the drivers of individual deer movement and habitat selection. We hypothesized that

movement is best predicted by 1) assumed risk of predation along industrial linear features 2) risk of predation in habitat with high predator frequency 3) selection of assumed forage availability associated with industrial block features and 4) selection of forage availability within natural habitat cover. For each tested hypothesis we accounted for differences in movement due to time of day and biological season. We predicted that individual deer will spend more time (move shorter net displacements) near features associated with forage acquisition such as industrial cut blocks and natural habitat, and move faster (move longer net displacement) near areas associated with risk such as predator habitat and industrial roads, trails, and seismic lines.

3.1 Methods

3.11 Study Area

We used 3000km^2 of intensively disturbed, mixed-wood boreal landscape of northeastern Alberta near Winifred Lake and the town on Conklin (Figure 3.1) to examine individual deer movement at fine scales of selection (Schneider *et al*. 2010). The landscape is a heterogeneous mosaic of boreal forest, bog, lakes and rivers, and extensive human disturbance arising from oil and gas development to the south and forestry in the north. Petroleum extraction, timber harvesting, and industrial camps in particular have superimposed a mosaic of disturbance across the study region (Pickell *et al*. 2013, Pickell *et al*. 2015). These anthropogenic disturbances include linear features such as road and trail networks, pipelines, and seismic lines and industrial polygonal or "block" features such as cut blocks, well pads, industrial camps and facilities (Pickell *et al*. 2013, Pickell *et al*. 2015).

The mammalian community in this region includes white-tailed deer, gray wolf, black bear, Canada lynx, coyote, red fox, snowshoe hare, and endangered woodland caribou (Fisher & Burton, 2018). In particular, the northeast portion of the study area intersects with the Eastside Athabasca River caribou range and the southern portion intersects with the Cold Lake caribou range (Alberta Environment & Parks, 2017).

3.12 Landscape covariates & telemetry data

We quantified land cover data (Table 3.1) for natural habitat characteristics such as wetlands and dominant tree species canopy and understorey cover (cover > 70%) from the Alberta Vegetation Index (Alberta Environment & Parks, 2010). Industrial linear features such as road and trail networks, pipelines, seismic lines, and 3D seismic lines were quantified from the University of Alberta human footprint project (U of A, 2012). Industrial block features including cut blocks, well pads, and industrial mines were obtained from the Alberta Biodiversity Monitoring Institute (ABMI, 2010).

We measured indirect predation risk using extrapolated camera trap data to model species-habitat relationships. Detections for gray wolf (*Canis lupus, n*=2,508) and black bear (*Ursus americanus, n*=2,657) were collected from 62 camera traps in a stratified random design across the study area between October 2011-2014. Fisher & Burton (2018) generated proportional binomial General Linear Models (GLMs) (Zuur *et al*. 2007) using monthly occurrence frequency against anthropogenic and natural landscape covariates. We extrapolated relative predator occurrence frequency values for gray wolf and black bear from these top GLM model beta coefficients and linearly scaled the estimates in ArcGIS 10.5 as an index for indirect predation risk.

We measured deer movement from thirty-eight females fitted with LOTEK Iridium Track M 3D telemetry collars from October 2011-2014 (Figure 3.1) in accordance with animal care protocols by InnoTech Alberta's Animal Care Committee, and permitted by Alberta Environment and Parks. Does were captured using clover traps (Clover 1956) and programmed to record locations at 2-hour fixed intervals (Fisher & Burton, 2016). A total of 111,978 telemetry locations were obtained over the three-year period with a mean of 2,946 locations per individual. Mortality and collar malfunction reduced our sample size to thirty-five individuals and limitations in sample size (< 30 collar days) across multiple seasons further reduced our total individuals analyzed to twenty.

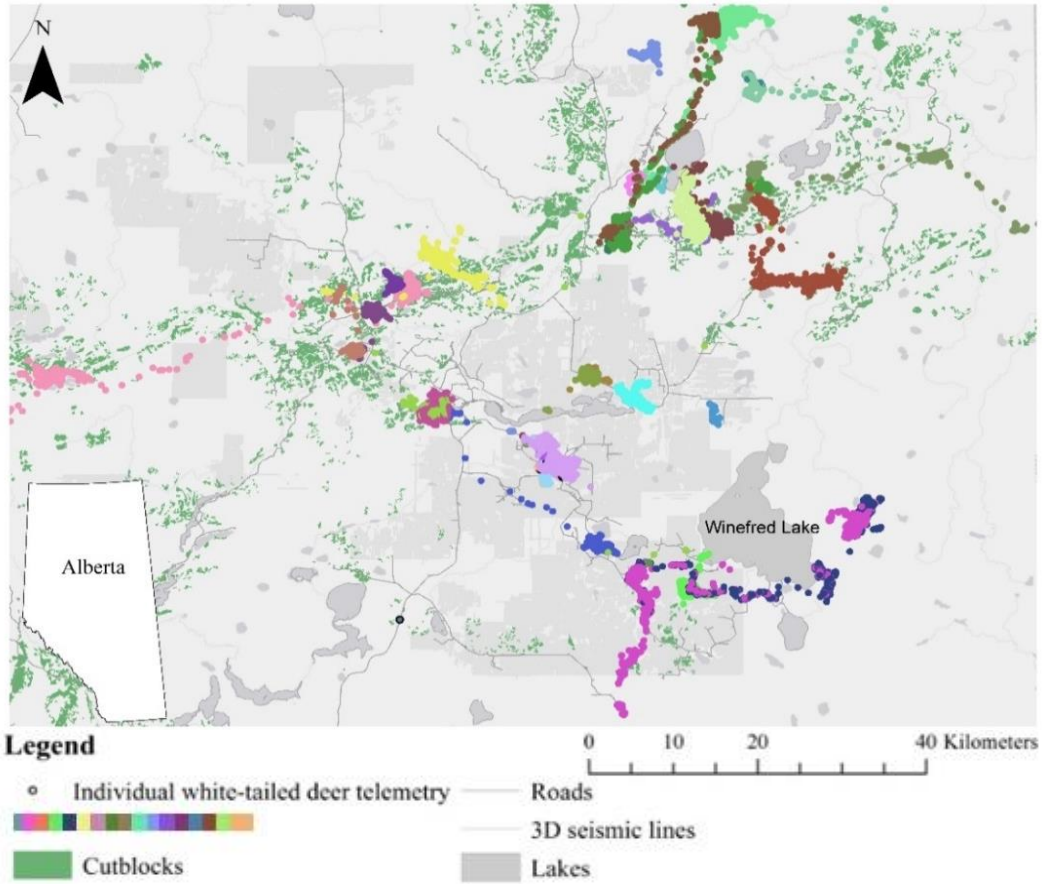


Figure 3.1. Study area and data distribution in Northeastern AlbertaTelemetry locations for 35 female white-tailed deer collared from October 2011-2014
in relation to roads and dense 3D seismic lines as gray linear features, large lakes as gray polygons, and cut blocks as green polygons across the 3000km^2 study area in northeastern Alberta.

Table 3.1. Hypotheses and corresponding landscape covariates and data sources

The landscape variables used in the white-tailed deer models include vegetation classification from the Alberta Vegetation Inventory (AVI), industrial linear features from the University of Alberta (U of A) updated to 2012, and industrial block features from the Alberta Biodiversity Monitoring Institute (ABMI) human footprint project updated from 2010.

Hypothesis	Variable Name	Description	Source
Resource subsidy	Distance to cut block	Forest harvesting areas with mature trees removed and saplings regrowing	ABMI 2010
	Distance to well sites	Well pads deforested for in-situ oil extraction	
	Distance to industrial mines✦	Borrow Pits, Industrial Sites, Mine Sites, Well Sites, Peat Mines	
Linear Features	Distance to seismic line	Traditional seismic petroleum exploration line *ca.* 7-10 m wide	U of A 2012
	Distance to 3D seismic line	Seismic petroleum exploration line *ca.* 1-3 m wide	
	Distance to pipeline	Petroleum pipeline and grassy right of way	
	Distance to rail	Railway line and associated vegetated right of way	
	Distance to road	Hard surface road, Roads including vegetated verge, Unimproved (gravel) roads, truck trails, winter roads	
	Distance to trail	Unimproved dirt track ca. 5-10 m wide navigable by off-highway vehicle or foot	
Natural Features	Distance to open wetland	Open wetland including lakes, streams, and bogs	AVI
	Percent cover Aw*	Trembling aspen *Populus tremulodies*	
	Percent cover Bw	White birch *Betula papyrifera*	
	Percent cover Fb	Balsam fir *Abies balsamea*	
	Percent cover Lt	Tamarack *Larix laricina*	
	Percent cover Pb	Balsam poplar *Populus balsamifera*	
	Percent cover Pj	Jack pine *Pinus banksiana*	
	Percent cover Sb	Black spruce *Picea mariana*	
	Percent cover Sw	White spruce *Picea glauca*	
	Percent coverUdec	Understorey deciduous species.	
	Percent cover Uconif	Understorey coniferous species	
Indirect Predation Risk	Wolf GLM	Predicted gray wolf relative abundance scaled from 0-1	Fisher & Burton 2016
	Bear GLM	Predicted black bear relative abundance scaled from 0-1	

All distance-to metrics are measured in metres (m) ✦These are composite variables; measuring the distance to the closest of any of these features, regardless of type.*PCT refers to the *percent* of the forest canopy overstorey dominated by this leading tree species. We also included variable denoted uPCT, referring to the percent of the forest understorey dominated by each of these tree species.AVI data were created and provided by Alberta Environment and Parks. 2010 Provincial Human Footprint layers and 2012 linear features were provided by ABMI and University of Alberta, Integrated Landscape Management Lab.

