# Calving Behavior of Boreal Caribou in a Multi-predator, Multi-use Landscape

by

Craig Allen DeMars

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# ABSTRACT

The boreal ecotype of woodland caribou (*Rangifer tarandus caribou*) is federally listed as *Threatened* due to population declines throughout its distribution. High mortality rates of neonate calves (≤ 4 weeks old) due to predation are a key demographic factor contributing to population declines and increasing predation has been linked to landscape disturbance within and adjacent to caribou range. To inform management strategies for improving rates of calf survival, I investigated the space use and habitat requirements of female boreal caribou during calving. Space is integral to the calving behaviour of boreal caribou with parturient females dispersing widely on the landscape, a behaviour hypothesized to reduce predation risk. I assessed potential evolutionary drivers of dispersion using simulation analyses that tracked caribou-wolf encounters during the calving season. I specifically assessed whether dispersion decreased predation risk by: (*i*) increasing predator search time, (*ii*) reducing predator encounters because individuals are inconspicuous relative to groups, or (*iii*) eliminating the risk of multiple kills per predator encounter of caribou groups. Simulation outputs show that dispersion only becomes favourable when differential detectability based on group size is combined with the risk of multiple kills per encounter. This latter effect, however, is likely the primary mechanism driving parturient females to disperse because group detectability effects are presumably constant year round. Simulation outputs further demonstrate that if females become increasingly clumped – a pattern that may result if caribou avoid disturbance in highly impacted landscapes – then calf survival is negatively affected. To specifically identify key attributes of calving habitat, I used a three-step process. First, I identified GPS locations where females were accompanied by neonate calves by developing two novel methods for predicting parturition events and neonate survival status based on female movement patterns. These methods predicted parturition with near certainty and provided reasonable estimates of neonate survival, which I further augmented with aerial survey data. Using the partitioned GPS location data, I then developed resource selection functions using a generalized mixed effects modelling approach that explicitly maintained the individual as the sampling and comparative unit. I discriminated calving areas from other areas within caribou range by conducting multiple comparisons based on season and maternal status. These comparisons show that parturient females shifted from bog-dominated winter ranges to calving areas dominated by fens. In general, reducing predation risk was a dominant factor driving calving habitat selection although the shift to fen landscapes indicates that females may be trading off increased predation risk to access higher quality forage because fens are riskier than bogs. As a third step, I explicitly evaluated calving habitat quality by relating maternal selection and use of resources to the probability of neonate survival. These analyses included spatially explicit covariates of predator-specific risk. Surprisingly, variation in landscape disturbance had minimal effect on calf survival; rather, survival was best explained by predation risk from black bears (*Ursus americanus*). Collectively, my findings yield important insights into the habitat requirements of boreal caribou during calving and highlight that management actions aimed at improving calving habitat quality will need to be conducted at large spatial scales.

# PREFACE

Throughout this thesis, I use the first person singular to maintain consistency. Modern ecological research, however, often requires collaboration. To that end, two of the chapters in this thesis represent collaborative work with fellow researchers.

*Chapter* 2 has been published as DeMars, C.A., Auger-Méthé, M., Schlägel, U.E. & Boutin, S., "Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou", *Ecology and Evolution*, vol. 3, 4149–4160. For this analysis, I conceived the concept, designed the study, collected the data and composed the manuscript. I assisted Marie Auger-Méthé and Ulrike Schlägel in method development and data analysis.

*Chapter 3* represents collaborative work with Drs. Greg Breed and Jonathan Potts. For this work, I conceived the research question and was responsible for data collection, study design, and manuscript composition. I assisted Drs. Breed and Potts in method development and data analyses.

*Chapters 1, 4*, *5* and *6* are my own original work.

The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Animal Care and Use Committee, Project Name "Assessing Spatial Factors Affecting Predation Risk to Boreal Caribou Calves: Implications for Management", Nos. 748/02/12; 748/02/13 and AUP00000019.

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Completing a graduate degree is never a solo endeavour. Fortunately, I had an extensive and knowledgeable support group to guide me through the journey. Of primary assistance was my advisor, Dr. Stan Boutin, whose incredible ability to think critically always impresses me. I am hopeful that over the past five years a tiny bit of that ability has been able to rub off on me. Stan, thanks for taking a chance on a “mature” student undergoing a mid-life career change. I am also grateful for the advice and support of my committee members Dr. Andrew DeRocher, Dr. Scott Nielsen, and, initially, Dr. Mark Boyce. Andy always made sure that the animal’s biology and natural history stayed in the picture and continually pushed – gently – that the thesis be completed in a timely manner. Scott was instrumental in guiding me through the arcane world of resource selection functions and arriving at appropriate statistical inference. Unfortunately for Scott, I directed many other students his way because of his ability to explain complex concepts in easy to understand language. I always remarked that I could learn more from Scott in 30 seconds than I could in an hour from most anyone else on the subject. Mark unfortunately had to leave the committee just prior to my candidacy exam but he provided sound critical advice on study design during the initial stages of my research.

A graduate degree is also never completed without considerable leaning on your fellow grad students. For that, I thank the members of the Boutin and Bayne labs, in particular Kim Dawe, Jessica Haines, Kristin Van Katwyck, Dario Moreira, Meghan Anderson, Eric Neilson, Jamie Gorrell, Melanie Dickie, Samuel Hache, Erin Cameron, Corey Scobie, Janet Ng, Diana Stralberg and Jeff Ball. Two others from the Boutin lab deserve special recognition. The first is Ainsley Sykes, who showed incredible patience from my excessive door knocking during the

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I extend a big thank you to Charlene Nielsen for providing invaluable assistance in all GIS analyses. Charlene is one of those good people who never says no when her assistance is asked, even when the queried task could probably be accomplished by the grad student on his/her own with a little more diligence. I also thank Al Richard and Kevin Smith (Ducks Unlimited Canada) for facilitating my use of Ducks Unlimited GIS data and providing technical support in its use.

The backbone of any ecology thesis is its research project. For initiating the project on which this thesis is based, I am indebted to Conrad Thiessen, a BC government biologist who approached Stan about putting a grad student on some caribou data he had. Over the course of the project, Conrad has become a good friend and assisting him with animal capture and collaring activities during the project's first two years are memories I will simply never forget. Conrad has since relocated to Smithers, BC and his positive outlook and dedication to boreal caribou conservation in NE BC are missed. For facilitating continued assistance on the part of the BC government, I extend thanks to Megan Watters (BC MFLNRO, Fort St. John) and Morgan Anderson (BC MFLNRO, Fort St. John).

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For general oversight of the project, I thank the members of the project's steering committee: Chris Ritchie (BC Ministry of Forests, Lands, and Natural Resource Operations), Gary Sargent (Canadian Association of Petroleum Producers), Scott Wagner (Nexen), and Steve Wilson, Ph.D. (EcoLogic Research). Their collective contributions greatly improved the overall structure of the project and their insight helped me navigate through occasional logistical challenges.

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One should never stop learning; but after 15 years in post-secondary school and four degrees, I hope I am now “educated”.....

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# CHAPTER 1

## GENERAL INTRODUCTION

Fundamental to species conservation is identifying and protecting habitat that is critical to population persistence (Camaclang *et al.* 2014). Yet, identifying a species' habitat requirements is not a trivial task. The concept of habitat itself can be difficult to define. In reviewing the habitat concept, Hall *et al.* (1997) suggested that habitat is most appropriately defined as the biotic and abiotic resources and conditions that determine the presence of a species in a defined area. This definition implicitly incorporates key components of a species' niche, specifically its environmental or structural attributes (Grinnell 1917) and its interactions with other species (Elton 1927). Moreover, the presence of a species in a defined area, if long term, suggests that the biotic and abiotic conditions defining a species' habitat also reflect the conditions required for the species to survive and reproduce (i.e. its fitness; Hutchinson 1957).

The definition by Hall *et al*. (1997) implies that identifying habitat is a multi-step process. Typically, the first step is to identify potentially important relationships between the species of interest and key environmental variables or resources (e.g. land cover type, climate, forage indices). In the last two decades, evaluating such relationships has increasingly relied on species distribution models (SDMs; Elith & Leathwick 2009), a broad suite of models that includes habitat suitability models (Dijak & Rittenhouse 2008), resource selection functions (Manly *et al.* 2002), ecological-niche factor analysis (Hirzel *et al.* 2002) and machine learning approaches (e.g. program Maxent; Phillips *et al.* 2006). In general, SDMs identify gradients in habitat quality by comparing the distribution and abundance of a species' spatial locations to the distribution and abundance of resources within a spatial scale of interest (Guisan & Thuiller 2005; Boyce 2006). Areas with a disproportionately high number of animal locations are indicative of higher habitat quality and resources are said to be selected if they are used disproportionate to their availability (Johnson 1980). This frequency-dependent process thus assumes a direct relationship between habitat quality and animal density (Boyce & McDonald 1999; Boyce *et al.* 2015), with variation in animal density in turn reflecting an area's relative fitness value (Fretwell & Lucas 1970).

Ensuring that inferences of habitat quality from SDMs scale linearly with relative fitness values might be considered a second step in identifying a species' habitat requirements. In natural landscapes, this assumption likely holds because as an adaptive behaviour, resource selection should reflect a strategy that maximizes fitness (Morris 2003). Inferences of habitat quality from SDMs, however, may break down in landscapes undergoing rapid environmental change. In such instances, animals may not be responding to novel environmental cues that have high influence on fitness, resulting in a decoupling of fitness from resource selection (Bock & Jones 2004; Sih 2013; DeCesare *et al.* 2014). This decoupling may not be captured by SDMs – which represent a static depiction of a species' Grinnellian niche (Hirzel & Le Lay 2008) – because resource selection may remain unchanged yet relative fitness values among areas may alter due to changes in the Eltonian niche (e.g. from altered species interactions; DeCesare *et al.* 2009). The potential decoupling of resource selection from relative fitness therefore limits the utility of SDMs for evaluating habitat quality in altered landscapes, a limitation that has particular relevance for conserving endangered species as many occur in landscapes highly altered by human activities (Pimm *et al.* 2014). Indeed, the prevalence of rapid environmental change in most global environments (Lawler *et al.* 2014) has resulted in an increased emphasis on explicitly evaluating habitat-fitness relationships to better inform conservation decisions (Gaillard *et al.* 2010; Heinrichs *et al.* 2010; Fordham *et al.* 2012).

A third step in identifying a species' habitat is understanding its spatial requirements, as indicated by the "in a defined area" clause within Hall *et al*.'s (1997) habitat definition. Having sufficient space is critical for individuals to obtain the necessary resources (e.g. food, refugia from competitors and/or predators) to survive and reproduce. For a species to persist in an area long-term, then sufficient space is required for multiple individuals (e.g. a minimum population size; Shaffer 1981). Effectively evaluating the spatial requirements for population persistence often involves data-intensive modelling approaches (e.g. spatially-explicit population viability analyses; Lamberson *et al.* 1992). For many species, however, such data may be unavailable. Nevertheless, insights into a species' spatial requirements may be gained from less data-intensive models such as home range analyses (Worton 1987; Moorcroft *et al.* 2006) and movement analyses, particularly those that relate movement patterns to fitness or demographic metrics (Morales *et al.* 2010).

In this thesis, I apply this multi-dimensional framework of habitat to investigate the habitat requirements and space use of boreal caribou (*Rangifer tarandus caribou*) during the calving season. Boreal caribou, an ecotype of woodland caribou, occur in a wide distribution that closely follows the boreal forest biome within Canada. Within this distribution, these animals inhabit low-productivity old-growth forests, subsisting on a winter diet dominated by low protein terrestrial lichens (Thompson *et al.* 2015). This unique dietary adaptation spatially separates boreal caribou from other ungulates (e.g. moose [*Alces alces*]) and their associated predators (e.g. wolves [*Canis lupus*]), a strategy that likely evolved to reduce predation risk (Bergerud 1974; James *et al.* 2004).

Since 2003, boreal caribou have been federally listed as *Threatened* under the *Species At Risk Act* due to population declines through much of their distribution (Environment Canada 2012). Population declines are believed to be caused by human-mediated apparent competition (Seip 1992; Rettie & Messier 1998), a process where human alteration of natural landscapes creates negative interactions between two or more species facilitated by a generalist predator (Holt 1977; DeCesare *et al.* 2009). For boreal caribou, unsustainable predation has resulted from increasing predator numbers (e.g. wolves), which track the increasing populations of other ungulate species (e.g. moose) that arise from increasing early seral conditions within and adjacent to caribou range (Seip 1992). Increasing predation may further be enhanced by linear disturbances (e.g. seismic lines, secondary roads and pipelines), which are hypothesized to increase the hunting efficiency of predators (i.e. the functional response; McKenzie *et al.* 2012) and increase predator-caribou spatial overlap (Latham *et al.* 2011). Climate change may also interact with disturbance to alter caribou-predator dynamics (Latham *et al*. 2013b; Dawe *et al*. 2014).

I focus on the calving season because this time period can play an important role in caribou population dynamics. Like other ungulates, caribou populations are sensitive to changes in adult female survival and juvenile recruitment (Gaillard *et al.* 2000; DeCesare *et al.* 2012). In many declining populations, adult female mortality can be particular high during calving (~ mid-May to mid-July; McLoughlin *et al.* 2003; Courtois *et al.* 2007) and high mortality rates of neonate calves (< 4 weeks old) contribute to unsustainably low rates of calf recruitment (Stuart-Smith *et al.* 1997; Pinard *et al.* 2012). Yet, despite this high influence on population dynamics, only a small number of studies have investigated the calving behaviour of female boreal caribou and none have been conducted within the western distribution of this ecotype (see Bergerud 1985; Hirai 1998; Carr *et al.* 2010; Pinard *et al.* 2012; Leclerc *et al.* 2012; and Dupont 2014 for eastern populations). Differences in geography, predator-prey communities and the behavioural plasticity of caribou as a species (Hummel & Ray 2008) suggest that inferences gained from eastern populations may not necessarily apply to western ranges.

Understanding the habitat requirements and space use of boreal caribou during calving has direct implications for effectively managing and conserving caribou populations. Critical habitat for boreal caribou has been designated as the range of individual populations (Environment Canada 2008), and the federal *Recovery Strategy* mandates that disturbance impacts be restricted to ≤ 35% of a population's range (Environment Canada 2012). Because many ranges exceed this threshold, the *Recovery Strategy* further specifies habitat restoration as a key management lever for stabilizing or recovering populations in decline (Environment Canada 2012). Most caribou ranges, however, have a wide geographic extent and encompass lands managed for multiple uses, necessitating that areas within ranges be prioritized for any potential conservation or restoration actions. Key to such prioritization strategies is discriminating demographically important habitats from others at scales that are conducive to management and biologically relevant to caribou (Heinrichs *et al.* 2010).

### *Overview of Thesis*

I structured this thesis as a series of inter-related yet separate papers. In *Chapter 2*, I collaborated with colleagues to develop two novel methods for inferring parturition and survival of neonate calves from movement patterns of adult female caribou. This chapter is foundational to *Chapters 4* and *5* as analyses in these later chapters relied on the developed methods to identify data specific to females accompanied by neonates. The development of these methods was necessary for two reasons. First, few quantitative methods existed for identifying parturition events in ungulates and the dependency of later analyses to effectively do so necessitated the development of methods that were both broadly applicable and rigorously tested within my study system. The second reason was to track neonate survival without using traditional methods such as radio-tagging, which is logistically infeasible in western ranges because of the forested and water-logged conditions in which caribou occur.

In *Chapter 3*, I investigated the spacing behaviour of boreal caribou at calving. This chapter is the most theoretical of the thesis as it assessed plausible evolutionary mechanisms for why females disperse from groups just prior to calving. This dispersive behaviour, which is a defining characteristic of the ecotype, is thought to be a strategy for reducing predation risk (Bergerud & Page 1987). The mechanisms by which it reduces predation risk, however, have not been explicitly tested. Using simulation analyses parameterized with empirical movement data, I evaluated three potential mechanisms by tracking the mean number of calves surviving per female as a proxy of individual fitness. While simulation outputs do not yield quantitative predictions as to how much space caribou require to reduce predation risk, results provide inferences on the potential impacts to caribou reproductive success if landscape disturbance causes females to become increasingly clumped.

In *Chapter 4*, I evaluated the selection of calving areas by female caribou. Specifically, I determined whether calving areas constituted a discrete habitat type within caribou range by contrasting these areas to other seasonal areas and by comparing resource selection based on maternal status. I used an analytical approach that explicitly maintained the individual as the sampling and comparative unit. Within this framework, I further assessed whether females selected calving areas that reduced predation risk or contained higher forage quality and/or quantity to meet lactation demands, a trade-off commonly faced by other ungulate species (Festa-Bianchet 1988; Bowyer *et al.* 1999; Parker *et al.* 2009).

The high degree of anthropogenic impacts within boreal caribou ranges suggests that inferences from maternal resource selection may not reflect calving habitat quality (DeCesare *et al.* 2014). Therefore, I explicitly evaluated habitat-performance relationships in *Chapter 5* by assessing how maternal variation in resource selection and/or use influenced the probability of neonate survival. For these analyses, I assumed predation was the primary cause of neonate mortality and discriminated among four predation-oriented hypotheses for explaining spatial variation in neonate survival. To guide potential habitat restoration or conservation strategies, three of these hypotheses were formulated to assess whether specific landscape features contributed disproportionately to neonate mortality rates. For the fourth hypothesis, I used data from wolves and black bears (*Ursus americanus*) to develop covariates representing spatially explicit predictions of predator-specific predation risk. Because factors affecting the predation process are likely scale-dependent (Lima 2002), I evaluated each hypothesis at multiple spatial scales.

In *Chapter 6*, I summarize the key findings of the thesis, discuss the potential management implications for conserving caribou populations in multi-use landscapes, and suggest directions for future research.

### *Study System*

My study system encompassed all six boreal caribou ranges currently recognized in northeast British Columbia (Fig. 1.1). This area, part of the Taiga Plains ecozone, is a mosaic of deciduous and mixed-wood uplands, poorly drained low-lying peatlands, and riparian areas (DeLong *et al.* 1991). Terrain is predominantly flat to undulating (elevation range: 410-700 m) and the climate is northern continental, characterized by long, cold winters (January mean temperature: -21.2$^{o}$C) and short summers (July mean temp.: 16.8$^{o}$C; DeLong *et al*. 1991). Common upland tree species include white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populous tremuloides*), and paper birch (*Betula papyrifera*). Low-lying peatlands are characterized by black spruce (*Picea mariana*) with occasional stands of tamarack (*Larix laricina*). Forest fire is a frequent form of natural disturbance with a mean fire interval of ~100 years (Johnstone *et al.* 2010). Moose and caribou are the dominant ungulates in the system although small populations of white-tailed deer (*Odocoileus virginanus*) and elk (*Cervus elaphus*) occur along major river valleys and near agricultural areas. For caribou, dominant predators include wolves, black bears and, occasionally, grizzly bears (*Ursus horriblis*). Lynx (*Lynx canadensis*) and wolverine (*Gulo gulo*), both of which can prey on caribou calves (Bergerud 1971; Gustine *et al.* 2006), are also present. The study area is further notable because it contains the Horn River Basin, a geologic formation that holds one of the largest shale gas deposits in Canada. Consequently, oil and gas extraction activities are the dominant form of anthropogenic disturbance (Thiessen 2009).

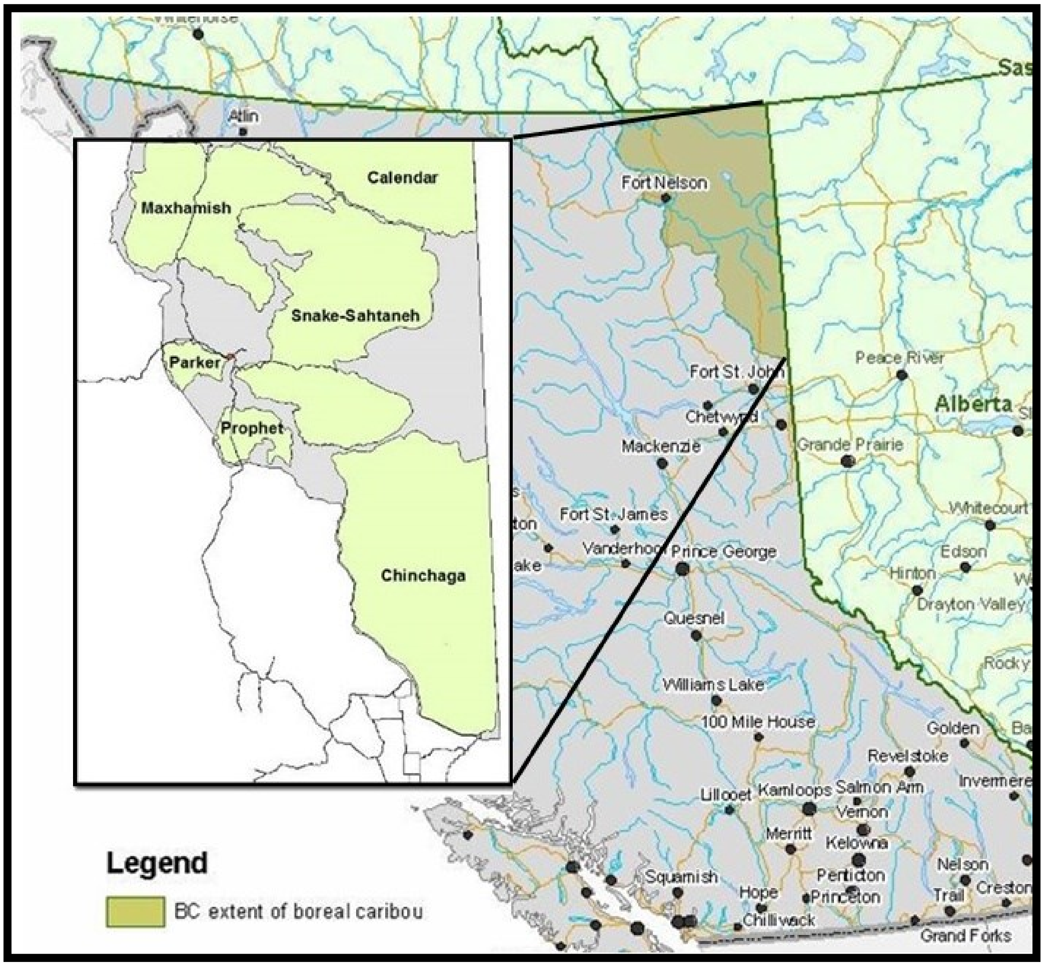

Figure 1. 1: The distribution and six recognized ranges of boreal caribou in northeast British Columbia.

## LITERATURE CITED

Bergerud, A.T. (1985). Antipredator strategies of caribou: dispersion along shorelines. *Canadian Journal of Zoology*, **63**, 1324–1329.

Bergerud, A.T. (1974). Decline of caribou in North America following settlement. *The Journal of Wildlife Management*, **38**, 757–770.

Bergerud, A.T. (1971). The population dynamics of Newfoundland caribou. *Wildlife Monographs*, **25**, 3–55.

Bergerud, A.T. & Page, R.E. (1987). Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology*, **65**, 1597–1606.

Bock, C.E. & Jones, Z.F. (2004). Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment*, **2**, 403.

Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. & Maier, J.A. (1999). Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy*, **80**, 1070–1083.

Boyce, M.S. (2006). Scale for resource selection functions. *Diversity and Distributions*, **12**, 269–276.

Boyce, M.S., Johnson, C.J., Merrill, E.H., Nielsen, S.E., Solberg, E.J. & van Moorter, B. (2015). Can habitat selection predict abundance? *Journal of Animal Ecology*, doi: 10.1111/1365-2656.12359.

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

Camaclang, A.E., Maron, M., Martin, T.G. & Possingham, H.P. (2014). Current practices in the identification of critical habitat for threatened species. *Conservation Biology*, doi: 10.1111/cobi.12428.

Carr, N.L., Rodgers, A.R. & Walshe, S.C. (2010). Caribou nursery site habitat characteristics in two northern Ontario parks. *Rangifer*, **27**, 167–179.

Courtois, R., Ouellet, J.-P., Breton, L., Gingras, A. & Dussault, C. (2007). Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*, **14**, 491–498.

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

DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K.G., Hervieux, D. & Neufeld, L. (2012). Estimating ungulate recruitment and growth rates using age ratios. *The Journal of Wildlife Management*, **76**, 144–153.

DeCesare, N.J., Hebblewhite, M., Robinson, H.S. & Musiani, M. (2009). Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation*, **13**, 353–362.

DeLong, C., Annas, R.M. & Stewart, A.C. (1991). Boreal white and black spruce zone. In: *Ecosystems of British Columbia.* D. Meidinger and J. Pojar (editors). BC Ministry of Forests, Research Branch, Victoria, BC. Special Report Series, 237–250.

Dijak, W.D. & Rittenhouse, C.D. (2008). Development and application of habitat suitability models to large landscapes. In: *Models for planning wildlife conservation in large landscapes*, J.J. Millspaugh and F.R. Thompson (editors). Academic Press, Burlington, MA. 720 pp.

Dupont, D.J. (2014). *Calving ground habitat selection of boreal woodland caribou (Rangifer tarandus caribou) in the Owl-Flintstone range*. M.Sc. thesis. University of Manitoba, Winnipeg, MB.

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**, 677–697.

Elton, C. (1927). *Animal ecology*. Sedgwick and Jackson, London, UK. 296 pp.

Environment Canada. (2012). *Recovery strategy for the woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa, ON. xi + 138 pp.

Environment Canada. (2008). *Scientific review for the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Environment Canada, Ottawa, ON. 72 pp. plus 180 pp. Appendices.

Festa-Bianchet, M. (1988). Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**, 580–586.

Fordham, D.A., Resit Akçakaya, H., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C. & Brook, B.W. (2012). Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.

Fretwell, S.D. & Lucas, H.J. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **14**, 16–36.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010). Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2255–2265.

Grinnell, J. (1917). The niche-relationships of the California Thrasher. *Auk*, **34**, 427–433.

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.

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

Heinrichs, J.A., Bender, D.J., Gummer, D.L. & Schumaker, N.H. (2010). Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence. *Biological Conservation*, **143**, 2229–2237.

Hirai, T. (1998). *An evaluation of woodland caribou (Rangifer tarandus caribou) calving habitat in the Wabowden area, Manitoba*. M.Sc. thesis, University of Manitoba, Winnipeg, MB.

Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology*, **83**, 2027–2036.

Hirzel, A.H. & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, **45**, 1372–1381.

Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.

Hummel, M. & Ray, J.C. (2008). *Caribou and the north: A shared future*. Dundurn Press, Toronto, ON. 288 pp.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology*, **22**, 415–427.

James, A.R., Boutin, S., Hebert, D.M. & Rippin, A.B. (2004). Spatial separation of caribou from moose and its relation to predation by wolves. *The Journal of Wildlife Management*, **68**, 799–809.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Johnstone, J.F., Chapin, F.S., Hollingsworth, T.N., Mack, M.C., Romanovsky, V. & Turetsky, M. (2010). Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research*, **40**, 1302–1312.

Lamberson, R.H., McKelvey, R., Noon, B.R. & Voss, C. (1992). A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology*, **6**, 505–512.

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

Lawler, J.J., Lewis, D.J., Nelson, E., Plantinga, A.J., Polasky, S., Withey, J.C., Helmers, D.P., Martinuzzi, S., Pennington, D. & Radeloff, V.C. (2014). Projected land-use change impacts on ecosystem services in the United States. *Proceedings of the National Academy of Sciences*, **111**, 7492–7497.

Leclerc, M., Dussault, C. & St-Laurent, M.-H. (2012). Multiscale assessment of the impacts of roads and cutovers on calving site selection in woodland caribou. *Forest Ecology and Management*, **286**, 59–65.

Lima, S.L. (2002). Putting predators back into behavioral predator-prey interactions. *Trends in Ecology & Evolution*, **17**, 70-75.

Manly, B.F.J., McDonald, L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*, 2nd ed. Kluwere Academic Publishers, New York, NY. 221 pp.

McKenzie, H.W., Merrill, E.H., Spiteri, R.J. & Lewis, M.A. (2012). How linear features alter predator movement and the functional response. *Interface Focus*, **2**, 205–216.

McLoughlin, P.D., Dzus, E., Wynes, B.O.B. & Boutin, S. (2003). Declines in populations of woodland caribou. *The Journal of Wildlife Management*, **67**, 755–761.

Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (2006). Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1651–1659.

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H. & Haydon, D.T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2289–2301.

Morris, D.W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13.

Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752–1246752.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D. & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, **76**, 189–199.

Rettie, W.J. & Messier, F. (1998). Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology*, **76**, 251–259.

Seip, D.R. (1992). Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology*, **70**, 1494–1503.

Shaffer, M.L. (1981). Minimum population sizes for species conservation. *BioScience*, **31**, 131–134.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, **85**, 1077–1088.

Stuart-Smith, K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M. & Rippin, A.B. (1997). Woodland caribou relative to landscape patterns in northeastern Alberta. *The Journal of Wildlife Management*, **61**, 622–633.

Thiessen, C. (2009). *Peace region boreal caribou monitoring: annual report 2008-09*. British Columbia Ministry of Environment, Fort St. John, BC.

Thompson, I.D., Wiebe, P.A., Mallon, E., Rodgers, A.R., Fryxell, J.M., Baker, J.A. & Reid, D. (2015). Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus tarandus*) in boreal forests in Ontario. *Canadian Journal of Zoology*, **93**, 87–98.

Worton, B.J. (1987). A review of models of home range for animal movement. *Ecological Modelling*, **38**, 277–298.

# CHAPTER 2

## INFERRING PARTURITION AND NEONATE SURVIVAL FROM MOVEMENT PATTERNS OF FEMALE UNGULATES: A CASE STUDY USING WOODLAND CARIBOU [1]

In the last 20 years, the analysis of animal movement has been a fundamental component of wildlife research and management. Movement analyses have been used to infer a broad range of animal behaviour and to assess the spatial dynamics of individuals and populations. For example, movement models based on step lengths, turning angles (the relative directional change in movement trajectory) and autocorrelation (the tendency to move in a similar direction or pattern) have yielded insights as to how animals move in heterogeneous landscapes (Morales & Ellner 2002; Johnson *et al.* 2002; Forester *et al.* 2007) and establish home ranges (Moorcroft *et al.* 2006; Börger *et al.* 2008; Moorcroft 2012). Specific behaviours such as foraging can be inferred using models that classify segments of movement paths based on the expected differences in movement characteristics of distinct behavioural states (Frair *et al.* 2005; Gurarie *et al.* 2009; Breed *et al.* 2012). The increasingly finer spatial and temporal resolution of GPS radio-telemetry data has facilitated an expansion in the variety and complexity of movement models (Schick *et al.* 2008; Smouse *et al.* 2010). However, the primary objectives for most movement studies remain similar: relating animal movement to environmental variation, behavioural states, or predictions of space use.

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Here, I analyze animal movement data to infer components of individual fitness. Specifically, I develop and evaluate two methods for inferring parturition and survival of neonatal offspring (0-4 weeks of age) using movement data from female woodland caribou (*Rangifer tarandus caribou*). For each parameter, I scale up individual predictions to estimate population rates, an important extension because parturition and neonate survival are components of calf recruitment, a key driver of ungulate population dynamics (Gaillard *et al.* 2000; Raithel *et al.* 2007; DeCesare *et al*. 2012).

Previous methods for assessing parturition in wild ungulates have included aerial surveys during the calving season (Whiting *et al.* 2012), serum progesterone tests on blood samples taken from captured animals (Wittmer *et al.* 2005), and vaginal implant transmitters (Powell & DelGiudice 2005; Barbknecht *et al.* 2011). Parturition has also been inferred by subjectively assessing for spatial clustering of GPS locations or changes in movement patterns (e.g., depressed daily movement rates for > 3 days) but these visual approximation methods have not been rigorously validated (Bowyer *et al.* 1999; Ferguson & Elkie 2004; Long *et al.* 2009; but see Nagy 2011). Recently, Dzialak *et al.* (2011) used a general additive modelling approach to infer parturition from movement data of female elk (*Cervus canadensis*). Their correlative approach, however, resulted in a high rate of false-negatives. I expand on the idea of inferring parturition from female movement patterns by more explicitly modelling the movement process and objectively evaluating model predictions across three data sets.

I further extend these analyses to develop a novel approach for estimating rates of neonate survival. Rates of neonate calf survival are usually determined by late spring aerial surveys or by radio-collaring newborn calves (Gustine *et al.* 2006; Barber-Meyer *et al.* 2008). By using only movement data of maternal females, I develop methods for estimating both parturition and survival that are potentially more cost-effective and less invasive to newborn offspring than traditional methods. Moreover, effective movement-based methods could be used to retroactively analyze historical radio-telemetry data sets to examine long-term trends in both rates.

I tested whether parturition status and neonate survival can be reliably inferred from female caribou movement patterns using population-based and individual-based methods. I predicted that calving events could be identified by a sudden and marked change – or break point – in normal female movement patterns, specifically a significant reduction in mean step length. For those females that calved, I predicted that movement rates would remain depressed as long as the calf was alive due to the relative immobility of the neonatal calf acting as a spatial “anchor”. Conversely, if the calf was lost during the neonatal period, I hypothesized that a second break point would be evident with female movement rates abruptly returning to pre-calving levels. Female movement patterns lacking a second break point would be indicative of calf survival through the neonate period. I limited my analysis to the neonate period because calf mobility after four weeks of age likely begins to approach adult movement rates – as evidenced by a sharp decline in bear predation of ungulate calves beyond this age (Zager & Beecham 2006; Barber-Meyer *et al.* 2008; Pinard *et al.* 2012) – thereby making breaks in movement patterns less discernible.

## METHODS

### *Caribou Movement Data*

I developed and tested the two methods using GPS location data collected from reproductive-aged (≥ 3 years old) female caribou captured from four caribou ranges (Maxhamish, Parker, Prophet, Snake-Sahtaneh) within my study area. For method development, I used data from females captured in 2011 (*n* = 25) and 2012 (*n* = 2). These animals were fitted with Iridium GPS radio-collars (model G2110E, Advanced Telemetry Systems (ATS), Isanti, MN) programmed to acquire one GPS location (or fix) every two hours from April 15 – July 15 and once per day otherwise. For three-dimensional GPS locations (3D; see below), the mean horizontal measurement error of the collars was estimated to be 7.7 m (C. DeMars, *unpublished data*). Approximately half of the collars deployed in 2011 remained operational through two calving seasons. I partitioned the locations from these collars into two data sets, using 2011 data for method training (*n* = 24) and 2012 data for method testing (*n* = 15; 3 individuals unique from 2011 data). To further evaluate method performance, I used data from a study conducted in the same area during 2004 (*n* = 10). Individuals from this study were fitted with GPS radio-collars programmed to record locations at four-hour intervals continuously (models POSREC C600 or C900, Televilt/TVP Positioning AB, Lindesberg, Sweden; or model G2000, ATS, Isanti, MN). The mean horizontal measurement error associated with the 2004 collars was unknown.

All caribou were captured and handled in accordance with approved governmental and institutional animal care protocols (British Columbia Resource Inventory Committee 1998; University of Alberta animal use protocol # 748/02/12). Individual females in each data set were captured by aerial net-gunning from a helicopter during the mid- to late-winter months (January – March). Captured animals were physically restrained during collar attachment and were not anesthetized.

For the 2011 data, the pregnancy status of all females is known from blood serum progesterone tests performed on samples taken upon capture (pregnancy: ≥ 2.0 ng/ml; Prairie Diagnostic Services, Saskatoon, SK). I confirmed calving events by conducting weekly aerial surveys during the calving season. All collared females received at least two surveys and all individuals classified as pregnant on progesterone testing were observed with a calf. I estimated calving dates by visually estimating calf age based on a calf's size, relative mobility and pelage colour (Lent 1966). I corroborated this information by assessing for a significant drop in female movement rates (Nagy 2011). For a subset of 12 females that calved, I continued aerial surveys after calving to assess calf survival to four weeks of age. Females observed to have lost their calf on a survey were subsequently re-surveyed to confirm calf status. As none of these females were subsequently observed with a calf, I assumed that true calf survival status for this subset was known. For 2012 data, the pregnancy status of females is unknown. I therefore classified these females as either calf presence or absence by aerial survey with absence indicating either calf loss or non-pregnancy. For the 2004 data, pregnancy status is known from serum progesterone tests and calving events and calf survival to four weeks of age were confirmed by aerial survey.

To standardize data sets, I used a sampling rate of every four hours and limited the time-series to GPS locations taken from April 15 to June 30 inclusively – the calving season of caribou in my study area. I further rarefied the data by excluding locations with low accuracy (e.g. fixes < 3D; < 3% of all locations; Frair *et al.* 2010) and locations from 10:00 to 18:00 hrs on dates of aerial surveys to remove step lengths potentially influenced by helicopter-associated disturbance. After rarefaction, the mean per-collar fix rate (number of successful fixes / number of attempts; Frair *et al.* 2010) was 95% (range: 86-98%) in 2011, 96% (range: 92-99%) in 2012, and 77% (range: 49-90%) in 2004. To ensure a consistent time interval across the time-series of each individual, I assigned a missing value to locations removed by the rarefying procedures and those associated with occasional missed GPS fixes by the radio-collars. In all analyses, I used only step lengths calculated from successive GPS locations (i.e. steps initiated or ending at a missing value were excluded).

### *Population-based Method*

For the first method, hereafter referred to as the population-based method (PBM), I developed population-level thresholds of three-day average movement (TDAM) rates (m/hr) to predict calving events and calf survival (Fig. 2.1; Appendix 2.1). To establish each threshold, I used empirical distributions of TDAM rates derived from step lengths contained within the 2011 data set. I used the calving and calf loss thresholds in a three-day moving window analysis applied to the time-series of movement data for individual caribou across all data sets. During preliminary analyses, I considered alternate time intervals (e.g. one- and two-day windows) but these did not improve method performance.

To estimate a calving threshold, I first created a distribution of TDAM rates using step lengths taken from the first three days post-calving of females known to have a calf surviving at least one week (*n* = 10). I converted this empirical distribution into a smooth kernel density estimate (KDE) using the 'density' function in R 2.15.0 (R Development Core Team, 2012). This KDE represents an estimate of the population-level distribution of possible TDAM rates of females with calves less than three days old. I then transformed the KDE into a cumulative distribution function (CDF), which represents the proportion of the population expected to move at or below a given rate (Fig. 2.2). I used the 99.9% quantile of the resultant CDFs as a calving threshold. In the subsequent moving window analysis performed on individual time-series data, females with TDAM rates dropping below this threshold would be indicative of calving.