3.12 Step generation & habitat metrics

The basis of the iSSA analysis is to compare the steps actually used by individual deer with those that were available to them. We generated used steps and turn angles from consecutive telemetry locations with a 2-hour fix rate for all individuals using the *movement.ssf* function in Geospatial Modeling Environment (GME) (www.spatialeclogy.com/gme). Available steps and turn angles were randomly generated in GME with a 5:1 ratio to observed steps based on similar studies (Van Beest *et al.* 2012; Thurfjell *et al.* 2014) by fitting a uniform distribution to turn angles between – π and π and fitting available step lengths to a lognormal distribution of the used step lengths (Avgar *et al*. 2016). Endpoints for available steps were generated in ArcMap 10.5. Habitat characteristics in an SSF can be measured from endpoints, along the step, or from the centre of the step (Thurfjell *et al*. 2014). The steps linking consecutive points are representative of the net straight-line distance and directions travelled by an animal only and are not reflective of their actual movement path. Therefore, we argue that endpoints are the most logical choice for measuring habitat metrics. The mean step length of the population (165 m) was used as a proximate radius for measuring the proportion of natural habitat features around the endpoints of used and available steps for all individuals.

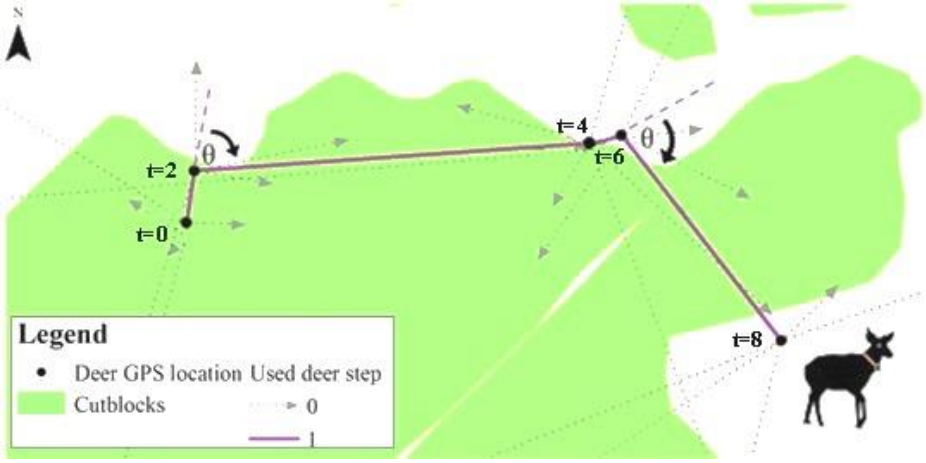


Figure 3.2. Used and available step lengths and turn angles generated from GPS data for use in the ISSA analysis

Step selection function for an individual white-tailed deer moving across a cut block from time t=0 to t=8. Used "steps" are the straight-line distance between consecutive telemetry locations and are paired with a set of available steps drawn from the individual's step length and turn angle distribution. The turn angle (θ) is calculated as the directional angle between the current step and the following step as a numeric value between –π and π (Adapted from Thurfjell, 2014).

3.13 Core Model

A core model was developed as a "null" hypothesis for deer movement based on co-variates that are expected to affect decision-making and activity patterns regardless of habitat selection (Prokopenko, 2017). Directionality of movement is measured by using the cosine of the turn angle (*cosTurnAngle*) measured in radians as a value between -1 (backward movement) to 1 (forward movement) with zero indicating a random walk (Benhamou, 2006). Including *cosTurnAngle* as a core model covariate accounts for directional persistence and is especially relevant during periods of migration or dispersal by deer from winter yards (DeYoung *et al*. 2011). Movement rate is calculated by the distance traveled divided by the 2-hour period time interval between consecutive points. Longer steps in a 2-hour time frame indicate a greater net displacement and faster movement rate. We used a natural log (ln) transformation of step length (*lnStepLeng*) as a measure of an individual deer's net displacement and rate of movement over two hours.

Time of day is an important factor that may influence the rate of movement of an animal due to its diel activity patterns (Halle, 2000; Frey *et al*. 2017). White-tailed deer are crepuscular -– most active at dawn and dusk when foraging (Masse & Cote, 2013). We used the R package "suntime" to categorize the GPS fix times depending on the time of day (Nouvellet *et al*. 2012). We used a simple interaction between *lnStepLeng* and *TimeofDay* categorized as twilight hours, daytime and nighttime, to account for differences in movement during crepuscular activity. We defined twilight as the combined period of dusk and dawn (Prokopenko *et al*. 2016). "Dawn" was defined as the period between one hour before sunrise to one hour after, and "dusk" as the period between one hour before sunset and one hour after (Masse & Cote, 2013).We defined daytime as the period between dawn end and dusk start, and nighttime from dusk end to dawn start (Masse & Cote, 2013).

Season affects habitat selection and movement rates, as environmental conditions or life history stages require more or less energy conservation (Masse & Cote, 2013; Darlington, 2018). We use an interaction between *lnStepLeng* and *season* to account for general changes in movement during important life history stages coinciding with changing climatic conditions. We defined biological seasons for deer (Hewitt *et al*. 2011; Williams *et al*. 2012) wherein winter

occurs from January 1st-April 30th, parturition from May 1st to June 30th, summer from July 1st to September 30th and rut from October 1st to December 31st.

Table 3.1. Core model parameters used in iSSA models
Core model parameter denotations for null hypothesis predicting individual deer movement.

Movement metrics	Core model parameter
Directionality	*cos(TurnAngle)*
Base rate of movement	*lnStepleng*
Time of day	*lnStepleng:TimeofDay*
Biological season	*lnStepleng:Season*

3.15 Competing hypotheses

We tested five principal hypotheses to explain individual habitat selection and movement responses to landscape characteristics associated with perceived predation risk and foraging behaviour (Table 2). Prey increase their movement rates and thus energetic costs to reduce their time spent in habitat associated with risk (Frair *et al*. 2005). We predicted that deer would respond negatively to features associated with greater risk of predation by making longer net displacements between consecutive steps, indicating reduced time spent near these features. We predicted that deer would select habitats associated with forage production by positively selecting these features and taking shorter steps, indicating increased time spent near those habitats. Furthermore, we competed each hypothesis against a global model (Burnham *et al*. 2010) representing cumulative effects (i.e. the additive effect of all individual variables) to evaluate the relative strengths of each model in describing individual deer habitat selection and movement.

Table 3.2. Deer habitat selection and movement hypotheses and predictions for iSSA
Predicted movement responses by deer to features associated with foraging versus features associated with perceived risk.

Hypothesis	Model parameters	Predicted response
Deer increase movement rate in risky places	Linear features	Avoidance + longer steps
	Indirect Predation risk	Avoidance + longer steps
Deer reduce movement rate in forage habitat	Block resource subsidies	Selection + shorter steps
	Natural habitat	Selection + shorter steps

3.16 ISSA Models

We used conditional logistic regression to fit the core model, four hypothesis models and one StepAIC global model (R package *MASS*; Venables & Ripley, 2002) for each individual deer. Movement rate was represented within each candidate model by an interaction between the *lnStepleng* and other model covariates - where a positive beta coefficient represents an increase in step length corresponding with an increase in parameter values, and inversely a negative beta coefficient represents a decrease in step length with an increase in parameter values (Avgar *et al*. 2016). We used fixed 2-hour intervals for each step length, therefore greater step lengths correspond to a greater net displacement, or rate of movement over time.

The StepAIC function uses a stepwise model selection approach by retaining parameters with the lowest AIC score which minimizes information loss and represents the closest and most parsimonious representation of "full reality" (Burnham & Anderson 2002; Burnham *et al*. 2010). We used this approach to reduce our total number of parameters in the global models without bias and to improve model performance. We used conditional logistic regression to compare matched cases and controls of used and available steps respectively (Fortin *et al*. 2005). We used the function *clogit* in the R package *survival* (version 3.3) to fit conditional models using start point ID as the strata for each individual (Therneau, 2015). Models with the lowest AIC score were considered the best-supported model and hence the hypothesis with the most evidentiary support (Akaike, 1973; Burnham & Anderson, 2002).

3.2 Results

We obtained sufficient GPS data from 20 individuals of the 38 captured and collared does to analyze seasonal movement by including individuals with at least 30 collar days in each season. These 20 collars collected a total of 408,078 GPS fixes, and an average of 648.4 days of continuous movement data per individual. Deer step length over a 2 hour fix rate approximated a lognormal distribution (165 m ± 1.21m, min = 0.1 m, max = 10,774 m), and turn angles were on average negative (-0.0068 rad ± 0.0066 rad).

3.21 Cumulative effects best predict individual habitat selection & movement

The cumulative effects of anthropogenic disturbance, natural habitat, and predator abundance best described habitat selection and movement for 19 of 20 individual white-tailed. This model had the lowest AIC score and 100% of the weight of evidence compared to other models (Figure 3.21, Table 3, see Appendix II Table 4). The strongest principal hypothesis was the influence of natural habitat on selection and movement, followed by linear features (Figure 3.21). The core model alone was consistently ranked last in all individual candidate model selection.

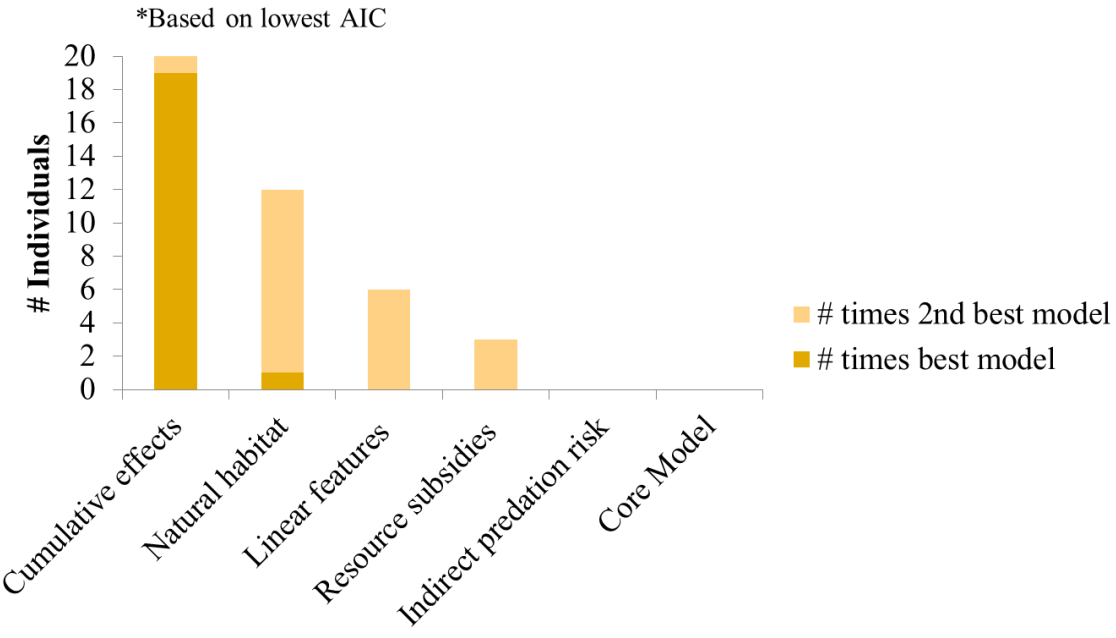


Figure 3.21 Cumulative effects best predict individual deer movement
Summary of model rankings across individual white-tailed deer (n=20) by lowest AIC score. Models are summarized by the number of times the model was ranked as the top model and second best model predicting individual deer movement.

3.22 Individuals vary in habitat selection

We summarized the selection beta coefficients β from the Global StepAIC models across individuals to compare trends by weighting the mean and calculating the 95% confidence envelope (Symonds & Moussalli, 2011). We did not average models to estimate population trends due to limitations of averaging for models with differences in retained parameters (Cade, 2015) rather; we report here the variation in parameter estimates. Directional movement was positive but not significant across individuals ($\overline{\beta}$ = 0.2795, 95% CI [0.0631- 0.4960]) and observed step lengths were shorter than the random distribution ($\overline{\beta}$ = -0.1956, 95% CI [-0.4603 - 0.0691]).

Deer more consistently selected for close proximity to cut blocks ($\overline{\beta}$= -0.1093, 95% CI [-0.2259 - 0.0073]) and trails ($\overline{\beta}$= -0.0741, 95%CI [-0.2704 - 0.1221]), and avoided well sites ($\overline{\beta}$ =0.0886, 95%CI [-0.1209 - 0.2982]), seismic lines ($\overline{\beta}$ =0.1557, 95%CI [0.0599 - 0.2515]), roads ($\overline{\beta}$ =0.0834, 95%CI [-0.0920 - 0.2589]), percent white spruce ($\overline{\beta}$ = -0.1036, 95% CI [-0.2027 - 0.0044]), and white birch stands ($\overline{\beta}$ = -0.0774, 95% CI [-0.2155 - 0.0607]). All other mean beta coefficients resulted in more variable responses (Table 5).

3.23 Deer move faster near risky features

Deer most consistently and strongly increased their rate of movement when in proximity to well sites (95% CI: $0.2 > \beta > -0.65$), roads (95% CI: $-0.01 > \beta > -0.7$), and conventional seismic lines (95% CI: $0.01 > \beta > -0.6$) (Figure 3.22). Each of these anthropogenic features had a median negative effect on step length with increasing distance, indicating a faster movement rate within close proximity to a feature. Deer responded more variably to other anthropogenic factors, and these parameters were included in fewer top models. All individuals exhibited seasonal differences in movement, with greatest net displacement during parturition and lowest during winter (Figure 3.22). Day-time differences in movement were more variable across individuals, with the most movement occurring during the day (default level) and the least at night (95% CI: $-0.2 > \beta > -0.3$) (Figure 3.22).

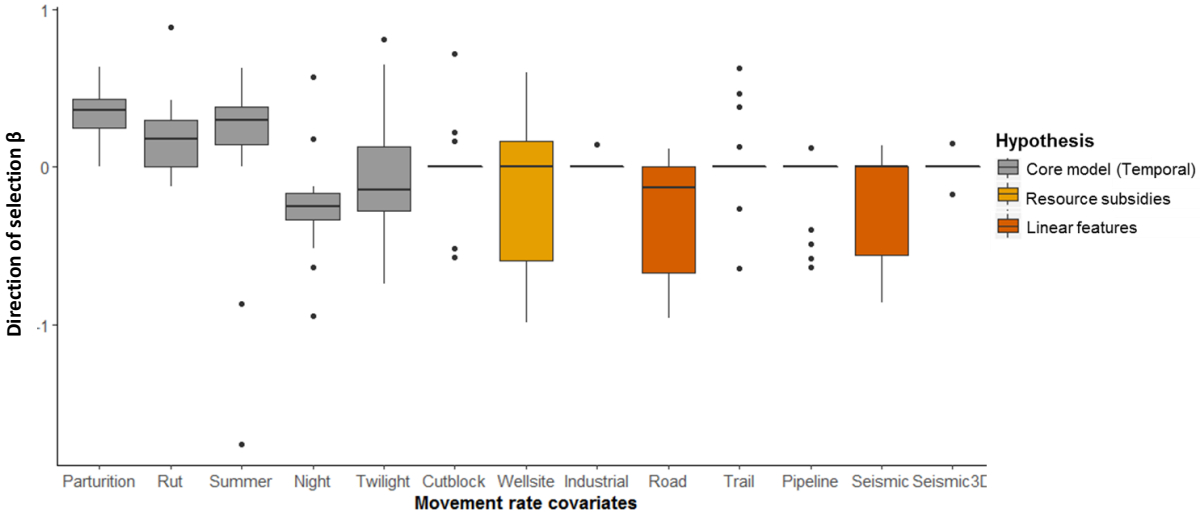


Figure 3.22. Direction of selection (β) across individual white-tailed deer movement rate parameters I

Boxplots of beta coefficients for core model and resource subsidy movement rate parameters (*lnStepleng*: *Coefficient*) across global cumulative effects models for individual white-tailed deer (*n*=20). Categorical covariates "season" is modelled against 'winter' and "time of day" is modelled against 'day time'. All anthropogenic covariates are distance-to metrics. Incomplete boxes indicate low occurrence of a variable across individual global models.

The effect of predicted relative occurrence frequency of gray wolves on deer movement rate was significantly positive for almost all individuals (95% CI: $0.68 > \beta > 0.2$) (Figure 3.4). The effects of percent aspen (95% CI: $0.55 > \beta > 0.1$) and white birch (95% CI: $0.6 > \beta > 0.05$) canopy cover on step length were important predictors across individuals, and indicate increased movement with increased canopy cover (Figure 3.23). Increasing percent coniferous understorey negatively affected step length, indicating slowed movement (Figure 3.23). Movement rate covariates for other anthropogenic and natural features were less represented in global models and individuals varied in their responses with less discernable trends.