I applied a similar approach to establish a calf loss threshold using step lengths from two to four weeks post-calving of females with calves surviving to four weeks (i.e. calving date and calf survival confirmed by aerial survey – see above; *n* = 6). Prior to calculating TDAM rates, however, I first rarefied the data to exclude the top 1% of step lengths. I considered these movements to be abnormal, perhaps related to instances of predator avoidance, and their removal ensured TDAM rates more accurately reflected average movement behaviour over the time interval (three days), thereby increasing the method's sensitivity to correctly identify instances of true calf loss. As for previous rarefaction procedures, steps removed were assigned a missing value. After rarefying, I calculated a CDF of TDAM rates using the same procedures as per the calving threshold. I used the 99.9% quantile of this CDF as a calf loss threshold, which represents the maximum expected TDAM rate of females with calves up to four weeks old. In the subsequent moving window analysis, I applied the same rarefying procedure to post-calving steps of females known to have calved, then calculated TDAM rates and identified instances of calf loss when TDAM rates first exceeded the calf loss threshold.

As the threshold values are dependent on the individuals sampled, I evaluated the robustness of PBM predictions to variation in threshold specification. I calculated 95% bootstrap confidence intervals for both the calving and calf loss thresholds by iteratively resampling with replacement individual caribou used to estimate each threshold (*n* = 1000 iterations for each threshold). Using the upper and lower bounds of these confidence intervals, I repeated the moving window analysis on all data sets to determine the extent to which predictions changed depending on the threshold value used.

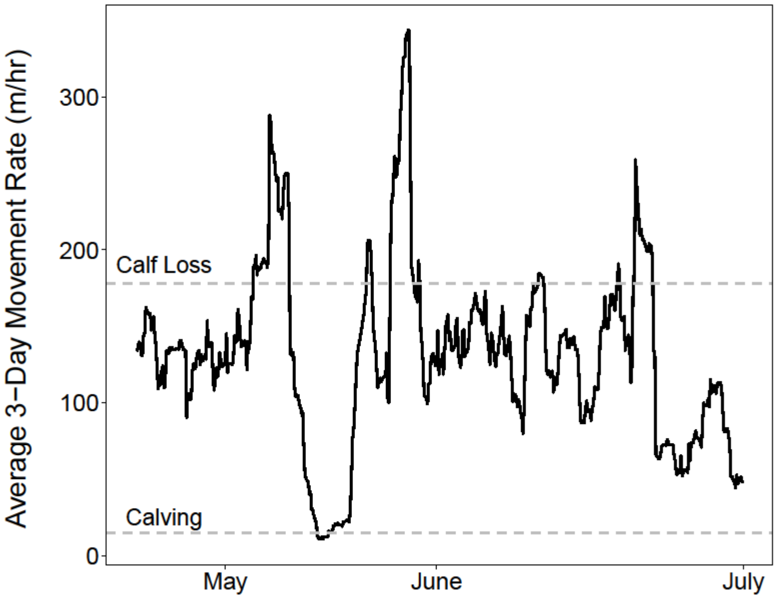


Figure 2.1: Analysis of movement patterns of female woodland caribou using the population-level method to infer parturition and offspring survival status. In this example, the female is predicted to have calved in the middle of May with the calf lost approximately one week later.

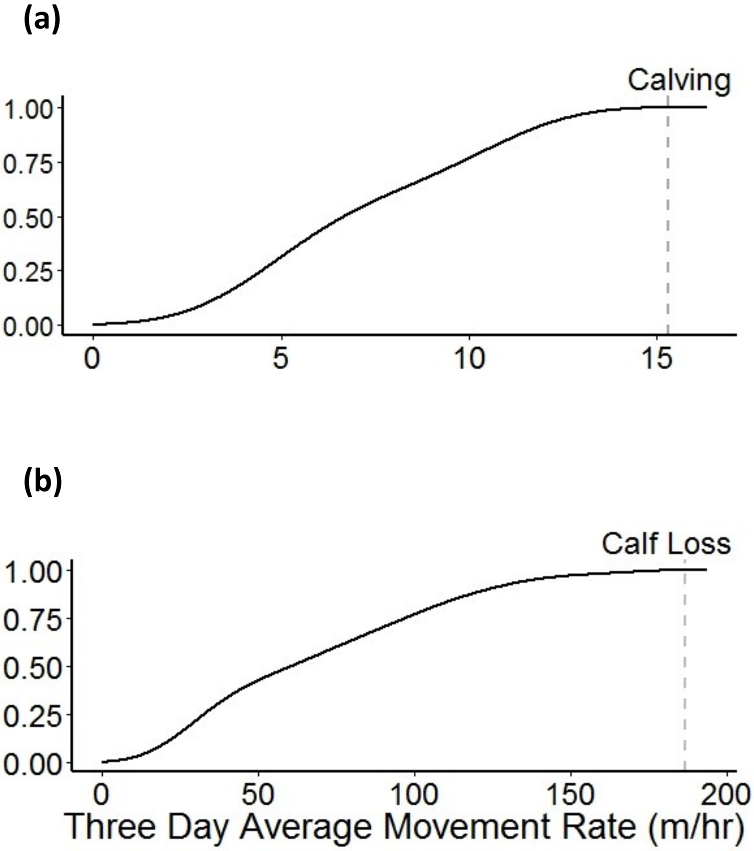


Figure 2.2: Cumulative distribution functions (CDFs) used to calculate the calving (a) and calf loss (b) thresholds for the population-based method (PBM). Grey dotted lines represent three day average movement rates at the 99.9% quantile of each CDF.

### *Individual-based Method*

For the second method, referred hereafter as the individual-based method (IBM), I developed *a priori* movement models representing the three states of females during the calving season (i.e., did not calve, calved and calf survived to four weeks, and calved with subsequent calf loss; Appendices 2.2 and 2.3). All models assume step lengths are exponentially distributed and differ only in their scale parameter – the only parameter of the exponential distribution – which in this analysis can be interpreted as mean step length (Fig. 2.3). For the model representing females that do not calve ($M_0$), the scale parameter ($b_0$) remains constant over time. For the model representing females with calves surviving to four weeks ($M_1$), the scale parameter abruptly drops at calving from its pre-calving constant ($b_1$), creating a break point ($BP_{1,c}$). The scale parameter then linearly increases with a slope of $b_1/k_1$, where $k_1$ is the time, defined in number of steps, required for the calf to achieve adult movement rates. For the model representing females losing calves ($M_2$), there is an abrupt change in the slope of the linear increase post-calving, creating a second break point ($BP_{2,l}$) after which the scale parameter immediately recovers its pre-calving value ($b_2$). The models therefore differ in their number of parameters to estimate: $M_0$ has one - $b_0$; $M_1$ has three – $b_1$, $k_1$ and $BP_{1,c}$; and $M_2$ has four – $b_2$, $k_2$, $BP_{2,c}$ and $BP_{2,l}$.

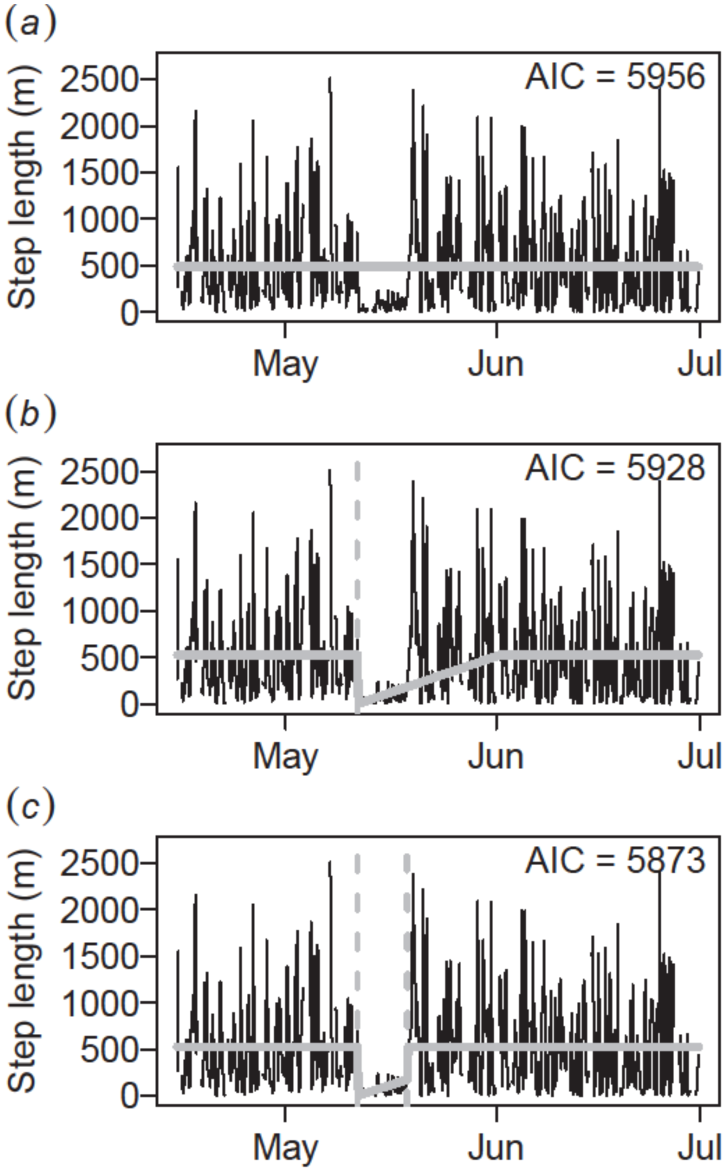


Figure 2.3: Movement models used in the individual-based method to infer parturition and offspring survival status in female woodland caribou. The black line represents the movement pattern of a female that gave birth ~ May 11 then lost her calf ~ May 19 [note: each graph represents the same movement data]. Solid grey lines represent the scale parameter of the exponential distribution, interpreted here as the mean step length. Vertical dashed lines represent estimated break points in the time series. A constant scale parameter with no break point indicates no calving (a), a single break point indicates a female with a calf that survived (b), while two break points indicates a female that calved then subsequently lost the calf (c). In this instance, the model with two break points (c) was the best fit to the data.

I discriminated among models using Akaike's Information Criterion (AIC) with the best model being the one with the lowest AIC value. Prior to model fitting, I removed the top 1% of step lengths from the whole time-series, which contrasts with the PBM where the rarefaction is applied only to post-calving steps. This *a priori* rarefaction was necessary to ensure that the three IBM movement models were evaluated against the same data set. I estimated all model parameters using an approximation of maximum likelihood estimation (Appendix 2.2) and applied the following constraints to each parameter. First, the scale parameters of the exponential distribution ($b_0$, $b_1$, and $b_2$) by definition should be greater than zero. Second, I constrained the values of $k$ to fall between three and six weeks of age because, as noted earlier, within this interval calf movement rates likely approach adult rates. Third, I constrained break points to be a minimum of 24 step lengths away from either end of the time series and from one another. This constraint allows for a sufficient number of observations for each movement phase to accurately estimate parameters and subsequently discriminate among models.

### *Evaluating Method Performance*

To evaluate predictive performance for each method, I calculated measures of sensitivity (proportion of true positives correctly identified), specificity (proportion of true negatives correctly identified) and accuracy (overall rate of true predictions). As both methods yield predictions of calving and calf loss dates (see Appendix 2.1, 2.3), I also evaluated whether predicted dates fell within the appropriate aerial survey interval (e.g., estimated calving date was after a female was seen without a calf and before the same female was seen with calf on a subsequent survey). Because management of ungulates often relies on population-level estimates of parturition and survival (Gordon *et al*. 2004), I summed individual predictions to estimate rates of parturition and neonate survival. I compared these predicted rates to the true sample rates, which in turn are estimates of population rates for parturition and neonate survival. This comparison explicitly evaluates each method for any directional bias (e.g. under- or over-estimating neonate survival; Altman & Royston 2000).

I also evaluated the effects of data quality on method performance by conducting post-hoc sensitivity analyses where I reduced fix rate and simulated data gaps (Appendix 2.4). Because parturition predictions for each method remained unchanged in all analyses, I focus primarily on neonate survival. For each analysis, I used all individuals from the 2011 and 2012 data sets whose parturition and neonate survival statuses were correctly predicted by both methods and had fix rates > 90%. To assess the effect of fix rate, I randomly subsampled within each individual to simulate fix rates of 90% down to 60% in 5% increments. To evaluate the effect of data gaps, I randomly removed intervals of one day, two non-consecutive days and two consecutive days from the post-calving period within the original time-series of each individual female. I further assessed the interacting effects of fix rate and data gaps. For all analyses, I ran 30 simulations across the data set of 13 individuals and calculated the mean accuracy rate (the percentage of correct predictions) for each method.

All analyses were performed with R 2.15.0 (R Development Core Team, 2012) and detailed descriptions of the R code used can be found in Appendices 2.1 and 2.3.

## RESULTS

### *Parturition Status*

Both methods predicted calving events with near certainty (Table 2.1). For the PBM, I calculated a calving threshold of 15.3 m/hr (Fig. 2.2a; sample range of TDAM rates three days post-calving: 3.78, 11.35 m/hr) which correctly discriminated among females that calved and non-pregnant females in 2011 and 2004 (*n* = 34). This threshold also correctly predicted the calving status of the six females visually confirmed to have calved in 2012 (pregnancy status is unknown for this data set). Further, all estimated calving dates fell within the appropriate aerial survey interval across data sets. The PBM was relatively robust to changes in the threshold value as no predictions changed when using the upper 95% CI value (18.8 m/hr) and only one female was misclassified when using the lower 95% CI value (13.2 m/hr).

The IBM correctly predicted calving status for 33 of 34 females across the 2011 and 2004 data sets and all six females confirmed to have calved in 2012. Estimated calving dates all fell within the appropriate survey interval. One female in 2011 was misclassified as not calving when in fact this individual was pregnant and observed with a calf. This female had the movement path with the smallest sample of step lengths in the 2011 data set (*n* = 331; range: 331-438).

Assessing sample rates of parturition, the PBM correctly estimated a rate of 19/24 for 2011 while the IBM produced an estimate of 18/24. Both methods correctly estimated a rate of 9/10 for 2004 and produced identical estimates of 12/15 for 2012 where the true sample rate is unknown.

### *Neonate Survival Status*

The two methods differed more in the ability to predict calf survival to four weeks of age (Tables 2.1, 2.2). For the PBM, I calculated a calf loss threshold of 186.5 m/hr (Fig. 2.2b sample range of TDAM rates: 12.9, 178.6 m/hr), which correctly predicted the survival status of nine of

12 calves in 2011, all six calves visually observed in 2012, and six of nine calves in 2004. For calves correctly predicted as lost, all estimated loss dates fell within the correct survey interval. Because both methods had high predictive power for calving, I further examined calf survival for all females predicted to have calved in 2012. Given this assumption, the PBM correctly predicted nine of 12 calves, misclassifying three lost calves. The PBM was less robust to changes in threshold specification for calf loss compared to calving (Table 2.2). While the lower 95% CI value (153.0 m/hr) minimally changed values of sensitivity – the proportion of lost calves correctly identified – and specificity– the proportion of surviving calves correctly identified –, the upper 95% CI value (249.5 m/hr) underestimated calf loss.

The IBM correctly predicted the survival status of nine of 11 calves in 2011 – excluding the female misclassified as not calving –, all six calves visually observed in 2012, and five of nine calves in 2004. For all females predicted to have calved in 2012, the IBM correctly predicted the survival status of 11 of 12 calves, misclassifying one lost calf. For calves correctly predicted as lost, seven of eight estimated loss dates fell within the appropriate survey interval.

In general, the IBM had higher rates of sensitivity and specificity than the PBM (Table 2.2). As a result, the IBM had higher accuracy (78%) than the PBM (73%) across all data sets. Performance of both methods decreased in 2004. Notably, this data set had a higher number of missing observations resulting in a lower mean number of steps per caribou (*n* = 283, range: 119-374) compared to the 2011 (n = 412; range: 331-438) and 2012 (n = 423; range: 394-446) data sets. With the 2004 data excluded, accuracy was 87% for the IBM and 75% for the PBM.

For assessing sample rates of calf survival, I pooled data across years because of small per-year sample sizes. The IBM estimated 13 surviving calves (true survival = 17 / 33 calves) while the PBM estimated 20. Considering only 2011 and 2012 data (true survival = 12 / 24 calves), the IBM estimated 11 surviving calves while the PBM estimated 14.

### *Effects of Data Quality*

I used all correctly predicted individuals from 2011 ($n$ = 7) and 2012 ($n$ = 6) for assessing the sensitivity of neonate survival predictions to data quality. In general, the PBM was more robust to decreasing data quality (Appendix 2.4). With decreasing fix rate, PBM mean accuracy was > 90% until fix rates were < 80% while IBM mean accuracy was < 90% with fix rates < 90% (Appendix 2.4). Data gaps had less effect than fix rate. When one day, two non-consecutive days and two consecutive days were removed, PBM mean accuracy remained > 98% while IBM mean accuracy was slightly lower (88% -94%). When fix rate was interacted with data gaps, method performance was primarily dictated by fix rate with data gaps only slightly decreasing mean accuracy compared to fix rate alone. In all analyses, the majority (> 95%) of incorrect predictions resulted from surviving calves being misclassified (i.e. neonate survival was underestimated).

Table 2.1: Parturition and calf survival status predicted by the population-based (PBM) and individual-based (IBM) methods.

| | | | Correct Predictions | | Correct Interval | |
|---|---|---|---|---|---|---|
| Year | Status | Known Status: Number | PBM | IBM | PBM | IBM |
| 2011 | calving | pregnant, calved: 19 | 19 | 18 | 19 | 18 |
| | | not pregnant: 5 | 5 | 5 | - | - |
| | calf survival | survived: 8 | 6 | 6 | - | - |
| | | lost [a]: PLM=4; IBM=3 | 3 | 3 | 3 | 3 |
| 2012 [b] | calf presence | confirmed calved: 6 | 6 | 6 | 6 | 6 |
| | | no calf: 9 | 6 | 8 | - | - |
| | calf survival | survived: 4 | 4 | 4 | - | - |
| | | lost: 2 | 2 | 2 | 2 | 2 |
| 2004 | calving | pregnant, calved: 9 | 9 | 9 | 9 | 9 |
| | | not pregnant: 1 | 1 | 1 | - | - |
| | calf survival | survived: 5 | 4 | 2 | - | - |
| | | lost: 4 | 2 | 3 | 2 | 2 |

[a] The total number of calves known to be lost is one less for IBM as I excluded the female misclassified as not calving.

[b] For 2012, pregnancy status is unknown therefore a status of no calf could indicate either not pregnant or calved and subsequently lost before the calf was observed.

Table 2.2: Sensitivity (the proportion of lost calves correctly identified), specificity (the proportion of surviving calves correctly identified) and accuracy (the proportion of correct predictions) of the population-level (PBM) and individual-based (IBM) methods for predicting calf survival across all data sets. For the PBM, the estimated threshold value (186.5 m/hr) and the bounding values of its 95% bootstrap confidence interval are shown. For 2012 data, I assumed the predicted calving status was true and therefore included all females predicted to have calved.

| Performance Measure | Data Set | PBM | | | IBM |
|---|---|---|---|---|---|
| | | 153.0 m/hr | 186.5 m/hr | 249.5 m/hr | |
| Sensitivity | 2011 (*n*= 4[3]) [a] | 1.0 | 0.75 | 0.25 | 1.0 |
| | 2012 (*n*=8) | 0.63 | 0.63 | 0.38 | 0.88 |
| | 2004 (*n*=4) | 0.75 | 0.50 | 0.25 | 0.75 |
| Specificity | 2011 (*n*=8) | 0.63 | 0.75 | 1.0 | 0.75 |
| | 2012 (*n*=4) | 1.0 | 1.0 | 1.0 | 1.0 |
| | 2004 (*n*=5) | 0.80 | 0.80 | 1.0 | 0.40 |
| Accuracy | 2011 (*n*=12) | 0.75 | 0.75 | 0.75 | 0.82 |
| | 2012 (*n*=12) | 0.75 | 0.75 | 0.58 | 0.92 |
| | 2004 (*n*=9) | 0.78 | 0.67 | 0.67 | 0.56 |

[a] The total number of calves known to be lost in 2011 is three for IBM as I excluded the female misclassified as not calving.

## DISCUSSION

Extracting information from animal movement data has been an active area of research for the past two decades but insights gained have been primarily restricted to understanding animal space use and the underlying behavioural processes driving these patterns (McLoughlin *et al.* 2010; Smouse *et al.* 2010). The two quantitative methods developed here expand the scope of information to be gained from animal movement patterns by inferring rates of parturition and neonate offspring survival, both components of individual fitness and often key drivers of population dynamics in wild animals (Stirling *et al.* 1999; Mahoney & Schaefer 2002; Ogutu *et al.* 2010). Both methods produced highly accurate estimates of parturition rates and, when applied to high quality data obtained by modern GPS radio-collars, good estimates of neonate survival using the IBM.

### *Parturition Status*

As predicted, a sudden and sustained drop in movement rate was indicative of parturition. While other studies have similarly suggested that parturition is correlated with depressed movement rates in ungulates (Poole *et al.* 2007; Long *et al.* 2009; Brook 2010), I validated two objective and quantitative methods for determining parturiency from time-series movement data. Both methods were highly accurate (>97%) in predicting parturition and provided appropriate predictions of parturition dates. Moreover, both methods had extremely low false-negative rates (PBM = 0%; IBM < 3%), which contrasts with the high false-negative rate (46%) that confounded the modelling approach of Dzialak *et al.* (2011; see Table 3 therein) for inferring parturition in elk.

The PBM performed slightly better for predicting parturition, likely due to its increased sensitivity to short duration changes in movement rates. By only considering movements within a three-day moving window, the PBM may detect parturition even in instances where offspring are lost shortly after birth. In contrast, the IBM considers the entire time-series to calculate likelihoods and discriminate among models. For this reason, it is critical that the time-series be restricted to the expected parturition period of the species because detecting differences in movement rates will become increasingly difficult as the volume of movement data outside of the parturition period increases. Nevertheless, even with this requirement, if parturition is close in time to offspring loss, only a small number of data points will be available to create significant changes in the likelihoods and differences among models. In such instances, the non-parturient model will be the most parsimonious fit to the data because movement rates will have changed relatively little when the entire time-series is considered. I attempted to partially overcome this limitation by constraining parturition and offspring loss break points to be at least 24 time steps apart. This constraint explicitly inhibits the ability of the IBM to detect parturition events where offspring loss is within four days of birth, or slightly longer if the data have significant gaps. However, given that the IBM still correctly predicted the parturition status of 33 out of 34 females, offspring losses occurring shortly after birth seem to constitute a small proportion of overall offspring losses, at least for the woodland caribou I monitored.

Both methods likely provide more accurate and cost-effective estimates of true parturition rates than traditional methods such as aerial surveys using radio-telemetry. When considering the 2012 data, only six of 15 females were confirmed to have calved by aerial survey whereas both movement-based methods estimated 12 females to have calved. Nagy (2011) reported a similar finding, suggesting that aerial surveys of woodland caribou underestimated parturition rates by 12-19%. The high correlation of both the IBM and the PBM with serum progesterone tests for pregnancy further validates the use of movement-based approaches for estimating population-level parturition rates.

### *Neonate Survival Status*

For predicting neonate survival, the IBM generally performed better, producing reasonably accurate estimates particularly when using the higher quality data of 2011 and 2012 (87% accuracy across both data sets). I attempted to improve the accuracy of both methods by incorporating information other than step length. I considered changes in turning angles and autocorrelation (Gurarie *et al.* 2009) as well as spatial information (e.g. net-squared displacement from calving site; Fryxell *et al.* 2008) but found these additional parameters to be uninformative for predicting neonate survival from caribou movement patterns.

At the sample level, predicted rates of neonate survival were close to true sample rates, particularly for the IBM. It is important to note, however, that predicted survival rates incorporate both correct and false predictions of individual survival. This method of comparing grouped predicted outcomes to grouped known outcomes – known as calibration (Alston & Royston 2000) – is necessary because of the difficulty in translating evaluative measures of individual-based binary classification tests (e.g. accuracy) into estimates of uncertainty for population rates. Calibration yields more explicit insight into potential directional biases associated with each method. The comparison of predicted to known sample rates of survival suggests that neonate survival is overestimated by the PBM and slightly underestimated by the IBM though a more rigorous evaluation of potential bias would require additional years of data.

The better performance of the IBM was likely due to its predictive ability being less influenced by inter-individual variability. By assigning to each individual a distinct baseline for movement rates, prediction by the IBM is confined to evaluating information solely within each individual. In contrast, the PBM compares individual movement rates to population-level thresholds and is thus contingent on variation within the population. This difference becomes increasingly important as the magnitude of movement variability among individuals increases. Variability in movement rates among females likely increases with offspring age such that the variability among females with four week old offspring is much greater than the variability among females in the first few days post-partum (Testa *et al.* 2000; Odonkhuu *et al.* 2009). With increasing variability, selecting a threshold that is adequate for all individuals becomes increasingly difficult, particularly in populations where individual personalities may vary widely from “slow” to “active” (Sih *et al.* 2004; Boon *et al.* 2008). If a threshold indicative of calf loss is too low, “active” mothers and offspring may exceed the threshold, resulting in an overestimation of offspring loss. Conversely, if a threshold is too high, females with normally “slow” movement rates may not exceed the threshold after offspring loss, resulting in an overestimation of offspring survival. This latter scenario was illustrated by the low sensitivity values recorded when I used the upper bound of the threshold’s 95% confidence interval for prediction. Because high inter-individual variation in movement rates is prevalent in many animal populations (Odonkhuu *et al.* 2009; Olson *et al.* 2010; Mueller *et al.* 2011), individual-based approaches such as the IBM will be preferable for predicting neonate survival in most instances.

Misclassification of calf status may also be influenced by the agent of mortality. In most ungulate populations, predation is the primary cause of mortality in neonatal offspring with a relatively small proportion lost to disease and other natural causes (Gustine *et al*. 2006; Barber-Meyer *et al*. 2008; Carstensen *et al*. 2009). In predation events where the predator represents a threat to the female as well as her offspring (e.g. wolves [*Canis lupus*] for ungulates), the change in maternal movement should be sudden and sustained, creating a break point that is clearly evident. Conversely, if offspring are lost to natural causes or to a predator that does not directly threaten the female, then a break point may be less discernible, particularly if the female remains in the area for a few days before slowly moving away. This latter scenario could result in a false prediction of offspring survival. For this case study, I did not have information regarding the true causes of calf mortality to directly assess this potential effect; however, determining whether female movement patterns contain information regarding the possible cause of offspring mortality represents an area for future research.

Due to the analytical framework of both methods, false predictions of offspring survival can result when offspring mortalities occur near the end of the time-series data. For the IBM, this situation results in a small number of post-loss steps being available to differentiate between the models of offspring survival and offspring loss. Moreover, pre-loss and post-loss movement rates will be similar because offspring movement rates are approaching adult rates at this time. Because the IBM uses the entire time-series to compare models, parsimony may favour the model of offspring survival. With the PBM, if offspring loss occurs on the last day of the time-series (i.e. when the calf is three weeks and six days old), the number of data points post-loss may be insufficient to raise the average of the three-day moving window above the threshold value indicative of calf loss. Overall, when estimating survival rates at the population level, any potential bias resulting from the timing of offspring loss should be small unless true offspring losses are skewed toward the end of the neonatal period (e.g., near four weeks of age for caribou).

Data quality was the most significant factor influencing the ability to predict offspring survival. Increasing gappiness in the time-series data negatively affected predictive performance of both methods. On average, the 2004 data set had a 30% reduction in the number of steps available for estimation compared to the other data sets, with some individuals missing complete days of data. Data quality affected each method differently. For the IBM, specificity was reduced because consecutive missed steps could affect the assumption that offspring movement rates increase linearly post-partum. If movement rates after the data gap significantly differed from movement rates before the gap, then a second break point in the time-series could be created regardless of true offspring survival status, resulting in overestimation of offspring loss (see also Appendix 2.3). For ungulates in particular, data gaps would be especially problematic in the two to four week interval post-partum when offspring movement rates can change substantially over a short interval (Testa *et al.* 2000; Odonkhuu *et al.* 2009). Alternatively, if the PBM is used, data gaps could result in a small number of data points within the three-day moving window, increasing the probability of sampling error. As a result, estimated movement rates within these data-deficient windows may differ significantly from true values.  Because of these issues, data quality needs to be assessed prior to the application of movement-based methods for estimating offspring survival rates.  For data sets with fix rates of < 90%, estimates of offspring survival may be unreliable, particularly when gaps spanning more than a day are present.  However, with fix rates and location accuracy continuing to improve in modern GPS radio-collars (Frair *et al.* 2010), issues related to data quality should be less problematic with more recent data sets.

The better performance of both methods with the 2011 and 2012 data sets may have been influenced by the carryover of some individuals from 2011 into 2012, creating an issue of non-independence. Note, however, that for the PBM only three of the individuals used to establish the calf loss threshold were included in the 2012 data set and all three had different known statuses in 2012 (e.g. calf survived in 2011, calf lost in 2012).  Further, of the 12 females predicted to have calved in 2012 and therefore considered for further analysis of calf survival, only five were carried over from 2011 and of these five, four had different known statuses between years.  Based on this information, any non-independence issues likely had minimal impact on the overall results and inferences of each method.

### *Conclusion*

With GPS radio-collars increasingly being used in the study and management of animal populations (Hebblewhite & Haydon 2010), movement-based methods are a viable approach for estimating rates of parturition and offspring survival in ungulates.  The methods described here could easily be adapted to other species though the reliance on movement data of independent individuals precludes species that aggregate during the parturition season and therefore are influenced by group movement dynamics (e.g. barren-ground caribou [Lent

1966]). Non-independence of movement behaviour may also result from abnormal weather events (e.g. deep snow); thus, it is recommended that the raw movement data be inspected prior to method application to assess for correlations between environmental conditions and sample-wide aberrations in movement patterns. Of the two methods tested, the IBM is more directly applicable as it does not require training data to establish *a priori* species-specific thresholds. For caribou, step length was the most informative variable for determining parturition and offspring survival rates. For other species, incorporating additional movement information such as turning angle and autocorrelation into movement models may prove useful for identifying break points indicative of parturition and offspring loss.

## LITERATURE CITED

Altman, D.G. & Royston, P. (2000). What do we mean by validating a prognostic model? *Statistics in Medicine*, **19**, 453-473.

Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008). Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs*, **169**, 1–30.

Barbknecht, A.E., Fairbanks, W.S., Rogerson, J.D., Maichak, E.J., Scurlock, B.M. & Meadows, L.L. (2011). Elk parturition site selection at local and landscape scales. *The Journal of Wildlife Management*, **75**, 646–654.

Boon, A., Réale, D. & Boutin, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, **117**, 1321–1328.

Bowyer, R., Van Ballenberghe, V. & Kie, J. (1999). Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy*, **80**, 1070–1083.

Breed, G.A., Costa, D.P., Jonsen, I.D., Robinson, P.W. & Mills-Flemming, J. (2012). State-space methods for more completely capturing behavioral dynamics from animal tracks. *Ecological Modelling*, **235-236**, 49–58.

British Columbia Resource Inventory Committee. (1998). *Live animal capture and handling guidelines for wild mammals, birds, amphibians, and reptiles*. Standards for components for British Columbia's biodiversity number 3. Victoria, BC.

Brook, R.K. (2010). Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes. *Canadian Journal of Zoology*, **88**, 968–976.

Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–50.

Carstensen, M., DelGiudice, G.D., Sampson, B.A., & Kuehn, D.W. (2009). Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *The Journal of Wildlife Management*, **73**, 175-183.

DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K.G, Hervieux, D., & Neufeld, L. (2012). Estimating ungulate recruitment and growth rates using age ratios. *The Journal of Wildlife Management*, **76**, 144-153.

Dzialak, M.R., Harju, S.M., Osborn, R.G., Wondzell, J.J., Hayden-Wing, L.D., Winstead, J.B. & Webb, S.L. (2011). Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PloS One*, **6**, e14597.

Ferguson, S.H. & Elkie, P.C. (2004). Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology*, **262**, 125–134.

Forester, J.D., Ives, A.R., Turner, M.G., Anderson, D.P., Fortin, D., Beyer, H.L., Smith, D.W. & Boyce, M.S. (2007). State–space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, **77**, 285–299.

Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2187–200.

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**, 273–287.

Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh, T. & Rosatte, R.C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19114–9.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gordon, I.J., Hester, A.J., & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology,* **41**, 1021-1031.

Gurarie, E., Andrews, R.D. & Laidre, K.L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**, 395–408.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.

Hebblewhite, M. & Haydon, D.T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2303–12.

Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002). A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications*, **12**, 1840–1860.

Lent, P.C. (1966). Calving and related social behavior in the barren-ground caribou. *Zeitschrift für Tierpsychologie*, **23**, 701-756.

Long, R.A., Kie, J.G., Terry Bowyer, R. & Hurley, M. A. (2009). Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. *Wildlife Biology*, **15**, 288–298.

Mahoney, S.P. & Schaefer, J.A. (2002). Long-term changes in demography and migration of Newfoundland caribou. *Journal of Mammalogy*, **83**, 957–963.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.

Moorcroft, P.R. (2012). Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy*, **93**, 903–916.

Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (2006). Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1651–1659.

Morales, J.M. & Ellner, S.P. (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, **83**, 2240–2247.

Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Wattles, D., DeStefano, S., Calabrese, J.M. & Fagan, W.F. (2011). How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, **20**, 683–694.

Nagy, J. (2011). *Use of space by caribou in northern Canada*. University of Alberta. PhD thesis. 184 pp.

Odonkhuu, D., Olson, K.A., Schaller, G.B., Ginsberg, J.R. & Fuller, T.K. (2009). Activity, movements, and sociality of newborn Mongolian gazelle calves in the Eastern Steppe. *Acta Theriologica*, **54**, 357–362.

Ogutu, J.O., Piepho, H.-P., Dublin, H.T., Bhola, N. & Reid, R.S. (2010). Dynamics of births and juvenile recruitment in Mara–Serengeti ungulates in relation to climatic and land use changes. *Population Ecology*, **53**, 195–213.

Olson, K.A., Fuller, T.K., Mueller, T., Murray, M.G., Nicolson, C., Odonkhuu, D., Bolortsetseg, S. & Schaller, G.B. (2010). Annual movements of Mongolian gazelles : nomads in the Eastern Steppe. *Journal of Arid Environments*, **74**, 1435–1442.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D. & Courtois, R. (2012). Calving rate, calf survival rate , and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, **76**, 189–199.

Poole, K., Serrouya, R. & Stuart-Smith, K. (2007). Moose calving strategies in interior montane ecosystems. *Journal of Mammalogy*, **88**, 139–150.

Powell, M.C. & DelGiudice, G.D. (2005). Birth, morphologic, and blood characteristics of free-ranging white-tailed deer neonates. *Journal of Wildlife Diseases*, **41**, 171–83.

Raithel, J.D., Kauffman, M.J. & Pletscher, D.H. (2007). Impact of spatial and temporal variation in calf survival on the growth of elk populations. *The Journal of Wildlife Management*, **71**, 795–803.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M. & Clark, J.S. (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, **11**, 1338–50.

Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology*, **79**, 241–277.

Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forester, J.D. & Morales, J.M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2201–11.

Stirling, I., Lunn, N. & Iacozza, J. (1999). Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic*, **52**, 294–306.

Testa, J., Becker, E.F. & Lee, G. (2000). Movements of female moose in relation to birth and death of calves. *Alces*, **36**, 155–162.

Whiting, J., Olson, D. & Shannon, J. (2012). Timing and synchrony of births in bighorn sheep: implications for reintroduction and conservation. *Wildlife Research*, **39**, 565–572.

Wittmer, H.U., Mclellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S. & Hamilton, D. (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (Rangifer tarandus caribou) in British Columbia, Canada. *Canadian Journal of Zoology*, **83**, 407–418.

Zager, P. & Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus*, **17**, 95–108.

## APPENDIX 2.1: R CODE FOR THE POPULATION-BASED METHOD

This appendix explains the two central R (R Development Core Team, 2012) functions that were developed for the population-based method (PBM). As described in the main chapter, the analysis is performed on three-day average movement rates. For the remainder of this appendix, three-day average movement rates will be referred to as "TDAM rates".

### *Threshold Establishment*

To detect calving events and, if applicable, calf loss events, I tested whether TDAM rates fell below or exceed, respectively, specific threshold values. These threshold values were determined using a training data set. The `makeThresh()` function provided here can be used to establish both the calving and the calf loss threshold by applying it to the corresponding subset of the data. For the calving threshold, I used data from the first three days post-calving of females known to have a calf surviving at least one week. For the calf loss threshold, I used data from two to four weeks post-calving of females with calves known to have survived to four weeks of age.

The data needed as input to the `makeThresh()` function is a matrix of regular movement rates, where columns correspond to individual females. To calculate such movement rates, I first generated a time-series of step lengths, defined as the distance between consecutive GPS locations. This time-series has to be regular, meaning all calculated step lengths must span the same time interval (in the current study, every four hours). Because GPS locations are often not recorded at exact times, I allowed a deviation up to a tolerance of one tenth of the time interval (i.e. 24 minutes). For missing GPS locations (e.g., missed fixes by the radio-collars), a value of "NA" is assigned thereby ensuring there is a record (i.e. row) for every fourth hour in the time-series. Note that every missed GPS location will result in at least two missed step lengths. After generating the time-series of step lengths, each step length was divided by the length of the time interval to obtain movement rates. These movement rates were transformed into a matrix where each column contains the movement rates of an individual female.

The `makeThresh()` function contains the option to rarefy the data prior to calculating a specific movement threshold. The default of this option is no rarefaction. As noted in the main chapter, I rarefied the two-to-four week post-calving data used to calculate the calf loss threshold by removing the top 1% of step lengths, movements considered to be abnormal and possibly associated with instances of predator avoidance. Removal of these outliers increases the sensitivity of the PBM to correctly identify instances of true calf loss. Steps removed by rarefaction are assigned a value of “NA”.