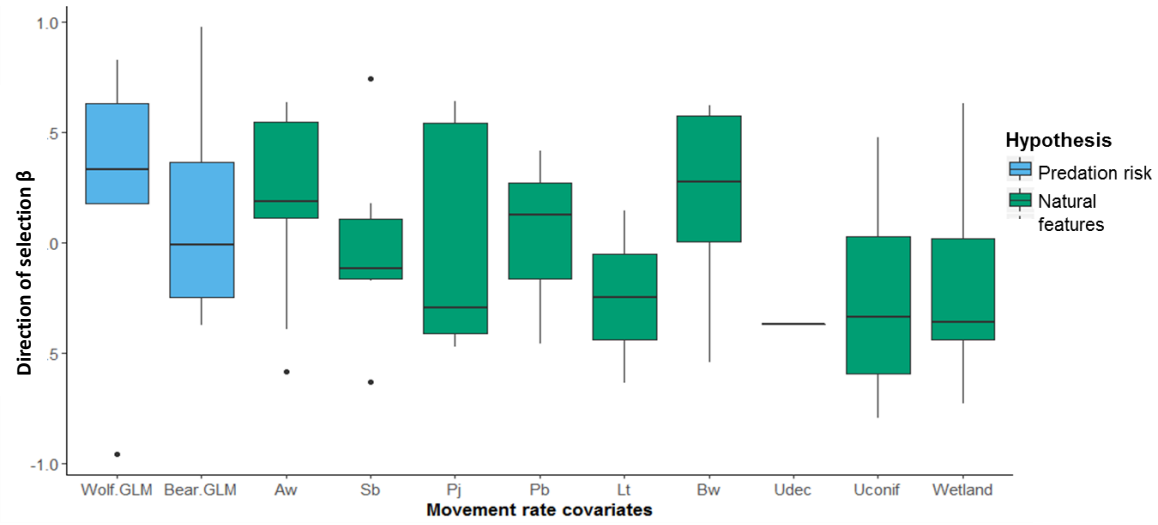


Figure 3.23. Direction of selection (β) across individual white-tailed deer movement rate parameters II

Boxplots of beta coefficients for predation risk and natural habitat movement rate parameters (*ln*Stepleng: Coefficient) across global cumulative effects models for individual white-tailed deer (n=20). Predator covariates are measured as relative abundance from extrapolated General Linear Model predictions. Vegetation covariates are measured as percent canopy cover and wetlands are a measure of distance in meters (details of variables in Table 3.1). Incomplete boxes indicate low occurrence of a variable across individual global models.

3.3 Discussion

In an intensively human-altered landscape, the cumulative effects of human land use, predator distributions, and natural habitat drive the movement behaviour of white-tailed deer. Our results provide support for the risk-avoidance hypothesis ,as evidence by an increase in deer movement rate when approaching industrial linear features and higher predicted wolf occurrence. Deer did not reduce their movement rate when approaching quality forage habitat, and instead showed increased movement through deciduous stands closely associated with apex predators (Fisher & Burton, 2018). Temporal differences in movement rate may be attributed to increased energetic requirements depending on biological season and crepuscular activity. For example, movement rate was significantly reduced in the winter months and during the night when deer are less active. The differences in movement rate near certain habitat features may be attributed to energetic trade-offs between time spent foraging and time spent avoiding risk (Kie *et al.* 1999). These findings suggest white-tailed deer may employ a time-minimizing approach to foraging in areas with a greater likelihood of wolf encounters and linear disturbance.

3.31 Energetic trade-offs

White-tailed deer exhibited differential movement responses to landscape features associated with risk versus those associated with quality forage. Optimal foraging theory (Kie, 1999) predicts that animals will strive to maximize energy gained or minimize time spent to obtain a fixed amount of energy. A time-minimizing approach implies that an animal is minimizing time spent exposed to predators while foraging (Kie, 1999; Frair *et al*. 2005). Energetic trade-offs in ungulates are increasingly important to consider in the context of expansive human land-use change and the colonization of invasive species such as white-tailed deer.

The conditions by which this invasive ungulate is able to sustain its population through Alberta's severe winters are largely attributed to the presence of early seral vegetation provided by converting mature forest to early seral vegetation in the boreal forest (Fisher & Wilkinson, 2005; Fisher & Burton, 2016; Fisher & Burton, 2018). White-tailed deer significantly reduced their rate of movement during the winter months, suggesting an energy-saving strategy for winter survival (Moen, 1976). During this period, forage is scarce and more difficult to access due to severe winter conditions, while increasing snow depth limits mobility (Moen, 1976; Parker *et al*. 1984). Reduced energy intake and movement in turn make deer more vulnerable to predators such as gray wolves that are adapted to run on snow (Telfer & Kelsall, 1984; Huggard, 1993). The effects of predation risk associated with linear features may be more pronounced during the winter where snow accumulation on seismic lines is reduced, allowing wolves more efficient access to deep snow areas (Paquet *et al*. 2010; Droghini & Boutin, 2018). Linear features may exacerbate the level of risk to deer during winter when they are most vulnerable to predation and least capable of increasing their movement rate.

We hypothesized that deer would respond to high predator frequency areas by avoidance and increasing their natural movement rate. We found this to be the case in 19 of 20 individuals in areas with high wolf frequency. Similarly, individuals significantly increased their rate of movement through aspen stands, which are spatially correlated with the occurrence of wolves (Fisher & Burton 2018). Our predicted wolf distribution showed high spatial overlap with the deer telemetry data, indicating that wolves may be occurring in greater frequencies where deer

are. For example, gray wolves in Yellowstone National Park have been shown to travel more often to habitat in which elk are more vulnerable to predation such as forest edges and deep snow (Bergman *et al*. 2006). Aspen stands and other natural habitat best predicted deer habitat selection and movement of our primary hypotheses, indicating that deer are likely selecting for forage while wolves are likely selecting for deer. Deer restricted their time spent in aspen stands and moved at a faster rate when percent canopy cover increased, indicating that deer are employing a time-minimizing approach to avoid predation (Kie, 1999).

Deer increased their rate of movement most significantly during parturition when calving occurs (Hewitt, 2011) and snow cover is reduced, becoming more widespread across the landscape with greater net displacements than other seasons. Where winters are apparently restricting movement (Moen, 1976), our findings suggest that post-winter months are the most important for expanding home-ranges as rate of movement and distance travelled increase. While deer migrate some distance in the spring to acquire resources after snowmelt (Hewitt, 2011), this time period coincides with the fawning period. The increased risk of predation to neonates by black bears may be an additional consideration affecting increased movement rate as we assume that the majority of our collared females had one or two fawns at heel in the spring due to high reproductive rates (Fisher & Burton, 2016).

We conclude that anthropogenic land-use by extractive industries is altering movement of white-tailed deer by providing forage subsidies and increasing risk response to predators. Previous research on mammalian responses to industrial linear features have focused on their use as travel corridors (Latham *et al.* 2011; Squires *et al*. 2013; Dickie *et al*. 2017) though few have examined ungulate behaviour. If deer were persistently using linear features as travel corridors to move faster we would expect deer to strongly select linear features, have increased movement rate, and significant forward directional movement (Dickie *et al*. 2017). We did not detect significant directional movement and individuals largely avoided linear features while increasing their rate of movement. Our findings suggest that deer are making energetic trade-offs between natural and anthropogenic forage subsidies and risk avoidance, highlighting the importance of human land-use to deer occupancy and survivorship in this landscape.

3.32 Management implications

White-tailed deer have been expanding their range within caribou habitat over the past fifty years (McCabe & McCabe, 1984; DeYoung, 2011), a phenomena simultaneously driven by climate change and human landscape change (Dawe *et al*. 2016; Fisher & Burton, 2016). The impact of increasing deer populations in the north is three-fold: 1) providing primary prey enrichment for apex predators such as gray wolves (Latham *et al*. 2011); 2) indirectly increasing predation pressure on alternative prey (DeCesare *et al.* 2010) and 3) altering vegetation communities by extensive browsing (Côté *et al*. 2004). Currently, the trajectory of deer expansion is across northern Alberta and as far north as the southern Yukon (Dawe *et al*. 2016).

The widespread forest clearing for oil and gas exploration in Alberta has raised questions regarding the mass reduction of critical woodland caribou habitat and populations through multiple processes (Latham *et al*. 2011; Hervieux *et al*. 2014; Dickie *et al*. 2017; Hebblewhite, 2017). All woodland caribou herds whose ranges overlap with oil and gas activities are in rapid decline by as much as 50% every eight years (Hebblewhite, 2017). The current provincial and federal recovery plans for woodland caribou cite predator control as a principal method of stabilizing caribou populations; however, wolf reduction alone has not resulted in the recovery of any caribou herd (Hervieux *et al*. 2014) and is considered a short-term solution to a long-term problem (Hebblewhite, 2017). It is evident that effective caribou management strategies must address the cumulative effects of anthropogenic land-use where linear features play a critical role in supporting both apex predators (Latham *et al.* 2011; Dickie *et al.* 2017) and driving apparent competitor distribution and movement.

Unravelling the mechanisms by which deer successfully occupy caribou ranges and evade predation is an important step towards addressing the consequences of apparent competition. Linear features not only facilitate movement for wolves, they also elicit behavioural changes in deer. Reducing forage opportunities for deer by minimizing the extent of regenerating clear-cuts and linear disturbance may indirectly reduce deer populations and predation pressure on woodland caribou.

3.33 Caveats & Future Directions

We used a relatively new approach to movement modelling to examine fine-scale behavioural responses by white-tailed deer to various landscape features and habitat types. The effectiveness of the iSSA approach for accurately modelling behaviour is dependent on the scale of the parameters used and the fix-rate of the telemetry data. We used a 2-hour fix rate which leaves significant room for interpretation with regard to movement responses. For example, Avgar *et al*. (2016) suggest measuring habitat several ways for this analysis including along the step length to capture the habitat that animals move through. However, in a two-hour period it is not likely that an animal has moved in a straight line between successive GPS fixes. We attempted to account for this by measuring habitat from the GPS points, or "end point", though an increase in fix-rate on the order of minutes may make alternative measurements of habitat possible. Secondly, our mean step length for the population was 165 m for an ungulate that is capable of moving as fast as 48 km/hr (Hewitt, 2011) indicating that the individuals in this population do not move far in a two-hour period. We recommend that future studies aiming to quantify movement using this approach implement shorter fix-rates to better explain fine-scale movement patterns, particularly when examining risk response.