After inputting the movement rate matrix and specifying whether to rarefy the data, the `makeThresh()` function generates TDAM rates for each time-series by calculating a moving average with window size of three days. To calculate TDAM rates, I used the `rollapply()` function from the R package ‘zoo’ (Zeileis & Grothendieck 2005). Because missing data points are included as “NA” in the time-series, the moving average is calculated from the available data points within the three-day window (as opposed to calculating a moving average for a fixed number of available data points). Note that for the calving threshold data, this analysis results in exactly one TDAM rate per female. For the calf loss threshold, multiple TDAM rates are generated per female because the data considered spans 14 days (i.e. from two to four weeks post-calving).

Calculated TDAM rates are then pooled together into one vector to generate an empirical distribution of possible TDAM rates within the considered time frame. From this vector, the `makeThresh()` function estimates a probability density function for TDAM rates using the `density()`function in R. To calculate the corresponding cumulative distribution function (CDF), which requires integrating the density, the resulting output from `density()` is converted into a function via the `approxfun()` function in R. After calculating the CDF, I used the 99.9% quantile of the CDF as the threshold value. This particular quantile was chosen because I wanted to obtain the largest TDAM rate possible under the estimated probability distribution. Many analytical probability distributions have a CDF that asymptotes at 1.0; hence, I chose a quantile very close to 1.0. However, practically, the distribution of TDAM rates has a finite domain so it may also be possible to use the 100% quantile. The obtained quantile is set as the threshold and returned as the value of the function.

The `makeThresh()` function provides the option to plot the histogram of TDAM rates, together with the estimated probability density function. A vertical bar indicates the threshold value.

```
makeThresh <- function(moveRates, timeInt, rare=F, draw=F){
    if (rare==T){
        rarIndex <- apply(moveRates, 2, function(x)
            quantile(x, probs=0.99, na.rm=T))
        for (i in 1:ncol(moveRates)) moveRates[moveRates[,i]   >
        rarIndex[i],i] <- NA
        }
    rollAverage <- rollapply(moveRates, 3*24/timeInt, mean,
        na.rm=T, by.column=T)
    rollPool <- as.vector(rollAverage)
    rollDensity <- density(rollPool)
    densityFun <- approxfun(rollDensity$x, rollDensity$y,
        yleft=0, yright=0)
    y <- seq(1, max(rollPool)+20, 0.1)
```

```
rollCumu <- rep(NA, length(y))
for (i in 1:length(y)) rollCumu[i] <- integrate(densityFun, -
Inf, y[i], stop.on.error=F)$value
quant <- 0.999
threshold <- y[which(rollCumu >= quant)[1]]
if (draw==T){
    hist(rollPool, 50, freq=F, xlim=c(0,threshold+10),
    xlab="TDAM mean movement rates", main="Histogram, Density
    and Threshold")
    lines(rollDensity, col='red', lwd=2)
    abline(v=threshold, lwd=2, col='blue')
    }
return(threshold)
}
```

*Data Analysis*

To perform the PBM using the thresholds established above, I developed the function `getStatus()`. This function analyzes data for one individual female, and therefore has to be applied to each individual separately (e.g., within some wrapper).

The data input for this function is a list, which contains at least three elements. An element named “MR” is a complete time-series of regular movement rates. This time-series should span the parturition and neonate season of the species under consideration. An element named “tp” is a vector of dates and times – in the R class POSIXct format – at which the movement rates were measured. Because of the format of MR, the vector tp should contain regular times, up to a certain tolerance (as explained in the previous section). An element named “interval” is a numeric value indicating the time interval spanning one step (here, 4). In addition to the data list, the calving threshold and the calf loss threshold need to be passed to the function. It is important that the unit for the movement rates is the same for threshold generation and data analysis (e.g., meters/hour).

After inputting the data list and threshold values, the `getStatus`() function first converts the time-series of movement rates into a series of TDAM rates, analogous to the previous section. Next, the calving status is determined by querying the series of TDAM rates for values that fall below the calving threshold. For the first TDAM rate falling below the calving threshold, I set the calving date as the date and time of the last step within the corresponding three-day window. If a calving event is detected, the data is further analyzed to determine calf survival to four weeks of age. Starting from the previously estimated calving date, a four week subset of MR is isolated and then rarefied to remove outliers, defined here as the upper 1% of movement rates (see main chapter for rationale). After rarefaction, TDAM rates are again calculated and searched for values that exceed the calf loss threshold. For the first TDAM rate exceeding the calf loss threshold, the estimated date of calf loss is the date and time of the last step in the corresponding three-day window. If no TDAM rate exceeds the threshold, the calf is predicted to have survived to four weeks of age.

The `getStatus`() function returns a data frame that contains the following information. “Calved” is logical and indicates whether a female calved. “Calving Date” returns the estimated date of calving and “NA” if the female was predicted to not have calved. “Lost” is logical and indicates whether a calf was lost. If there was no calf, “Lost” is set to “NA”. “LostDate” returns either the estimated date of calf loss or “NA” if the calf survived.

```
getStatus <- function(movF, threshCalf, threshLoss){
    meanMR <- rollapply(movF$MR, 3*24/movF$interval, mean,
        na.rm=T)
    calved <- any(meanMR < threshCalf)
    calfIndex <- which(meanMR < threshCalf)[1] + 17
    calfDate <- movF$tp[calfIndex]
```

```
if (!is.na(calfIndex)){
    wk4 <- calfIndex + 28*24/movF$interval
    postCalfMR <- movF$MR[calfIndex:wk4]
    postCalfDate <- movF$tp[calfIndex:wk4]
    rarIndex <- quantile(postCalfMR, probs=0.99, na.rm=T)
    postCalfMR[postCalfMR > rarIndex] <- NA
    meanPcMR <- rollapply(postCalfMR, 3*24/movF$interval,
        mean, na.rm=T)
    calfstatus <- any(meanPcMR > threshLoss)
    lossIndex <- which(meanPcMR > threshLoss)[1] + 17
    lossDate <- postCalfDate[lossIndex]
    }else{
        calfstatus <- NA
        lossDate <- NA
        }
results <- data.frame(Calved = calved, CalvingDate =
    calfDate, Lost = calfstatus, LossDate =
    as.character(lossDate))
return(results)
}
```

An R script containing the two functions can be found on the website

https://sites.google.com/site/babybou2013.

*Literature Cited*

Zeileis, A. & Grothendieck, G. (2005). zoo: S3 Infrastructure for regular and irregular time series. *Journal of Statistical Software*, **14**, 1-27. URL http://www.jstatsoft.org/v14/i06/

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

## APPENDIX 2.2: LIKELIHOOD FUNCTIONS USED IN THE INDIVIDUAL-BASED METHOD

In this appendix the likelihood functions are described for each of the three models of the Individual-based Method (IBM). These likelihood functions are for time-series of observed step lengths, $\vec{x} = (x_{t_1}, x_{t_2}, \ldots, x_N)$, where $S = (t_1, t_2, \ldots, t_N) \subseteq (1, 2, \ldots, T)$, and T is the full span of the time-series. A step length is defined as the distance between locations taken at regular time intervals. Missing locations are handled by excluding the associated step lengths from the time-series and by keeping the associated true time indices. For example, if step lengths at time t=2 and t=3 are missing from the time–series, this yields $\vec{x} = (x_1, x_4, x_5, \ldots, x_T)$, $S = (1, 4, 5, \ldots, T)$, and thus $N < T$. The likelihood functions are appropriate for time-series with missing steps because the step lengths are assumed to be independently distributed. See Appendix 2.3 for more details on the construction of step length time-series.

The three models assume that step lengths are exponentially distributed. This distribution is characterized by a scale parameter, $b_t$, which varies in time according to the specified model. For the model of a female that does not calve, $M_0$, the scale parameter remains constant through time. Thus $b_t = b_0$ for all $t$. The likelihood function for $M_0$ is:

$$L_0(b_0) = \prod_{t \in S} \frac{1}{b_0} \exp\left(-\frac{x_t}{b_0}\right) \tag{1}$$

For the model of a female with a calf that survives, $M_1$, the scale parameter, $b_t$, varies as a function of three parameters: the pre-calving scale parameter, $b_1$, the calving break point, $BP_{1,c}$, and the number of steps required by the calf to attain an adult movement rate, $k_1$. Specifically, $b_t$ is defined for $M_1$ by:

$$b_t = \begin{cases} b_1 & \mathit{for}\ t \le BP_{1,c} \\[2ex] \dfrac{(t-BP_{1,c})b_1}{k_1} & \mathit{for}\ BP_{1,c} < t \le BP_{1,c}+k_1 \\[2ex] b_1 & \mathit{for}\ t > BP_{1,c}+k_1 \end{cases} \tag{2}$$

Thus, the likelihood function for $M_1$ is:

$$L_1(b_1,k_1,BP_{1,c}) = \prod_{\substack{\{t\in S, t\le BP_{1,c}\} \\ \{t\in S, t>BP_{1,c}+k_1\}}} \frac{1}{b_1}\exp\left(-\frac{x_t}{b_1}\right) \times \prod_{\{t\in S, BP_{1,c}<t\le BP_{1,c}+k_1\}} \frac{k_1}{(t-BP_{1,c})b_1}\exp\left(-\frac{x_t k_1}{(t-BP_{1,c})b_1}\right) \tag{3}$$

For the model of a female with a lost calf, $M_2$, the scale parameter, $b_t$, is affected by parameters equivalent to those of $M_1$ as well as the calf loss break point, $BP_{2,l}$. Specifically, $b_t$ is defined for $M_2$ by:

$$b_t = \begin{cases} b_2 & \mathit{for}\ t \le BP_{2,c} \\[2ex] \dfrac{(t-BP_{2,c})b_2}{k_2} & \mathit{for}\ BP_{2,c} < t \le BP_{2,l} \\[2ex] b_2 & \mathit{for}\ t > BP_{2,l} \end{cases}, \tag{4}$$

where $BP_{2,l} \le BP_{2,c}+k_2$. Thus the likelihood for $M_2$ is:

$$L_2(b_2,k_2,BP_{2,c},BP_{2,l}) = \prod_{\substack{\{t\in S, t\le BP_{2,c}\} \\ \{t\in S, t>BP_{2,l}\}}} \frac{1}{b_2}\exp\left(-\frac{x_t}{b_2}\right) \times \prod_{\{t\in S, BP_{2,c}<t\le BP_{2,l}\}} \frac{k_2}{(t-BP_{2,c})b_2}\exp\left(-\frac{x_t k_2}{(t-BP_{2,c})b_2}\right) \tag{5}$$

where $BP_{2,l} \le BP_{2,c}+k_2$.

To be able to compare the models using Akaike's Information Criterion (AIC), maximum likelihood estimates (MLE) are required for the parameters of each model. This is easily achieved for $M_0$ which has only one parameter to estimate. The analytical solution for the MLE of $b_0$ is:

$$\hat{b}_0 = \frac{1}{N}\sum_{t\in S} x_t \tag{6}$$

where N is the number of step lengths included in the time-series $\vec{x}$. In contrast, models M$_1$ and M$_2$ have no known analytical solution for the MLE of its parameters. Thus, these models require simultaneous numerical maximization of the likelihood with respect to all parameters: $MLE = \underset{b,k,BP}{\arg\max} L(b,k,BP)$, where *BP*, *b* and *k* stand for their corresponding versions in models M$_1$ and M$_2$. Such maximization can be computationally intense. This is particularly true for the likelihood functions because the values of two important parameters, the calving and calf loss break points, are natural numbers and many of the fast optimization methods are inappropriate for discrete parameters. A precise numerical maximization of a likelihood with such discrete-value parameters can be achieved by profiling the likelihood. To do so, the likelihood is first maximized at all possible *BP* values and then the chosen BP value is the one that maximizes the overall likelihood, $MLE = \underset{BP}{\text{argmax}}(\underset{b,k}{\text{argmax}} L(b,k,BP))$. To reduce part of the computational complexity, the likelihood functions are altered. For M$_1$ the likelihood function becomes:

$$\tilde{L}_1(\hat{b}_1, k_1, BP_{1,c}) = \prod_{\substack{\{t\in S,\, t\le BP_{1,c}\} \\ \{t\in S,\, t>BP_{1,c}+k_1\}}} \frac{1}{\hat{b}_1}\exp\left(-\frac{x_t}{\hat{b}_1}\right) \times \prod_{\{t\in S,\, BP_{1,c}<t\le BP_{1,c}+k_1\}} \frac{k_1}{(t-BP_{1,c})\hat{b}_1}\exp\left(-\frac{x_t k_1}{(t-BP_{1,c})\hat{b}_1}\right) \tag{7}$$

where $\hat{b}_1 = \frac{1}{N_{BP_{1,c}}}\sum_{t\in S} x_t$ and $N_{BP_{1,c}}$ is the number of step lengths in the time-series $\vec{x}$ with $t \le BP_{1,c}$. Thus, the approximation of the MLE uses the mean observed step length prior to the calving break point as the estimate of *b$_1$* and maximizes eqn. 7 with respect to only the parameters BP$_{1,c}$ and *k$_1$*: $M\tilde{L}E = \underset{k_1, BP_{1,c}}{\arg\max} \tilde{L}_1(\hat{b}_1, k_1, BP_{1,c})$. A similar procedure is performed for M$_2$.

The altered likelihood function is:

$$\tilde{L}_2(\hat{b}_2, k_2, BP_{2,c}, BP_{2,l}) = \prod_{\substack{\{t \in S, t \le BP_{2,c}\} \\ \{t \in S, t > BP_{2,l}\}}} \frac{1}{\hat{b}_2} \exp\left(-\frac{x_t}{\hat{b}_2}\right) \times \prod_{\{t \in S, BP_{2,c} < t \le BP_{2,l}\}} \frac{k_2}{(t - BP_{2,c})\hat{b}_2} \exp\left(-\frac{x_t k_2}{(t - BP_{2,c})\hat{b}_2}\right)$$

,

(8)

where *BP$_{2,l}$* ≤ *BP$_{2,c}$*+*k$_2$*, $\hat{b}_2 = \frac{1}{N_{BP_{2,c}}} \sum_{t \in S} x_t$ and $N_{BP_{2,c}}$ is the number of step lengths in the time-series $\vec{x}$ with $t \le BP_{2,c}$. The approximation of the MLE in this case is found using:

$M\tilde{L}E = \underset{k_2, BP_{2,c}, BP_{2,l}}{\arg\max} \tilde{L}_1(\hat{b}_2, k_2, BP_{2,c}, BP_{2,l})$. For more details on how the MLE was approximated please see Appendix 3 for the R code and its explanation.

Similar to others (e.g., Gurarie *et al.* 2009), I mainly used an approximation of the MLE to reduce computational time and complexity. This approach is an important consideration for the IBM method given that tens of thousands of break point combinations are evaluated for each individual. In addition to its computational efficiency, this approximation is also biologically relevant. Interest lies in identifying the moment in the time-series when the female recovers her normal, pre-calving movement. As such, using only mean pre-calving movement to estimate *b$_1$* and *b$_2$* focuses the movement model on changes from the pre-calving movement rather than on averaging the overall movement. As a further test, the analysis was also performed using the true (full) likelihood functions (eqns. 3 and 5). This analysis produced similar results and the R code for the full likelihood is available on the website:

https://sites.google.com/site/babybou2013.

### *Literature Cited*

Gurarie, E., Andrews, R.D. & Laidre, K.L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**, 395–408.

## APPENDIX 2.3: R CODE FOR THE INDIVIDUAL-BASED METHOD

This appendix includes the four R (R Development Core Team, 2012) functions necessary to apply the individual-based method (IBM) to an individual movement trajectory and their explanation. The R scripts and other R related information can be found on the website: https://sites.google.com/site/babybou2013. As mentioned in the main text, the IBM has three models: $M_0$ for a female that does not calve, $M_1$ for a female with a calf surviving to four weeks, and $M_2$ for a female losing a calf prior to four weeks of age. When taken together, the first three R functions calculate the negative log-likelihood (nll) of $M_1$ and $M_2$ and are used to numerically estimate the minimum negative log-likelihood (mnll) and the maximum likelihood estimate (MLE) of the parameters of these two models. The fourth function calculates the mnll, MLE, and Akaike's Information Criterion (AIC) of the three models and does so by calling the previous functions and, in the case of the $M_0$, by directly calculating the analytical MLE and mnll.

The four functions rely on similar data inputs. `SL` is a numeric vector containing the step lengths measured at a regular time interval. `ti` is an integer vector identifying the time, in number of steps, of the step lengths present in `SL`. `SL` and `ti` should be of the same length and cannot contain NAs. `tp` is a POSIXct (an R class for dates and time) vector that identifies the real date and time of the `SL`. If there are missing steps, these should be represented with NAs in `tp`; thus, `tp` will be longer than `SL` and `ti`. These three vectors together represent the movement path of one individual. For example, for the (x,y) locations {(0,0), (0,1), (0,3), (1,3), (7,3)} at time {(2012/01/01 00:00), (2012/01/01 04:00), (2012/01/01 08:00), (2012/01/01 16:00), (2012/01/01 20:00)} from a radio-collar programmed to record a GPS location every 4 hours, `SL` would be {1, 2, 6}, `ti` would be {1, 2, 5}, and `tp` would be{(2012/01/01 00:00), (2012/01/01 04:00), NA, NA, (2012/01/01 16:00), NA}. Note that the time-series should be limited to the parturition and neonate season of the species under consideration. For woodland caribou in my study area, I only included movement from April 15th to June 30th. Using the R function `quantile()`, I also assign as missing steps all step lengths greater than the 99% quantile of `SL`.

As explained in the main chapter and in Appendix 2.2, all models assume step lengths are exponentially distributed and differ only in their scale parameters, *b*. Using the R function `dexp()`, the log-likelihood of all models is calculated by summing the log of the exponential probability density function of step lengths given a scale parameter. Note that `dexp()` requires the input of the rate rather than the scale parameter. The rate parameter of the exponential distribution is simply the inverse of the scale parameter (Forbes *et al.* 2011).

For models $M_1$ and $M_2$, the time-series is divided into pre-calving and post-calving sections. $M_2$ further divides the post-calving section into pre-calf loss and post-calf loss sections. Thus, for functions `nll1()` and `nll2()`, which calculate nll of $M_1$ and $M_2$ respectively, `SL` and `ti` are divided into subsections defined by the calving and calf loss break points. *Section a* represents the time-series up to and including the calving break point. *Section b* represents the time-series after the calving break point, where the female is with her calf. For $M_1$, *section b* includes the rest of the time-series. However, for $M_2$, *section b* only includes the time-series up to and including the calf loss break point. After this second break point, the rest of the time-series is in *section c*.

The first function, `nllk()`, calculates the nll of *section b*, the section of the time-series where the female is with her calf. The scale parameter during this section increases linearly with a slope of $b_1/k_1$ or $b_2/k_2$, represented in the code by `ba/k`, where `ba` is the pre-calving scale parameter and `k` is the time, in number of steps, it takes a female with a calf that survives to recover pre-calving movement. After *k* steps, the scale parameter returns to its pre-calving value, `ba`, and remains at this value for the rest of the time-series. `nllk()` is used in both functions `nll1()` and `nll2()` to numerically estimate the mnll of *section b* of the time series and the MLEs of $k_1$ and $k_2$.

```
nllk <- function(k, SLb, tib, ba, tiBP1){
     bb <- (tib - tiBP1) * ba / k
     bb[ bb > ba ] <- ba
     nllb <- -sum(dexp(SLb, 1/bb, log=TRUE))
     return(nllb)
}
```

The second function, `nll1()`, calculates the nll of $M_1$. This function first divides the time-series in two sections using the $BP_{1,c}$ value contained in the object `BP`. For *section a*, the pre-calving section, the scale parameter, `ba`, is estimated by the mean of the observed step lengths for this section. The mnll of *section a* is calculated directly using `ba`. For *section b*, the post-calving section, the mnll is numerically estimated using `nllk()` and the R function `optimize()`. The nll of *section a* and *b* are added together to get the overall nll of $M_1$.

```
nll1 <- function(BP, SL, ti, kc){
     SLa <- SL[1:BP]
     n <- length(SL)
     SLb <- SL[ (BP + 1):n]
     tib <- ti[ (BP + 1):n ]
```

```
	ba <- mean(SLa)
	mnlla <- -sum(dexp(SLa, 1/ba, log=TRUE))
	mnllb <- optimize(nllk, kc, SLb=SLb, tib=tib, ba=ba,
		tiBP1=ti[BP])$objective
	nll <- mnlla + mnllb
	return(nll)
}
```

Using methods similar to `nll1()`, the third function, `nll2()`, calculates the nll of $M_2$. The function first divides the time-series into sections using the $BP_{2,c}$ and $BP_{2,l}$ values contained in object `BP`. For *section a*, the pre-calving section, and *section c*, the post-calf loss section, the MLE of the scale parameter, object `ba`, is the mean of the observed step lengths of *section a*. The mnll of *sections a* and *c* are calculated directly using `ba`. As for `nll1()`, function `nllk()` is used to calculate the mnll of *section b*. The nll of all sections are summed to calculate the overall nll.

```
nll2 <- function(BP, SL, ti, kc){
	SLa <- SL[1:BP[1]]
	SLb <- SL[(BP[1]+1):BP[2]]
	tib <- ti[(BP[1]+1):BP[2]]
	SLc <- SL[(BP[2]+1): length(SL)]
	ba <- mean(SLa)
	mnlla <- -sum(dexp(SLa, 1/ba, log=TRUE))
	mnllc <- -sum(dexp(SLc, 1/ba, log=TRUE))
	mnllb <- optimize(nllk, kc, SLb=SLb, tib=tib, ba=ba,
		tiBP1=ti[BP[1]])$objective
	nll <- sum(mnlla, mnllc, mnllb)
	return(nll)
}
```

The fourth function, `mnll3M()`, estimates the mnll and AIC of all three models and the MLEs of all parameters. In addition to `SL`, `ti`, and `tp`, `mnll3M()` requires the input of two other objects: `int` and `kcons`. As described in the main chapter, the values for the calving and calf loss break points are constrained to be at least 24 step lengths away from the beginning and the end of the time-series and from one another. The object `int` specifies this constraint and in my analyses was set to equal 24. The main reason for this constraint is that a minimum number of data points are required in each section of the time-series to be able to estimate model parameters. The choice of the exact value for this constraint is somewhat arbitrary. The number needs to be small enough to allow for the detection of calves born close to the start of the time-series and for detecting calf loss events occurring shortly after birth or near the end of the time-series. However, the number needs to be large enough to ensure a sufficient amount of data within each section to accurately estimate parameters. In addition, as AIC selects a model based on the likelihood over the entire time-series, the models can only appreciably differ in AIC if the amount of data points in each section is large enough compared to the length of the time-series. The object `int` can be changed by the user, although `int` should be at the very least 1 and very small values might cause the function to return warnings and errors. Note that this constraint is in terms of observed step lengths. In fact, in the following code, break point values can only be at times for which there is data thereby ensuring that data points are available within each section of the time-series for parameter estimation. This restriction on break points could potentially explain why the IBM performs poorly with time-series containing large numbers of missing data points. For example, if calving occurs at a time where there is a missing location, the calving break point is likely to be assigned to the last non-missing location before the calving event. This approximation should be adequate if the data gap is small. However, as the data gap increases between the last available data point and the calving event, this approximation will become increasingly inadequate. The main reason the models are coded in this manner was to handle missing data points. There are likely ways to code these models without this restriction but the implementation of such code on time-series with large data gaps would be difficult.

The other additional input to `mnll3M()` is a numeric vector, `kcons`, which contains two values that specify the minimum and maximum values for parameters $k_1$ and $k_2$. As mentioned in the main chapter, these values are constrained to be equivalent to the number of steps between three and six weeks. `kcons` is required in part because an interval is needed for the R function `optimize()`. In addition, constraining the values of $k_1$ and $k_2$ helps the IBM to accurately distinguish between the three models.

The function `mnll3M()` can be divided into five parts, three of which apply one of the three models to data. The first part of `mnll3M()` creates objects that will contain the results and calculates the sample size. The second part of `mnll3M()` fits $M_0$ to data. To do so, it estimates the MLE of the scale parameter, represented in the code by `b0`, by taking the mean of the observed step lengths and uses `b0` to directly calculate the mnll. The third part of `mnll3M()` fits $M_1$ to data by first creating a vector, `BP1ser`, which contains all possible values for the calving break point, $BP_{1,c}$. To get the mnll, the `nll1()` function is applied to all possible $BP_{1,c}$ values and the minimum nll value is selected. The $BP_{1,c}$ value that produced mnll is selected as the MLE of $BP_{1,c}$. The MLE of the two other parameters, $b_1$ and $k_1$, are estimated as in `nll1()`. The fourth part of `mnll3M()` fits $M_2$ to data. As for $M_1$, it first identifies all possible combinations of $BP_{2,c}$ and $BP_{2,l}$. To get the mnll and the MLEs for $BP_{2,c}$ and $BP_{2,l}$, the `nll2()` function is applied to all possible combinations of break points. The minimum nll value is selected as the mnll and the two BP values producing mnll are selected as $BP_{2,c}$ and

$BP_{2,l}$. The two other parameters to estimate, $b_2$ and $k_2$ are estimated as in `nll2()`. The fifth part of `mnll3M()` uses the mnll values calculated for each model to calculate their AIC values. The model with the lowest AIC is selected as the best model. Finally, `mnll3M()` returns a list of three objects, which contains the MLE values of all parameters and the mnll and AIC of all models.

```
mnll3M <- function(SL, ti, tp, int, kcons){
     resCA <- matrix(NA, 1, ncol=8)
     colnames(resCA) <- c("n",  "mnll_0", "mnll_1", "mnll_2",
          "AIC0", "AIC1", "AIC2", "BM")
     BPs <- data.frame(matrix(NA, 1, ncol=6))
     colnames(BPs) <- c("BP1c", "BP2c", "BP2l", "iBP1c",
"iBP2c",
          "iBP2l")
     mpar <- matrix(NA, 1, 5)
     colnames(mpar) <- c("b0", "b1", "b2", "k1", "k2")
     resCA[1] <- length(SL)
     mpar[1] <- mean(SL) #b0
     resCA[2] <- -sum(dexp(SL, 1/mpar[1], log=TRUE)) #mnll0
     BP1ser <- int:(resCA[1]-int) #All possible BP1c
     NLL1 <- lapply(BP1ser, nll1, SL=SL, ti=ti, kc=kcons)
     MNLL1i <- which.min(NLL1)
     resCA[3] <- NLL1[[MNLL1i]] #mnll1
     BPs[4] <- BP1ser[MNLL1i] #BP1c MLE in terms of index of SL
     BPs[1] <- as.character(tp[ti[BPs[[4]]]]) #BP1c in real time
     mpar[2] <- mean(SL[1:BPs[[4]]]) #b1
     mpar[4] <- optimize(nllk, kcons,
          SLb=SL[(BPs[[4]]+1):resCA[1]],
          tib=ti[(BPs[[4]]+1):resCA[1]], ba=mpar[2],
          tiBP1=ti[BPs[[4]]])$minimum #k1
     BP2ser <- combn(int:(resCA[1]-int), 2) #2 BPs combinations
     BP2ser <- BP2ser[,diff(BP2ser) >= int]
     BP2ser <- BP2ser[,diff(BP2ser) <= kcons[2]]
     BP2ser <- split(t(BP2ser),1:ncol(BP2ser))
     NLL2 <- lapply(BP2ser, nll2, SL=SL, ti=ti, kc=kcons)
     MNLL2i <- which.min(NLL2)
     resCA[4] <- NLL2[[MNLL2i]] #mnll2
     BPs[5:6] <- BP2ser[[MNLL2i]] #mle of BP as index of SL
     BPs[2] <- as.character(tp[ti[BPs[[5]]]]) #BP2c in real time
     BPs[3] <- as.character(tp[ti[BPs[[6]]]]) #BP2l in real time
```

```
     mpar[3] <- mean(SL[1:BPs[[5]]]) #b2
     mpar[5] <- optimize(nllk, kcons,
          SLb=SL[(BPs[[5]]+1):BPs[[6]]],
          tib=ti[(BPs[[5]]+1):BPs[[6]]],
          ba=mpar[3], tiBP1=ti[BPs[[5]]])$minimum #k2
     resCA[5] <- 2*(resCA[2] + 1) #AIC0
     resCA[6] <- 2*(resCA[3] + 3) #AIC1
     resCA[7] <- 2*(resCA[4] + 4) #AIC2
     resCA[8] <- which.min(resCA[,5:7])-1
     return(list(resCA=resCA, BPs=BPs, mpar=mpar))
}
```

To apply the IBM to data, first run all of the code sections included in this appendix, then create the `SL`, `ti`, `tp`, `int`, and `kcons` objects, and finally run:

```
mnll3M(SL, ti, tp, int, kcons)
```

*Literature Cited*

Forbes, C., Evans, M., Hastings, N. & Peacock, B. (2011). *Statistical distributions*, 4th edn. John Wiley & Sons, Inc., Hoboken, New Jersey.

R Development Core Team. (2012). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

## APPENDIX 2.4: POST-HOC ANALYSES OF THE EFFECTS OF DATA QUALITY ON METHOD PERFORMANCE

I conducted post-hoc analyses to assess the effects of fix rate and data gaps on method performance. Fix rate is the number of successful GPS locations acquired by the radio-collar divided by the number of attempts (Frair *et al.* 2010). I tested for these effects by using female caribou whose calf survival status was correctly predicted by both methods in 2011 ($n$ = 7) and 2012 ($n$ = 6) using the original data. For this subset of females, the mean fix rate for the original data was 96% (range: 94 - 98%). Nine females had calves surviving to four weeks of age while four lost calves. In all analyses, parturition predictions for both methods remained unchanged. I therefore focus primarily on how data quality affects predictions of neonate survival.

To assess the effects of fix rate, I randomly subsampled within each individual female to simulate fix rates of 90% down to 60% in 5% increments. To assess the effect of data gaps, I randomly removed intervals of one day, two non-consecutive days and two consecutive days from the post-calving period within the original time-series of each individual female. I then assessed the interacting effects of fix rate and data gaps. For all analyses, I ran 30 simulations across the data set of 13 individuals and calculated the mean accuracy rate (the percentage of correct predictions) for each method.

In general, the PBM was more robust to decreasing data quality. With decreasing fix rate, mean accuracy of the PBM stayed above 90% until fix rates fell below 80% while mean accuracy for the IBM fell below 90% with fix rates < 90% (Fig. A2.4.1). Data gaps had less effect than fix rate. Mean accuracy of the PBM was > 98% in all three scenarios (one day removed: 99% [SE: 2%]; two non-consecutive days: 98% [SE: 3%]; two consecutive days: 98% [SE: 3%]) while IBM mean accuracy was slightly lower (one day: 88% [SE: 5%]; two non-consecutive days:

94% [SE: 6%]; two consecutive days: 93% [SE: 6%]). Assessing the interacting effects of fix rate and data gaps, method performance was largely dictated by fix rate with the removal of days only slightly decreasing mean accuracy compared to fix rate alone (Fig. A2.4.2).

In all analyses, the majority (> 95%) of incorrect predictions resulted from surviving calves being misclassified (i.e. neonate survival was underestimated).

### *Literature Cited*

Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2187–200.

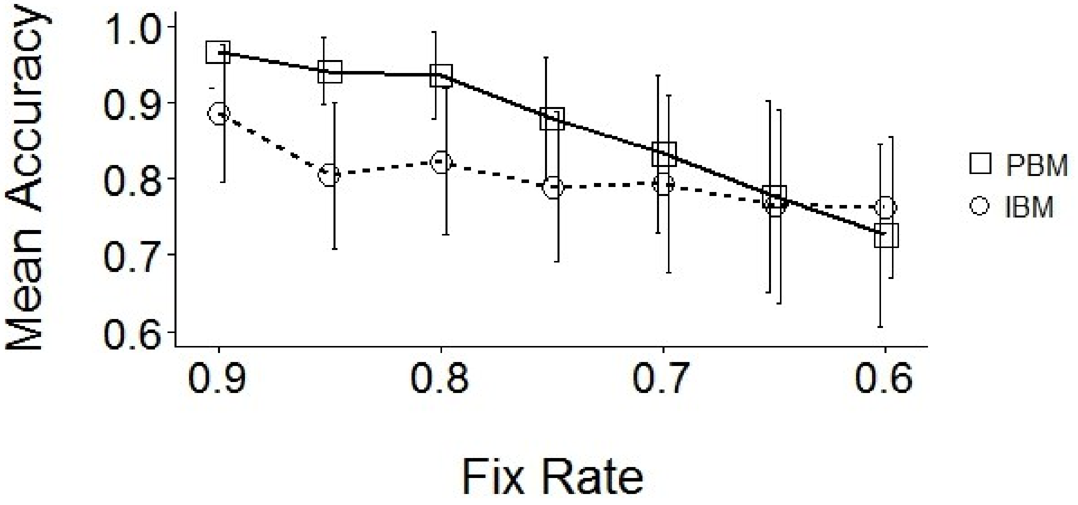


Figure A2.4.1: Predictive performance of the PBM and IBM when fix rate was reduced from 90% down to 60%. Thirty simulations were performed for each level of fix rate. Accuracy is the percentage of correct predictions of calf survival status (error bars = 1 SE).

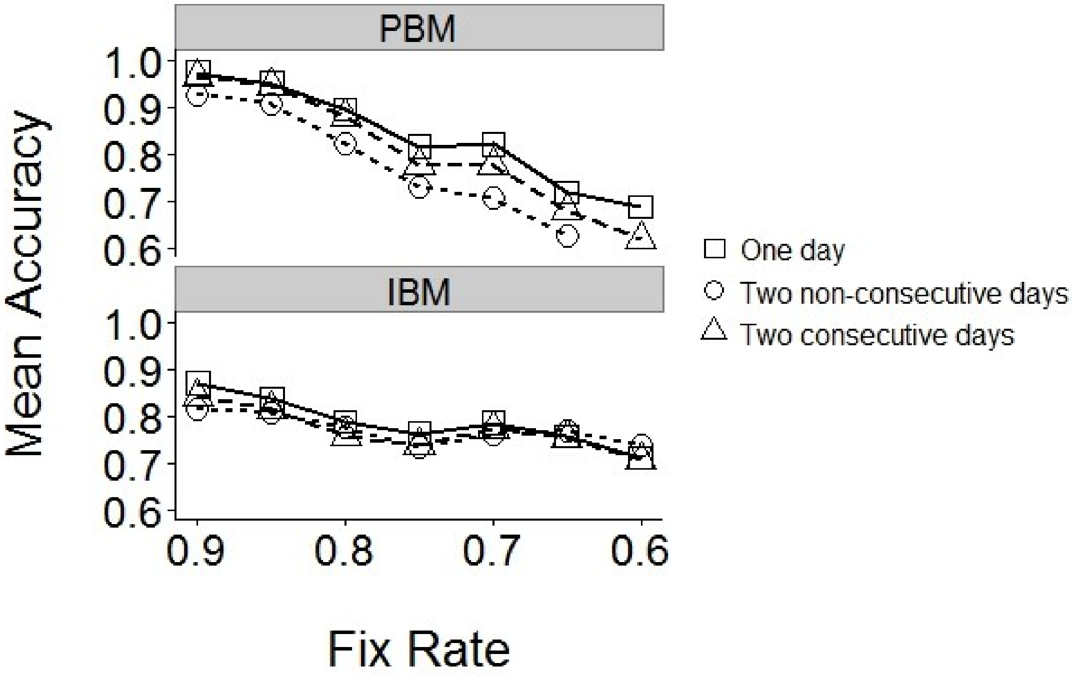


Figure A2.4.2: Predictive performance of the PBM (top) and the IBM (bottom) when fix rate is reduced and data gaps are present. Data gaps of one day, two non-consecutive days and two consecutive days were simulated in the post-calving interval of individual time-series. Thirty simulations were performed for each level of fix rate. Accuracy is the percentage of correct predictions of calf survival status. For clarity, error bars are not shown.

# CHAPTER 3

## SPATIAL PATTERNING OF PREY AT REPRODUCTION TO REDUCE PREDATION RISK: WHAT DRIVES DISPERSION FROM GROUPS?

Predator-prey interactions can be important drivers in the evolution of social behaviour in organisms (Hamilton 1971; Alexander 1974). One outcome of such interactions is the adaptation of sociality, or group-living, a widespread behaviour occurring in birds, mammals, and fish (Krause & Ruxton 2002). Mechanistic explanations for this behaviour have primarily centered on its effects for reducing predation risk (Hamilton 1971; Hart & Freed 2005). For example, sociality may afford early predator detection (Pulliam 1973), decrease each individual's capture probability through dilution effects (Hamilton 1971; Foster & Treherne 1981), or aid defence (Garay 2009). Sociality may also reduce the probability of predator encounter if increasing prey aggregation effectively lowers the number of groups available to predators (Travis & Palmer 2005; Ioannou *et al.* 2011).

Yet, given these apparent advantages to sociality, many organisms considered to be group-living spend a portion of their life cycles as dispersed individuals (Alexander 1974). This behavioural shift suggests that the relative costs and benefits associated with group-living can vary temporally. While other factors (e.g. access to food; parasite avoidance) may influence social behaviour in animals (Krause & Ruxton 2002), here I focus on temporal trade-offs to sociality in terms of predation risk. In certain situations, the dispersion of individuals may be advantageous over group-living: for example, if groups are more detectable than individuals (Hebblewhite & Pletscher 2002; Ioannou & Krause 2008), if aggregation leads to area-restricted search behaviour from predators (Tinbergen *et al.* 1967; Scharf *et al.* 2011) or if the number of individuals predated per encounter is greater than one (Treisman 1975).

Within this context, I evaluated mechanistic hypotheses for explaining individual dispersion as a strategy for reducing predation risk at reproduction in an otherwise group-living animal. Specifically, I tested the ability of these hypotheses to explain the dispersive behaviour of female boreal caribou (*Rangifer tarandus caribou*) at calving. For most of the year, boreal caribou occur in small groups of 5-10 individuals (Rettie & Messier 1998). During calving, however, parturient females disperse widely on the landscape, a spatial tactic that differs from barren-ground caribou (*Rangifer tarandus groenlandicus*) which undergo long-distance migrations and subsequently calve in large aggregations (Bergerud 1996). Both tactics – the ‘spacing out’ of boreal caribou and the ‘spacing away’ of barren-ground caribou (*sensu* Bergerud & Page 1987) – are considered to be primarily strategies for reducing predation risk as they do not afford other maternal benefits such as maximizing nutrition or minimizing parasite harassment (Russell *et al.* 1993; Bergerud *et al.* 2008). For barren-ground caribou, spacing away reduces predation risk because migration moves females from winter ranges with relatively high predator density to calving areas with lower predator density (Heard *et al.* 1996). For boreal caribou, spacing out may reduce predation risk by increasing the search time of predators and because solitary females with calves are less conspicuous than female-calf groups (Bergerud & Page 1987, Bergerud 1996). This latter point becomes increasingly advantageous in forested environments where the benefits of early predator detection afforded by groups are minimized. To date, these mechanisms for spacing out have not been explicitly tested.

Using simulation analyses, I tested various hypotheses for explaining dispersion of boreal caribou at calving. I focused simulations on the interaction between female caribou with neonate calves (< 4 weeks old) and wolves (*Canis lupus*), a primary predator of caribou calves. Simulations tracked caribou-wolf encounters from which I calculated the mean number of calves surviving per female per generation (7 years for caribou; COSEWIC 2002) as a proxy of lifetime reproductive success (hereafter, lifetime neonate survival [LNS]). Using this framework, I specifically tested the two hypotheses suggested by Bergerud & Page (1987); that is, that dispersion increases predator search time (search time hypothesis; see also Tinbergen *et al*. 1967) and that dispersion is driven by the relative inconspicuousness of individuals compared to groups (group detectability hypothesis). The search time hypothesis predicts that increasing dispersion of individuals would be correlated with increasing LNS. The group detectability hypothesis predicts that dispersed individuals would have a higher LNS than grouped caribou and the magnitude of this difference would be driven by differential detectability based on group size.

I also evaluated a third hypothesis: that female dispersion is favoured when more than one individual per group is predated per predator encounter (multiple kills hypothesis; Treisman 1975). This hypothesis, in effect, is the opposite of the “selfish herd” hypothesis (Hamilton 1974); that is, the positive individual effect of dilution associated with grouping is negated, and in fact reversed, when high vulnerability of prey causes a concentrative effect from the predator, resulting in multiple kills on group encounter. Multiple kills on encounter have been documented in many predator-prey interactions (Kruuk 1972) and for caribou, the killing of multiple calves per wolf encounter has been observed in the barren-ground subspecies, which congregates at calving (Miller *et al.* 1985). Under the multiple kills hypothesis, dispersed females are predicted to have a higher LNS than those in groups.

## METHODS

### *Wolf GPS Data*

To model wolf movements, I used location data from GPS radio-collared wolves (*n* = 15) captured within boreal caribou ranges of northeast British Columbia, Canada (~ lat. 58.2500 to 60.0000, long. -120.9000 to -123.5000). Animals were captured by aerial darting from a helicopter in either March 2012 (*n* = 3) or March 2013 (*n* =12) and fitted with Iridium satellite GPS collars (Advanced Telemetry Systems; model #2110E). All capture and handling procedures followed approved institutional animal care protocols (University of Alberta Animal Use protocol # 748/02/12). GPS collars were programmed to acquire one location (or fix) every 15 minutes during the calving season of caribou (May 1 – June 30) and once per day otherwise. For all analyses, I used only location data from the calving season and I screened this data to exclude locations with low precision (< 3-dimensional fixes; Lewis *et al.* 2007) and/or associated with biologically unrealistic movements (Bjørneraas *et al*. 2010). I further excluded locations between 10:00 and 18:00 hrs, an interval coinciding with limited movement presumably due to animals bedding down to avoid warm daytime temperatures.

### *Simulation Model Setup and Parameterization*

I assessed caribou-wolf encounter rates under varying spatial conditions by creating a simulated caribou range of 4900 km$^2$ (50-m grid cell resolution), a size that approximates the median range size of caribou populations in northeast British Columbia. I populated the simulated range with 300 caribou calves and 10 wolves [note: sensitivity analyses varying the number of caribou and wolves did not fundamentally alter simulation inferences]. Caribou-wolf encounters were primarily driven by wolves searching for stationary calves. Calves were considered to be stationary because of their limited movement during the neonate period (< 1-km displacement from the calving site; Gustine *et al*. 2006). In simulations where calves occurred in groups, I considered all individuals in the group to be occupying the same grid cell.

Wolf movements were modelled using a correlated random walk (Turchin 1998). Within this framework, I modelled the distribution of step lengths (distance between successive fixes) as a Weibull distribution, which is a generalization of the exponential distribution and has the following form

$$f(r) = \frac{a}{b}\left(\frac{x}{b}\right)^{a-1} e^{-(x/b)^{a}} \qquad (1)$$

where $r$ is the step length, $a$ is the shape parameter, and $b$ is the scale parameter. To model the turning angles between successive steps, I used a von Mises distribution

$$g(\theta) \propto e^{k\cos(\theta)} \qquad (2)$$

where $\theta$ is the turning angle, $k$ measures the amount of correlation between the direction of successive steps, and the constant of proportionality is chosen to ensure $g(\theta)$ integrates to 1 between 0 and $2\pi$. Maximum likelihood estimation (MLE) was used to determine the values of $a$, $b$, and $k$ for each wolf. For the simulations, I picked a single set of parameters (*a*, *b*, *k*) that was representative because parameters did not vary much among wolves. For each likelihood maximization calculation, I used the Nelder-Mead simplex algorithm (Lagarias *et al*. 1998), as implemented in the Python maximize() function from the SciPy library (Jones *et al*. 2001).

Assuming the wolf stays within the simulated caribou range, I used the following probability density function for a single step

$$p(\boldsymbol{x}_n|\boldsymbol{x}_{n-1},\theta_{n-1}) = f(|\boldsymbol{x}_n - \boldsymbol{x}_{n-1}|)g(\theta_{n-1} - \theta_n) \tag{3}$$

where $\boldsymbol{x}_1, \boldsymbol{x}_2, \dots , \boldsymbol{x}_N$ are the successive positions of the wolf and $\theta_n$ is the bearing from $\boldsymbol{x}_{n-1}$ to $\boldsymbol{x}_n$. Each time step in the simulations modelled 15 minutes of wolf movement, mirroring the resolution of the GPS data. Successive positions were found by drawing from the probability distribution in equation (3). Each simulation lasted a total of 1200 steps, which given the 16-hr day due to excluding 10:00 – 18:00 locations, equates to a time period of 18.75 days.

For the initial simulations, I started with the following assumptions. First, if a wolf encountered a calf, the calf was killed (i.e. the probability of death given encounter = 1.0). This assumption is not unreasonable given the small size of neonate calves and their high vulnerability to predation (Adams *et al.* 1995). Owing to the calf's small size, I imposed a one hour handling time – or pause in wolf movement – to reflect the time required to process captured prey (Holling 1959). Second, I assumed that wolves could detect a calf at a distance up to 1-km. This distance is similar to detection distances used in other wolf studies (1.5-km, Muhly *et al.* 2010; 1.3-km, Whittington *et al.* 2011) and within the sensory detection range reported for wolves (Mech & Boitani 2003). I further note that sensitivity analyses conducted using different detection radii did not affect overall inferences (i.e. simulation outputs changed linearly with detection radius).

### *Testing the Search Time Hypothesis*

I evaluated the search time hypothesis – which states that dispersion by females increases predator search time – in two ways. First, I assessed how the magnitude of dispersion by individual females affected the mean LNS. For this analysis, I evaluated nine scenarios representing varying degrees of dispersion from highly clumped (scenario 0) to highly dispersed (scenario 8; Appendix 3.1). I maintained the basic assumptions as outlined above, specifically that the detection radius of wolves was 1-km and that once a calf was detected, the wolf moved toward it and killed it. I then evaluated how dispersed calves (scenario 8; hereafter, the reference scenario) compared against calves that were grouped. I tested group sizes ranging from 2-13 – running independent simulations for each group size – and groups were randomly dispersed within the simulated range prior to each run. I maintained the 1-km detection radius regardless of group size and when a wolf encountered a caribou group, only one calf was killed per encounter. After a wolf encounter, caribou groups were relocated within the simulated range with the distance moved determined by randomly drawing from an exponential distribution with a mean of 8-km, a value based on observations of movements made by radio-collared maternal females following apparent predator or human-mediated disturbance (C. DeMars, unpublished data).

### *Testing the Group Detectability Hypothesis*

I tested the group detectability hypothesis by varying the detection radius of wolves as a function of group size. For this analysis, I assumed that the primary means of prey detection by wolves is by olfaction or audition, particularly in forested environments (Mech & Boitani 2003). I assumed that detection distances for these senses are predominantly influenced by the olfactory or auditory intensity of the point source and that this intensity increases linearly with the number of caribou in a group (Andersson *et al*. 2013). I therefore modelled the relationship between group size and detectability using the inverse square law, which states that the influence of a point source emitting a physical quantity will decay as the square root of the distance from the point source (Self *et al*. 2009). For example, where I assumed that wolves could detect an individual calf at a distance of 1-km, a group of three calves would have a detection radius of $\sqrt{3} \approx 1.73$. Using this relationship, I again evaluated the effects of grouping on the mean LNS, testing group sizes ranging from 2-13 independently, and comparing these effects to the reference scenario where individuals are highly dispersed. For these simulations, I maintained the rules that only one calf was killed per wolf encounter and that groups were randomly relocated following each encounter.

### *Testing the Multiple Kills Hypothesis*

To evaluate the multiple kills hypothesis, I varied the number of calves killed per group encounter while holding the detection radius constant at 1-km regardless of group size and randomly relocating groups after each encounter. I varied kills per encounter by including a parameter in the simulation model that specified the number of encounters needed to kill all the calves in a group. I varied the kills-per-encounter parameter from one kill per encounter to values where all calves were killed on first encounter and tested the multiple kills hypothesis on group sizes of 3, 7 and 13.

### *Testing Multiple Mechanisms*

I further evaluated the effects of multiple mechanisms by combining differential group detectability with variation in the number of kills per encounter. For these simulations, I modelled group detectability using the inverse square law as above and varied the number of kills per encounter from one to where all calves in a group were killed. I also tested scenarios where < 1 individual was killed per encounter by substituting the kills-per-encounter parameter with a parameter specifying the probability of a calf being killed on encounter. I set this kill success parameter at 50%, a value close to empirical values of kill success for wolves when encountering groups of adult caribou (Haber 1977). Thus, this latter scenario provides a specific test of how the effects of grouping might differ between adults and neonate calves.

### *Simulation Analysis*

For each scenario tested, I ran 250 simulations to generate a distribution of the number of calves killed per calving season (Appendix 3.2). Note that for analyses assessing group size or kills-per-encounter effects, I ran 250 simulations for each group size and for each change in the number of calves killed per encounter. I used the distribution of kills to calculate the mean LNS for each scenario. For a given female, I randomly drew from the distribution of kills, used this proportion (*x*/300 calves) as the probability of a binomial draw to determine whether a calf survived and repeated this seven times, summing the total to calculate LNS. I repeated this process 50,000 times then calculated the mean LNS and its associated variance. To evaluate each hypothesis, I assessed for trends in the mean and variance of LNS and specifically noted how group-living compared to the reference scenario. Simulations were coded in the C programming language while LNS calculations were performed in R, version 3.1.2 (R Core Team 2014).

## RESULTS

### *Search Time Hypothesis*

Under the assumptions that wolves detected caribou at a constant radius of 1-km and killed one calf per encounter, dispersion appeared to be a favourable tactic when caribou occurred as individuals (Fig. 3.1A). Increasing dispersion resulted in an increasing trend in mean LNS (scenario 0 [highly aggregated] = 1.88; scenario 8 [highly dispersed] = 2.12; Appendix 3.3 Table A3.3.1) and variance tracked the mean trend, albeit at a slower rate, in a Poisson-like distribution (range: 1.37, 1.49). Dispersing as individuals, however, was not advantageous over group-living under these assumptions as dispersed individuals had a lower mean LNS than grouped caribou. (Fig. 3.1B, Appendix 3.3 Table A3.3.2). Moreover, increasing group size led to an increasing trend in the mean and a decreasing trend in variance (group size 2: 1.72; group size 13: 0.79) of LNS.

### *Group Detectability Hypothesis*

The advantage of group living greatly diminished when the detection radius of wolves varied as a function of caribou group size (Fig. 3.2, Appendix 3.3 Table A3.3.3). Small groups ($2 \leq n \leq 4$) had a lower mean LNS on average than dispersed individuals and the mean for small groups trended lower with increasing group size. This trend, however, reversed at intermediate to large group sizes (≥ 5) and, as a result, when group size was ≥ 10, mean LNS was higher than dispersed individuals. Variance in LNS remained relatively constant across group sizes (range: 1.32, 1.55).

### *Multiple Kills Hypothesis*

Varying the number of kills per encounter while holding the detection radius constant resulted in grouped caribou having a higher mean LNS than dispersed individuals in all simulations except those where all calves were killed on initial encounter (Fig. 3.3, Appendix 3.3 Table A3.3.4). Variance showed a slight curvilinear effect, being higher at middle values of mean LNS.

### *Multiple Mechanisms*

Combining the effects of multiple kills per encounter and differential group detectability resulted in dispersed individuals having a higher mean LNS than grouped caribou (Fig. 3.4, Appendix 3.3 Table A3.3.5). This outcome was evident even in simulations where only 1.5 calves were killed on average per encounter. Variance again showed a Poisson-like property, mirroring the trend in mean LNS.

Modelling a lowered rate of kill success (50%) with differential group detectability resulted in a consistent increase in mean LNS across group sizes (Fig. 3.4, Appendix 3.3 Table A3.3.6). As a consequence, results from this interaction were similar to the group detectability simulations where dispersed individuals had a higher mean LNS than small groups (here, group sizes of 2-4) but not large groups (> 6 individuals). Notably, the increasing trend in mean LNS associated with group sizes > 6 was steeper than when the kills-per-encounter is 1.0. Variance in LNS was relatively constant across group sizes (range: 1.67, 1.76).

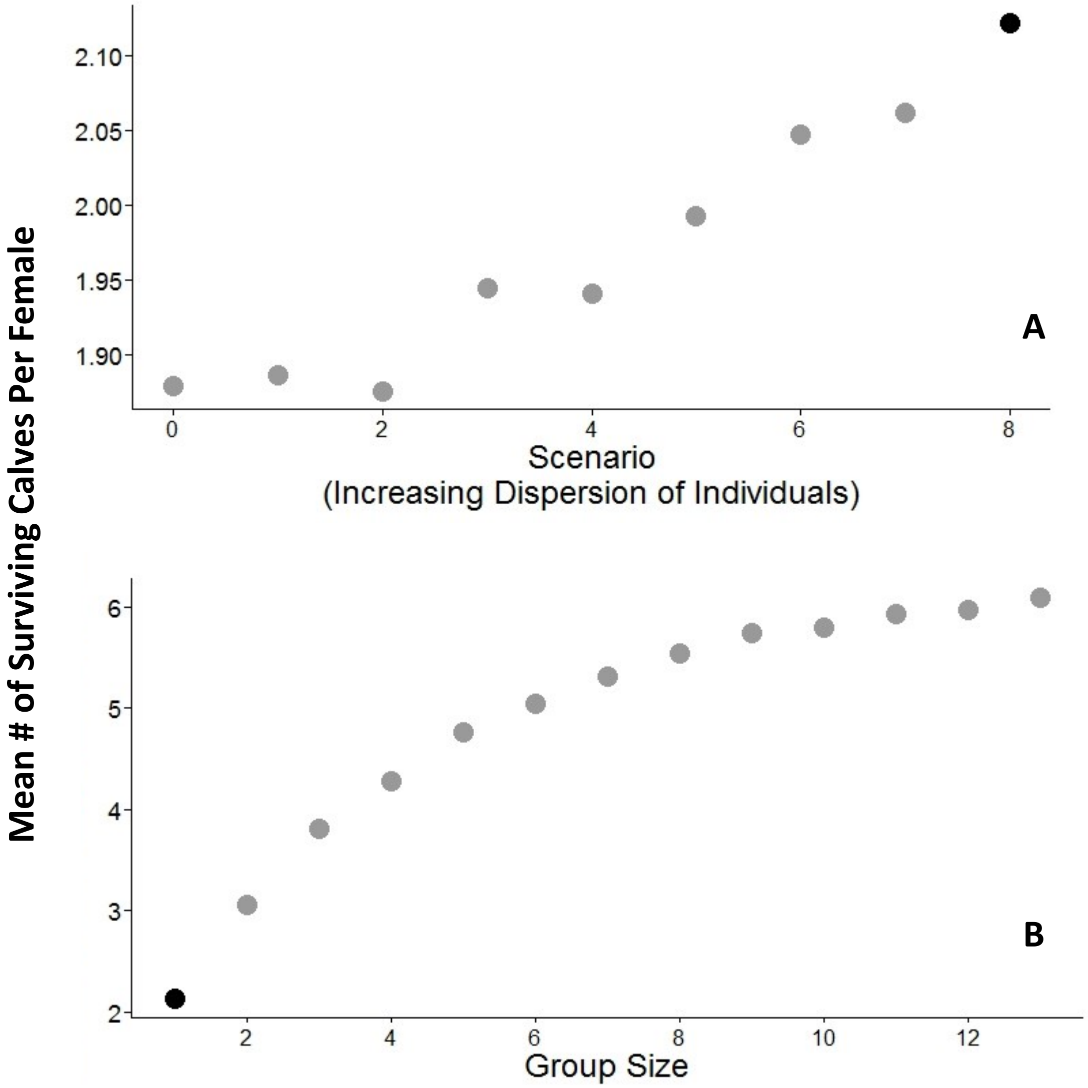


Figure 3.1: The effect of individual dispersion (search time hypothesis) on the mean number of surviving calves per female per generation (7 years) during simulations (n = 250 / scenario or group size) tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves was 1-km regardless of group size and one calf was killed per encounter. Black circles and dashed lines refer to the values of the reference scenario where caribou occur as highly dispersed individuals. In (A), the spatial configuration of individual caribou was varied from highly clumped (scenario 0) to highly dispersed (scenario 8). In (B), highly dispersed individuals are compared to dispersed caribou groups.

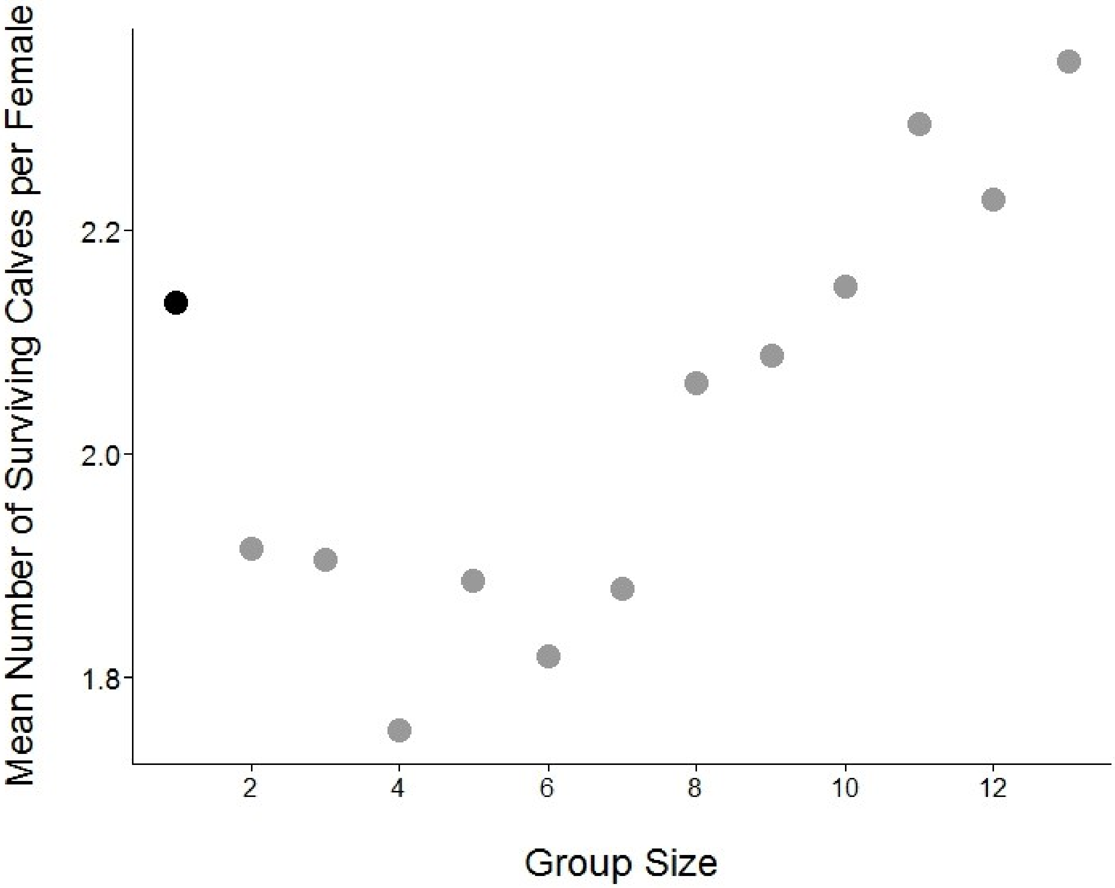


Figure 3.2: The effect of differential detectability by group size (group detectability hypothesis) on the mean number of surviving calves per female per generation (7 years) during simulations (n = 250 / scenario or group size) tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves varied as the square root of caribou group size and only one calf was killed per wolf encounter. The black circle refers to the values of the reference scenario where caribou occur as highly dispersed individuals.

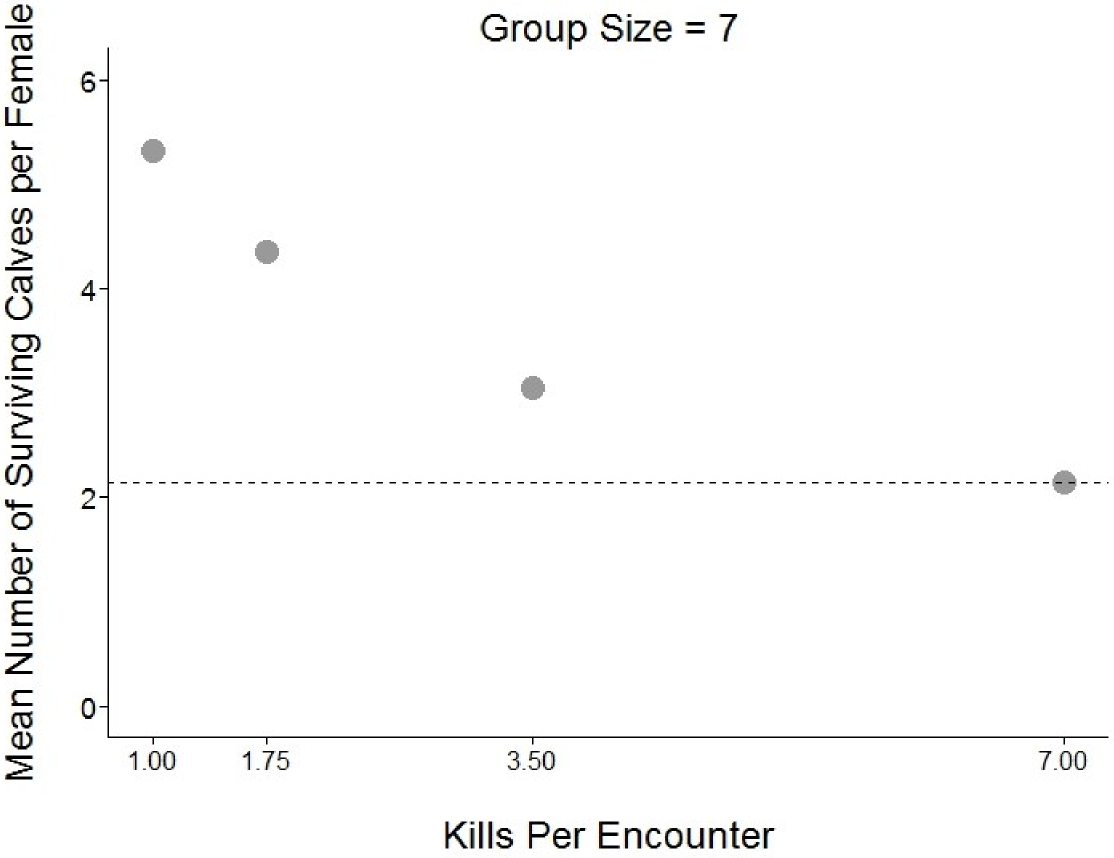


Figure 3.3: The effect of multiple kills per encounter (multiple kills hypothesis) on the mean number of surviving calves per female per generation (7 years) during simulations (n = 250 / scenario or group size) tracking caribou-wolf encounters during the calving season. Here, I show the effects when caribou occur in groups of seven, the mean group size of caribou during the winter in northeast British Columbia. The dashed line indicates the mean number of surviving calves in the reference scenario where caribou are dispersed as individuals.

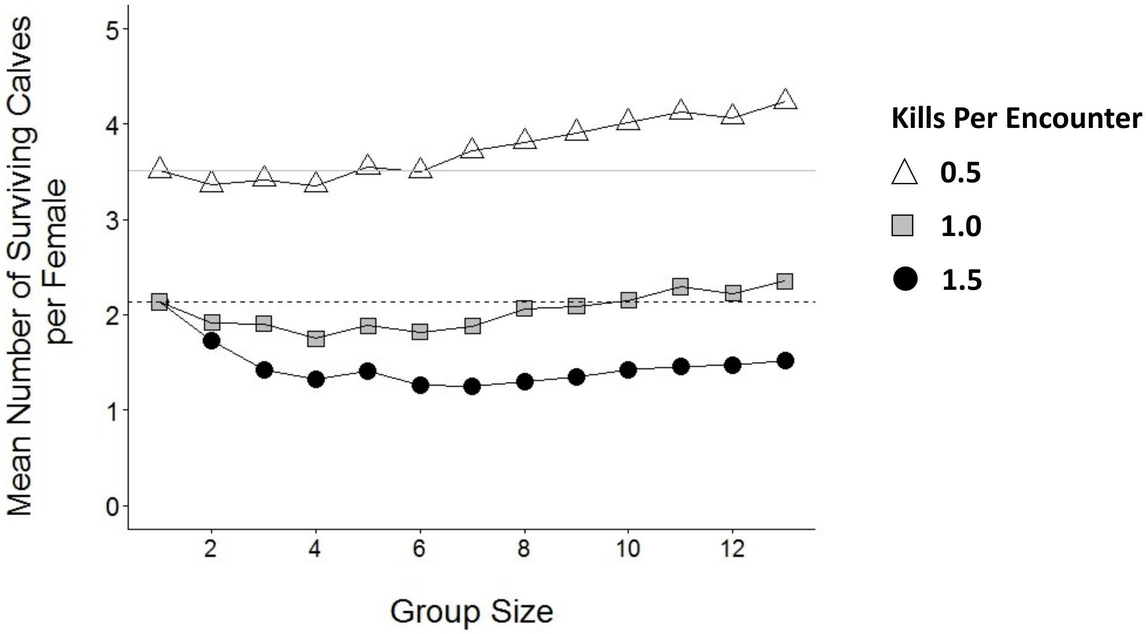


Figure 3.4: The effects of multiple mechanisms on the mean number of surviving calves per female per generation (7 years) during simulations (n = 250 / scenario or group size) tracking caribou-wolf encounters during the calving season. Differential group detectability was separately combined with multiple kills per encounter (black circles) and a 50% rate of kill success (white triangles). For multiple kills, the average kills per encounter was 1.5. The results of simulations assessing only differential group detectability (grey squares; kills-per-encounter = 1.0) are also presented for comparison. Black dashed line represents the value of the reference scenario where caribou are dispersed as individuals and kill success is 100%. Grey solid line represents the value of the reference scenario when kill success is 50%.

## DISCUSSION

The evolution of life history traits can often be driven by multiple causes (Hilborn & Stearns 1982). My results suggest that multiple mechanisms interact to selectively favour dispersion as a strategy for reducing predation risk at reproduction in otherwise group-living prey. Dispersion was only a consistently favourable strategy when detectability increased with group size and predators killed more than one offspring per encounter. The risk of multiple kills per encounter, however, may be the primary mechanism causing females to disperse at reproduction as differential group detectability is likely to remain relatively constant throughout the year for most species. During reproduction, dispersion is favoured because the vulnerability of neonatal offspring results in a high risk of multiple kills if offspring are grouped (Miller *et al*. 1985) and this risk outweighs the benefits afforded by group living. Outside of reproduction, the risk of multiple kills is greatly reduced because groups consist of adults and juveniles, individuals with a considerably lower probability of capture than neonates. This low risk of multiple kills therefore favours living in larger groups (e.g. > 6 for boreal caribou) – as evidenced by simulations modelling a kill success of 50% - with the benefits of group living likely due to the increased search time and lowered predator encounter rates associated with increasing group size (Ioannou *et al*. 2011).

Temporal variation in predation vulnerability has been shown to be a driver in the evolution of other behaviours in addition to the potential effect demonstrated here. In common lizards (*Zootoca vivipara*), gravid females will maintain a static, cryptic behaviour longer than non-gravid females upon predator approach because the increased weight of pregnancy makes fleeing less effective (Bauwens & Thoen 1981). In bream (*Abramis brama*), a freshwater fish, migratory behaviour is thought to be a size-dependent response to predation risk with smaller, high-risk individuals showing a greater propensity to migrate (Skov *et al*. 2011). In both examples, predation-sensitive behaviours likely evolved because of the positive effects on individual survival, and therefore fitness. For caribou in forested environments, dispersion at calving may have become fixed over aggregation because of dispersion's positive effect on neonate survival, a contributing factor to fitness. Because offspring survival affects the fitness of all organisms, this mechanism likely generalizes beyond caribou in explaining dispersive behaviour at reproduction. For example, within ungulates – where calving behaviour has been primarily assessed in terms of habitat selection – offspring vulnerability may be an influencing factor in the dispersive behaviour of parturient moose (*Alces alces*; Poole *et al.* 2007) and elk (*Cervus elaphus*; Vore & Schmidt 2001). Within birds, offspring vulnerability could be a contributing mechanism in the dispersion of pairs at breeding in otherwise flocking species (Lima 2009).

The dominant mechanisms driving spatial strategies of organisms are likely context specific (Treisman 1975; Taylor 1976; Scharf *et al.* 2011). This idea is exemplified by caribou where the surrounding environment likely plays an important role in determining whether to disperse (boreal caribou) or aggregate (barren-ground caribou) at calving. In my simulations, I assumed that wolves primarily detected caribou by olfaction and/or audition because forest cover limits visual detection. Environmental effects on vision may also determine the spatial strategy of prey as it directly affects the benefit of early predator detection provided by groups (Pulliam 1973). In open environments, group living is likely maintained during reproduction because early visual detection of predators enhances predator evasion (e.g. bighorn sheep

[*Ovis canadensis*], Berger 1978; common degu [*Octodon degus*], Ebsenperger & Wallem 2002) or the organization of group defence (e.g. muskoxen [*Ovibos moschatus*], Tener 1965; bison [*Bison bison*], Carbyn & Trottier 1988) and these benefits may outweigh the risk of multiple kills when offspring are grouped. Indeed, in a predator removal experiment Banks (1990) found that female eastern grey kangaroos (*Macropus giganteus*) foraging in the open with dependent young were more likely to occur in groups in areas where predators were present compared to areas where they were removed. For boreal caribou, the weight of importance is placed on minimizing the risk of multiple kills because early visual detection of predators is limited in the boreal forest. The importance of vision in determining grouping patterns has also been demonstrated in other taxa including freshwater fish (Emery 1973) and dolphins (Scott & Cattanach 1998).

Differential group detectability strongly influenced the relative differences between dispersion and group-living in my simulations. When detectability was held constant for all group sizes, group-living was highly advantageous over dispersion regardless of group size (Fig. 3.1B); conversely, when detectability varied as a function of group size, dispersion was somewhat advantageous over small to intermediate groups but not large groups (Fig. 3.2). These results are similar to empirical findings of encounter rates between wolves and elk groups where intermediate group sizes of elk had higher encounter rates with wolves than individuals or large groups (Hebblewhite & Pletscher 2002). Together, these results suggest that at small to intermediate group sizes, group detectability effects have a stronger influence on encounter rates than the minimizing effect associated with increasing group size (Ioannou *et al*. 2011). Note, however, that the encounter-detectability relationship is dependent on how detectability is modelled. Because the true nature of prey detections in my wolf-caribou system is largely unknown, I used the inverse square law to model detectability as the square root of group size (Andersson *et al*. 2013). This approach is likely not an exact representation of how wolves detect caribou and may be biologically liberal when group sizes are large (e.g. the detection radius of a group of 13 in my simulations is 3.6 km). If the true detection radius is smaller, then group-living becomes increasingly advantageous even at small group sizes. These relationships therefore suggest that while differential group detectability discounts the advantages of group-living relative to dispersion (Figs. 3.1B & 3.2), it is by itself an insufficient explanation for why female caribou disperse at calving unless detection radii exceed distances that may be biologically implausible.

Of the three *a priori* hypotheses evaluated, the search time hypothesis – which isolated the effect of simply spacing out – was the least informative for explaining dispersion at reproduction. In simulations comparing groups to dispersed individuals, group-living was advantageous over individuals across all group sizes (Fig. 3.1B). Moreover, group-living becomes increasingly advantageous as group size increased, an effect caused by the increasing search time required for wolves to locate the decreasing number of available caribou groups (Travis & Palmer 2005, Ioannou *et al*. 2011). Dispersion only became effective when caribou occurred as individuals (Fig. 3.1A). In these simulations, increasing dispersion resulted in increasing mean LNS. While this finding does not directly answer my central question of why organisms disperse from groups, it does have important ramifications for the management of species that disperse at reproduction to reduce predation risk. If human-altered landscapes force such species to become increasingly clumped, an effect that has been shown for boreal caribou (Fortin *et al.* 2013), then lowered or more variable offspring survival may result, potentially leading to population declines and increased extinction risk (Boyce *et al.* 2006). Thus, conservation strategies for species that disperse at reproduction will require the protection of sufficient space to allow their dispersive behaviour to effectively reduce predation risk.

## LITERATURE CITED

Adams, L.G., Singer, F.J. & Dale, B.W. (1995). Caribou calf mortality in Denali National Park, Alaska. *The Journal of Wildlife Management*, **59**, 584–594.

Alexander, R.D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, **5**, 328–383.

Andersson, P., Löfstedt, C. & Hambäck, P.A. (2013). How insects sense olfactory patches - the spatial scaling of olfactory information. *Oikos*, **122**, 1009–1016.

Banks, P.B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour*, **61**, 1013-1021.

Bauwens, D. & Thoen, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology*, **50**, 733.

Berger, J. (1978). Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. *Behavioral Ecology and Sociobiology*, **4**, 91–99.

Bergerud, A.T. (1996). Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer*, **16**, 95–116.

Bergerud, A.T., Luttich, S.N. & Camps, L. (2008). *The return of caribou to Ungava*. McGill-Queen's University Press. 586 pp.

Bergerud, A.T. & Page, R.E. (1987). Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology*, **65**, 1597–1606.

Bjørneraas, K., Van Moorter, B., Rolandsen, C. M., & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *The Journal of Wildlife Management*, **74**, 1361–1366.

Boyce, M., Haridas, C., Lee, C. & the NCEAS Stochastic Demography Working Group. (2006). Demography in an increasingly variable world. *Trends in Ecology & Evolution*, **21**, 141–148.

Bulmer, M.G. (1985). Selection for iteroparity in a variable environment. *The American Naturalist*, **126**, 63–71.

Carbyn, L.N. & Trottier, T. (1988). Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. *Arctic*, **41**, 297–302.

COSEWIC. (2002). *COSEWIC assessment and update status report on the woodland caribou (Rangifer tarandus caribou) in Canada*. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON. *xi* + 98 pp.

Ebsenperger, L.A. & Wallem, P.K. (2002). Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. *Oikos*, **98**, 491–497.

Emery, A.R. (1973). Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. *Canadian Journal of Zoology*, **30**, 761–774.

Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Tye Gingras, C., Moorcroft, P.R., Courtois, R. & Dussault, C. (2013). Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. *The American Naturalist*, **181**, 827–836.

Foster, W.A. & Treherne, J.E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, **293,** 466–467.

Garay, J. (2009). Cooperation in defence against a predator. *Journal of Theoretical Biology*, **257**, 45–51.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.

Haber, G.C. (1977). *Socio-ecological dynamics of wolves and prey in a subarctic ecosystem*. Ph.D. dissertation. University of British Columbia, Vancouver, BC.

Hamilton, W.D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.

Hart, P.J. & Freed, L.A. (2005). Predator avoidance as a function of flocking in the sexually dichromatic Hawaii akepa. *Journal of Ethology*, **23**, 29–33.

Heard, D.C., Williams, T.M. & Melton, D.A. (1996). The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics. *Rangifer*, Special Issue **9**, 37–44.

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

Hilborn, R. & Stearns, S.C. (1982). On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheoretica*, **31**, 145–164.

Holling, C.S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**, 293–320.

Ioannou, C.C., Bartumeus, F., Krause, J. & Ruxton, G.D. (2011). Unified effects of aggregation reveal larger prey groups take longer to find. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2985–2990.

Ioannou, C.C. & Krause, J. (2008). Searching for prey: the effects of group size and number. *Animal Behaviour*, **75**, 1383–1388.

Jones, E., Oliphant, T., & Peterson, P., et al. (2001). SciPy: Open source scientific tools for Python. URL http://www.scipy.org/

Krause, J. & Ruxton, G.D. (2002). *Living in groups*. Oxford University Press, New York, NY. 224 pp.

Kruuk, H. (1972). Surplus killing by carnivores. *Journal of Zoology*, **166**, 233–244.

Lagarias, J. C., Reeds, J. A., Wright, M. H., & Wright, P.E. (1998). Convergence properties of the Nelder-Mead simplex method in low dimensions. *SIAM Journal on Optimization*, **9**, 112-147.

Lewis, J.S., Rachlow, J.L., Garton, E.O. & Vierling, L.A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology*, **44**, 663–671.