Though indirect predation risk was not among our top models explaining individual deer behaviour, encounters with predators are difficult to capture because species are dynamic (Creel *et al*. 2008) and these interactions likely play a more significant role in increasing deer movement rate than predicted by our models. Studies on predator-prey interactions over space and time using radio-telemetry can be costly and time consuming (Proulx *et al*. 2012) and seldom include sample sizes sufficient to make robust statistical inferences. Our metric for indirect predation risk was a coarse spatial representation of predicted predator frequencies derived from camera data over a three-year period (Fisher & Burton, 2018). Therefore we could only account for habitat used by predators and test the "risky places hypothesis", and not predator movement timed to deer movement to test the "risky times" hypothesis (Creel *et al.* 2008). We were unable to retain sufficient samples sizes to run logistic regression models for predator frequency by season and therefore may not fully capture the variation in predator space-use.

We limited our scope to examine a set of hypotheses that broadly explain movement behaviour in prey and only included movement parameters that measure the effect size of step length on landscape features. Our study was further limited by only collaring female deer; however, with high reproductive rates in deer populations (Fisher & Burton, 2016) this allowed us to make some inferences regarding behaviour during the calving season that would be difficult to disentangle with the inclusion of captured males. Deer exhibit many behaviours that we are unable to account for including resting, mating, calving, search time, and migrating under some circumstances (Hewitt, 2011). Other studies have used accelerometers on GPS collars to determine rest periods in which fixes are only taken when the animal moves at a certain rate (Stewart *et al*. 2018 *in review*). Similarly, movement rate has been used to examine calving periods in caribou (DeMars *et al*. 2013) during parturition using GPS collars. This technology would allow behaviours to be categorized in more detail including those associated with evading predators or areas with high levels of human disturbance. Nevertheless, for the first time we were able to detect significant changes in deer movement with proximity to human land use, natural vegetation canopy cover, and predator frequency derived from camera trap data.

3.34 Conclusion

The cumulative effects of human land-use, natural resources, and indirect predation risk drive deer movement, and may contribute to deer expansion in the boreal forest. Management of white-tailed deer populations must account for these cumulative drivers and for seasonal variation, where deer move farther and occupy the landscape to a greater degree during the spring and summer months and movement is restricted during the winter months. The vast network of industrial features across the boreal forest are utilized by apex predators to increase hunting efficiency (Latham *et al*. 2011; Dickie *et al*. 2017) and white-tailed deer appear to be adjusting their movements accordingly to evade predation, while also occupying habitats with abundant forage where predators are more likely. Widespread landscape change not only affects where large mammals go (Fisher & Burton, 2018) – it also changes their behaviour by introducing risks for some species, and rewards for others. The boreal north is a harsh, predator-rich environment that white-tailed deer have successfully adapted to – made possible by thousands of kilometers of forage opportunity and a quicker stride to their step.

Appendix A

Individual deer sample size and model rankings

Candidate model selection ranked by AIC score by individual white-tailed deer collar identification (n=20). Values include K model parameters, AIC score, delta AIC, AIC weight and Log Likelihood (LL).

Collar ID 32798 *n*= 55806	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	27	31997.56	0	1	-15971.8
Linear distance	15	32254.79	257.23	0	-16112.4
Natural features	19	32413.37	415.81	0	-16187.7
Block distance	11	32465.78	468.22	0	-16221.9
Predators	11	32611.1	613.54	0	-16294.6
Core model	7	32818.43	820.87	0	-16402.2
Collar ID 32806 *n*= 38328	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	19	21240.52	0	1	-10601.3
Natural features	13	21461.77	221.25	0	-10717.9
Linear distance	13	21802.43	561.92	0	-10888.2
Predators	11	21825.49	584.97	0	-10901.8
Block distance	9	22162.17	921.65	0	-11072.1
Core model	7	22243.96	1003.44	0	-11115
Collar ID 32796 *n*= 36846	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	21	21233.63	0	1	-10595.8
Natural features	19	21277.33	43.7	0	-10619.7
Block distance	11	21382.06	148.42	0	-10680
Linear distance	13	21385.33	151.7	0	-10679.7
Predators	9	21477.01	243.38	0	-10729.5
Core model	7	21621.22	387.59	0	-10803.6
Collar ID 328083 *n*= 33600	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	17	19170.99	0	1	-9568.49
Linear distance	13	19364.11	193.12	0	-9669.05
Natural features	13	19501.07	330.09	0	-9737.54
Block distance	11	19528.13	357.14	0	-9753.06
Predators	9	19666.97	495.98	0	-9824.49
Core model	7	19689.78	518.79	0	-9837.89
Collar ID 32809 *n*= 33390	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	21	18681.7	0	1	-9319.85
Natural features	19	18696.01	14.32	0	-9329.01
Linear distance	11	19329.33	647.63	0	-9653.67
Block distance	11	19330.88	649.18	0	-9654.44
Predators	11	19352.86	671.16	0	-9665.43
Core model	7	19367.09	685.4	0	-9676.55
Collar ID 33454 *n*= 26100	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	17	14858.46	0	1	-7412.23
Linear distance	11	15007.4	148.94	0	-7492.7
Natural features	13	15014.39	155.93	0	-7494.2
Block distance	11	15064.95	206.49	0	-7521.47
Predators	9	15115.69	257.23	0	-7548.85
Core model	7	15174.31	315.85	0	-7580.15
Collar ID 33456 *n*= 22314	K	AIC	ΔAIC	AICWt	LL

Cumulative effects	21	12339.81	0	1	-6148.91
Linear distance	13	12529.3	189.49	0	-6251.65
Block distance	11	12541.01	201.19	0	-6259.5
Natural features	15	12590.51	250.7	0	-6280.26
Predators	9	12813.98	474.16	0	-6397.99
Core model	7	12840.28	500.46	0	-6413.14
Collar ID 33457 *n*= 20670	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	21	11997.62	0	1	-5977.81
Natural features	17	12055.46	57.83	0	-6010.73
Predators	11	12161.5	163.88	0	-6069.75
Block distance	11	12179.43	181.8	0	-6078.71
Linear distance	9	12205.87	208.25	0	-6093.94
Core model	7	12246.4	248.78	0	-6116.2
Collar ID 32440 *n*= 18378	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	15	10513.93	0	1	-5241.97
Block distance	11	10533.5	19.56	0	-5255.75
Linear distance	13	10586.45	72.51	0	-5280.22
Natural features	13	10693.65	179.72	0	-5333.83
Predators	9	10793.97	280.03	0	-5387.98
Core model	7	10798.45	284.51	0	-5392.22
Collar ID 334552 *n*= 15996	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	17	9051.52	0	1	-4508.76
Natural features	15	9138.38	86.86	0	-4554.19
Block distance	11	9152.37	100.86	0	-4565.19
Linear distance	13	9187.7	136.18	0	-4580.85
Predators	9	9240.94	189.43	0	-4611.47
Core model	7	9270.33	218.82	0	-4628.17
Collar ID 328052 *n*= 15102	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	15	8778.64	0	1	-4374.32
Natural features	11	8800.63	21.99	0	-4389.32
Predators	9	8864.15	85.51	0	-4423.08
Linear distance	11	8878.76	100.12	0	-4428.38
Core model	5	8922.25	143.61	0	-4456.13
Block distance	9	8926.22	147.58	0	-4454.11
Collar ID 32791 *n*= 14262	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	20	8145.19	0	1	-4052.59
Block distance	10	8267.19	122	0	-4123.6
Linear distance	12	8284.73	139.54	0	-4130.37
Natural features	14	8293.27	148.08	0	-4132.64
Predators	10	8424.47	279.28	0	-4202.24
Core model	6	8425.92	280.73	0	-4206.96
Collar ID 32194 *n*= 12186	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	20	6821.68	0	1	-3390.84
Linear distance	12	6973.78	152.09	0	-3474.89
Predators	8	6976.97	155.28	0	-3480.48
Natural features	12	7068.67	246.99	0	-3522.34
Block distance	10	7097.37	275.69	0	-3538.69
Core model	6	7138.02	316.33	0	-3563.01
Collar ID 32805 *n*= 11904	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	22	6747.82	0	1	-3351.91

Block distance	10	6888.31	140.49	0	-3434.15
Predators	10	6919.62	171.8	0	-3449.81
Linear distance	12	6937.3	189.48	0	-3456.65
Natural features	14	6988	240.18	0	-3480
Core model	6	7042.49	294.67	0	-3515.25
Collar ID 32793 *n*= 10974	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	22	6239.16	0	1	-3097.58
Natural features	14	6284.66	45.5	0	-3128.33
Block distance	10	6355.5	116.34	0	-3167.75
Linear distance	12	6417.61	178.45	0	-3196.8
Predators	10	6483.96	244.8	0	-3231.98
Core model	6	6504.96	265.8	0	-3246.48
Collar ID 32810 *n*= 9072	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	16	5264.22	0	1	-2616.11
Natural features	12	5278.67	14.45	0	-2627.33
Predators	8	5283.39	19.17	0	-2633.69
Block distance	10	5309.89	45.67	0	-2644.95
Linear distance	10	5310.41	46.19	0	-2645.21
Core model	6	5360.97	96.75	0	-2674.49
Collar ID 32794 *n*= 8946	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	18	5132.99	0	1	-2548.5
Linear distance	10	5170.75	37.76	0	-2575.37
Block distance	10	5193.74	60.74	0	-2586.87
Natural features	14	5219.69	86.69	0	-2595.84
Predators	10	5250.4	117.41	0	-2615.2
Core model	6	5273.65	140.65	0	-2630.82
Collar ID 32807 *n*= 8268	K	AIC	ΔAIC	AICWt C	LL
Natural features	14	4748.56	0	0.91	-2360.28
Cumulative effects	16	4753.26	4.7	0.09	-2360.63
Block distance	10	4844.4	95.84	0	-2412.2
Predators	10	4876.33	127.77	0	-2428.17
Core model	6	4876.84	128.28	0	-2432.42
Linear distance	10	4878.68	130.12	0	-2429.34
Collar ID 32197 *n*= 8250	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	17	4836.57	0	1	-2401.29
Natural features	11	4860.17	23.6	0	-2419.09
Predators	9	4899.12	62.54	0	-2440.56
Block distance	7	4899.73	63.15	0	-2442.86
Linear distance	9	4919.97	83.4	0	-2450.99
Core model	5	4926.75	90.17	0	-2458.37
Collar ID 32195 *n*= 7686	K	AIC	ΔAIC	AICWt	LL
Cumulative effects	20	4365.96	0	1	-2162.98
Natural features	14	4413.12	47.16	0	-2192.56
Linear distance	12	4531.01	165.05	0	-2253.51
Block distance	10	4547.84	181.88	0	-2263.92
Predators	10	4559.71	193.75	0	-2269.85
Core model	6	4574.28	208.32	0	-2281.14

Appendix B

Range in direction of habitat selection for cumulative effects models

Weighted mean beta coefficients, 95% confidence interval (CI), and p value range for individual global StepAIC (cumulative effects) model habitat selection parameters (*n*=20).

Covariate	Mean β coefficient	95% CI
cos(TurnAngle)	0.2795	[0.0631- 0.4960]
*ln*StepLeng	-0.1956	[-0.4603 - 0.0691]
Wolf GLM	0.0040	[-0.0990 - 0.1069]
Bear GLM	-0.0107	[-0.1688 - 0.1475]
Distance-to well sites	0.0886	[-0.1209 - 0.2982]
Distance-to trails	-0.0741	[-0.2704 - 0.1221]
Distance-to seismic	0.1557	[0.0599 - 0.2515]
Distance-to 3D seismic	0.0531	[-0.0236 - 0.1297]
Distance-to cut blocks	-0.1093	[-0.2259 - 0.0073]
Distance-to pipelines	-0.0015	[-0.2027 - 0.1996]
Distance-to roads	0.0834	[-0.0920 - 0.2589]
Distance-to wetlands	0.0214	[-0.1107 - 0.1535]
Percent Aw	-0.0161	[-0.2343 - 0.2020]
Percent Bw	-0.0774	[-0.2155 - 0.0607]
Percent Pj	-0.0242	[-0.0941 - 0.0466]
Percent Pb	-0.0515	[-0.1616 - 0.0585]
Percent Sb	0.0544	[-0.0752 - 0.1840]
Percent Lt	-0.0492	[-0.1860 - 0.0875]
Percent Sw	-0.1036	[-0.2027 - 0.0044]
Percent Uconif	0.0674	[-0.0122 - 0.1469]
Percent Udec	-0.0280	[-0.1093 - 0.0534]

Literature Cited

Alberta Environment & Parks. (2017). Alberta Caribou Ranges Map. Retrieved from: http://aep.alberta.ca/fish-wildlife/wildlife-management/caribou-range-planning/caribou-range-maps.aspx

Alberta Biodiversity Monitoring Institute. (2010). Human Footprint Report. Retrieved from: http://abmi.ca/home/data-analytics/da-top/da-product-overview/GIS-Land-Surface/HF-inventory.html

Akaike, H. (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika, 60*, 255–265.

Avgar, T., Potts, J. R., Boyce, M.S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution,7*: 619–630.

Benhamou, S. (2006) Detecting an orientation component in animal paths when the preferred direction is individual-dependent. *Ecology.87*, 518–528.

Bergman, E.J., Garrott, R.A., Creel, S., Borkowski, J.J., Jaffe, R., Watson, F.G.R. (2006). Assessment of Prey Vulnerability through Analysis of Wolf Movements and Kill Sites. *Ecological Applications, 16(1*): 273–284.

Burnham, K. P., & Anderson, D. R. (2016). Multimodel Inference. Sociological Methods & Research, 33(2), 261-304.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2010). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23-35.

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology, 96*(9), 2370–2382.

Cattarino, L., McAlpine, C.A., Rhodes, J.R. (2016). Spatial scale and movement behaviour traits control the impacts of habitat fragmentation on individual fitness. *British Ecological Society, 85*(1):168-177.

Côté, S.D., Rooney, T.P., Tremblay, J-P., Dussault, C., Waller, D.M. (2004). Ecological Impacts of Deer Overabundance. *Annual Reviews, 35*: 113-147.

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.M., Hewison, A.J.M. (2008). Inferring the effects of landscape structure on roe deer (Capreolus, capreolus) movements using a step selection function. *Landscape Ecol. 23*: 603–614.

Creel, S., Winnie, J. A., Christianson, D., & Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour, 76*(4), 1139-1146.

DeMars, C.A, Auger-éthé M., Schlägel, U.E., Boutin, S. (2013). Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution; 3*(12): 4149–4160.

DeYoung, R. W., Miller, K.V., & Hewitt, D. (2011). White-tailed deer behaviour. Biology and management of white-tailed deer. 311-351.

Dickie, M., Serrouya, R., McNay, R. S., Boutin, S., & du Toit, J. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology, 54*(1), 253-263.

Dietz, H. & Edwards, P.J. (2006). Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology, 87, 1359–1367.

Dingle, H. (2015). Animal Movement Across Scales edited by Lars-Anders Hansson and Susanne Åkesson. *The Quarterly Review of Biology, 90*(4), 437-438.

Droghini, A., & Boutin, S. (2018). Snow conditions influence grey wolf (Canis lupus) travel paths: the effect of human-created linear features. *Canadian Journal of Zoology*, *96*(1): 39-47.

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics, 40*(1), 677-697.

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, *21*(6): 1003-1015

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics, 34*: 487–515.

Fisher, J.T., & Burton, A.C. (2018). Wildlife winners and losers in an oil sands landscape. *Front Ecol Environ. 16*(6): 323-328.

Fisher, J.T., & Burton, A.C. (2016). Moose and Predator Numerical Responses to Anthropogenic Features in the Alberta Oil Sands Region of Alberta. Alberta Innovates – Technology Futures, Vegreville, AB. 34 pp.

Fisher, J.T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev 35*: 51–81.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005). Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. *Ecology 86*:1320-1330.

Frair, J. L., Merrill, E. H., Visscher, D. R., Fortin, D., Beyer, H. L., & Morales, J. M. (2005). Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, *20*(3), 273-287.

Frey, S., Fisher, J.T., Burton, A.C. (2017). Investigating animal activity patterns and temporal niche partitioning using camera trap data: Challenges and Opportunities. *Remote Sensing in Ecology and Conservation*: 1-10.

González-Moreno, P., Diez, J. M., Richardson, D. M., & Vilà, M. (2015). Beyond climate: disturbance niche shifts in invasive species. *Global Ecology and Biogeography, 24*(3): 360-370.

Greenwood, Paul J. & Swingland, I. R. 1946- (1983). The Ecology of animal movement. Clarendon Press, Oxford [Oxfordshire]

Halle, S., 2000. Ecological relevance of daily activity patterns.Pp. 67–90. In Activity Patterns in Small Mammals. Springer, Berlin Heidelberg.

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation, 206*: 102-111.

Hervieux, D., Hebblewhite, M., DeCesare, N. J., Russell, M., Smith, K., Robertson, S., &Boutin, S. (2013). Widespread declines in woodland caribou (Rangifertaranduscaribou) continue in Alberta. *Canadian Journal of Zoology, 91*(12), 872-882.

Hervieux, D., Hebblewhite, M., Stepnisky, D., Bacon, M. Boutin, S. (2014). Managing wolves (Canis lupus) to recover threatened woodland caribou (Rangifer tarandus caribou) in Alberta. *Can. J. Zool. 92*: 1029–1037.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol 12*:197-229.

Huggard, D.J. (1993). Effect of snow depth on predation and scavenging by gray wolves. *J. Wildl. Manage. 57*(2): 382–388.

Kie, J.G. (1999). Optimal Foraging and Risk of Predation: Effects on Behaviour and Social Structure in Ungulates. *Journal of Mammology, 80*(4): 1114-1129.

Latham, A. D. M., Latham, M. C., Boyce, M.C., Boutin, S. (2011). Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications, 21*(8), 11.

Latham, A. D. M., Latham, M.C., McCutchen, N.A., &. Boutin, S. (2011)b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management 75*:204-212.