Lima, S.L. (2009). Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, **84**, 485–513.

Mech, L.D. & Boitani, L. (2003). *Wolves: behavior, ecology, and conservation*. The University of Chicago Press, Chicago, IL. 448 pp.

Miller, F.L., Gunn, A. & Broughton, E. (1985). Surplus killing as exemplified by wolf predation on newborn caribou. *Canadian Journal of Zoology*, **63**, 295–300.

Muhly, T.B., Alexander, M., Boyce, M.S., Creasey, R., Hebblewhite, M., Paton, D., Pitt, J.A. & Musiani, M. (2010). Differential risk effects of wolves on wild versus domestic prey have consequences for conservation. *Oikos*, **119**, 1243–1254.

Poole, K.G., Serrouya, R. & Stuart-Smith, K. (2007). Moose calving strategies in interior montane ecosystems. *Journal of Mammalogy*, **88**, 139–150.

Pulliam, H.R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, **38**, 419–422.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rettie, W.J. & Messier, F. (1998). Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology*, **76**, 251–259.

Rubenstein, D.R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences*, **108**, 10816–10822.

Russell, D.E., Martell, A.M. & Nixon, W.A. (1993). Range ecology of the Porcupine caribou herd in Canada. *Rangifer*, **13**, 1–168.

Scharf, I., Ovadia, O. & Foitzik, S. (2011). The advantage of alternative tactics of prey and predators depends on the spatial pattern of prey and social interactions among predators. *Population Ecology*, **54**, 187–196.

Scott, M.D. & Cattanach, K.L. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. *Marine Mammal Science*, **14**, 401–422.

Self, D., Duncan, B., Sinclair, I., Brice, R., Hood, J.L., Singmin, A., Davis, D., Patronis, E., & Watkinson, J. (2009). *Audio engineering: know it all*. Newnes Press, Burlington, MA.

Skov, C., Baktoft, H., Brodersen, J., Bronmark, C., Chapman, B.B., Hansson, L.-A. & Nilsson, P.A. (2011). Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1414–1418.

Taylor, J. (1976). The advantage of spacing out. *Journal of Theoretical Biology*, **59**, 485–490.

Tener, J.S. (1965). *Muskoxen in Canada: a biological and taxonomic review*. Dept. of Northern Affairs and National Resources, Canadian Wildlife Service, Ottawa, ON.

Tinbergen, N., Impekoven, M. & Franck, D. (1967). An experiment on spacing-out as a defence against predation. *Behaviour*, **28**, 307–321.

Travis, J.M.J. & Palmer, S.C.F. (2005). Spatial processes can determine the relationship between prey encounter rate and prey density. *Biology Letters*, **1**, 136–138.

Treisman, M. (1975). Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour*, **23**, 779–800.

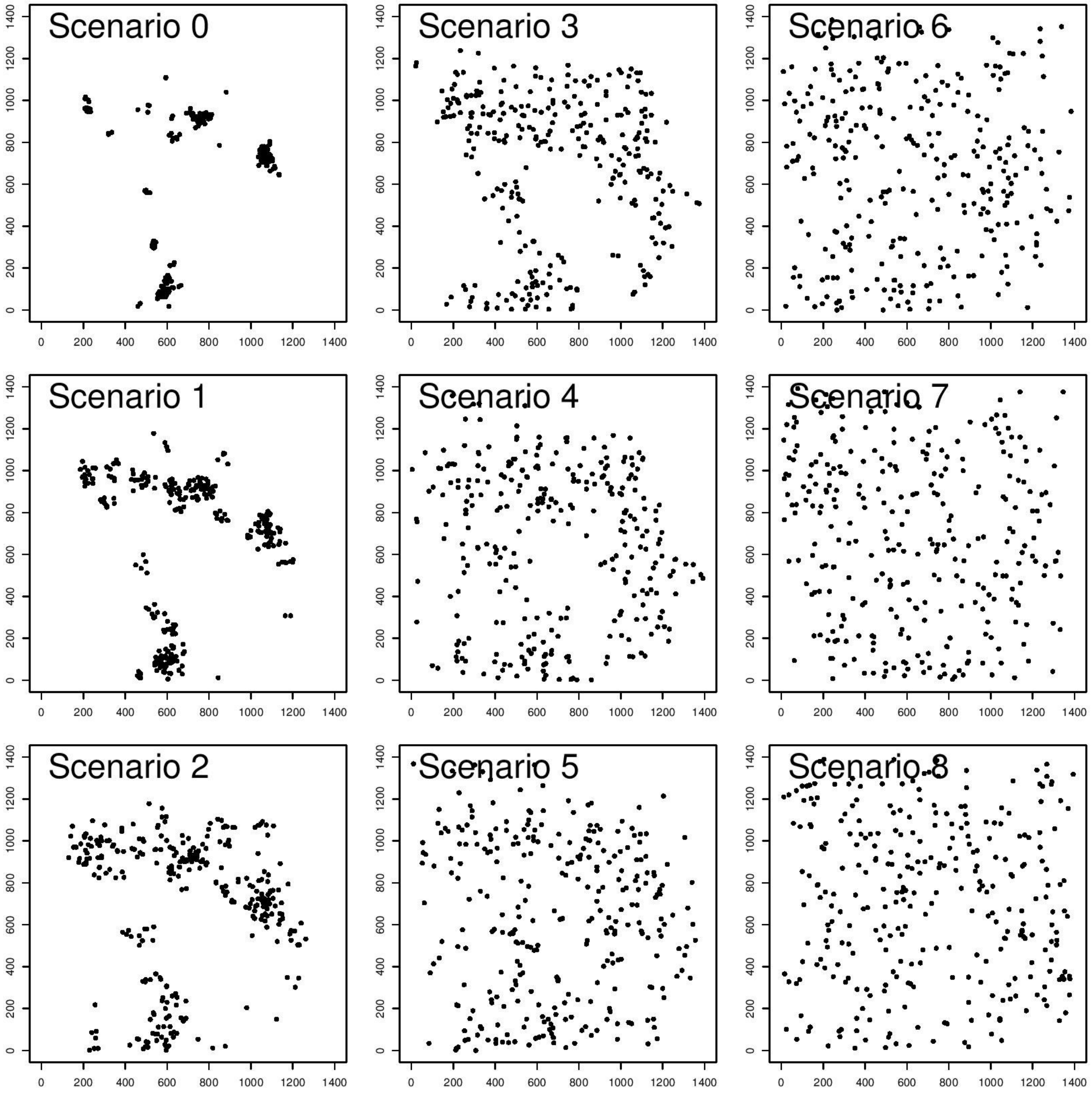
Turchin, P. (1998). *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*, 1st ed. Sinauer Associates, Inc., Sunderland, MA. 396 pp.

Vore, J.M. & Schmidt, E.M. (2001). Movements of female elk during calving season in northwest Montana. *Wildlife Society Bulletin*, **29**, 720–725.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J. & Musiani, M. (2011). Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *Journal of Applied Ecology*, **48**, 1535–1542.

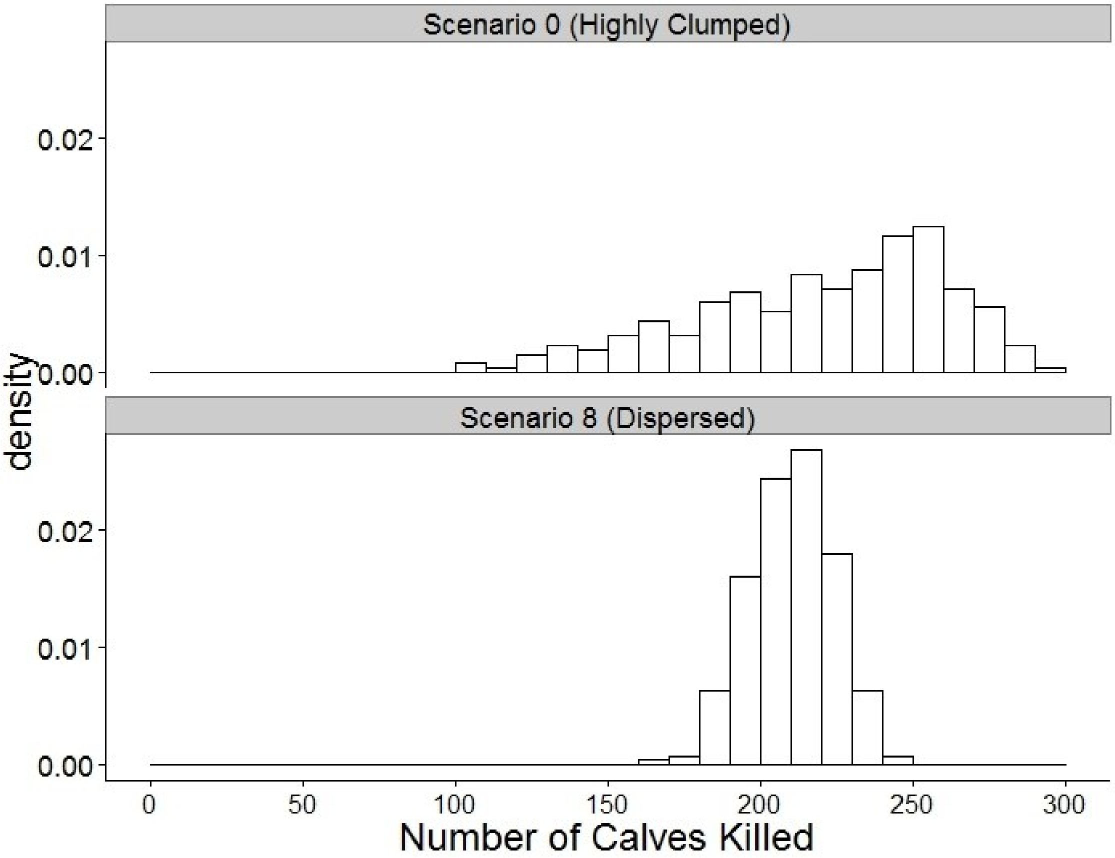
## APPENDIX 3.1: DISPERSION SCENARIOS TO TEST THE SEARCH TIME HYPOTHESIS

To test the search time hypothesis, which assessed the effectiveness of female caribou spacing out during calving, I evaluated nine scenarios representing varying degrees of dispersion ranging from highly clumped (Scenario 0) to highly dispersed (Scenario 8). Each scenario was populated with 300 caribou in a simulated caribou range of 4900 km$^2$ at a grid cell resolution of 50-m.



## APPENDIX 3.2: OUTPUTS FROM CARIBOU-WOLF ENCOUNTER SIMULATIONS: EXAMPLE DISTRIBUTIONS OF THE NUMBER OF CALVES KILLED

Simulations of caribou-wolf encounters during the calving season tracked the number of calves killed (out of 300). For each scenario tested, I ran 250 simulations (i.e. 250 calving seasons), generating an estimated distribution of the number of calves killed during a calving season. Below are two example distributions when testing the search time hypothesis: one when caribou are highly clumped (scenario 0) and one when caribou are highly dispersed (scenario 8).



## APPENDIX 3.3: ESTIMATES OF LIFETIME NEONATE SURVIVAL FROM SIMULATIONS TRACKING CARIBOU-WOLF ENCOUNTERS DURING THE CALVING SEASON

The following tables list the lifetime neonate survival values (mean and variance of the number of surviving calves per female per generation) calculated from simulations evaluating the search time, group detectability and multiple kills hypotheses as well as their interactions. I ran 250 simulations for each group size or scenario tested and each simulation started with 300 caribou calves and 10 wolves.

Table A3.3.1: The effect of individual dispersion (search time hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves was 1-km and one calf was killed per encounter.

| Scenario (Increasing Dispersion) | Number of Surviving Calves Per Female | |
|---|---|---|
| | Mean | Variance |
| 0 | 1.88 | 1.37 |
| 1 | 1.89 | 1.39 |
| 2 | 1.88 | 1.36 |
| 3 | 1.94 | 1.40 |
| 4 | 1.94 | 1.40 |
| 5 | 1.99 | 1.44 |
| 6 | 2.05 | 1.45 |
| 7 | 2.06 | 1.45 |
| 8 | 2.12 | 1.49 |

Table A3.3.2: The effect of group size (search time hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves was 1-km regardless of group size and one calf was killed per encounter.

| | Number of Surviving Calves Per Female | |
|---|---|---|
| Group Size | Mean | Variance |
| 1 | 2.14 | 1.50 |
| 2 | 3.06 | 1.72 |
| 3 | 3.81 | 1.74 |
| 4 | 4.28 | 1.66 |
| 5 | 4.76 | 1.53 |
| 6 | 5.04 | 1.40 |
| 7 | 5.31 | 1.28 |
| 8 | 5.54 | 1.15 |
| 9 | 5.74 | 1.03 |
| 10 | 5.80 | 1.00 |
| 11 | 5.94 | 0.90 |
| 12 | 5.97 | 0.88 |
| 13 | 6.09 | 0.79 |

Table A3.3.3: The effect of differential detectability by group size (group detectability hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves varied as the square root of caribou group size and one calf was killed per encounter.

| | Number of Surviving Calves Per Female | |
|---|---|---|
| Group Size | Mean | Variance |
| 1 | 2.14 | 1.50 |
| 2 | 1.92 | 1.38 |
| 3 | 1.90 | 1.38 |
| 4 | 1.75 | 1.32 |
| 5 | 1.89 | 1.37 |
| 6 | 1.82 | 1.35 |
| 7 | 1.88 | 1.37 |
| 8 | 2.06 | 1.45 |
| 9 | 2.09 | 1.46 |
| 10 | 2.15 | 1.49 |
| 11 | 2.30 | 1.55 |
| 12 | 2.23 | 1.52 |
| 13 | 2.35 | 1.55 |

Table A3.3.4: The effect of multiple kills per encounter (multiple kills hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. Group sizes of three, seven and thirteen were evaluated.

| | | Number of Surviving Calves Per Female | |
|---|---|---|---|
| Group Size | Average Kills Per Encounter | Mean | Variance |
| 3 | 1.0 | 3.80 | 1.74 |
| | 1.5 | 3.20 | 1.73 |
| | 3.0 | 2.20 | 1.54 |
| 7 | 1.0 | 5.32 | 1.29 |
| | 1.8 | 4.36 | 1.63 |
| | 3.5 | 3.04 | 1.73 |
| | 7.0 | 2.14 | 1.48 |
| 13 | 1.0 | 6.10 | 0.79 |
| | 2.2 | 5.00 | 1.41 |
| | 4.3 | 3.80 | 1.75 |
| | 6.5 | 2.96 | 1.71 |
| | 13.0 | 2.09 | 1.48 |

Table A3.3.5: The combined effects of differential group detectability (group detectability hypothesis) and multiple kills per encounter (multiple kills hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. In these simulations, the number of kills per encounter averaged 1.5 for group sizes ≥ 2.

| | Number of Surviving Calves Per Female | |
|---|---|---|
| Group Size | Mean | Variance |
| 1 | 2.14 | 1.50 |
| 2 | 1.73 | 1.30 |
| 3 | 1.42 | 1.14 |
| 4 | 1.32 | 1.07 |
| 5 | 1.41 | 1.12 |
| 6 | 1.26 | 1.03 |
| 7 | 1.25 | 1.03 |
| 8 | 1.30 | 1.05 |
| 9 | 1.34 | 1.08 |
| 10 | 1.42 | 1.13 |
| 11 | 1.46 | 1.16 |
| 12 | 1.47 | 1.16 |
| 13 | 1.52 | 1.18 |

Table A3.3.6: The combined effects of differential group detectability (group detectability hypothesis) and a kill success rate of 50% on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season.

| | Number of Surviving Calves Per Female | |
|---|---|---|
| Group Size | Mean | Variance |
| 1 | 3.51 | 1.76 |
| 2 | 3.37 | 1.77 |
| 3 | 3.42 | 1.73 |
| 4 | 3.36 | 1.75 |
| 5 | 3.55 | 1.73 |
| 6 | 3.50 | 1.74 |
| 7 | 3.72 | 1.74 |
| 8 | 3.81 | 1.73 |
| 9 | 3.91 | 1.73 |
| 10 | 4.02 | 1.71 |
| 11 | 4.12 | 1.69 |
| 12 | 4.07 | 1.70 |
| 13 | 4.23 | 1.67 |

# CHAPTER 4

## AN INDIVIDUAL-BASED, COMPARATIVE APPROACH TO IDENTIFY CALVING HABITAT FOR A THREATENED FOREST UNGULATE

With global demands for natural resources increasing (Nepstad *et al.* 2013), many threatened and endangered species must coexist in landscapes managed for multiple uses. Maintaining species within these landscapes represents a challenge because habitat conservation – a fundamental management strategy (Kerr & Deguise 2004) – is often balanced against more immediate social and economic interests (Naidoo *et al.* 2006; Schneider *et al.* 2012). In many instances, conservation of all potential habitat is not possible; consequently, management strategies for multi-use landscapes frequently entail prioritizing areas for conservation (Moilanen *et al.* 2005). Inherent to this process is identifying habitats with high influence on population dynamics at scales that are both amenable to management and biologically relevant to the species of interest (Newbold & Siikamaki 2009; Dzialak *et al.* 2011).

The effectiveness of prioritization strategies depends on strong inference from models used to identify important habitats. Such a modelling process may require two types of models: those that first identify life history stages with high influence on population dynamics (e.g. demographic models; Crouse *et al.* 1987) and those that identify habitats associated with these life stages (e.g. predictive habitat distribution models [hereafter, habitat models]; Guisan & Zimmermann 2000). Here, I focus on the second phase of prioritization modelling; that is, discriminating demographically important habitats from other areas on the landscape. The discriminative ability of a habitat model is commonly tested through its predictive performance

(Boyce *et al.* 2002), although thoroughly testing this ability requires comparing model outputs to those generated for other non-targeted areas (Gustine & Parker 2008). Habitat models also need to be evaluated to determine the amount of individual variation that is captured in their predictions. Many modelling approaches focus primarily on population-level responses yet individuals can vary significantly in their habitat use thereby limiting the effectiveness of conservation strategies based solely on population-level responses (Bolnick *et al.* 2003; Gillingham & Parker 2008b). Finally, model inferences need to be spatially explicit and easily transferrable to maps in order to guide prioritization strategies, particularly when prioritization is conducted over large spatial scales (Apps *et al.* 2001; Schneider *et al.* 2012).

I applied these modelling tenets to develop an individual-based, comparative approach for identifying calving habitat of boreal caribou (*Rangifer tarandus caribou*). Boreal caribou occur within the boreal forest biome of Canada and the vast majority of population ranges are situated in landscapes managed for multiple uses (Environment Canada 2008). Identifying calving habitat for boreal caribou has become a conservation priority because for many populations low rates of neonate survival during the calving period have resulted in low rates of calf recruitment, a key demographic factor contributing to population declines (Stuart-Smith *et al.* 1997; Environment Canada 2008; Pinard *et al.* 2012). Predation is the primary cause of calf mortality (Pinard *et al.* 2012; Leclerc *et al.* 2014) and increasing predation of caribou has been linked to indirect effects of anthropogenic disturbance occurring within caribou range (McLoughlin *et al.* 2005; Dussault *et al.* 2012; Leclerc *et al.* 2014). To date, few conservation strategies have been developed to limit disturbance within calving areas because of an inability to adequately discriminate such areas on the landscape.

Identifying reproductive habitats of ungulates can be challenging, particularly for species like boreal caribou that do not congregate in defined areas to calve (c.f. barren-ground caribou [*Rangifer tarandus groenlandicus*]; Bergerud *et al.* 2008). Nevertheless, considerable research has been directed toward evaluating habitat selection (*sensu* Johnson 1980) by ungulates during the reproductive season. For the most part, such studies can be categorized into two types of analyses: those that assess birth site selection (e.g., Bowyer *et al.* 1999; Poole *et al.* 2007; Singh *et al.* 2010; Barbknecht *et al.* 2011; Rearden *et al.* 2011; Pinard *et al.* 2012; Leclerc *et al.* 2012) versus those that encompass the entire reproductive period (e.g., Gillingham & Parker 2008a; Gustine & Parker 2008; McLoughlin *et al.* 2011; Moreau *et al.* 2012). For informing management strategies that aim to conserve reproductive habitat to increase offspring survival, studies of birth site selection may have limited value because these site-specific analyses do not represent the extent of habitat used during the entire neonate period when offspring are most vulnerable (Gaillard *et al.* 2000; Zager & Beecham 2006). Moreover, many studies of birth site selection include fine-scale analyses (e.g., site-specific shrub cover) that do not translate easily into habitat characteristics that can be mapped. For larger-scale seasonal analyses, few studies are restricted to only females with offspring (but see Gustine *et al.* 2006; Dzialak *et al.* 2011); thus, these analyses may simply represent a seasonal habitat shift of the entire population (e.g., parturient and barren females) rather than identifying reproductive habitat *per se*.

To identify calving habitat characteristics of boreal caribou, I evaluated whether the presence of a neonate calf (≤ 4 weeks old) induced changes in habitat selection by females at scales that are easily mapped and thus amenable to landscape-level management. To do so, I used an individual-based, comparative approach that assessed for: *i*) differences between habitats selected during calving and other seasons; *ii*) differences in habitat selection between females with calves and barren females; and iii) changes in habitat selection after females lost their calves. The latter two comparisons provide a powerful test for determining whether calving areas are a discrete, identifiable habitat within caribou range.

Within this comparative framework, I also assessed whether females selected calving areas to further reduce predation risk or to access higher forage quantity and/or quality to meet maternal nutritional demands (Parker *et al.* 2009). This trade-off is one faced by most maternal ungulates (Festa-Bianchet 1988; Rachlow & Bowyer 1998; Panzacchi *et al.* 2010). For boreal caribou, previous research has suggested that females select calving sites to reduce predation risk (Bergerud *et al.* 1990; Pinard *et al.* 2012; Leclerc *et al.* 2012) but it is unclear how females manage this trade-off as the calving period progresses. Because caribou enter the calving season with a protein deficit – due to a winter diet consisting mostly of lichen –, females may be forced to trade-off increasing predation risk to access higher forage quality to meet increasing lactation demands associated with calf growth (Parker *et al*. 2009).

## METHODS

### *Caribou Spatial Data*

I used location data from 46 reproductive-aged (>3 years old) female caribou fitted with Iridium satellite GPS collars (Advanced Telemetry Systems; model #2110E). Individual females were captured by aerial net-gunning from a helicopter during the winter months (January – March) of 2011 (*n* = 24), 2012 (*n* = 2) and 2013 (*n* =20). During collar deployment, animals were physically restrained and not anaesthetized. All animals were captured and handled following approved institutional animal care protocols (University of Alberta Animal Use protocol # 748/02/13). For animals captured in 2011 and 2012, collars were programed to acquire one GPS location (or fix) every two hours during the calving season (April 15 – July 15) and once per day otherwise. The mean data collection period for 2011-12 collars was 542 days (range: 254, 647) with 19 collars remaining operational through two calving seasons. For 2013 animals, collars acquired one GPS location every four hours during calving and every eight hours otherwise. I used data up to September 12, 2013 for these females, resulting in a mean per-collar data collection period of 226 days (range: 192, 268).

Prior to data analysis, I applied the following screening procedures to the raw GPS data. First, I removed the first two weeks of GPS locations post-capture to reduce the effects of captured-related behavioural alterations (Morellet *et al.* 2009). Second, I removed locations from 10:00 to 18:00 on dates of aerial surveys (see below) to reduce behavioural effects associated with helicopter disturbance. Third, I removed all locations with low positional accuracy (e.g. < three-dimensional fixes; Lewis *et al.* 2007). For the retained three-dimensional fixes, the mean horizontal measurement error of the ATS collars was estimated to be ± 7.7 m (C. DeMars, *unpublished data*). Finally, I used the methods of Bjørneraas *et al*. (2010) to exclude outlying locations that were beyond the range of possible caribou movement. Following these procedures, the mean per-collar fix rate during the calving season was 98.5% (range: 94.3 – 100) for 2011, 98.4% (95.4 – 99.9) for 2012 and 87.8% (69.8-96.3) for 2013. Outside of the calving season, mean per-collar fix rates were 87.9% (60.6, 97.8) for 2011, 90.0% (55.4-97.9) for 2012 and 94.7% (84.2-1.0) for 2013.

### *Identifying Calving Habitat: General Framework*

To identify calving habitat, I developed resource selection functions (RSFs), a widely used modelling approach whereby environmental attributes associated with GPS (or "used") locations are compared to environmental attributes of random (or "available") locations generated within the spatial scale of interest (Manly *et al.* 2002). For convenience, I use the term "resources" to describe these environmental attributes but recognize that RSFs frequently incorporate geophysical and topographical variables (e.g. temperature, slope) and are not necessarily restricted to consumable resources (e.g. forage; Matthiopoulos *et al.* 2011). To specifically determine key characteristics of calving habitat, I compared RSFs developed for females with neonate calves (≤ 4 weeks old) to RSFs developed for barren females and to RSFs developed for other seasonal periods (see below). I also compared RSFs calculated pre- and post-calf loss for females losing calves prior to four weeks of age.

All RSFs were estimated at a second-order scale (*sensu* Johnson 1980) to determine how calving areas and other seasonal areas differed from random areas within a herd's range. This scale of selection likely reflects the primary selective decision of female caribou as many individuals undertake long distance, migratory-type movements just prior to calving – indicating that selection is occurring at large spatial scales – and show considerable inter-annual fidelity to calving areas (Edmonds 1988; Schaefer *et al.* 2000; Faille *et al.* 2010). Compared to finer (e.g. third- and fourth-order) scales of selection, results derived from second-order selection analyses are likely more informative for potential management decisions (Boyce 2006), particularly for a wide-ranging ungulate such as caribou. Further, this RSF framework allows for a more straightforward comparison of selection differences as the scale of availability is constant for large groups of individuals (i.e. all animals within a given range).

I assessed for seasonal differences in habitat selection by partitioning the screened GPS data into calving, fall, and winter seasons. Within the calving season, I further partitioned the data based on maternal status. I defined calving areas as those areas used by females with neonate calves (≤ 4 weeks old). To identify calving GPS locations, I estimated the reproductive status (i.e., parturient versus barren) of individual females and the survival status of neonate calves by using the two movement-based methods described in *Chapter 2*. These methods yield predictions of parturition date and calf loss date, where appropriate. To predict parturition status, I used the population-based method due to its higher accuracy. For females predicted to have calved, I compared predictions of neonate survival from both of the movement-based methods and corroborated these predictions with data from aerial surveys that attempted to visually observe each female at four weeks post-calving. If model predictions of calf survival differed, I used the prediction which matched the status (e.g. calf presence / absence) on aerial survey. In one instance, I truncated the post-calving data to the date the calf was last observed as the predicted date of calf loss fell before this aerial survey, which was conducted prior to four weeks post-calving. For females with differing model predictions and no aerial survey data ($n$ = 5), I used the predictions of the individual-based method to assign calf survival status as this analysis has a higher accuracy rate (see *Chapter 2*). In subsequent calving habitat selection analyses, I used all calving locations from estimated parturition date to the estimated date of calf loss or four weeks post-calving, whichever came first.

For females losing calves prior to four weeks of age, I assessed for selection differences depending on maternal status by comparing RSFs estimated from with-calf locations to RSFs estimated from post-loss locations. For each individual post-loss RSF, I used GPS locations collected from a time period equal to the with-calf time period. To exclude behavioural alterations potentially related to the calf loss event, I allowed two days between the estimated time of calf loss and the start of data for the post-loss period (e.g., for a female losing her calf at 10 days post-calving, I used locations from days 2-12 post loss).

For developing RSFs for females considered to be barren, I used GPS locations starting from May 15 – the peak of calving in my study area – to June 12 (four weeks total). To assess habitat selection outside of the calving season (in our study area, April 15 – July 15), I followed Nagy's (2011) delineation of seasonal activity periods for boreal caribou and estimated RSFs for late summer (August 13 – September 12), late fall (October 21 – November 30) and midwinter (January 26 – March 15). All seasonal RSFs were estimated at the same second-order scale as for calving RSFs.

For each RSF analysis, I characterized the extent of the area used by constructing 80% utilization distributions (UDs) from the GPS location data as described by Börger *et al*. (2006). Within each UD, I generated sufficient random points to accurately represent the area (Benson 2013, Northrup *et al*. 2013). To determine the number of random points required, I conducted a sensitivity analysis on the largest UD, plotting the mean of each covariate against the number of random points used to calculate the mean (Appendix 4.1). I selected the number of random points where the mean of each covariate changed < 1%. I repeated this analysis to determine the number of points necessary to adequately represent a herd's range. Subsequent RSF analyses thus entailed a comparison between UD random points and herd range random points. Because home range estimators like UDs can be sensitive to insufficient sampling (Börger *et al*. 2006), I excluded individuals with <80% fix rates within a particular seasonal period from the corresponding RSF analysis.

### *Environmental Covariates*

I modelled RSFs using explanatory variables derived from GIS data representing vegetation characteristics (land cover type and normalized difference vegetation index [NDVI]), slope, aquatic features (lakes, rivers) and disturbed habitat (forest fires < 50 years old, forestry cut blocks < 50 years old, oil and gas well sites and linear features; see Appendix 4.2 for further details and a list of data sources). For characterizing land cover type, I used Enhanced Wetlands Classification data developed by Ducks Unlimited Canada, which I collapsed into eight categories that were biologically meaningful to caribou. For all analyses, I set treed bog as the reference category by omitting it from RSF models; thus, all land cover rankings derived from model estimates are relative to treed bog. I modelled forage productivity using NDVI data, an index that has been used in other caribou studies (Gustine *et al.* 2006; DeCesare *et al.* 2012). NDVI is correlated with above-ground net primary productivity and NDVI values in forested habitats are significantly influenced by forest floor greenness (Suzuki *et al.* 2011). For each year of our study and all RSF models, I used NDVI data spanning the calving season only (end-April to mid-July) and calculated an average NDVI value for each pixel during this time period. By using NDVI data only from the calving season, I could more directly evaluate the forage quality hypothesis by concurrently comparing NDVI values of calving areas with other seasonal areas.

For modelling disturbance, I combined forestry cut blocks and forest fires < 50 years old to create a unified variable describing early seral vegetation, which has been associated with increased predation risk to caribou (Rettie & Messier 1998; Kinley & Apps 2001; Wittmer *et al.* 2007). Linear features are also thought to increase predation risk to caribou (James & Stuart-Smith 2000; Latham *et al.* 2011b; Whittington *et al.* 2011). I created a linear feature data set by merging data representing pipelines, seismic lines and roads. I did not model road effects separately because road density in the study area is low ($\leq 0.2$ km/km$^2$) and the majority of roads have low traffic volume. To assess caribou response to non-linear oil and gas disturbance, I used data representing active and completed well sites.

I conducted preliminary analyses to determine the most predictive spatial scale for each of the explanatory covariates (Levin 1992; Boyce 2006; Leblond *et al.* 2011; Appendix 4.3). For each analysis, I pooled the data across individuals and conducted univariate logistic regression analyses at each spatial scale. I selected the scale with the lowest Akaike's Information Criterion (AIC) score as the scale to be included in further RSF modelling. While the most predictive scale can vary across seasons (Leblond *et al*. 2011), I conducted these analyses on the calving data only and kept the scale of each covariate constant across seasonal analyses to facilitate more direct comparison of seasonal selection coefficients. For land cover, I evaluated predictive power at the pixel scale (30-m) as well as for the proportion of each cover type in a moving window analysis with radii varying from 400-m to 6000-m, the radius of the largest calving area UD (100-m increments from 400- to 1000-m, 500-m increments thereafter). I assessed the density of lakes, rivers, early seral vegetation and well sites at the same scales and further evaluated whether distance-to measures were more predictive than density measures.

For linear features, I assessed density only as I was specifically interested in caribou response to changes in linear feature density. I kept NDVI and slope at the scale of the original data (250-m and 30-m, respectively) as I did not want to obscure fine-scale heterogeneity in these variables. Because my objective was to compare seasonal differences in selection at the individual level, I did not include quadratic terms or interactions in my models to facilitate more straightforward comparison of variable coefficients.

*Data Analysis*

I estimated RSFs using generalized linear mixed effect models (GLMMs; Zuur *et al.* 2009), which account for the hierarchical structure inherent in GPS location data. In all GLMMs, I assigned individual caribou as a random grouping effect thereby creating a random intercept for each caribou. I further evaluated for functional responses in selection – where selection may change as a function of resource availability (Mysterud & Ims 1998) – by nesting individual caribou within herd range (i.e., a two-factor mixed-effects model). For second-order selection analyses where availability is defined at the range level, only five sets of availability are possible for each resource. To assess variation among individual caribou to specific explanatory covariates, I fit random slope GLMMs of the form

$$ln\left[\frac{\pi(y_i=1)}{1-\pi(y_i=1)}\right] = \beta_0 + \beta_1 x_{1ijk} + \ldots + \beta_n x_{nijk} + \gamma_{0j} + \gamma_{0jk} + \gamma_{nij} x_{nij} + \gamma_{nijk} x_{nijk}$$

(Gillies *et al.* 2006)

where the left-hand side of the equation is the logit transformation for location $y_i$, $\beta_0$ is the fixed-effect – or population mean – intercept, $\beta_n$ is the fixed-effect coefficient for covariate $x_n$, $\gamma_{0j}$ and $\gamma_{0jk}$ are the random intercepts for range $j$ and caribou $k$, respectively, and $\gamma_{nj}$ and $\gamma_{njk}$ are the respective random slopes (or coefficients) for range *j* and caribou *k* for covariate $x_n$. Note that the coefficients for random intercepts ($\gamma_{0j}$ and $\gamma_{0jk}$) represent the differences of range *j* and caribou *k* from $\beta_0$ while the random slope coefficients ($\gamma_{nj}$ and $\gamma_{njk}$) represent the differences of range *j* and caribou *k* from $\beta_n$. The fixed-effects, or marginal, coefficients ($\beta_n$) yield population-level inferences that can be interpreted within the classic use-availability design of

$$\omega(x_i) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n) \qquad \text{(Manly } et\ al.\text{ 2002)}$$

where $\omega(x_i)$ is the relative selection value of a sample unit (or pixel) in category *i* as a function of the explanatory covariates.

I used the conditional coefficients of the GLMMs – the random slopes estimated for each individual – to explicitly maintain individual caribou as the sampling unit when evaluating caribou response to specific covariates (Schielzeth & Forstmeier 2009). This approach is similar to two-stage RSF models where RSFs are estimated using logistic regression for each individual then population-level coefficients are generated by averaging across individuals (Fieberg *et al.* 2010). Two-stage RSF approaches, however, can be hampered when certain model coefficients cannot be estimated for all individuals (i.e. models fail to converge). GLMMs, in contrast, are less susceptible to this problem because they use information from the population to estimate coefficients for individuals where data are limited (Zuur *et al*. 2009). Statistical software and computing limitations constrain the number of random slopes that can be estimated in a given GLMM. I therefore estimated a suite of calving RSF models as follows, all with random intercepts for individual ranges and caribou:

i. A null model of no fixed-effects;

ii. A model with only fixed-effects specified (see below; hereafter the Random Intercept model);

iii. A Disturbance model where early seral vegetation, well site, and linear feature variables were specified as random slopes;

iv. A Water model where river and lake variables were specified as random slopes;

v. A Forage Quality model where NDVI was specified as the random slope;

vi. Three Landscape Context models where the following land cover types were specified as random slopes:

    a. Upland conifer and conifer swamp (hereafter, the Conifer model)
    b. Poor fen and rich fen (Fen model)
    c. Upland deciduous and deciduous swamp (Deciduous model)

For all models, the fixed-effects component of the model was the same, specifically:

*Land cover + slope + NDVI + river + lake + early seral + well site + line density*

Within this model structure, none of the explanatory variables were found to be significantly correlated (variance inflation factors < 2; Zuur *et al*. 2010). To better compare relative effect sizes, I standardized all variables before model fitting. For individuals calving in both 2011 and 2012, I pooled the data across years.

For other seasonal analyses and for analyses based on maternal status, I estimated the Disturbance, Water, Forage, and Landscape Context models only. I used the individual random slope coefficients – calculated as $\beta_n + \gamma_{njk}$ – in a paired design to evaluate differences in selection. For seasonal comparisons, I assessed the number of individuals whose selection coefficient increased during calving compared to selection coefficients estimated for the same set of individuals during other time periods. For females losing calves prior to four weeks of age, I determined the number whose selection coefficient was higher pre-loss versus post-loss. I evaluated the strength of selection differences (i.e. the number of individuals whose coefficient increased at calving) using binomial exact tests. I could not use a paired design for evaluating differences between barren females and calving females because of the 18 females that had data spanning two calving seasons, most calved in both seasons. I therefore compared the distributions of individual selection coefficients between calving and barren females and conducted Mann-Whitney U tests to determine whether selection differed between the two groups.

### *Assessing Model Performance*

I evaluated performance of the calving RSF models using AIC scores and *k*-fold cross-validation (Boyce *et al.* 2002). For cross validation, I specifically evaluated model performance for predicting calving areas within caribou range. To do so, I randomly partitioned the data by individual caribou into five folds, using four folds for model training then testing model predictions on the withheld individuals. For each test, I used the fixed-effects output from the training data to predict values for both the random locations generated within each range and the locations of the withheld caribou. I partitioned the predicted values of the range random points into 10 ordinal bins of equal number (i.e. deciles) then assessed model prediction by comparing the frequency of predicted values for withheld caribou falling within a bin to bin rank using Spearman's correlation coefficient ($r_s$; DeCesare *et al.* 2012). I repeated the *k*-fold process 30 times for each calving RSF model. The 30 tests were held constant across all models evaluated (i.e., the groups of training and testing data sets were constant for each calving RSF model evaluated). I calculated $\bar{r}_s$ for each model with higher $\bar{r}_s$ values indicating better predictive performance. I did not evaluate the performance of other seasonal RSF models as my motivation was not to develop predictive models outside of calving *per se* but rather to determine how individual- and population-level selection differed from calving.

All statistical analyses were performed in R, version 3.0.2 (R Core Team 2014). I used the R packages 'adehabitatHR' (Calenge 2006) to estimate UDs, 'lme4' (Bates *et al*. 2013) to estimate GLMMs and 'arm' to calculate standard errors of random slope coefficients (Gelman & Su 2013).