Latombe, G., Fortin, D., Parrott, L. (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology, 83*: 185–198.

Lawler, J.J., Ruesch, A.S., Olden, J.D., & McRae, B.H. (2013). Projected climate-driven faunal movement routes. *Ecology Letters, 16:* 1014–1022.

Leblond, M., Dussault, C., Ouellet, J.P. (2013). Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology, 289*: 32–40.

McGreer, M.T., Mallon, E. E., Vander Vennen, L. M., Wiebe, P. A., Baker, J. A., Brown, G. S., Avgar, T., Hagens, J., Kittle, A.M., Mosser, A,. Street, G. M., Reid, D. E. B., Rodgers, A. R., Shuter, J., Thompson, I. D., Turetsky, M. J, Newmaster, S. G., Patterson, B. R., Fryxell, J.M. (2015). Selection for forage and avoidance of risk by woodland caribou (Rangifer tarandus caribou) at coarse and local scales. *Ecosphere 6*(12): 288.

Massé, A., Côté, S.D. (2013). Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. *Can. J. Zool. 91*: 252–263.

May, R., Landa, A., van Dijk, J., Linnell, J.D.C. & Andersen, R. (2006). Impact of infrastructure on habitat selection of wolverines Gulo gulo. Wildl. Biol. 12, 285–295.

McCabe, R. E., & McCabe, T.R.. 1984. Of slings and arrows: a historical retrospective. Pp. 19–72 in L. Halls, ed. White-tailed deer ecology and management. Wildlife Management Institute, Washington, DC.

Miller, J. R. B. (2015). Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. *Biodiversity and Conservation, 24*(12), 2887-2911.

Nouvellet, P., Rasmussen, G. S. A., Macdonald, D. W., Courchamp, F. (2012). Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *Journal of Zoology, 286(*3): 179-184.

Paquet, P.C., Alexander, S., Donelon, S., and Callaghan, C. (2010). Influence of anthropogenically modified snow conditions on wolf predatory behaviour. In The world of wolves: new perspectives on ecology, behaviour, and management. Edited by M. Musiani, L. Boitani, and P.C. Paquet. University of Calgary Press, Calgary, Alta. pp. 157–173

Parker, K. L., Robbins, C.T., & Hanley, T.A. (1984). Energy expenditures for locomotion by mule deer and elk. *J. Wildl.Manage. 48*: 474-488.

Prokopenko, C. M., Boyce, M. S., Avgar, T., & Tulloch, A. (2017). Characterizing wildlife behavioural responses to roads using integrated step selection analysis. *Journal of Applied Ecology, 54*(2), 470-479.

Proulx, G, Cattet M.R.L., Powell R.A. (2012). Humane and efficient capture and handling of carnivores. In: Boitani L, Powell RA, editors. Carnivore ecology and conservation: a handbook of techniques, Oxford: Oxford University Press. pp. 70–129.

Rogala, J.K., Hebblewhite, M., Whittington, J., White, C.A., Coleshill, J. & Musiani, M. (2011). Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. *Ecol. Soc. 16,* 16.

Schneider R.R., Hauer, G., Adamowicz, W.L., & Boutin S. (2010). Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biol Conserv 143:* 1603-11.

Squires, J.R., DeCesare, N.J., Olson, L.E., Kolbe, J.A., Hebblewhite, M., Parks, S.A. (2013). Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation, 157*: 187–195.

Stewart, F.E.C., Darlington, S., Volpe, J.P., McAdie, M., Fisher, J.T. (2019). The matrix matters: natural habitat patches within working landscapes predicts functional connectivity better than protected areas. *Journal of Applied Ecology, In Review*.

Symonds, M.R.E., & Moussalli A. (2011). A brief guide to model selection, multimodel inference and model averaging inbehavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*(1): 13-21.

Telfer, E.S., Kelsall, J.P. (1984). Adaptation of some large North American mammals for survival in snow. *Ecology, 65*(6):1828–1834.

Therneau T. (2015). A Package for Survival Analysis in S. version 2.38. URL: https://CRAN.R-project.org/package=survival>.

Therneau, T.M., &. Grambsch, P.M. (2000). Modeling Survival Data: Extending the Cox Model. Springer, New York. ISBN 0-387-98784-3.

Thurfjell, H., Ciuti, S., & Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology 2*:4.

Turchin, P. (1998). Quantitative analysis of movement. Sinuaer Associates, Sunderland, Massachussetts, USA.

Van Beest, F.M., Van Moorter, B., Milner, J.M. (2012). Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim Behav.84*: 723–735.

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0ISSA

Williams, D.M., Dechen Quinn, A.C., Porter, W.F. (2012). Landscape effects on scales of movement by white-tailed deer in an agricultural–forest matrix. *Landscape Ecol. 27*:45–57.

Zuur A, Ieno EN, and Smith GM. 2007. Analysing ecological data. Berlin, Germany: Springer Science+Business Media.

CHAPTER 4: Moving Forward

Are linear features paving the way to white-tailed deer range expansion?

Human altered landscapes are quickly becoming the norm as the global human population exceeds 7 billion and more land is converted to meet our growing needs (Sanderson *et al*. 2002). From urbanization to resource development, human footprint – the transformation of native ecosystems to infrastructure and land use change that supports human activity (ABMI, 2017) – is spreading across every continent (Sanderson *et al.* 2002). Habitat loss from human altered landscapes is the largest threat to biodiversity loss globally (Maxwell *et al.* 2016) with both direct and indirect implications for species interactions and survival (Godsoe & Harmon, 2012). The scale, shape, and pattern of habitat loss can affect how animals perceive and move through their immediate surroundings (Dingle, 2015). The implications of altered habitat selection and movement by species in the wild depend on their adaptive responses to environmental change (Dingle, 2015). The study of animal movement and predator-prey interactions on human altered landscapes can help us understand how various modes of landscape disturbance are perceived and used by wildlife.

The impact of accelerated human development in the northeastern Alberta boreal forest is evident in the mammal community, where resource extraction has paved the way for thousands of kilometers of linear disturbance through important caribou habitat (Hebblewhite, 2017). Though the modes of linear disturbance vary, from seismic lines and pipelines to road networks and game trails, the result is a grid-like mosaic of cleared forest (Pickell *et al*. 2013) that facilitates predator movement as travel corridors (Latham *et al*. 2011) and is perceived as risky by some species of prey (Creel *et al*. 2008; DeCesare *et al.* 2010). The effect of linear features on habitat selection and movement has been studied in wolves (James & Stuart-Smith, 2000; Latham *et al*. 2011; Dickie *et al*. 2016), moose and caribou (DeCesare *et al*. 2010), elk (Prokopenko *et al*. 2017), and now white-tailed deer.

White-tailed deer have successfully invaded the mixed-wood boreal forest, and their presence has provided apex predators with an abundance of primary prey and contributed indirectly to increasing predation pressure on local caribou herds (DeCesare *et al.* 2010). As such, the role of linear features in driving deer distributions is important to consider for wildlife

managers; where the underlying mechanisms driving caribou decline are subsequently linked to habitat loss from industrial activity (Schneider *et al*. 2010) and apparent competition with deer (Fisher & Wilkinson, 2005). Furthermore, the primary drivers of deer range expansion - climate and human land use change (Dawe & Boutin, 2016) - are inextricably linked and linear features comprise a majority of land use change in Alberta (Pickell *et al.* 2015). Previous research on deer range expansion in northeastern Alberta has been limited by the exclusion of proximate linear features and the inclusion of winter only data and snow tracking to determine habitat use (Dawe & Boutin, 2016). By analyzing seasonal trends in population-scale habitat selection using 38 radio-collared individuals I found that human land use is indeed important for supporting deer populations throughout the year. Though the strength of selection for certain landscape characteristics varied, distance to cut blocks, roads, trails, and seismic lines were highly significant in predicting deer occurrence. Deer distributions were best predicted by cumulative effects models across all seasons, with total human footprint as the second best model during winter and parturition, and linear features alone during summer and rut. I was unable to account for differences in winter severity given the three-year study period, however my findings corroborated Dawe & Boutin (2016) in which human land use is an important driver of deer habitat selection in winter. Industrial linear and block features outweighed both natural habitat and predator frequency models during the winter months, indicating their increased importance when forage availability is lowest and energetic costs are greater (Delgiudice *et al.* 2002).

The continued use of anthropogenic features from summer into winter suggests that deer may be locally expanding their ranges (VerCauteren, 2003), gradually moving northward as average temperatures increase and development of the boreal forest continues. Deer occupied the landscape to a greater extent during parturition when conditions are milder, calves are born, and the risk of bear predation on neonates increases (DeYoung *et al.* 2011). In the predictive seasonal distribution maps in Chapter 2 I show that predicted winter deer occurrence hot spots are occupied by the collared deer during parturition. I suggest that parturition is when local range expansion occurs, as deer leave winter yards in pursuit of quality forage and remain where resources are plentiful through the following winter. Future research on local range expansion could include long-term home-range analysis for individuals to examine spatio-temporal shifts in distributions.