## RESULTS

I predicted 35 of the 46 female caribou to have calved in at least one year. Eighteen females had data sets spanning two seasons with 12 calving in both seasons, five calving in only one season and one was barren both seasons. Of the 35 calving females, 22 were predicted to have lost their calf prior to four weeks of age, including two females that lost calves in both years in which they calved.

### *Calving Habitat Selection*

I used the data from the 35 calving females to assess calving habitat selection. The most predictive scale of response for calving habitat selection varied among explanatory covariates (Appendix 4.3). For land cover, caribou selection was strongest at a radius of 1500-m. For linear feature density, the best scale was 400-m. For all other explanatory covariates evaluated (excluding NDVI and slope – see above), distance-to measures were stronger than density measures. Across the calving RSF models considered, a functional response in habitat selection by caribou was not supported as two-factor GLMMs – where herd range and individual caribou were specified as random intercepts – consistently ranked below one-factor models (random intercept for individual caribou only; Table 4.1). For the remaining analyses, I only consider one-factor RSF models for inference. Evaluating model performance by AIC, the top ranked model was Disturbance and all random slope models were ranked higher than the Random Intercept model. The Disturbance model, however, was not the top model for prediction, ranking fifth out of six models ($\bar{r}_s$ = 0.51). The best models for prediction were the Random Intercept ($\bar{r}_s$ = 0.77) and the Deciduous ($\bar{r}_s$ = 0.79). I was unable to estimate a Forage model using calving season data as this model would not statistically converge. Also, I dropped upland conifer as a random slope variable from the Conifer model as the model would not converge with upland conifer specified as a random slope because a large portion of caribou ($n$ = 17) had < 1% upland conifer within their calving UDs.

I used the random slope RSF models to specifically assess caribou response to individual covariates (Table 4.2). In general, caribou strongly avoided upland deciduous forests and situated their calving areas away from well sites, early seral vegetation, rivers and lakes. Caribou also avoided areas with high densities of linear features. Poor fen was the land cover most strongly selected while rich fen was selected at a rate similar to the reference category, treed bog. All other land covers were relatively avoided. Overall, female caribou showed considerable variation in calving habitat selection as many coefficients had 95% confidence intervals overlapping zero, although most intervals were directionally skewed toward either selection or avoidance. I further note that the magnitude of the population-level coefficient did not always correlate with the number of individuals associated with the direction of the coefficient. For example, the population-level coefficient for upland forest had the highest magnitude for avoidance (β = -5.20) yet four females had positive coefficients; conversely, the population-level coefficient for deciduous swamp showed a much lower magnitude of avoidance (β = -0.62) yet all females had negative coefficients.

Inferences gained from the analyses of individual random-slope covariates across model sets differed somewhat to inferences derived from the fixed-effect coefficients of the top AIC and predictive models (Table 4.3). First, effect sizes for a given variable were generally higher when it was specified as a random slope compared to models specifying it as a fixed-effect only. Second, 95% confidence intervals for random slope variables were considerably wider than the 95% confidence intervals for variables specified as fixed-effects only. Third, the coefficient direction (i.e., selection versus avoidance) changed for a few variables depending on the specifications of random-effects within the model. For land cover variables, a directional change equates to a change in the variables ranking relative to treed bog, the reference category.

Table 4.1: Performance of RSF models for assessing calving habitat selection of female boreal caribou in northeast BC from 2011-13. Akaike's Information Criterion (AIC) measures model parsimony while mean Spearman's rank correlation ($\overline{r_s}$) measures model predictive performance. Two-factor RSFs refer to models where herd range and individual caribou were specified as random intercepts while one-factor RSFs specified only individual caribou as a random intercept. Predictive performance ($\overline{r_s}$) was evaluated for one-factor RSF models only.

| Model | One-factor RSF AIC | Two-factor RSF AIC | $\overline{r_s}$ [1] |
|---|---|---|---|
| Null | 2606237 | 2606239 | n/a |
| Random Intercept | 2046717 | 2046719 | 0.77 |
| Disturbance | 1186310 | 1186330 | 0.51 |
| Forage | did not converge | did not converge | n/a |
| Water | 1531568 | 1531579 | 0.75 |
| Conifer | 1576912 | 1576917 | 0.61 |
| Fen | 1292386 | 1292397 | 0.37 |
| Deciduous | 1715288 | 1715301 | 0.79 |

[1] $\overline{r_s}$ for each model calculated from 30 tests (6 iterations of 5 folds) except for Deciduous (n=28) where 2 training sets failed to converge

Table 4.2: Fixed-effect coefficients, their 95% confidence intervals and the number of females with positive coefficients for the variables specified as random slopes in the suite of one-factor, random-slope GLMMs estimated for the calving season. Random slopes explicitly maintain the individual as the sampling unit and give a better representation of individual variability within the population.

| Model | Variable | β Estimate | 95% CI | Females (*n*=35) with Positive β 's |
|---|---|---|---|---|
| Disturbance | Dist. to early seral | 1.42 | -0.08, 2.92 | 26 |
| | Dist. to well site | 1.91 | 0.08, 3.74 | 33 |
| | Line density (400-m) | -0.86 | -1.79, 0.08 | 9 |
| Water | Dist. to river | 0.77 | 0.19, 1.36 | 32 |
| | Dist. to lake | 0.94 | -0.09, 1.96 | 31 |
| Conifer | Conifer swamp | -0.96 | -2.03, 0.12 | 10 |
| Fen | Poor fen | 1.31 | -0.38, 3.00 | 26 |
| | Rich fen | 0.05 | -1.49, 1.59 | 16 |
| Deciduous | Upland deciduous | -5.20 | -11.25, 0.85 | 4 |
| | Deciduous swamp | -0.62 | -1.20, -0.04 | 0 |

Table 4.3: Fixed-effect parameter estimates and their 95% confidence intervals (in brackets) for three one-factor GLMMs – the Random Intercept model, the Disturbance model, and the Deciduous model – for evaluating calving habitat selection by female boreal caribou in northeast British Columbia. The Disturbance model was the top model selected by AIC while the Deciduous model had the highest predictive power (see Table 2).

| | Model | | |
|---|---|---|---|
| Variable | Disturbance | Random Intercept | Deciduous |
| Conifer swamp | 0.03 | -0.11 | 0.19 |
| | (0.02, 0.04) | (-0.11, -0.10) | (0.19, 0.2) |
| Deciduous swamp | -0.39 | -0.50 | -0.62 |
| | (-0.39, -0.38) | (-0.51, -0.50) | (-1.20, -0.04) |
| Other | -0.55 | -0.47 | -0.50 |
| | -0.56, -0.55) | (-0.47, -0.46) | (-0.51, -0.50) |
| Poor fen | -0.22 | -0.10 | 0.33 |
| | (-0.23, -0.21) | (-0.10, -0.09) | (0.32, 0.34) |
| Rich fen | 0.53 | 0.56 | 0.84 |
| | (0.52, 0.54) | (0.56, 0.57) | (0.83, 0.84) |
| Upland conifer | 0.42 | 0.42 | 0.33 |
| | (0.41, 0.43) | (0.42, 0.43) | (0.32, 0.34) |
| Upland deciduous | -1.14 | -1.05 | -5.20 |
| | (-1.15, -1.13) | (-1.06, -1.04) | (-11.24, 0.84) |
| Slope | -0.24 | -0.16 | -0.10 |
| | (-0.25, -0.24) | (-0.16, -0.15) | (-0.10, -0.09) |
| NDVI | -0.02 | 0.11 | 0.15 |
| | (-0.03, -0.01) | (0.11, 0.12) | (0.14, 0.15) |
| Dist. to river | 0.24 | 0.33 | 0.32 |
| | (0.24, 0.25) | (0.32, 0.33) | (0.32, 0.33) |
| Dist. to lake | 0.25 | 0.16 | -0.01 |
| | (0.25, 0.26) | (0.15, 0.16) | (-0.02, -0.01) |
| Dist. to early seral | 1.42 | -0.20 | -0.25 |
| | (-0.08, 2.92) | (-0.20, -0.20) | (-0.26, -0.25) |
| Dist. to well | 1.91 | 0.19 | 0.25 |
| | (0.08, 3.74) | (0.18, 0.19) | (0.24, 0.25) |
| Line density | -0.86 | -0.12 | -0.06 |
| | (-1.79, 0.08) | (-0.12, -0.11) | (-0.07, -0.06) |

### *Seasonal Comparisons*

I compared calving habitat selection to the selection of other seasonal areas using 24 females for each comparison (Table 4.4, Appendix 4.4), a number reduced from the 35 above due to my criterion of excluding animals with seasonal fix rates <80% and because of differences in the timing of collar deployments and life spans of collar batteries. These factors also resulted in the set of 24 females differing for each comparison (i.e., the set of 24 used to compare calving to mid-winter was different than the set used to compare calving to late summer). Across all seasonal comparisons, the most consistent characteristics defining calving areas were relatively higher proportions of poor fens and lower densities of linear features. The relative selection or avoidance of other variables depended on the seasonal comparison. Comparing calving to mid-winter, female caribou showed relative selection for poor fens (23/24 individuals, $p < 0.001$ from binomial exact test) and moved into areas that were relatively lower in linear feature density (19/24, $p = 0.007$), higher in forage quality (20/24, $p = 0.002$) and closer to lakes (21/24, $p < 0.001$). Compared to late summer, calving females relatively selected both poor (19/24, $p = 0.007$) and rich fens (20/24, $p = 0.002$), were closer to lakes (23/24, $p < 0.001$) and avoided conifer swamps (18/24, $p = 0.02$), upland deciduous forests (24/24, $p < 0.001$) and areas higher in linear feature density (23/24, $p < 0.001$). Relative to late fall, females selected calving areas that had higher proportions of poor fens (22/24, $p < 0.001$), were lower in linear feature density (19/24, $p = 0.007$), and were situated farther from lakes (23/24, $p < 0.001$) and rivers (24/24, $p < 0.001$). Calving areas were also situated relatively closer to well sites (22/24, $p < 0.001$) and had lower proportions of upland deciduous forests (19/24, $p = 0.007$), conifer swamps (18/24, $p = 0.02$) and deciduous swamps (24/24, $p < 0.001$) than late fall areas.

Table 4.4: Relative seasonal differences in habitat selection by female boreal caribou in northeast British Columbia. Conditional coefficients of random-slope variables from calving RSF models were compared to coefficients derived from the same set of models estimated during other seasonal time periods. Listed numbers refer to the number of females that had a higher variable coefficient (i.e. relative selection) during calving compared to the other seasonal periods. Bold numbers refer to comparative differences where $p < 0.05$ from a binomial exact test.

| | | No. of Females with Relative Selection at Calving Versus: | | |
|---|---|---|---|---|
| Model | Variable | Mid Winter (*n* = 24) | Late Summer (*n* = 24) | Late Fall (*n* = 24) |
| Disturbance | Dist. to early seral [1] | 9 | 7 | 8 |
| | Dist. to well site | 10 | 17 | **2** |
| | Line density (400-m) | **5** | **1** | **5** |
| Water | Dist. to river | 15 | 10 | **24** |
| | Dist. to lake | **3** | **1** | **23** |
| Forage | NDVI | **20** | 17 | 9 |
| Conifer | Conifer swamp | 12 | **6** | **6** |
| Fen | Poor fen | **23** | **19** | **22** |
| | Rich fen | 9 | **20** | 9 |
| Deciduous | Upland deciduous | 17 | **0** | **5** |
| | Deciduous swamp | 13 | 8 | **0** |

[1] For distance-to variables, numbers refer to the number of individuals that were further way from the habitat element compared to the other time periods.

### *Maternal Status Comparisons*

The presence of a dependent calf also influenced female habitat selection during the calving season (Table 4.5, Appendix 4.4). Comparing areas used by females with calves ($n = 22$) to areas used by the same females after calf loss, the presence of a calf resulted in females selecting areas that were further away from early seral vegetation (21/22 individuals, $p < 0.001$ from binomial exact test), well sites (17/22, $p < 0.02$), rivers (17/22, $p < 0.02$) and lakes (20/22, $p < 0.001$). Females with calves also relatively avoided rich fens (20/22, $p < 0.001$), upland deciduous forests (20/22, $p < 0.001$), and deciduous swamps (22/22, $p < 0.001$). Compared to barren females ($n = 11$; Table 4.6), calving females (n = 35) selected for areas higher in proportion of poor and rich fens ($p < 0.002$ and $p < 0.01$, respectively, from Mann Whitney U tests), lower in linear feature density ($p < 0.004$) and that were situated further away from early seral vegetation ($p = 0.03$), well sites ($p < 0.001$), rivers ($p < 0.007$) and lakes ($p < 0.004$). Calving females also showed relatively stronger avoidance of upland deciduous forests ($p < 0.001$).

Table 4.5: Relative differences in habitat selection by female caribou based on calf status. Conditional coefficients of random-slope variables are compared from RSF models calculated pre- and post-calf loss for females losing calves prior to four weeks of age. Bold numbers refer to comparative differences where $p < 0.05$ from a binomial exact test.

| Model | Variable | No. of Females (*n* = 22) with Relative Selection Pre- versus Post-Calf Loss |
|---|---|---|
| Disturbance | Dist. to early seral | **21** |
| | Dist. to well site | **17** |
| | Line density (400-m) | 12 |
| Water | Dist. to river | **17** |
| | Dist. to lake | **20** |
| Forage | NDVI | 14 |
| Conifer | Conifer swamp | 5 |
| Fen | Poor fen | 6 |
| | Rich fen | **2** |
| Deciduous | Upland deciduous | **2**[1] |
| | Deciduous swamp | **0** |

[1] For upland hardwood, the sample size is 19 female caribou. Because of non-convergence with the original sample of 22, we removed three females that did not have upland hardwood in their utilization distributions.

Table 4.6: Relative differences in habitat selection between female boreal caribou with calves and barren females during the calving season in northeast British Columbia. The distributions of individual selection coefficients for covariates specified as random-effects in generalized linear mixed-effects models were compared between the two groups using Mann-Whitney U tests. The median coefficient value (β) for each group is presented for each covariate.

| | | Median β | | |
|---|---|---|---|---|
| Model | Variable | Calving (*n* = 35) | Barren (*n* = 11) | *p* |
| Disturbance | Dist. to early seral | 1.52 | 0.05 | 0.03 |
| | Dist. to well site | 2.30 | 0.51 | 0.001 |
| | Line density (400-m) | -1.82 | 0.22 | 0.004 |
| Water | Dist. to river | 1.07 | 0.17 | 0.007 |
| | Dist. to lake | 1.26 | -0.03 | 0.004 |
| Conifer | Conifer swamp | -1.79 | -1.25 | 0.86 |
| Fen | Poor fen | 2.29 | -0.75 | 0.002 |
| | Rich fen | -0.15 | -1.90 | 0.01 |
| Deciduous | Upland deciduous | -6.39 | -1.58 | < 0.001 |
| | Deciduous swamp | -0.83 | -1.29 | 0.19 |

## DISCUSSION

Developing effective conservation strategies for threatened and endangered species requires identifying key attributes of habitat critical to population persistence at scales amenable to regional planning (Apps *et al.* 2001; Gordon *et al.* 2004). The individual-based, comparative approach outlined here identified key characteristics of calving areas used by boreal caribou and this approach effectively discriminated calving areas from other areas within caribou range. Moreover, the use of seasonal and maternal status comparisons at the individual level allowed for an explicit evaluation of the relative strength of selection trends exhibited by females with neonate calves, trends that may not have been readily apparent in modelling approaches that only estimate population-level effects during the season of interest (Gillingham & Parker 2008b).

### *Calving Habitat Selection by Female Caribou*

In general, reducing predation risk appeared to be a dominant factor driving female selection of calving areas. Across most seasonal and maternal status comparisons, females with neonate calves consistently avoided habitat types associated with increasing predation risk, such as upland deciduous forests (McLoughlin *et al.* 2005) and areas of natural and anthropogenic disturbance (Rettie & Messier 1998; Latham *et al.* 2011b). Predation risk has been suggested to be an important driver of caribou behaviour during reproduction (Bergerud *et al.* 1984; Bergerud 1992) with boreal caribou dispersing – or 'spacing out' (*sensu* Bergerud & Page 1987) to avoid predator encounters (*Chapter 3*). Within this dispersion strategy, my results indicate that females select calving areas that likely further reduce the probability of predator encounter. Moreover, the predator avoidance strategy of calving females is evident at relatively large spatial scales (i.e., second-order selection). With predation considered to be the primary factor limiting boreal caribou populations (Rettie & Messier 1998; McLoughlin *et al.* 2003; Festa-Bianchet *et al.* 2011) and the main cause of calf mortality (Pinard *et al.* 2012; Dussault *et al.* 2012), the response of caribou at this scale is consistent with the hypothesis that broad-scale selection should reflect important factors limiting individual fitness (Rettie & Messier 2000).

Across the resources I assessed, the response of calving females was strongest for upland deciduous forests, which were avoided presumably because of their high predation risk (McLoughlin *et al.* 2005). Effect sizes for this variable were consistently among the highest within the top calving RSF models (Table 4.3) and there was a large difference in the strength of avoidance between calving and barren females (Table 4.6). Only when comparing winter ranges to calving did a majority of females show relative selection for this habitat type. This seasonal difference in selection, however, is likely a result of females shifting from winter ranges dominated by large peatland complexes to more mosaic-type landscapes in the spring and I note that within this seasonal comparison no females showed absolute selection (i.e., a positive coefficient) for upland deciduous forest during calving (Appendix 4.4). Although avoidance of deciduous forests was strong in my system, this behaviour does not seem to be consistent across the distribution of boreal caribou. In eastern Canada, females selected for upland deciduous forest when calving (Pinard *et al.* 2012; Dussault *et al.* 2012). This plasticity in habitat selection is likely due to topography-driven differences in predation risk (Lima & Dill 1990; Forstmeier & Weiss 2004; Creel *et al.* 2005). In these eastern studies, the landscapes had more topographic relief than our study area, with females selecting higher elevation deciduous forests presumably to avoid valley bottoms frequented by wolves (Pinard *et al.* 2012; Lesmerises *et al.* 2012). In much of our study system, topographic relief is minimal with uplands often separated by < 10 m in elevation change from peatlands.

A similar east-west dichotomy in habitat selection occurs when assessing caribou response to lakes. Calving females in my study area relatively avoided lakeshore habitats, a finding corroborated by the raw use data where < 7% of GPS locations for females with neonate calves were within 500-m of a lake and < 20% were within 1-km (C. DeMars, *unpublished data*). This result contrasts with other studies from eastern Canada where caribou used lakeshores and islands for calving (Bergerud 1985; Carr *et al.* 2011; Dupont 2014). In my system, the avoidance of lakes by calving females may be another behaviour linked to reducing predation risk. Many lakes in my study area were inhabited by beaver (*Castor canadensis*), which become a primary prey item of wolves in the spring and summer (Latham et al. 2013b) and as such may lead to high use of lakeshores by wolves. Further, the effectiveness of lakes as escape terrain may be limited in my study area because the majority of lakes are devoid of islands and relatively shallow (e.g < 10-m mean depth; Prepas *et al.* 2001).

The avoidance of areas representing increased predation risk was also evident in female response to anthropogenic features. Females generally avoided well sites and areas of high linear feature density. Caribou avoidance of anthropogenic features has previously been documented (Dyer *et al.* 2001; DeCesare *et al.* 2012; Leblond *et al.* 2013) and females have been shown to select calving sites away from roads and cut blocks (Leclerc *et al.* 2012). Based on my comparative analyses, avoidance of these features intensifies when a female is accompanied by a neonate calf. This avoidance results in a functional loss of calving habitat

(Dyer *et al*. 2001). Moreover, in highly modified landscapes, this avoidance response could negatively impact the spatial dispersion strategy of calving females (Bergerud & Page 1987), potentially resulting in females becoming increasingly clumped, and hence more predictable to predators (Fortin *et al.* 2013). Maintaining functional calving habitat within caribou range will therefore require management strategies that focus on restoring highly impacted areas in addition to conserving existing low-impact areas.

While my analyses indicate that predation risk is an important driver of calving area selection, forage quality and/or quantity may still factor into female selection of calving areas. Females appeared to shift from winter ranges comprised of lichen-rich bogs to landscapes with a higher proportion of poor fens at calving and the selective response for poor fens was consistent across other seasonal and maternal status comparisons. Relative to bogs, poor fens have higher primary productivity due to a higher abundance of sedges and shrubs (Thormann & Bayley 1997). This shift from bogs to fens likely accounted for the high number of females showing selection for calving areas with higher NDVI values relative to winter ranges. Calving females may therefore be moving to areas with higher forage quality to meet maternal nutritional demands (Parker *et al*. 2009). By making this shift, females may be trading off an increase in predation risk to access higher quality forage because fens provide less of a predator refuge than bogs (Latham *et al.* 2011a, 2013a). Increasing predation rates of caribou in the snow-free season have been linked to increasing spatial overlap between caribou and predators during this time period (Latham *et al.* 2011a, 2013b). This hypothesis has been primarily based upon studies assessing seasonal habitat shifts of predators. My results suggest that increasing spatial overlap between caribou and predators may also be driven by a habitat shift by caribou, at least during the calving season.

By making multiple seasonal and maternal comparisons at the individual level, I detected distinct trends in the selection of calving areas by female caribou. Across the population, however, females displayed considerable variation in calving area selection as reflected by the relatively wide 95% confidence intervals of the random-slope variables – with a few overlapping zero – and the predictive performance of the calving RSF models. This variation is consistent with studies of calving habitat selection by boreal caribou in eastern Canada – where calving RSF models yielded $r_s$ values < 0.80 (Dussault *et al.* 2012; Leclerc *et al.* 2012) – and for the northern ecotype of woodland caribou in northeast British Columbia (Gustine *et al.* 2006). Two mechanisms may account for individual variation in the selection of calving areas. First, individual variation may be an outcome of density dependent selection at calving. Parturient females disperse away from other females at calving (Bergerud 1992; *Chapter 3*) and the absence of other females may be a key constraint in the selection of calving areas. This constraint may directly result in variation of habitat features associated with calving areas. A second explanation is that individual variation may be a further life history strategy of caribou for reducing predator encounters. By preventing predators from associating calving areas with certain habitat types, behavioural plasticity in calving area selection may make females and their calves more unpredictable to predators (Mitchell & Lima 2002; Miner *et al.* 2005).

### *Evaluating Resource Selection Functions*

Generalized linear mixed-effects models have become an increasingly popular statistical approach for estimating RSFs in habitat selection studies, primarily for their utility in dealing with hierarchically clustered data (Gillies *et al.* 2006; Fieberg *et al.* 2010; Moreau *et al.* 2012). In many such studies, the hierarchical clustering is accounted for by specifying a random intercept for individual animals then interpreting the fixed-effect coefficients to assess resource selection at the population-level. With this model specification, ‘used’ and ‘available’ locations are pooled across individuals to estimate covariate effects, yielding standard errors for fixed-effect estimates that do not explicitly reflect the individual animal as the sampling unit (Schielzeth & Forstmeier 2009). In our analysis, 95% confidence intervals were extremely narrow when covariates were specified as fixed-effects only. When these same covariates were specified as random slopes, 95% confidence intervals were much wider and gave a more realistic evaluation of inter-individual variation within the population. Computing power and statistical software currently limits the number of random slopes that can be specified within a given model; however, for RSF studies utilizing GLMMs, my approach of estimating multiple random-slope models represents a viable way for thoroughly evaluating inter-individual variability within GLMMs.

My comparative approach also yielded new insights into evaluating the performance of RSF models. For most RSF studies using GPS data, a ‘use versus available’ design is employed and model parameters are estimated using logistic regression (Boyce & McDonald 1999; Johnson *et al.* 2006). The primary method for evaluating predictive performance of this type of RSF model is *k*-fold cross-validation (Boyce *et al.* 2002; Johnson *et al.* 2006). The majority of such studies, however, only evaluate the predictive performance of the top model selected through an information-theoretic (IT) process (e.g., AIC or Bayesian Information Criterion [BIC]). This standard evaluative process implies that model quality as determined by IT criterion is more important than model prediction and that the top model as ranked by IT criterion will necessarily be the best for prediction. My results clearly indicate that there is trade-off between IT model selection and prediction when evaluating RSF models, particularly in studies using large data sets. From a management perspective, fully evaluating model prediction may be as or more important than determining the top IT selected model for the data at hand.

The sole reliance on IT criteria for selecting a top model in RSF studies becomes increasingly problematic when samples sizes become large (e.g. > 1,000 per animal). In the typical regression analyses used in RSF studies, the individual GPS fix or animal location is statistically considered to be the sample unit, which results in large sample sizes that impact the ability of IT criterion to discriminate between model fit and model complexity. This issue is not overcome by two-stage RSF approaches (e.g., Sawyer *et al.* 2006; Nielsen *et al.* 2009) where separate regression analyses are conducted on individual animals because the number of fixes per animal is generally large. With increasingly large sample sizes, significant effects will be detected for even relatively uninformative variables (*sensu* Arnold 2010) and the penalties applied by IT criterion for these extra variables are relatively small. For example, in my study AIC values were >1,000,000, making the 2 point penalty for an extra parameter seem trivial and the use of BIC, which applies a penalty based on the natural log of the sample size, does little to overcome this problem. As a consequence, the most complex model is selected as the top model by IT criterion in many RSF studies using large sample sizes (e.g., Latham *et al.* 2011a).

Moreover, incorporating model uncertainty by calculating model-averaged parameter estimates (Burnham & Anderson 2002) is frequently not possible because the top ranked model has an AIC weight at or near 1.0.

In my study where sample sizes were large, the most complex model – the Disturbance model – was selected as the top model by AIC yet it had considerably less predictive power than the less complex Deciduous model. This difference in prediction was likely driven by the differences in the relative strengths (i.e., effect sizes) of the variables specified as random slopes. Caribou response was strongest to upland hardwoods (avoidance) with all individuals having negative coefficients for this variable. In contrast, effect sizes for the disturbance variables were smaller and consistent selection or avoidance across individual caribou was not evident for any of these variables.

I note that using *k*-fold cross-validation as the sole evaluative technique for RSF models is also problematic. For boreal caribou, a simple model with a binary habitat variable describing the land base as peatland or otherwise would likely have high predictive power. This simplistic model, however, would be inadequate for discriminating calving habitat from other seasonal ranges and ignores other environmental attributes that may have a strong influence on determining calving habitat. For habitat selection studies using an RSF modelling approach, I therefore recommend developing a plausible set of candidate models and evaluating this model set by both IT criterion and a measure of prediction (e.g. *k*-fold cross-validation) so that trade-offs between model discrimination and prediction can be explicitly evaluated.

## LITERATURE CITED

Apps, C.D., McLellan, B.N., Kinley, T.A. & Flaa, J.P. (2001). Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *The Journal of Wildlife Management*, **65**, 65–77.

Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management*, **74**, 1175–1178.

Barbknecht, A.E., Fairbanks, W.S., Rogerson, J.D., Maichak, E.J., Scurlock, B.M. & Meadows, L.L. (2011). Elk parturition site selection at local and landscape scales. *The Journal of Wildlife Management*, **75**, 646–654.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. http://CRAN.R-project.org/package=lme4

Benson, J.F. (2013). Improving rigour and efficiency of use-availability habitat selection analyses with systematic estimation of availability. *Methods in Ecology and Evolution*, **4**, 244-251.

Bergerud, A.T. (1985). Antipredator strategies of caribou: dispersion along shorelines. *Canadian Journal of Zoology*, **63**, 1324–1329.

Bergerud, A.T. (1992). Rareness as an antipredator strategy to reduce predation risk for moose and caribou. In: *Wildlife 2001: Populations*, D. McCullough & R.H. Barrett (editors). Springer Netherlands. 1164 pp.

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

Bergerud, A.T., Ferguson, R. & Butler, H.E. (1990). Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour*, **39**, 360–368.

Bergerud, A.T., Luttich, S.N. & Camps, L. (2008). *The return of caribou to Ungava*. McGill-Queen's University Press, Montreal, QC & Kingston, ON. 586 pp.

Bjørneraas, K., Van Moorter, B., Rolandsen, C.M. & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *The Journal of Wildlife Management*, **74**, 1361–1366.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1–28.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393–1405.

Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. & Maier, J.A. (1999). Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy*, **80**, 1070–1083.

Boyce, M.S. (2006). Scale for resource selection functions. *Diversity and Distributions*, **12**, 269–276.

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

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

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theorectic approach*, 2nd ed. Springer, New York, NY. 515 pp.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516-519.

Carr, N.L., Rodgers, A.R., Kingston, S.R. & Lowman, D.J. (2011). Use of island and mainland shorelines by woodland caribou during the nursery period in two northern Ontario parks. *Rangifer*, **31**, 49–61.

Creel, S., Winnie Jr, J., Maxwell, B., Hamlin, K. & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.

Crouse, D.T., Crowder, L.B. & Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68**, 1412.

DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., Bradley, M., Whittington, J., Smith, K.G. & Morgantini, L.E. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, **22**, 1068–1083.

Dupont, D.J. (2014). *Calving ground habitat selection of boreal woodland caribou (Rangifer tarandus caribou) in the Owl-Flintstone range*. M.Sc. thesis. University of Manitoba, Winnipeg, MB.

Dussault, C., Pinard, V., Ouellet, J.-P., Courtois, R. & Fortin, D. (2012). Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4481–4488.

Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S. (2001). Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management*, **65**, 531–542.

Dzialak, M.R., Harju, S.M., Osborn, R.G., Wondzell, J.J., Hayden-Wing, L.D., Winstead, J.B. & Webb, S.L. (2011). Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PLoS ONE*, **6**, e14597.

Edmonds, E.J. (1988). Population status, distribution, and movements of woodland caribou in west central Alberta. *Canadian Journal of Zoology*, **66**, 817–826.

Environment Canada. (2008). *Scientific review for the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Environment Canada, Ottawa, ON. 72 pp. plus 180 pp. appendices.

Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H. & Dussault, C. (2010). Range fidelity: The missing link between caribou decline and habitat alteration? *Biological Conservation*, **143**, 2840–2850.

Festa-Bianchet, M. (1988). Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**, 580–586.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D. & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology*, **89**, 419–434.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2233–2244.

Forstmeier, W. & Weiss, I. (2004). Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, **104**, 487–499.

Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Tye Gingras, C., Moorcroft, P.R., Courtois, R. & Dussault, C. (2013). Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. *The American Naturalist*, **181**, 827–836.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gelman, A. & Su, Y-S. (2013). arm: Data analysis using regression and multilevel/hierarchical models. R package version 1.6-10. http://CRAN.R-project.org/package=arm.

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

Gillingham, M.P. & Parker, K.L. (2008a). Differential habitat selection by moose and elk in the Besa-Prophet area of northern British Columbia. *Alces*, **44**, 41–63.

Gillingham, M.P. & Parker, K.L. (2008b). The importance of individual variation in defining habitat selection by moose in northern British Columbia. *Alces*, **44**, 7–20.

Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004). Review: the management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, **41**, 1021–1031.

Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Gustine, D.D. & Parker, K.L. (2008). Variation in the seasonal selection of resources by woodland caribou in northern British Columbia. *Canadian Journal of Zoology*, **86**, 812–825.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.

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

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

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. *The Journal of Wildlife Management*, **70**, 347–357.

Kerr, J.T. & Deguise, I. (2004). Habitat loss and the limits to endangered species recovery. *Ecology Letters*, **7**, 1163–1169.

Kinley, T.A. & Apps, C.D. (2001). Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Society Bulletin*, **29**, 158–164.

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

Latham, A.D.M., Latham, M.C., Boyce, M.S. & Boutin, S. (2011b). 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., Boyce, M.S. & Boutin, S. (2013a). Spatial relationships of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) with woodland caribou (*Rangifer tarandus caribou*) during the calving season in a human-modified boreal landscape. *Wildlife Research*, **40**, 250.

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

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

Leblond, M., Frair, J., Fortin, D., Dussault, C., Ouellet, J.-P. & Courtois, R. (2011). Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. *Landscape Ecology*, **26**, 1433–1446.

Leclerc, M., Dussault, C. & St-Laurent, M.-H. (2014). Behavioural strategies towards human disturbances explain individual performance in woodland caribou. *Oecologia*, **176**, 297–306.

Leclerc, M., Dussault, C. & St-Laurent, M.-H. (2012). Multiscale assessment of the impacts of roads and cutovers on calving site selection in woodland caribou. *Forest Ecology and Management*, **286**, 59–65.

Lesmerises, F., Dussault, C. & St-Laurent, M.-H. (2012). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management*, **276**, 125–131.

Levin, S. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. *Ecology*, **73**, 1943–1967.

Lewis, J.S., Rachlow, J.L., Garton, E.O. & Vierling, L.A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology*, **44**, 663–671.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Manly, B.F.J., McDonald, L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*, 2nd ed. Kluwere Academic Publishers, New York, NY. 221 pp.

Matthiopoulos, J., Hebblewhite, M., Aarts, G. & Fieberg, J. (2011). Generalized functional responses for species distributions. *Ecology*, **92**, 583–589.

McLoughlin, P.D., Dunford, J.S. & Boutin, S. (2005). Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology*, **74**, 701–707.

McLoughlin, P.D., Dzus, E., Wynes, B.O.B. & Boutin, S. (2003). Declines in populations of woodland caribou. *The Journal of Wildlife Management*, **67**, 755–761.

McLoughlin, P.D., Wal, E.V., Lowe, S.J., Patterson, B.R. & Murray, D.L. (2011). Seasonal shifts in habitat selection of a large herbivore and the influence of human activity. *Basic and Applied Ecology*, **12**, 654–663.

Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K. & Relyea, R.A. (2005). Ecological consequences of phenotypic plasticity. *Trends in Ecology & Evolution*, **20**, 685–692.

Mitchell, W.A. & Lima, S.L. (2002). Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos*, **99**, 249–259.

Moilanen, A., Franco, A.M.., Early, R.I., Fox, R., Wintle, B. & Thomas, C.D. (2005). Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1885–1891.

Moreau, G., Fortin, D., Couturier, S. & Duchesne, T. (2012). Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests: *Functional responses for wildlife conservation*. *Journal of Applied Ecology*, **49**, 611–620.

Morellet, N., Verheyden, H., Angibault, J.-M., Cargnelutti, B., Lourtet, B. & Hewison, M.A.J. (2009). The effect of capture on ranging behaviour and activity of the European roe deer (*Capreolus capreolus*). *Wildlife Biology*, **15**, 278–287.

Mysterud, A. & Ims, R.A. (1998). Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*, **79**, 1435–1441.

Nagy, J.A. (2011). *Use of space by caribou in northern Canada*. Ph.D. thesis. University of Alberta, Edmonton, AB.

Naidoo, R., Balmford, A., Ferraro, P., Polasky, S., Ricketts, T. & Rouget, M. (2006). Integrating economic costs into conservation planning. *Trends in Ecology & Evolution*, **21**, 681–687.

Nepstad, D.C., Boyd, W., Stickler, C.M., Bezerra, T. & Azevedo, A.A. (2013). Responding to climate change and the global land crisis: REDD+, market transformation and low-emissions rural development. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **368**, 20120167–20120167.

Newbold, S.C. & Siikamaki, J. (2009). Prioritizing conservation activities using reserve site selection methods and population viability analysis. *Ecological Applications*, **19**, 1774–1790.

Nielsen, S.E., Cranston, J. & Stenhouse, G.B. (2009). Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *Journal of Conservation Planning*, **5**, 38–60.

Northrup, J.M., Hooten, M.B, Anderson Jr., C.R., & Wittemyer. (2013). Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, **94**, 1456-1463.

Panzacchi, M., Herfindal, I., Linnell, J.D.C., Odden, M., Odden, J. & Andersen, R. (2010). Trade-offs between maternal foraging and fawn predation risk in an income breeder. *Behavioral Ecology and Sociobiology*, **64**, 1267–1278.

Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D. & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, **76**, 189–199.

Poole, K.G., Serrouya, R. & Stuart-Smith, K. (2007). Moose calving strategies in interior montane ecosystems. *Journal of Mammalogy*, **88**, 139–150.

Prepas, E.E., Planas, D., Gibson, J.J., Vitt, D.H., Prowse, T.D., Dinsmore, W.P., Halsey, L.A., McEachern, P.M., Paquet, S., Scrimgeour, G.J., Tonn, W.M., Paszkowski, C.A. & Wolfstein, K. (2001). Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1286–1299.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rachlow, J.L. & Bowyer, R.T. (1998). Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology*, **245**, 457–465.

Rearden, S.N., Anthony, R.G. & Johnson, B.K. (2011). Birth-site selection and predation risk of Rocky Mountain elk. *Journal of Mammalogy*, **92**, 1118–1126.

Rettie, W.J. & Messier, F. (1998). Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology*, **76**, 251–259.

Rettie, W.J. & Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.

Sawyer, H., Nielson, R.M., Lindzey, F. & McDonald, L. (2006). Winter habitat selection by mule deer before and during development of a natural gas field. *The Journal of Wildlife Management*, **70**, 396–403.

Schaefer, J.A., Bergman, C.M. & Luttich, S.N. (2000). Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology*, **15**, 731–739.

Schielzeth, H. & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioural Ecology*, **20**, 416-420.

Schneider, R.R., Hauer, G., Dawe, K., Adamowicz, W. & Boutin, S. (2012). Selection of reserves for woodland caribou using an optimization approach. *PLoS ONE*, **7**, e31672.

Singh, N.J., Grachev, I.A., Bekenov, A.B. & Milner-Gulland, E.J. (2010). Saiga antelope calving site selection is increasingly driven by human disturbance. *Biological Conservation*, **143**, 1770–1779.

Stuart-Smith, K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M. & Rippin, A.B. (1997). Woodland caribou relative to landscape patterns in northeastern Alberta. *The Journal of Wildlife Management*, **61**, 622–633.

Suzuki, R., Kobayashi, H., Delbart, N., Asanuma, J. & Hiyama, T. (2011). NDVI responses to the forest canopy and floor from spring to summer observed by airborne spectrometer in eastern Siberia. *Remote Sensing of Environment*, **115**, 3615–3624.

Thormann, M.N. & Bayley, S.E. (1997). Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecology*, **131**, 1–16.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J. & Musiani, M. (2011). Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *Journal of Applied Ecology*, **48**, 1535–1542.

Wittmer, H.U., Mclellan, B.N., Serrouya, R. & Apps, C.D. (2007). Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology*, **76**, 568–579.