I hypothesized that linear features would be perceived as risky places (Creel *et al*. 2008) by deer and predicted that deer would avoid these features both at the population level, and at the individual level. I found that at the population scale deer strongly selected for most types of linear disturbances throughout the year, including roads, trails, and seismic lines. Though our predictions were not supported, the linear features hypothesis was consistently one of the best supported core models. These results indicate that linear features attract deer at large scales. I suggest that some linear features such as conventional seismic lines provide sources of forage subsidies (Finnegan *et al.* 2018) similar to cut blocks (Fisher & Wilkinson, 2005). Seismic lines are estimated to contribute to 46% of total linear footprint in Alberta (Pascher *et al*. 2013) and are as dense as 10km/km^2 in parts of northeastern Alberta (Lee & Boutin, 2006). By area, seismic lines could provide more early seral vegetation across a greater extent than timber harvested areas combined.

Though deer may occupy more disturbed habitat at large scales, the results of the ISSA modeling approach (Avgar *et al*. 2016) for individuals showed that deer increase their rate of movement when in proximity to certain linear features. I hypothesized that deer would negatively respond to linear features by increasing their movement rate due to their use by gray wolves (Dickie *et al*. 2016). I found that deer not only increased their rate of movement when near linear features and areas frequented by wolves – they also increased their rate of movement in aspen stands with high canopy cover and near cut blocks. In contrast, deer moved slower in coniferous habitat, which is often associated with refugia (VerCauteren, 2003). I suggest that deer are making energetic trade-offs (Kie, 1999) between accessing quality forage in disturbed, and aspen dominated habitat with the risk of predation by wolves (Creel *et al*. 2008). That northeastern Alberta's mosaic of human land use plays an important role in sustaining deer populations while mediating a landscape of fear (Laundré *et al.* 2001; Ripple & Beschta, 2004).

Arguably, the winter months are when predation risk is greatest for deer, when energetic costs are greater (Delgiudice *et al.* 2002), movement is limited (Moen, 1976), and wolves have the adaptive advantage for running on snow (Telfer & Kelsall, 1984; Mech & Peterson, 2003). As such, I found that deer moved significantly less during the winter than other times of the year, and that deer more strongly selected for cut blocks and wolf frequented areas during this time. The wolf distribution from our camera data suggests that wolves occur where deer densities are

greater – namely in upland deciduous and timber harvested areas (Fisher & Burton, 2018). Industrial polygonal and linear clear-cuts may be facilitating primary prey enrichment of wolves indirectly by sustaining deer in heavily disturbed areas (Latham *et al.* 2011), perhaps most notably during the winter period. I recommend that future research regarding fine-scale movement behaviour and energetic trade-offs in human altered landscapes include fine-scale metrics of habitat selection such as snow depth, seismic line and cut block age, seral stage, and forest edge (Dabros *et al.* 2017) to examine these relationships more comprehensively. Furthermore, fine-scale analysis of predation risk could be improved by testing the risky times hypothesis (Creel *et al*. 2008) using radio-collared predators while vigilance behaviour may be examined using group size in ungulates (Cherry *et al.* 2015).

My findings support the hypothesis that the cumulative effects of human land use, predator frequency, and natural habitat drive deer distributions at the population, and individual level. The behavioural response of deer to areas associated with predation risk highlights the importance of energetic trade-offs in northern climates and the role that human land use plays in tipping the balance. The long-term consequences of rapid environmental change from anthropogenic sources on predator-prey dynamics and species invasion in Alberta are still unfolding and may be worsened by management decisions that are based on single species conservation (Sinclair & Byrom, 2006). Effective management of white-tailed deer and in part, woodland caribou recovery, must take into account the ecological impacts of human disturbance on multiple species, across scales, and temporal gradients. The vast network of linear disturbance in Alberta has been shown to facilitate predator movement and may also provide resource subsidies that support deer and other ungulates. Linear features may be paving the way for the colonization of white-tailed deer in Canada's boreal north.

"*The most visible example of unintended consequences, is what happens every time humans try to change the natural ecology of a place*." - Margaret J. Wheatley

Literature Cited

Alberta Biodiversity Monitoring Institute. (2017). The status of human footprint in Alberta. Human Footprint Report. Retrieved from: www.abmi.ca

Avgar, T., Potts, J. R., Boyce, M.S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution,7*: 619–630

Creel, S., Winnie, J.A, Christianson, D., & Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour 76*:1139-1146.

Cherry, M.J., Conner, L.M., Warren, R.J. (2015). Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. *Behavioral Ecology, 26*(4): 1091–1099.

Dabros, A., Hammond, H.E.J., Pinzon, J., Pinno, B., Langor, D. (2017). Edge influence of low-impact seismic lines for oil exploration on upland forest vegetation in northern Alberta (Canada). *For. Ecol. Manage. 400*: 278–288.

Dawe, K.L, & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (Odocoileus virginianus) range expansion at the northern extent of its range; land-use is secondary. *Ecology and Evolution. 6*(18); 6435-6451.

DeCesare, N. J., Hebblewhite, M., Robinson, H. S., Musiani, M. (2010). Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation, 13*: 353–362.

Delgiudice, G. D., Riggs, M. R., Joly, P., Pan, W. (2002). Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *The Journal of Wildlife Management*: 698-717.

DeMars, C.A., & Boutin, S. (2017). Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. *J. Anim. Ecol. 87*: 274–284.

DeYoung, R. W., Miller, K.V., & Hewitt, D. (2011). White-tailed deer behaviour. Biology and management of white-tailed deer:311-351.

Dickie, M., Serrouya, R., McNay, R. S., Boutin, S., & du Toit, J. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology, 54*(1), 253-263.

Dingle, H. (2015). Animal Movement Across Scales edited by Lars-Anders Hansson and Susanne Åkesson. *The Quarterly Review of Biology, 90*(4), 437-438.

Finnegan, L., MacNearney, D., Pigeon, K.E. (2018). Divergent patterns of understory forage growth after seismic line exploration: Implications for caribou habitat restoration. *For. Ecol. Manage. 409*: 634–652.

Fisher, J.T., & Burton, A.C. (2018). Wildlife winners and losers in an oil sands landscape. *Front Ecol Environ. 16*(6): 323-328.

Fisher, J.T., & Wilkinson, L.(2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev 35*: 51–81.

Godsoe, W., & Harmon, L. J. (2012). How do species interactions affect species distribution models? *Ecography, 35*(9), 811-820.

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation, 206*: 102-111.

James, A.R., Stuart-Smith, A.K. (2000). Distribution of Caribou and Wolves in Relation to Linear Corridors. *The Journal of Wildlife Management, 64*(1): 154-159.

Kie, J.G. (1999). Optimal Foraging and Risk of Predation: Effects on Behaviour and Social Structure in Ungulates. *Journal of Mammology*, *80*(4): 1114-1129.

Latham, A. D. M., Latham, M.C., Boyce, M.S., & Boutin, S. (2011)a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications 21*:2854-2865.

Laundré, J.W., Hernández, L., Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool. 79*: 1401–1409 .

Lee, P., & Boutin, S. (2006). Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. J. Environ. Manage. 78(3): 240–250.

Maxwell, S., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). The ravages of guns, nets and bulldozers. Nature, 536, 143–145.

Mech, L.D., and Peterson, R.O. 2003. Wolf–prey relations. In Wolves: behavior, ecology, and conservation. Edited by D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 131–160.

Moen, A. N. (1976). Energy conservation by white tailed deer in the winter. *Ecology* 57:192-198.

Pasher, J., Seed, E., Duffe, J. (2013). Development of boreal ecosystem anthropogenic disturbance layers for Canada based on 2008 to 2010 Landsat imagery. *Can. J. Remote Sensing, 39*(1): 42–58.

Pickell, P. D., D. W. Andison, and N. C. Coops. (2013). Characterizations of anthropogenic disturbance patterns in the mixedwood boreal forest of Alberta, Canada. *Forest Ecology and Management 304*:243-253.

Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. (2015). The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. *Canadian Journal of Forest Research 45*:732-743

Prokopenko, C. M., Boyce, M. S., Avgar, T., & Tulloch, A. (2017). Characterizing wildlife behavioural responses to roads using integrated step selection analysis. *Journal of Applied Ecology, 54*(2), 470-479.

Ripple, W.J., Beschta, R.L. (2004). Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience 54:* 755–766.

Sanderson, E.W., Jaiteh, M. , Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G. (2002). The Human Footprint and the Last of the Wild. *BioScience, 52*(10): 891-906.

Schneider, R.R., Hauer, G., Adamowiczb, W.L., Boutin, S. (2010). Triage for conserving populations of threatened species: The case of woodland caribou in Alberta. *Biological Conservation, 143*: 1603–1611.

Segan, D.B., Murray, K.A, Watson, J.E.M. (2016). A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. *Global Ecology and Conservation, 5*: 12-21.

Sinclair, A.R.E., & Byrom, A.E. (2006). Understanding ecosystem dynamics for conservation of biota. *Journal of Animal Ecology, 75*: 64–79.

Telfer, E.S., Kelsall, J.P. (1984). Adaptation of some large North American mammals for survival in snow. *Ecology, 65*(6):1828–1834.

VerCauteren, K.C. (2003). The Deer Boom: Discussions on Population Growth and Range Expansion of the White-Tailed Deer. U.S. Department of Agriculture: Animal and Plant Health Inspection Service. Pages 15-20 in G. Hisey and K. Hisey, editors. Bowhunting records of North American white-tail deer. Pope and Young Club, Chatfield, MN, USA.