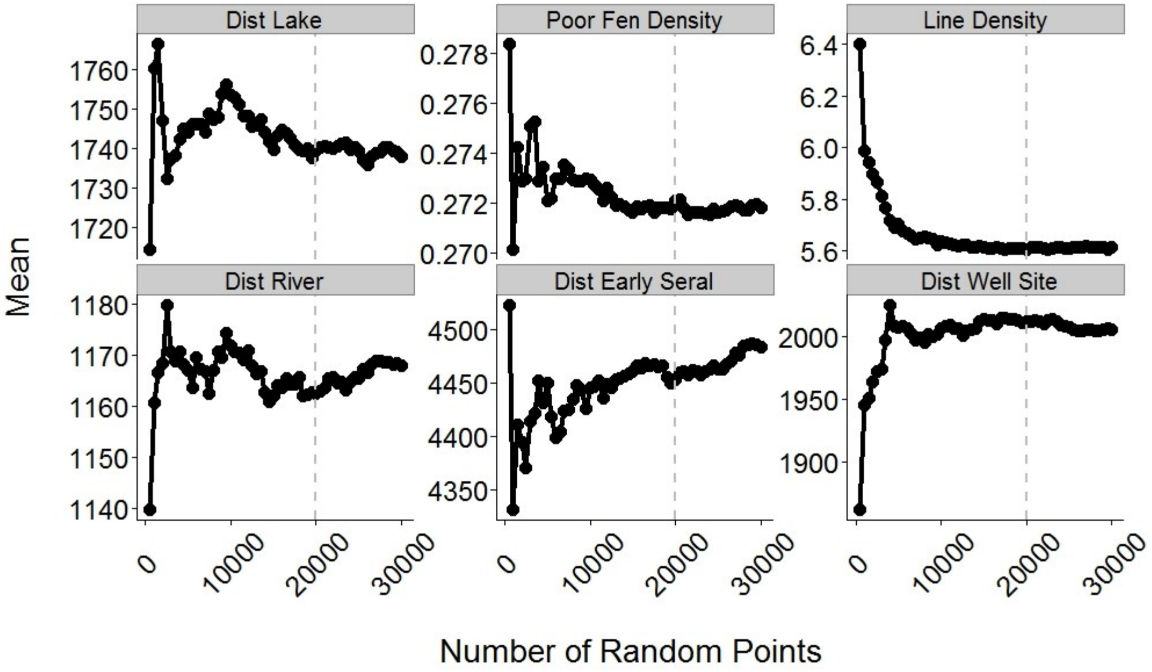
Zager, P. & Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus*, **17**, 95–108.

Zuur, A.F., Ieno, E., & 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., Ieno, E., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York, NY. 574 pp.

## APPENDIX 4.1: RANDOM POINT SENSITIVITY ANALYSIS

To assess habitat selection by female boreal caribou, I first conducted sensitivity analyses to determine the number of random points required to adequately characterize availability at the range scale (see main text). Fifty thousand random points were generated within the largest range of our study area (the Snake-Sahtaneh range) then the pixel values of GIS resource variables were extracted to these points. I calculated the mean value of each resource first using 500 points then at 1,000 point intervals from 1,000 to 50,000. The figure below represents sensitivity analyses on 6 resource variables used in habitat selection modelling (x-axis is truncated at 30,000). Because mean values for each variable remained unchanged (i.e., varied < 1%) after 20,000 points (grey dashed line), I used this number of random points to characterize availability in all habitat selection analyses.



## APPENDIX 4.2: GIS DATA SOURCES

The following two tables outline the GIS variables and data sources used for modelling habitat selection by female boreal caribou in northeast British Columbia.

Table A4.2. 1: Classification of land cover types used to model resource selection by boreal caribou in northeastern BC. Land cover types were developed from Ducks Unlimited Enhanced Wetlands Classification data clipped to the study area.

| Land cover | EWC Class | Description |
|---|---|---|
| **Treed bog** | Treed bog, Open bog, Shrubby bog | Black spruce and *Spaghnum* moss dominated bogs with no hydrodynamic flow. Areal coverage: ~20% |
| **Nutrient-poor fen** | Graminoid poor fen,<br>Shrubby poor fen,<br>Treed poor fen | Low nutrient peatland soils influenced by groundwater flows. Treed poor fens dominate, comprised of black spruce, tamarack and bog birch (25-60% tree cover). Areal coverage: ~22% |
| **Nutrient-rich fen** | Graminoid rich fen,<br>Shrubby rich fen,<br>Treed rich fen | Low nutrient peatland soils influenced by groundwater flows. Shrubby fens dominate, comprised of bog birch, willow and alder. Areal coverage: ~4% |
| **Conifer swamp** | Conifer swamp | Tree cover >60% dominated by black or white spruce. Occur on peatland or mineral soils. Areal coverage: ~9% |
| **Hardwood swamp** | Shrub swamp,<br>Hardwood swamp<br>Mixed-wood swamp | Mineral soils with pools of water often present. Dominant deciduous tree species: paper birch and balsam poplar. Areal coverage: ~14% |
| **Upland conifer** | Upland conifer | Mineral soils with tree cover >25%. Dominant tree species: black spruce, white spruce and pine. Areal coverage: ~5% |
| **Upland deciduous** | Upland deciduous,<br>Mixed-wood upland | Mineral soils with tree cover >25%. Dominant deciduous tree species: aspen and paper birch. Areal coverage: ~20% |
| **Other** | Upland other,<br>Cloud shadow,<br>Anthropogenic, Burn,<br>Aquatic | Uplands: mineral soils with tree cover <25%.<br>Anthropogenic: urban areas, roads and cut blocks.<br>Burns: vegetation is limited or covered by burn<br>Aquatic: includes a continuum of aquatic classes from low turbidity lakes to emergent marshes where aquatic vegetation is >20% of the cover.<br>Total areal coverage: ~6% (Cloud shadow <0.5%) |

Table A4.2.2: List of data sources used to model resource covariates for resource selection analyses of female boreal caribou in northeast British Columbia.

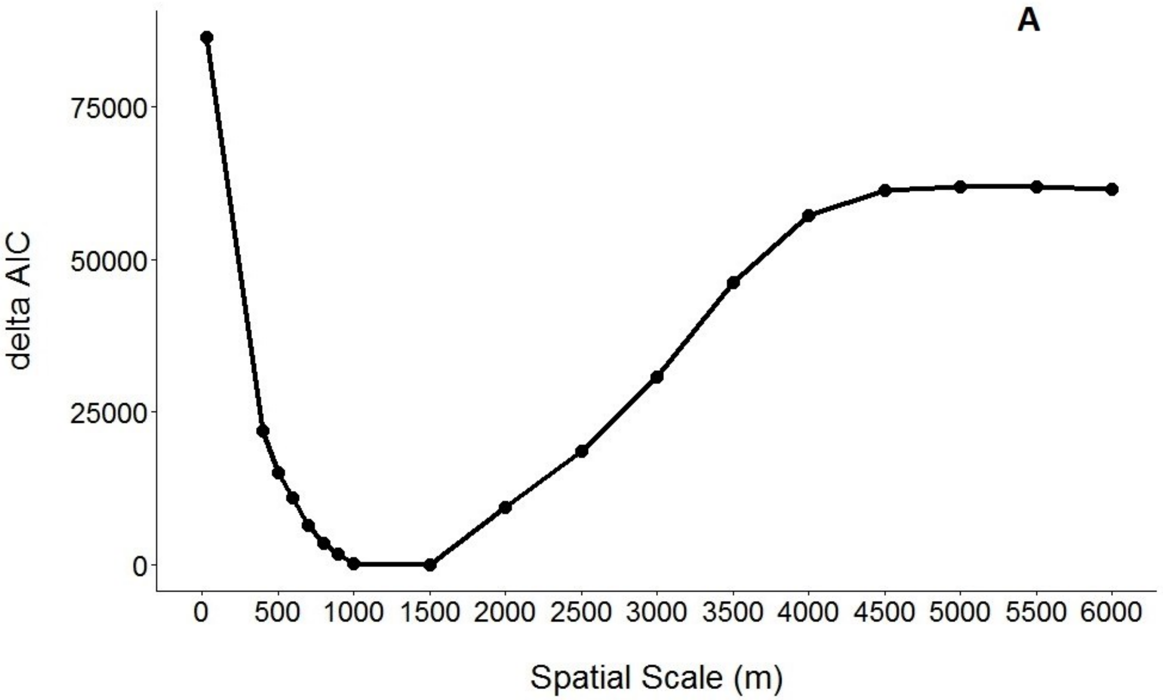
| Variable | Source | Access Information |
|---|---|---|
| **Land Cover** | Ducks Unlimited Canada | Ducks Unlimited Canada<br>100, 17958 106 Ave, Edmonton, AB T5S 1V4 |
| **Forest Structure** | Vegetation Resource Inventory, BC Ministry of Forests, Lands and Natural Resource Operations | https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=47574&recordSet=ISO19115 |
| **Rivers, Lakes** | Digital Baseline Mapping, BC Integrated Land Management Bureau, Geographic Data Discovery Service | https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=3679&recordSet=ISO19115 |
| **Forest Fire History** | Fire Perimeters – Historical, , BC Integrated Land Management Bureau (ILMB), Geographic Data Discovery Service | http://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=57060&recordSet=ISO19115 |
| **Cut Blocks** | Forest Tenure Cut Block Polygons, BC Ministry of Forests, Lands and Natural Resource Operations | https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=50580&recordSet=ISO19115 |
| **Pipelines** | BC Oil and Gas Commission | ftp://www.bcogc.ca/outgoing/OGC_Data/Pipelines/ |
| **OGC Seismic Lines** | BC Oil and Gas Commission | ftp://www.bcogc.ca/outgoing/OGC_Data/Geophysical/ |
| **Major Roads** | Digital Baseline Mapping, BC ILMB, Geographic Data Discovery Service | https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=3679&recordSet=ISO19115 |
| **Forestry Roads** | Forest Tenure As-Built Roads, BCGOV FOR Resource Tenures and Engineering | https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=45694&recordSet=ISO19115 |
| **Other Secondary Roads** | BC Oil and Gas Commission | ftp://www.bcogc.ca/outgoing/OGC_Data/Roads/ |
| **Well Sites** | BC Oil and Gas Commission | ftp://www.bcogc.ca/outgoing/OGC_Data/Wells/ |
| **TRIM Lines** | TRIM miscellaneous annotation, BC Integrated Land Management Bureau, Geographic Data Discovery Service | https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=4105&recordSet=ISO19115 |
| **NDVI** | U.S. National Aeronautics and Space Administration MODIS database | http://modis.gsfc.nasa.gov/data/dataprod/dataproducts.php?MOD_NUMBER=13 |

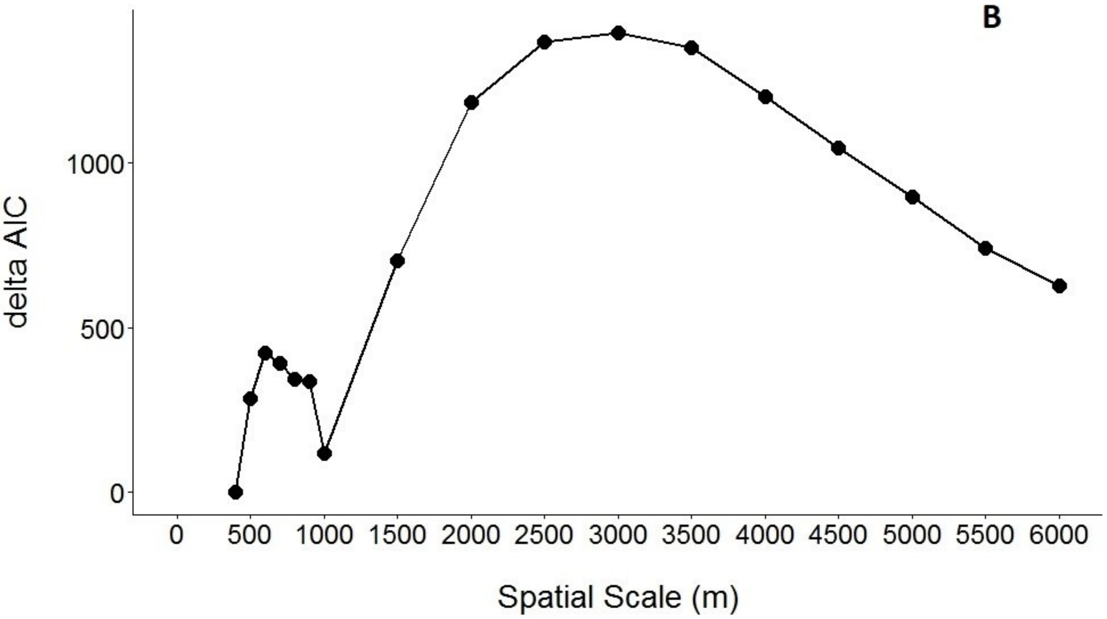
## APPENDIX 4.3: SPATIAL SCALE OF RESPONSE ANALYSES

I used repeated univariate logistic regression models to identify the most predictive scale of response for resource covariates used in habitat selection modelling of female boreal caribou (Leblond *et al.* 2011; DeCesare *et al.* 2012). For each analysis, I compared random points generated within 80% utilization distributions (UDs) of calving areas to random points generated with each herd's range (see main chapter). In all analyses, I pooled the data across individual caribou and across individual ranges. I tested spatial scales ranging from 400-m to 1,000-m in 100-m increments then from 1,000-m to 6,000-m, the radii of the largest calving UD, in 500-m increments. Values for each spatial scale were in calculated in moving window analyses centred on each 30-m pixel within the study area. Thus, the models took the form

$$\text{Logit(U)} \sim \beta_0 + \beta_1 x_i$$

where Logit(U) is the logit transformation of the binary response variable describing a calving or range random point, $\beta_0$ is the intercept, and $\beta_1$ is the coefficient of covariate $x$ at spatial scale $i$. The scale with the lowest AIC value was selected as the best predictor for each covariate. In the figures below, I show analyses for land cover (A) and linear feature density (B). For land cover, I also test the individual pixel scale (left uppermost point). Delta AIC refers to the difference in AIC values between a given spatial scale and the best predictive scale.


A
delta AIC
75000
50000
25000
0
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
5500
6000
Spatial Scale (m)


B
delta AIC
1000
500
0
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
5500
6000
Spatial Scale (m)

*Literature Cited:*

DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., Bradley, M., Whittington, J., Smith, K.G. & Morgantini, L.E. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, **22**, 1068–1083.

Leblond, M., Frair, J., Fortin, D., Dussault, C., Ouellet, J.-P. & Courtois, R. (2011). Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. *Landscape Ecology*, **26**, 1433–1446.

## APPENDIX 4.4: HABITAT SELECTION BY FEMALE BOREAL CARIBOU BASED ON SEASON AND MATERNAL STATUS

The following tables list the conditional – or individual-level – parameter estimates for variables specified as random slope variables in generalized linear mixed-effect models (see main text) used to model habitat selection by female boreal caribou. All estimates are calculated as $\beta_n + \gamma_{nj}$, where $\beta_n$ is the population-level slope for covariate $x_n$ and $\gamma_{nj}$ is the difference of the random slope for caribou *j* from $\beta_n$. Bold numbers indicate comparisons in which 95% confidence intervals overlapped (*n* = 1; see Table A4.19). Tables A4.1 – A4.6 are individual parameter estimates for mid-winter and calving, Tables A4.7 – A4.12 are estimates for late summer and calving, Tables A4.13 – A4.18 are estimates for late fall and calving, and Tables A4.19 – A4.24 are estimates for females with calves and females after calf loss.

Table A4.4. 1: Conditional parameter estimates for variables specified as random slopes in the Disturbance model for individual female caribou in mid-winter and calving.

| | Dist. to Early Seral | | Dist. to Well | | Line Density | |
|---|---|---|---|---|---|---|
| Animal ID | Mid-Winter | Calving | Mid-Winter | Calving | Mid-Winter | Calving |
| D030308 | -2.42 | -1.82 | -0.65 | -1.15 | -1.70 | -3.58 |
| D030309 | -1.07 | 0.51 | -1.26 | 0.61 | -0.83 | -9.54 |
| D030310 | -2.75 | -5.37 | -0.65 | 0.88 | -1.78 | -3.04 |
| D030312 | -2.31 | -8.62 | -1.59 | -0.84 | 0.02 | 0.18 |
| D030314 | 1.23 | -1.34 | -1.26 | 0.21 | -0.43 | -8.13 |
| D030316 | -2.30 | -2.42 | -1.20 | -0.61 | -0.15 | -0.96 |
| D030318 | -2.22 | -3.37 | -0.46 | -1.45 | 0.21 | -1.45 |
| D030319 | -2.15 | -5.41 | -1.14 | -3.45 | -0.97 | -5.11 |
| D030320 | -1.66 | -0.72 | -0.76 | -1.87 | -0.65 | -2.02 |
| D030321 | 0.44 | 1.00 | 0.12 | -0.11 | -0.21 | -0.31 |
| D030324 | -1.39 | -1.11 | -1.03 | -1.31 | -1.87 | -3.75 |
| D030325 | -1.67 | -4.83 | -0.56 | -0.53 | -0.81 | -3.94 |
| D030326 | -0.72 | -4.16 | -0.52 | -2.09 | -0.74 | -1.46 |
| D030327 | 0.41 | -1.54 | 0.68 | 0.50 | 0.54 | -3.25 |
| D030328 | -2.53 | -2.04 | 1.06 | -1.53 | -2.08 | -6.83 |
| D030329 | -2.03 | -2.55 | -1.24 | 1.64 | -0.95 | 1.07 |
| D030330 | -2.04 | -2.65 | -0.61 | -0.86 | -1.14 | -2.43 |
| D030331 | -1.65 | -4.14 | -0.52 | -1.36 | -0.76 | -4.23 |
| D030332 | -0.87 | 0.71 | -1.17 | -4.32 | -0.74 | 0.13 |
| D031237 | -1.25 | -0.51 | -0.66 | -3.19 | -2.61 | 1.88 |
| D031716 | -1.31 | -2.69 | -0.48 | -0.36 | -2.04 | -2.62 |
| D031726 | -1.60 | -3.89 | -2.73 | -0.90 | -1.33 | -3.51 |
| D031734 | -2.21 | -3.15 | -0.87 | -1.12 | -2.61 | -2.57 |
| D031748 | -3.61 | -1.30 | -2.53 | -0.46 | -2.09 | -3.05 |

Table A4.4. 2: Conditional parameter estimates for variables specified as random slopes in the Water model for individual female caribou in mid-winter and calving.

| | Dist. to River | | Dist. to Lake | |
|---|---|---|---|---|
| Animal ID | Mid-Winter | Calving | Mid-Winter | Calving |
| D030308 | 1.27 | 0.62 | 2.77 | 3.27 |
| D030309 | 0.17 | 1.18 | 4.36 | 0.75 |
| D030310 | 2.48 | 1.42 | 3.63 | 0.81 |
| D030312 | 0.37 | 0.10 | 4.61 | 0.17 |
| D030314 | 0.70 | 2.90 | 5.42 | 3.12 |
| D030316 | 1.51 | 0.08 | 3.48 | 2.13 |
| D030318 | 0.52 | 0.68 | 4.23 | 0.23 |
| D030319 | 1.58 | 0.87 | 3.47 | 0.30 |
| D030320 | 1.12 | 0.59 | 3.20 | 1.60 |
| D030321 | 0.46 | 2.44 | 3.66 | 0.39 |
| D030324 | 0.46 | -0.01 | 3.63 | 1.84 |
| D030325 | 0.16 | 3.40 | 5.29 | 14.70 |
| D030326 | 0.29 | 1.32 | 4.29 | 0.43 |
| D030327 | 0.42 | 0.62 | 3.72 | 0.81 |
| D030328 | 0.79 | 1.70 | 5.91 | 5.18 |
| D030329 | 1.21 | 1.08 | 3.99 | 1.01 |
| D030330 | 0.46 | 2.92 | 4.49 | 0.59 |
| D030331 | 0.14 | 0.72 | 5.29 | 3.07 |
| D030332 | 0.19 | 4.22 | 4.41 | 1.47 |
| D031237 | 0.27 | 6.13 | 3.22 | 2.25 |
| D031716 | 0.08 | 0.30 | 3.63 | 1.49 |
| D031726 | 0.82 | 1.34 | 4.68 | 8.61 |
| D031734 | 0.11 | 1.29 | 24.72 | 2.54 |
| D031748 | 1.96 | 0.44 | 7.65 | 4.69 |

Table A4.4. 3: Conditional parameter estimates for variables specified as random slopes in the Forage model for individual female caribou in mid-winter and calving.

| | NDVI | |
|---|---|---|
| Animal ID | Mid-Winter | Calving |
| D030308 | -3.02 | 0.44 |
| D030309 | -1.49 | 0.60 |
| D030310 | -2.68 | -0.04 |
| D030312 | 0.15 | 0.68 |
| D030314 | -0.80 | -1.08 |
| D030316 | -1.29 | 0.28 |
| D030318 | -0.51 | -1.10 |
| D030319 | -2.47 | 0.07 |
| D030320 | -3.17 | -1.55 |
| D030321 | -1.66 | -0.53 |
| D030324 | -2.09 | -2.20 |
| D030325 | 0.76 | 1.32 |
| D030326 | -1.64 | 0.69 |
| D030327 | -1.99 | 0.64 |
| D030328 | 0.05 | 0.85 |
| D030329 | -0.50 | 0.56 |
| D030330 | 0.08 | 0.26 |
| D030331 | 0.80 | 0.90 |
| D030332 | -1.42 | -1.66 |
| D031237 | -4.01 | -1.51 |
| D031716 | -4.45 | -1.41 |
| D031726 | -1.07 | 1.45 |
| D031734 | -0.83 | 0.90 |
| D031748 | -2.72 | 0.61 |

Table A4.4. 4: Conditional parameter estimates for variables specified as random slopes in the Conifer model for individual female caribou in mid-winter and calving.

| | Conifer Swamp | |
|---|---|---|
| Animal ID | Mid-Winter | Calving |
| D030308 | -2.05 | 0.55 |
| D030309 | -0.07 | -3.54 |
| D030310 | -1.58 | -0.87 |
| D030312 | -0.82 | -3.86 |
| D030314 | 0.62 | -2.37 |
| D030316 | -0.76 | 0.14 |
| D030318 | -1.58 | -6.42 |
| D030319 | -1.43 | -1.03 |
| D030320 | -5.47 | 0.52 |
| D030321 | -0.51 | -3.54 |
| D030324 | -2.77 | -4.13 |
| D030325 | 0.05 | 2.60 |
| D030326 | -0.34 | 0.79 |
| D030327 | -1.72 | 0.33 |
| D030328 | -0.49 | -2.96 |
| D030329 | -0.71 | -2.74 |
| D030330 | 1.01 | -0.20 |
| D030331 | 0.13 | -2.06 |
| D030332 | -0.18 | -5.46 |
| D031237 | -3.03 | 3.70 |
| D031716 | -2.63 | -4.70 |
| D031726 | -0.48 | 2.46 |
| D031734 | 0.70 | 1.16 |
| D031748 | -1.20 | 0.75 |

Table A4.4. 5: Conditional parameter estimates for variables specified as random slopes in the Fen model for individual female caribou in mid-winter and calving.

| | Poor Fen | | Rich Fen | |
|---|---|---|---|---|
| Animal ID | Mid-Winter | Calving | Mid-Winter | Calving |
| D030308 | 0.64 | 3.45 | -0.66 | -3.51 |
| D030309 | -0.94 | 0.77 | -0.54 | -0.83 |
| D030310 | 0.62 | 3.04 | -0.79 | -0.60 |
| D030312 | -2.66 | -0.09 | 0.10 | 1.36 |
| D030314 | -0.91 | 7.61 | -1.36 | -1.44 |
| D030316 | -1.67 | 3.63 | 0.71 | 0.34 |
| D030318 | -3.48 | -0.64 | 0.52 | 0.69 |
| D030319 | 0.22 | 3.42 | -0.65 | -0.68 |
| D030320 | 0.86 | 3.70 | 0.27 | -4.31 |
| D030321 | -1.49 | 4.28 | 0.77 | 0.95 |
| D030324 | -3.31 | -1.70 | 1.18 | 4.06 |
| D030325 | -1.70 | 3.92 | 0.02 | -0.93 |
| D030326 | -0.85 | 2.87 | -0.37 | -3.19 |
| D030327 | -1.33 | 4.18 | 0.43 | 1.70 |
| D030328 | -2.32 | 1.09 | -1.67 | -16.20 |
| D030329 | -2.42 | 2.63 | 0.59 | 1.51 |
| D030330 | -0.83 | 2.32 | 0.51 | -0.08 |
| D030331 | -1.64 | 0.58 | -0.03 | -9.76 |
| D030332 | -0.98 | 10.89 | -0.62 | 2.86 |
| D031237 | -3.80 | 6.38 | 1.78 | -2.74 |
| D031716 | -3.35 | -4.59 | 1.36 | 3.19 |
| D031726 | -0.45 | 4.00 | -0.66 | -1.40 |
| D031734 | -1.21 | 2.46 | -0.45 | -0.90 |
| D031748 | 0.39 | 4.03 | 0.05 | -5.34 |

Table A4.4. 6: Conditional parameter estimates for variables specified as random slopes in the Deciduous model for individual female caribou in mid-winter and calving.

| | Deciduous Swamp | | Upland Deciduous | |
|---|---|---|---|---|
| Animal ID | Mid-Winter | Calving | Mid-Winter | Calving |
| D030308 | -1.30 | -1.61 | -5.66 | -1.02 |
| D030309 | -1.01 | -0.23 | -2.75 | -0.41 |
| D030310 | -1.91 | -3.01 | -5.43 | -0.74 |
| D030312 | -2.28 | -0.86 | -1.15 | -3.45 |
| D030314 | -2.55 | -1.03 | -1.99 | -1.73 |
| D030316 | -1.19 | -1.68 | -2.89 | -1.74 |
| D030318 | -2.04 | -2.70 | -1.33 | -0.55 |
| D030319 | -2.29 | -1.61 | -3.55 | -1.75 |
| D030320 | -2.69 | -1.75 | -14.35 | -2.43 |
| D030321 | -0.48 | -0.16 | -2.59 | -1.77 |
| D030324 | -2.37 | -0.81 | -3.84 | -2.62 |
| D030325 | -1.11 | -1.86 | -1.38 | -2.45 |
| D030326 | -0.80 | -1.75 | -2.63 | -1.22 |
| D030327 | -2.47 | -0.89 | -1.66 | -2.18 |
| D030328 | -1.59 | -7.76 | -0.74 | -1.49 |
| D030329 | -0.88 | -1.78 | -1.78 | -1.18 |
| D030330 | -0.78 | -0.55 | -2.32 | -1.25 |
| D030331 | -1.15 | -6.93 | -1.42 | -1.80 |
| D030332 | -1.10 | -0.87 | -2.57 | -7.21 |
| D031237 | -2.55 | -1.77 | -5.25 | -1.85 |
| D031716 | -2.66 | -0.56 | -4.97 | -1.20 |
| D031726 | -0.53 | -0.85 | -1.68 | -1.90 |
| D031734 | -0.75 | -0.85 | -2.56 | -0.59 |
| D031748 | -4.49 | -1.03 | -4.64 | -1.67 |

Table A4.4. 7: Conditional parameter estimates for variables specified as random slopes in the Disturbance model for individual female caribou in late summer and calving.

| | Dist. to Early Seral | | Dist. to Well | | Line Density | |
|---|---|---|---|---|---|---|
| Animal ID | Late Summer | Calving | Late Summer | Calving | Late Summer | Calving |
| D030308 | -4.73 | -1.69 | -3.34 | -0.79 | -2.16 | -3.84 |
| D030309 | -0.51 | 0.56 | -0.18 | 1.21 | -1.14 | -9.06 |
| D030310 | -3.87 | -5.18 | -0.06 | 1.39 | -1.25 | -3.21 |
| D030311 | -0.64 | -2.23 | -0.73 | -2.67 | 2.79 | 1.12 |
| D030312 | -1.99 | -7.30 | -1.68 | 0.00 | 0.73 | 0.06 |
| D030313 | -0.77 | -0.54 | 0.05 | 1.20 | -2.40 | -7.91 |
| D030314 | -0.77 | -1.37 | -0.32 | 0.77 | -0.27 | -8.84 |
| D030316 | -1.09 | -2.50 | -0.19 | 0.07 | 3.44 | -1.07 |
| D030318 | -1.41 | -2.81 | -0.19 | -0.53 | 0.55 | -1.41 |
| D030319 | -2.30 | -5.23 | -1.11 | -3.39 | -1.76 | -5.27 |
| D030321 | 1.74 | 1.11 | -0.34 | 0.48 | 0.72 | -0.36 |
| D030324 | -1.65 | -1.17 | -1.38 | -0.50 | 0.60 | -3.86 |
| D030325 | -1.88 | -4.80 | -0.08 | 0.14 | -0.96 | -4.18 |
| D030327 | -1.90 | -1.34 | 1.16 | 1.14 | -1.92 | -3.38 |
| D030329 | -1.54 | -2.66 | -1.02 | 2.46 | 2.05 | 1.10 |
| D030331 | -2.36 | -4.25 | -0.41 | -0.67 | -1.42 | -5.01 |
| D030931 | -2.53 | -8.30 | 1.69 | 1.70 | 0.01 | -0.77 |
| D031237 | 0.02 | -0.45 | -1.88 | -2.64 | 4.31 | 2.09 |
| D031716 | -1.27 | -2.87 | -1.25 | 0.43 | -1.67 | -2.73 |
| D031726 | -1.47 | -3.92 | 0.26 | -0.22 | -0.20 | -3.77 |
| D031727 | 0.42 | 2.44 | -2.18 | 3.23 | 1.69 | -4.96 |
| D031734 | -1.56 | -3.18 | -1.00 | -0.48 | -0.67 | -2.84 |
| D031737 | 0.90 | -0.74 | -3.61 | -1.76 | -0.52 | -3.17 |
| D031738 | 1.02 | 1.29 | 1.25 | 5.29 | -0.24 | 0.02 |

Table A4.4. 8: Conditional parameter estimates for variables specified as random slopes in the Water model for individual female caribou in late summer and calving.

| | Dist. to River | | Dist. to Lake | |
|---|---|---|---|---|
| Animal ID | Late Summer | Calving | Late Summer | Calving |
| D030308 | 0.99 | 0.68 | 109.24 | 2.97 |
| D030309 | 1.16 | 1.23 | 8.83 | 0.50 |
| D030310 | 1.24 | 1.47 | 13.04 | 0.67 |
| D030311 | 2.04 | 8.25 | 11.37 | -0.38 |
| D030312 | 0.70 | 0.15 | 9.11 | -0.02 |
| D030313 | 0.59 | 0.19 | 8.69 | 0.94 |
| D030314 | 0.89 | 3.14 | 9.01 | 2.81 |
| D030316 | 0.59 | 0.22 | 10.07 | 1.90 |
| D030318 | 1.08 | 0.76 | 9.07 | 0.15 |
| D030319 | 0.90 | 1.07 | 8.87 | 0.08 |
| D030321 | 1.97 | 2.57 | 9.16 | 0.27 |
| D030324 | 1.66 | 0.15 | 8.84 | 1.70 |
| D030325 | 1.10 | 3.49 | 10.79 | 14.60 |
| D030327 | 1.00 | 0.70 | 9.12 | 0.56 |
| D030329 | 1.57 | 1.20 | 9.77 | 0.76 |
| D030331 | 1.21 | 0.87 | 40.16 | 3.35 |
| D030931 | 2.03 | 2.55 | 9.96 | 3.21 |
| D031237 | 19.56 | 6.52 | 9.93 | 2.11 |
| D031716 | 1.88 | 0.47 | 8.97 | 1.31 |
| D031726 | 1.42 | 1.44 | 9.18 | 8.38 |
| D031727 | 1.54 | -0.39 | 8.85 | -2.76 |
| D031734 | 1.60 | 1.31 | 10.30 | 2.46 |
| D031737 | 0.71 | 3.49 | 8.78 | -3.09 |
| D031738 | 1.57 | -0.17 | 9.21 | 0.10 |

Table A4.4. 9: Conditional parameter estimates for variables specified as random slopes in the Forage model for individual female caribou in late summer and calving.

| | NDVI | |
|---|---|---|
| Animal ID | Late Summer | Calving |
| D030308 | 1.49 | 0.66 |
| D030309 | -0.85 | 0.89 |
| D030310 | -0.43 | 0.28 |
| D030311 | -0.14 | -0.59 |
| D030312 | 0.62 | 0.98 |
| D030313 | -1.07 | -0.89 |
| D030314 | -0.77 | -1.09 |
| D030316 | -1.31 | 0.81 |
| D030318 | 0.46 | -0.72 |
| D030319 | 0.06 | 0.37 |
| D030321 | -1.02 | -0.18 |
| D030324 | -0.96 | -1.94 |
| D030325 | 0.34 | 1.97 |
| D030327 | -0.14 | 0.97 |
| D030329 | -0.10 | 1.09 |
| D030331 | 0.49 | 1.33 |
| D030931 | -2.94 | -4.77 |
| D031237 | -1.63 | -1.39 |
| D031716 | -2.26 | -1.18 |
| D031726 | -0.82 | 2.17 |
| D031727 | -0.95 | 6.03 |
| D031734 | 0.60 | 1.32 |
| D031737 | 0.42 | 1.61 |
| D031738 | -1.13 | -2.43 |

Table A4.4. 10: Conditional parameter estimates for variables specified as random slopes in the Conifer model for individual female caribou in late summer and calving.

| | Conifer Swamp | |
|---|---|---|
| Animal ID | Late Summer | Calving |
| D030308 | 2.20 | 1.08 |
| D030309 | -0.12 | -2.74 |
| D030310 | 1.59 | -0.17 |
| D030311 | 1.58 | 0.23 |
| D030312 | -2.16 | -2.93 |
| D030313 | -3.35 | -1.84 |
| D030314 | 0.32 | -1.83 |
| D030316 | 0.52 | 0.45 |
| D030318 | -2.62 | -5.10 |
| D030319 | 0.32 | -0.48 |
| D030321 | -0.85 | -3.12 |
| D030324 | 0.27 | -3.42 |
| D030325 | 0.68 | 2.59 |
| D030327 | 0.94 | 0.54 |
| D030329 | 0.67 | -2.27 |
| D030331 | -0.41 | -1.59 |
| D030931 | 0.05 | -3.17 |
| D031237 | 2.44 | 3.86 |
| D031716 | 0.36 | -4.25 |
| D031726 | 0.16 | 2.55 |
| D031727 | -0.57 | 2.12 |
| D031734 | 0.77 | 1.37 |
| D031737 | 2.25 | -1.39 |
| D031738 | -1.50 | -4.07 |

Table A4.4. 11: Conditional parameter estimates for variables specified as random slopes in the Fen model for individual female caribou in late summer and calving.

| | Poor Fen | | Rich Fen | |
|---|---|---|---|---|
| Animal ID | Late Summer | Calving | Late Summer | Calving |
| D030308 | 1.01 | 2.70 | -5.39 | -2.71 |
| D030309 | -0.37 | 0.17 | 0.20 | 0.47 |
| D030310 | 2.28 | 2.29 | -3.58 | 0.34 |
| D030311 | 1.24 | 7.10 | -4.92 | -1.45 |
| D030312 | -3.69 | -0.78 | -0.04 | 2.65 |
| D030313 | -4.84 | -4.10 | 1.28 | 4.76 |
| D030314 | -0.24 | 6.45 | -0.73 | -0.49 |
| D030316 | 0.43 | 2.74 | -0.65 | 1.52 |
| D030318 | -2.26 | -1.15 | -0.47 | 1.93 |
| D030319 | 1.16 | 2.76 | 0.54 | 0.24 |
| D030321 | -0.05 | 3.40 | 0.28 | 2.24 |
| D030324 | -1.37 | -2.50 | 0.00 | 5.57 |
| D030325 | 0.04 | 3.04 | -0.02 | 0.21 |
| D030327 | -0.46 | 3.39 | 0.00 | 3.03 |
| D030329 | -0.53 | 1.77 | -0.99 | 2.77 |
| D030331 | -2.01 | -0.10 | -7.78 | -9.65 |
| D030931 | -1.41 | -1.75 | -4.74 | -3.48 |
| D031237 | 0.21 | 5.68 | -1.54 | -1.93 |
| D031716 | -1.49 | -5.63 | -0.53 | 4.92 |
| D031726 | -0.67 | 3.03 | -0.13 | -0.30 |
| D031727 | 0.43 | -0.67 | -0.10 | 4.55 |
| D031734 | -1.23 | 1.78 | -0.92 | 0.30 |
| D031737 | -2.87 | -3.13 | -1.67 | -0.56 |
| D031738 | 1.39 | 8.80 | 0.87 | 10.23 |

Table A4.4. 12: Conditional parameter estimates for variables specified as random slopes in the Deciduous model for individual female caribou in late summer and calving.

| | Deciduous Swamp | | Upland Deciduous | |
|---|---|---|---|---|
| Animal ID | Late Summer | Calving | Late Summer | Calving |
| D030308 | 2.25 | -1.47 | -4.95 | -7.42 |
| D030309 | 0.45 | -0.20 | -2.68 | -6.80 |
| D030310 | -1.94 | -2.73 | -2.97 | -6.96 |
| D030311 | -0.24 | -0.64 | -1.95 | -8.55 |
| D030312 | -0.87 | -0.77 | -1.12 | -9.23 |
| D030313 | -1.86 | -1.33 | -2.70 | -7.91 |
| D030314 | -0.75 | -0.82 | -1.97 | -7.95 |
| D030316 | -1.12 | -1.48 | -3.13 | -7.88 |
| D030318 | 0.00 | -2.11 | -1.22 | -6.67 |
| D030319 | 0.58 | -1.65 | -3.17 | -8.45 |
| D030321 | 0.71 | 0.00 | -2.16 | -7.92 |
| D030324 | -0.84 | -0.70 | -2.03 | -8.38 |
| D030325 | -0.39 | -1.69 | -2.24 | -8.43 |
| D030327 | -0.53 | -0.77 | -1.33 | -8.15 |
| D030329 | -0.15 | -1.55 | -1.39 | -7.37 |
| D030331 | -5.68 | -6.77 | -2.02 | -8.30 |
| D030931 | -4.28 | -3.73 | -12.64 | -130.79 |
| D031237 | -1.19 | -1.53 | -1.83 | -7.92 |
| D031716 | -1.14 | -0.41 | -1.78 | -7.16 |
| D031726 | -0.40 | -0.68 | -2.37 | -7.93 |
| D031727 | -0.88 | -0.44 | -1.99 | -6.95 |
| D031734 | -0.17 | -0.75 | -0.67 | -6.73 |
| D031737 | -0.50 | 1.05 | -0.80 | -10.23 |
| D031738 | -0.37 | 0.65 | -1.89 | -24.33 |

Table A4.4. 13: Conditional parameter estimates for variables specified as random slopes in the Disturbance model for individual female caribou in late fall and calving.

| | Dist. to Early Seral | | Dist. to Well | | Line Density | |
|---|---|---|---|---|---|---|
| Animal ID | Late Fall | Calving | Late Fall | Calving | Late Fall | Calving |
| D030308 | -0.68 | -1.47 | -0.88 | -1.21 | -1.63 | -3.51 |
| D030309 | -0.37 | 0.91 | 0.40 | 0.71 | -0.65 | -9.49 |
| D030310 | -1.09 | -5.43 | 0.99 | 0.93 | -1.00 | -3.13 |
| D030311 | -1.50 | -1.80 | -0.04 | -3.00 | 2.93 | 1.04 |
| D030312 | -0.96 | -7.39 | -0.39 | -0.64 | 0.28 | 0.31 |
| D030313 | -0.55 | -0.12 | 0.44 | 0.86 | -1.67 | -8.06 |
| D030314 | -1.40 | -1.04 | -0.26 | 0.29 | -0.36 | -8.03 |
| D030315 | -0.44 | 0.84 | -0.68 | 0.85 | -0.40 | -2.15 |
| D030316 | -1.07 | -2.22 | -0.17 | -0.56 | 0.44 | -0.76 |
| D030318 | -1.10 | -3.01 | -0.57 | -1.20 | -0.04 | -1.28 |
| D030319 | -1.48 | -5.37 | -0.66 | -3.48 | -1.13 | -4.84 |
| D030320 | -0.15 | -0.32 | -0.87 | -1.88 | -0.64 | -1.74 |
| D030321 | -0.69 | 1.18 | 0.02 | -0.03 | -0.05 | -0.18 |
| D030324 | -0.76 | -0.79 | -0.05 | -1.31 | 0.33 | -3.68 |
| D030325 | -1.57 | -4.75 | -0.24 | -0.46 | -1.30 | -3.98 |
| D030326 | -1.44 | -4.00 | -0.26 | -2.06 | -0.35 | -1.35 |
| D030327 | -0.58 | -1.31 | 0.17 | 0.72 | 0.51 | -3.23 |
| D030328 | -1.92 | -1.77 | 0.52 | -1.46 | -1.33 | -6.50 |
| D030329 | -1.13 | -2.27 | -0.17 | 1.73 | 0.61 | 1.27 |
| D030330 | -1.37 | -2.41 | -0.34 | -0.84 | -0.91 | -2.25 |
| D030331 | -1.45 | -3.88 | -0.74 | -1.31 | -1.12 | -4.00 |
| D030332 | -0.82 | 0.85 | -0.18 | -4.08 | -0.24 | 0.24 |
| D031237 | -1.00 | -0.22 | -0.42 | -3.43 | 0.44 | 2.14 |
| D031238 | -0.54 | -1.18 | -0.58 | 0.65 | -0.06 | 3.22 |

Table A4.4. 14: Conditional parameter estimates for variables specified as random slopes in the Water model for individual female caribou in late fall and calving.

| | Dist. to River | | Dist. to Lake | |
|---|---|---|---|---|
| Animal ID | Late Fall | Calving | Late Fall | Calving |
| D030308 | 0.07 | 0.87 | -0.52 | 3.02 |
| D030309 | -0.17 | 1.44 | -0.75 | 0.39 |
| D030310 | 0.58 | 1.67 | -1.39 | 0.57 |
| D030311 | 0.07 | 7.83 | 1.12 | -0.36 |
| D030312 | -0.34 | 0.36 | -0.46 | -0.12 |
| D030313 | 0.22 | 0.35 | -0.33 | 0.73 |
| D030314 | -0.22 | 3.23 | -0.63 | 2.68 |
| D030315 | -0.13 | 2.41 | -0.38 | 3.75 |
| D030316 | -0.08 | 0.38 | -0.02 | 1.71 |
| D030318 | -0.12 | 0.92 | -0.42 | -0.08 |
| D030319 | 0.04 | 1.15 | -0.84 | -0.05 |
| D030320 | -0.20 | 0.85 | -0.09 | 1.27 |
| D030321 | -0.16 | 2.59 | -0.69 | 0.08 |
| D030324 | 0.11 | 0.22 | -0.42 | 1.52 |
| D030325 | -0.15 | 3.78 | -0.07 | 14.81 |
| D030326 | -0.21 | 1.54 | -0.53 | 0.08 |
| D030327 | -0.11 | 0.88 | -0.43 | 0.46 |
| D030328 | 0.03 | 1.99 | -0.11 | 4.77 |
| D030329 | -0.13 | 1.39 | 0.01 | 0.64 |
| D030330 | -0.01 | 3.28 | -0.01 | 0.26 |
| D030331 | -0.12 | 1.01 | 0.55 | 2.71 |
| D030332 | -0.12 | 4.20 | -0.73 | 1.08 |
| D031237 | 0.01 | 6.26 | -0.41 | 1.95 |
| D031238 | 0.04 | 1.34 | -0.48 | 2.70 |

Table A4.4. 15: Conditional parameter estimates for variables specified as random slopes in the Forage model for individual female caribou in late fall and calving.

| | NDVI | |
|---|---|---|
| Animal ID | Late Fall | Calving |
| D030308 | 0.32 | 0.33 |
| D030309 | 0.59 | 0.48 |
| D030310 | -0.50 | -0.06 |
| D030311 | -0.58 | -0.76 |
| D030312 | 0.93 | 0.42 |
| D030313 | 0.00 | -1.26 |
| D030314 | 0.26 | -1.16 |
| D030315 | 0.25 | -1.77 |
| D030316 | 0.44 | 0.27 |
| D030318 | 0.54 | -1.10 |
| D030319 | 0.19 | -0.02 |
| D030320 | 0.11 | -1.54 |
| D030321 | 0.45 | -0.62 |
| D030324 | 0.34 | -2.26 |
| D030325 | -0.37 | 1.22 |
| D030326 | 0.21 | 0.59 |
| D030327 | 0.34 | 0.54 |
| D030328 | 0.40 | 0.73 |
| D030329 | 0.42 | 0.50 |
| D030330 | -0.28 | 0.13 |
| D030331 | 0.15 | 0.80 |
| D030332 | 0.24 | -1.53 |
| D031237 | 0.16 | -1.37 |
| D031238 | 0.27 | 0.00 |

Table A4.4. 16: Conditional parameter estimates for variables specified as random slopes in the Conifer model for individual female caribou in late fall and calving.

| | Conifer Swamp | |
|---|---|---|
| Animal ID | Late Fall | Calving |
| D030308 | -0.12 | 0.21 |
| D030309 | -0.65 | -3.76 |
| D030310 | -1.49 | -1.04 |
| D030311 | 0.13 | -0.53 |
| D030312 | -1.14 | -3.73 |
| D030313 | -1.23 | -2.85 |
| D030314 | -0.38 | -2.58 |
| D030315 | -0.26 | -6.20 |
| D030316 | 0.11 | -0.15 |
| D030318 | -1.67 | -6.38 |
| D030319 | -0.58 | -1.39 |
| D030320 | 0.47 | 0.20 |
| D030321 | -0.53 | -3.62 |
| D030324 | -0.05 | -4.55 |
| D030325 | 0.36 | 2.30 |
| D030326 | -0.32 | 0.44 |
| D030327 | -1.09 | -0.01 |
| D030328 | 0.45 | -3.26 |
| D030329 | 0.19 | -3.03 |
| D030330 | 0.42 | -0.50 |
| D030331 | 0.49 | -2.39 |
| D030332 | -0.31 | -5.25 |
| D031237 | 0.41 | 2.94 |
| D031238 | -0.13 | -0.57 |

Table A4.4. 17: Conditional parameter estimates for variables specified as random slopes in the Fen model for individual female caribou in late fall and calving.

| | Poor Fen | | Rich Fen | |
|---|---|---|---|---|
| Animal ID | Late Fall | Calving | Late Fall | Calving |
| D030308 | -0.02 | 4.23 | 0.11 | -3.30 |
| D030309 | -0.65 | 1.41 | 1.38 | -0.66 |
| D030310 | 1.58 | 3.74 | 0.74 | -0.56 |
| D030311 | 2.28 | 8.08 | 2.29 | -2.16 |
| D030312 | -2.14 | 0.99 | 0.73 | 1.44 |
| D030313 | -1.42 | -3.28 | 1.62 | 3.64 |
| D030314 | -0.40 | 8.37 | 0.63 | -1.19 |
| D030315 | -0.26 | 25.81 | 0.23 | 11.07 |
| D030316 | -0.06 | 4.25 | 0.50 | 0.44 |
| D030318 | -2.20 | 0.18 | 0.73 | 0.88 |
| D030319 | 0.06 | 4.26 | 0.60 | -0.48 |
| D030320 | -0.50 | 4.39 | 0.38 | -4.11 |
| D030321 | -0.69 | 4.77 | 0.95 | 1.11 |
| D030324 | -0.37 | -0.97 | 1.10 | 4.41 |
| D030325 | 1.75 | 4.83 | 2.19 | -0.80 |
| D030326 | -0.30 | 3.48 | 0.54 | -3.01 |
| D030327 | -1.42 | 5.01 | 0.95 | 1.91 |
| D030328 | -0.20 | 1.77 | 0.12 | -15.25 |
| D030329 | 0.00 | 3.29 | 0.41 | 1.59 |
| D030330 | 0.63 | 3.04 | 1.44 | 0.11 |
| D030331 | -0.42 | 1.21 | 0.41 | -9.37 |
| D030332 | -0.42 | 10.63 | 0.78 | 2.69 |
| D031237 | -0.34 | 6.87 | 0.80 | -2.34 |
| D031238 | -0.52 | 3.39 | 0.82 | -1.02 |

Table A4.4. 18: Conditional parameter estimates for variables specified as random slopes in the Deciduous model for individual female caribou in late fall and calving.

| | Deciduous Swamp | | Upland Deciduous | |
|---|---|---|---|---|
| Animal ID | Late Fall | Calving | Late Fall | Calving |
| D030308 | 0.32 | -1.85 | -1.73 | -1.36 |
| D030309 | -0.37 | -0.52 | -0.86 | -0.74 |
| D030310 | -1.88 | -3.17 | -1.82 | -1.00 |
| D030311 | -0.85 | -1.18 | -3.55 | -2.59 |
| D030312 | -0.48 | -1.08 | -0.20 | -3.57 |
| D030313 | -0.73 | -1.85 | -1.59 | -2.48 |
| D030314 | -0.25 | -1.31 | -1.05 | -2.02 |
| D030315 | -0.74 | -3.77 | -0.89 | -9.19 |
| D030316 | -0.22 | -1.95 | -1.02 | -2.03 |
| D030318 | -0.35 | -2.83 | 0.08 | -0.94 |
| D030319 | -0.57 | -1.86 | -1.02 | -2.15 |
| D030320 | 0.25 | -1.80 | -1.26 | -2.92 |
| D030321 | -0.17 | -0.45 | -1.09 | -2.04 |
| D030324 | -0.38 | -1.01 | -1.38 | -2.98 |
| D030325 | -0.88 | -2.19 | -2.55 | -2.86 |
| D030326 | -0.23 | -2.15 | -1.10 | -1.56 |
| D030327 | -0.47 | -1.17 | -0.38 | -2.65 |
| D030328 | -0.54 | -8.00 | -1.25 | -1.85 |
| D030329 | -0.27 | -2.00 | -1.01 | -1.53 |
| D030330 | -0.43 | -0.82 | -2.22 | -1.61 |
| D030331 | -0.45 | -7.45 | -0.67 | -2.27 |
| D030332 | -0.25 | -1.17 | -1.22 | -6.95 |
| D031237 | -0.17 | -1.92 | -1.08 | -2.08 |
| D031238 | -0.11 | -1.89 | -0.88 | -2.18 |

Table A4.4. 19: Conditional parameter estimates for variables specified as random slopes in the Disturbance model for individual female caribou with neonate calves and after calf loss.

| | Dist. to Early Seral | | Dist. to Well | | Line Density | |
|---|---|---|---|---|---|---|
| Animal ID | Post Loss | Calving | Post Loss | Calving | Post Loss | Calving |
| D030308.2011 | 0.47 | 3.03 | -1.42 | 1.78 | -2.26 | -2.46 |
| D030308.2012 | 0.80 | 2.93 | 0.40 | 1.87 | -2.21 | -2.24 |
| D030309.2011 | 0.02 | 8.10 | 2.01 | 12.33 | -1.37 | -1.38 |
| D030309.2012 | 0.58 | 6.39 | 0.28 | 6.81 | -1.28 | -1.27 |
| D030312.2012 | -2.81 | -1.50 | 0.54 | -1.51 | 1.89 | 2.34 |
| D030313.2011 | 1.12 | 9.94 | 1.57 | 10.71 | -2.23 | -2.38 |
| D030314.2012 | 1.03 | 6.61 | 3.52 | 6.96 | -1.46 | -1.56 |
| D030315.2011 | 2.93 | 7.45 | 10.71 | 6.71 | -2.99 | -3.29 |
| D030316.2011 | 0.77 | 2.83 | 0.51 | 3.78 | 0.62 | 0.66 |
| D030319.2012 | 0.40 | -1.32 | 3.05 | -11.20 | -1.16 | -0.99 |
| D030320.2011 | 0.71 | 3.88 | 0.80 | 1.13 | 0.05 | 0.08 |
| D030321.2012 | 4.04 | 18.64 | 1.57 | -0.32 | 1.06 | 1.09 |
| D030325.2011 | -1.25 | 0.37 | 2.54 | 3.23 | -1.84 | -1.91 |
| D030327.2012 | 0.61 | 4.26 | 2.83 | 4.34 | -1.70 | -1.64 |
| D030328.2011 | 0.50 | 3.30 | 0.61 | 2.37 | -2.73 | -2.83 |
| D030329.2012 | 0.83 | 2.77 | 1.32 | 2.95 | 1.39 | 1.47 |
| D030331.2012 | -0.45 | 0.52 | 0.33 | 2.32 | -3.66 | -3.72 |
| D031237.2013 | 5.99 | 11.97 | -0.62 | 0.82 | 4.06 | 4.15 |
| D031726.2013 | 0.64 | 0.95 | 3.90 | 2.51 | 0.17 | 0.26 |
| D031731.2013 | 2.16 | 4.68 | 0.14 | 1.22 | 0.21 | 0.15 |
| D031737.2013 | 2.54 | 4.30 | -1.80 | 1.17 | -2.16 | -2.04 |
| D031738.2013 | 5.07 | 22.55 | 0.79 | 26.86 | 0.10 | 0.56 |

Table A4.4. 20: Conditional parameter estimates for variables specified as random slopes in the Water model for individual female caribou with neonate calves and after calf loss.

| | Dist. to River | | Dist. to Lake | |
|---|---|---|---|---|
| Animal ID | Post Loss | Calving | Post Loss | Calving |
| D030308.2011 | 0.29 | 0.39 | 2.52 | 4.87 |
| D030308.2012 | -0.16 | 1.83 | 3.16 | 3.41 |
| D030309.2011 | 1.09 | 1.54 | -0.23 | 1.94 |
| D030309.2012 | 1.04 | 1.68 | -0.15 | 1.19 |
| D030312.2012 | -0.05 | -0.15 | -0.18 | -1.41 |
| D030313.2011 | 0.44 | 0.52 | -0.06 | 2.21 |
| D030314.2012 | 0.41 | 2.77 | 1.46 | 5.64 |
| D030315.2011 | 3.39 | 2.65 | 3.41 | 5.31 |
| D030316.2011 | -0.43 | -1.65 | 1.49 | 4.69 |
| D030319.2012 | 0.87 | 1.08 | -0.64 | 2.02 |
| D030320.2011 | -1.12 | 0.99 | 7.58 | 2.61 |
| D030321.2012 | 1.19 | 22.51 | 0.66 | 0.93 |
| D030325.2011 | 0.93 | 5.49 | 9.95 | 20.05 |
| D030327.2012 | -0.28 | 0.77 | 1.15 | 1.43 |
| D030328.2011 | -0.31 | 0.63 | 3.57 | 6.93 |
| D030329.2012 | 0.44 | -0.23 | 1.08 | 4.68 |
| D030331.2012 | -0.08 | 1.28 | 4.18 | 5.25 |
| D031237.2013 | 1.94 | 7.02 | 2.19 | 3.40 |
| D031726.2013 | 0.26 | 1.98 | 0.80 | 10.56 |
| D031731.2013 | 0.44 | 1.17 | -0.12 | 1.40 |
| D031737.2013 | 0.96 | 2.83 | -1.75 | -0.52 |
| D031738.2013 | 0.31 | 0.24 | 0.69 | 0.95 |

Table A4.4. 21: Conditional parameter estimates for variables specified as random slopes in the Forage model for individual female caribou with neonate calves and after calf loss.

| | NDVI | |
|---|---|---|
| Animal ID | Post Loss | Calving |
| D030308.2011 | 0.28 | 0.76 |
| D030308.2012 | 0.45 | 0.99 |
| D030309.2011 | -1.14 | 0.46 |
| D030309.2012 | -2.37 | 0.66 |
| D030312.2012 | 1.04 | 3.70 |
| D030313.2011 | -0.51 | -1.62 |
| D030314.2012 | -3.15 | -6.23 |
| D030315.2011 | -0.38 | -1.91 |
| D030316.2011 | -0.51 | -1.42 |
| D030319.2012 | -2.37 | 0.78 |
| D030320.2011 | -3.58 | -1.89 |
| D030321.2012 | -1.28 | 0.10 |
| D030325.2011 | 0.00 | 2.14 |
| D030327.2012 | 0.93 | 0.89 |
| D030328.2011 | -0.56 | 0.32 |
| D030329.2012 | 0.31 | 0.47 |
| D030331.2012 | 0.79 | 1.66 |
| D031237.2013 | 0.15 | -1.37 |
| D031726.2013 | -0.40 | 2.70 |
| D031731.2013 | 0.61 | 0.27 |
| D031737.2013 | 1.02 | 1.63 |
| D031738.2013 | -1.33 | -2.81 |

Table A4.4. 22: Conditional parameter estimates for variables specified as random slopes in the Conifer model for individual female caribou with neonate calves and after calf loss.

| | Conifer Swamp | |
|---|---|---|
| Animal ID | Post Loss | Calving |
| D030308.2011 | -1.11 | -1.72 |
| D030308.2012 | -0.50 | -1.56 |
| D030309.2011 | -2.20 | -2.02 |
| D030309.2012 | -1.70 | -3.28 |
| D030312.2012 | -15.24 | -11.03 |
| D030313.2011 | -4.07 | -3.68 |
| D030314.2012 | -1.93 | -10.42 |
| D030315.2011 | -5.19 | -6.33 |
| D030316.2011 | -0.70 | -3.05 |
| D030319.2012 | -3.25 | -2.84 |
| D030320.2011 | 0.51 | -1.76 |
| D030321.2012 | -2.76 | -3.46 |
| D030325.2011 | 1.25 | -1.00 |
| D030327.2012 | -0.02 | -1.89 |
| D030328.2011 | -1.15 | -2.21 |
| D030329.2012 | -0.93 | -9.71 |
| D030331.2012 | -1.17 | -5.80 |
| D031237.2013 | 2.85 | -0.44 |
| D031726.2013 | -1.46 | -0.75 |
| D031731.2013 | -3.99 | -5.32 |
| D031737.2013 | -0.28 | -3.49 |
| D031738.2013 | -2.11 | -4.80 |

Table A4.4. 23: Conditional parameter estimates for variables specified as random slopes in the Fen model for individual female caribou with neonate calves and after calf loss.

| | Poor Fen | | Rich Fen | |
|---|---|---|---|---|
| Animal ID | Post Loss | Calving | Post Loss | Calving |
| D030308.2011 | -0.02 | -0.50 | -6.71 | -4.44 |
| D030308.2012 | 1.04 | 0.14 | -4.85 | -10.24 |
| D030309.2011 | -0.05 | -0.64 | -0.12 | -3.28 |
| D030309.2012 | -0.38 | -1.84 | 0.17 | -4.59 |
| D030312.2012 | -3.18 | -2.69 | -0.36 | -4.05 |
| D030313.2011 | -3.72 | -2.11 | -0.24 | -0.81 |
| D030314.2012 | 2.51 | -0.29 | -1.62 | -10.64 |
| D030315.2011 | -0.45 | -0.40 | -1.80 | -1.85 |
| D030316.2011 | 2.03 | -0.97 | -1.49 | -1.51 |
| D030319.2012 | 1.02 | 1.90 | -1.19 | -9.80 |
| D030320.2011 | 3.93 | 0.17 | -11.39 | -5.43 |
| D030321.2012 | 0.18 | 0.19 | -1.44 | -3.11 |
| D030325.2011 | 2.34 | -0.04 | -2.43 | -11.20 |
| D030327.2012 | 0.47 | -0.61 | -0.80 | -1.94 |
| D030328.2011 | -0.73 | -1.54 | -6.27 | -11.82 |
| D030329.2012 | 0.15 | 0.92 | -2.09 | -10.55 |
| D030331.2012 | -1.09 | -4.21 | -9.10 | -12.40 |
| D031237.2013 | 0.67 | -0.17 | -4.40 | -5.21 |
| D031726.2013 | -0.29 | -0.42 | -0.93 | -5.20 |
| D031731.2013 | -2.13 | -3.88 | -0.81 | -3.09 |
| D031737.2013 | -2.53 | -10.13 | -3.32 | -13.05 |
| D031738.2013 | 1.26 | -0.95 | -0.83 | -1.61 |

Table A4.4. 24: Conditional parameter estimates for variables specified as random slopes in the Deciduous model for individual female caribou with neonate calves and after calf loss.

| | Deciduous Swamp | | Upland Deciduous | |
|---|---|---|---|---|
| Animal ID | Post Loss | Calving | Post Loss | Calving |
| D030308.2011 | 0.11 | -2.71 | -2.16 | -4.31 |
| D030308.2012 | -0.43 | -9.82 | -2.83 | -7.45 |
| D030309.2011 | 0.84 | -3.12 | -2.82 | -4.11 |
| D030309.2012 | 1.09 | -2.38 | -3.14 | -3.01 |
| D030312.2012 | -1.52 | -4.10 | n/a | n/a |
| D030313.2011 | -2.15 | -3.14 | -5.61 | -4.68 |
| D030314.2012 | -0.52 | -10.46 | -3.27 | -4.41 |
| D030315.2011 | -1.55 | -2.99 | -1.05 | -9.86 |
| D030316.2011 | -1.11 | -2.36 | n/a | n/a |
| D030319.2012 | -3.16 | -10.65 | -5.58 | -7.28 |
| D030320.2011 | -1.77 | -4.03 | -5.29 | -5.99 |
| D030321.2012 | 0.60 | -2.06 | -1.86 | -3.56 |
| D030325.2011 | -1.13 | -3.31 | -3.56 | -5.41 |
| D030327.2012 | 0.08 | -2.08 | -2.16 | -3.68 |
| D030328.2011 | -4.66 | -5.95 | -1.69 | -3.23 |
| D030329.2012 | -0.49 | -2.80 | n/a | n/a |
| D030331.2012 | -5.83 | -11.68 | -1.76 | -2.93 |
| D031237.2013 | 0.22 | -3.37 | -1.96 | -4.31 |
| D031726.2013 | -0.37 | -2.48 | -3.10 | -4.26 |
| D031731.2013 | 1.25 | -1.18 | -2.25 | -9.47 |
| D031737.2013 | -1.16 | -10.70 | -2.41 | -4.89 |
| D031738.2013 | -0.14 | -1.82 | -3.14 | -16.60 |

# CHAPTER 5

## ASSESSING SPATIAL FACTORS INFLUENCING PREDATION RISK TO BOREAL CARBIOU CALVES IN A MULTI-USE LANDSCAPE

In natural landscapes, animals are expected to select biotic and abiotic resources and conditions (i.e. habitat, *sensu* Hall *et al.* 1997) in a density-dependent process that maximizes fitness (Fretwell & Lucas 1970; Morris 1989). This behaviour, which is shaped by natural selection, requires animals to integrate cues on food, cover, predation risk and information from conspecifics to select the best available habitat (Morris 2003). If habitat quality is measured solely on resource availability, then habitat selection should result in a positive correlation between animal density and habitat quality for species that are not strongly territorial. Indeed, many models of species distribution implicitly rely on this relationship to infer habitat quality (Boyce & McDonald 1999; Guisan *et al.* 2013).

Rapid and accelerating rates of environmental change, however, can impact the relationship between habitat quality and animal density if rates of change exceed the evolutionary potential of a particular species (Sih *et al.* 2011). In such instances, individuals may ignore or show maladaptive responses to novel cues that have high influence on fitness, which may result in lowered demographic performance in habitats with high animal densities (Van Horne 1983; Battin 2004; Bock & Jones 2004; Robertson & Hutto 2006; Chalfoun & Schmidt 2012). For endangered species management, the uncoupling of habitat quality from animal density would limit the effectiveness of habitat conservation strategies that rely primarily on inferences from species distribution models. Consequently, increasing emphasis has been placed on linking habitat characteristics or selection to demographic performance to more fully assess habitat quality (Olson *et al.* 2004; Nielsen *et al*. 2006; Wittmer *et al*. 2007; Aldridge & Boyce 2008; Heinrichs *et al.* 2010; DeCesare *et al.* 2014; Wirsing & Heithaus 2014).

Understanding how human-mediated environmental change (HMEC) affects demographic performance is integral to developing effective conservation strategies for boreal caribou (*Rangifer tarandus caribou*), a threatened ecotype of woodland caribou.  Population declines of boreal caribou have been attributed to elevated predation rates facilitated by HMEC within caribou range (McLoughlin *et al.* 2003; Courtois *et al.* 2007; Festa-Bianchet *et al.* 2011). Because of this relationship, the federal recovery strategy for boreal caribou has identified habitat protection and restoration as key management levers for stabilizing and sustaining caribou populations (Environment Canada 2012).  Both levers, however, may be problematic to implement without demographically-linked information on habitat quality.  For example, prioritizing areas for protection based on models of caribou habitat selection may be unreliable because the human-mediated increase in predation risk can discount habitat quality when indexed only by selection (DeCesare *et al.* 2014).  Restoration strategies will also be more effective if they are targeted toward specific landscape features that have high influence on caribou demographic rates.  The effectiveness of both levers will further be scale-dependent. Caribou have evolved a spatial separation strategy to reduce predation risk (Bergerud 1988) and determining the amount of space required for this strategy to be effective will be necessary to inform the appropriate scale of management actions.

Understanding drivers of caribou habitat quality is particularly important during the calving and summer seasons when predation rates of adult females and calves are highest

(Stuart-Smith *et al.* 1997; Courtois *et al.* 2007; Pinard *et al.* 2012). To that end, I focus here on evaluating habitat quality of calving areas, defined as those areas used by females with neonate calves (≤ 4 weeks old). Using GPS location data from female caribou, wolves (*Canis lupus*) and black bears (*Ursus americanus*), I evaluated calving habitat quality by assessing the influence of multiple spatial factors on the survival of neonates. I specifically assessed the relative importance of four hypotheses, each describing spatial factors linked to predation risk. The first – the disturbance hypothesis – suggests that landscape disturbance facilitates spatial overlap among caribou, other ungulates, and their predators, resulting in increased caribou predation rates (James & Stuart-Smith 2000; Latham *et al.* 2011b; Peters *et al.* 2013). Under this hypothesis, calf survival is predicted to be negatively correlated with increasing landscape disturbance. The second – the lake refuge hypothesis – suggests that lakeshores provide escape habitat and thus a predation refuge for female caribou with neonates (Bergerud 1985; Carr *et al.* 2011). Increasing proximity to lakes should therefore equate to an increased probability of neonate survival. The third hypothesis proposes a similar refuge effect for peatlands (e.g. nutrient-poor fens and bogs) where neonate survival should increase as the proportion of peatlands in the landscape increases (peatland refuge hypothesis; McLoughlin *et al.* 2005). The fourth hypothesis predicts that neonate survival will be negatively correlated to the proximity to – or density of – habitats favoured by wolves and/or black bears, the two main predators of caribou calves (predation risk hypothesis; Gustine *et al.* 2006). Compared to the first three hypotheses, which describe the risk effects of specific landscape features, the predation risk hypothesis can be considered the combined effects of multiple landscape features as reflected by predator habitat selection.

Assessments of habitat quality fundamentally depend on spatial scale and the metrics used to describe habitat and/or fitness (Chalfoun & Martin 2007). I therefore evaluated each hypothesis at multiple spatial scales using metrics of exposure and maternal selection of calving habitat. Exposure, which can be considered habitat use, measures the landscape attribute directly and any relationship to survival – and thus habitat quality – is contingent on the absolute value of these measurements (e.g. Wittmer *et al*. 2007; Apps *et al.* 2013). Selection, on the other hand, is the ratio of the measured attributed relative to its availability at a larger, pre-defined scale; thus, habitat quality in this sense is contingent on habitat availability (e.g., Dussault *et al.* 2012; Leclerc *et al.* 2014). All assessments of selection and exposure were conducted at the individual level and I used neonate survival as a surrogate of fitness. This individual-based framework yields inferences on the fitness potential, or the relative per capita contribution to population growth, of a given habitat (Wiens 1989; Franklin *et al.* 2000; Johnson 2007).

## METHODS

To assess spatial factors affecting neonate survival, I used location data from radio-collared caribou, wolves and black bears collected during the calving seasons from 2011-2013. All capture and handling procedures followed approved governmental and institutional animal care protocols (BC Wildlife Act Permits FJ12-76949 and FJ12-80090; University of Alberta Animal Use protocol # 748/02/13).

*Caribou Spatial Data*

Female caribou were captured by aerial net-gunning during the winter months of 2011 (*n* = 24), 2012 (*n* = 2) and 2013 (*n* = 27).[2] All captured caribou were physically restrained without anesthetic during collar deployment. For animals captured in 2011 and 2012, radio-collars were programmed to acquire a GPS location every two hours during the calving season (April 15 – July 15). For animals captured in 2013, radio-collars acquired GPS locations every four hours during calving. Prior to analyses, I applied the same screening procedures as described in *Chapter 4*, removing locations with low positional accuracy (< 3D fixes), biologically implausible locations and locations from 10:00 – 18:00 hrs on dates of aerial surveys.

Caribou data were restricted to locations where females were accompanied by a neonate calf. To identify these locations, I applied the movement-based methods described in *Chapter 2* to individual data sets. I used the population-based method to exclude females predicted to be barren in a particular calving season. For calving females, I applied both movement-based methods to predict neonate survival, corroborating method predictions with data from aerial surveys conducted at four weeks post-calving. Where method predictions differed, I used the prediction that matched calf status (e.g. calf presence / absence) recorded on aerial survey. For those females lacking aerial survey data (*n* = 6), I used the prediction of the individual-based method due to its higher accuracy rate. Two females were excluded from further analysis as their predicted dates of calf loss did not coincide with aerial survey data (e.g. predicted calf loss date was after the aerial survey where the calf was not observed). From

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[2] The larger sample size of caribou compared to *Chapter 4* is due to additional data becoming available upon completion of *Chapter 4* analyses.

these procedures, the remaining data set consisted of 38 females with individual data sets containing GPS locations from the estimated parturition date to the estimated date of calf loss or four weeks post-calving, whichever came first. Of these 38 females, 12 were predicted to have calved in two seasons, equating to 50 caribou-calving seasons of data. Mean fix rates per collar-season were 94.7% in 2011 (range: 75.8 – 100%), 95.7% in 2012 (85.0 – 100%) and 81.9% in 2013 (46 – 100%).

### *Predator Spatial Data*

Wolves were captured during the winter months of 2012 ($n$ = 3) and 2013 ($n$ = 12) while bears were captured in May 2012 ($n$ = 4) and May 2013 ($n$ = 15). Capture efforts focused on individuals occurring within or adjacent to caribou range. All wolves and bears were captured by aerial darting with targeted animals chemically immobilized using *Telazol* ® (4.0 mg/kg) delivered by an appropriate sized dart. Wolf collars were programmed to acquire a GPS location every 15 minutes from May 1 – June 30 while bear collars acquired a location every 30 minutes during the same time period. Data sets from predator collars contained data from one calving season only (i.e., no collars spanned two seasons). Two wolves captured in 2013 dispersed from the study area and were removed from further analyses. The final wolf data set therefore consisted of 13 individuals distributed among ten packs.

As with caribou, I screened predator data sets prior to analyses, removing biologically implausible locations and locations with low positional accuracy (< 3D fixes). For wolves, I removed all locations within 200-m of suspected den sites and further excluded locations between 10:00 – 18:00 hrs as all individuals had generally low movement rates (<100 m/hr) within this interval, presumably due to the animals bedding down to avoid warm daytime temperatures. For bears, I did not exclude specific time intervals as most individuals did not display a consistent daily period of inactivity. Bear data sets also contained all locations since the time of capture. Although locations within the first two week post-capture may reflect capture-related behavioural alterations (Morellet *et al.* 2009), I elected to retain this data because none of the individual data sets began before May 1 and I wanted to preserve all bear locations during the neonate period when caribou calves are most vulnerable to bear predation (Zager & Beecham 2006). Following these procedures, the mean per-collar fix rates were 65.5% (range: 37.9 – 95.2%) for wolves and 76.2% (51.3 – 87.0%) for bears. Testing of predator collars in different habitats suggested that the low fix rates of predator collars were likely due to inconsistent collar performance rather than habitat induced bias in fix acquisition (C. DeMars, *unpublished data*; Frair *et al.* 2010).

### *Selection and Exposure Metrics*

I assessed the effects of spatial factors on calf survival using two metrics: resource selection and exposure. For the first metric, I related calf survival to individual variation in maternal selection of resources. I developed individual-based measures of maternal selection using resource selection functions (RSFs; Manly *et al.* 2002) estimated at second- and third-order scales. To account for females calving in two seasons, I considered caribou-year as the sampling unit. For second-order RSFs, I followed the same framework described in *Chapter 4*, comparing random points generated within the 80% utilization distributions (UDs) of individual calving areas to random points generated within a given herd's range. Third-order RSFs compared the GPS locations of individual females to the random points of calving area UDs.

RSFs at both scales were estimated using generalized linear mixed-effects models (GLMMs; Zuur *et al.* 2009). For all GLMMs, I used the same suite of explanatory variables detailed in *Chapter 4*; specifically, I used variables describing land cover, normalized difference vegetation index (NDVI), slope, distance to river, distance to lake, distance to early seral vegetation (forest fires and cut blocks < 50 years old), distance to well sites and linear feature density (400-m radius). To evaluate the four hypotheses considered for explaining calf survival, I fit GLMMs with individual caribou-year as the random intercept and specified random slopes for those variables representative of a given hypothesis. For example, for the lake refuge hypothesis, the variable "distance to lake" was specified as a random slope. This model formulation yields selection coefficients specific to each caribou-year for variables specified as random slopes (see *Chapter 4: Data Analysis* for details on random-slope GLMMs). I used these individual-specific selection coefficients as covariates in calf survival analyses.

For second-order GLMMs evaluating the disturbance, lake refuge and peatland refuge hypotheses, the fixed effects component of the model was specified as

*Land cover + slope + NDVI + dist. to river + dist. to lake + dist. to early seral + dist. to well site + line density*

where land cover types were calculated as proportions in a 1500-m radius. For third-order caribou RSFs, I excluded river, lake, early seral, and well sites because the majority of calving UDs did not contain these features. Land cover types were also measured at the pixel (30-m) scale. Within these model structures, none of the explanatory variables were found to be correlated (i.e., variance inflation factor < 2; Zuur *et al.* 2010).

Prior to calf survival analyses, I further assessed RSFs to determine if differential availability of resources affected selection coefficients (i.e. a functional response in selection; Mysterud & Ims 1998), which could confound their use as covariates in calf survival models. For second-order RSFs, only six sets of availability were possible, representing the six boreal caribou ranges in my study area. I followed the same procedure outlined in *Chapter 4*, using Akaike's Information Criterion (AIC) to compare GLMMs with individual caribou as a random intercept to more complex GLMMs where random intercepts were specified for both individual caribou and herd range. Similar to *Chapter 4* results, the more complex GLMMs were unsupported and their results are not shown here. For third-order GLMMs, I plotted the individual selection coefficients for a given variable against the variable's availability and assessed whether a linear or quadratic relationship was evident. I also calculated $R^2$ statistics to measure the strength of potential correlations. Evidence for a functional response in selection was weak as no obvious trend was noted in the plotted data and all $R^2$ values were $< 0.17$.

For the second metric used to assess calf survival, I calculated measurements of exposure. In these analyses, I calculated the mean value of the "used" locations at varying spatial scales for variables representative of the four hypotheses. I calculated means at the following scales:

i. Local scale, representing the pixel value of each GPS location
ii. 500-m buffer around each GPS location
iii. 1000-m buffer around each GPS location
iv. 1500-m buffer around each GPS location
v. 2000-m buffer around each GPS location

vi. Calving area (i.e. 80% UD random points)
vii. Range (i.e. range random points)

Distance-to measures were only contained in models at the local scale. For density measures, I considered buffers extending to 2000-m, which is likely near the maximum distance a predator might reasonably detect a female caribou and calf (Mech & Boitani 2003).

*Spatial Predictions of Predation Risk*

Assessing the predation risk hypothesis required the development of selection and exposure metrics based on spatially explicit predictions of predator habitat suitability. To do so, I first estimated predator-specific RSFs at multiple spatial scales. For predator RSFs estimated at second- and third-order scales, I followed a similar framework as for caribou. I note that assessing second-order selection for predators is complicated by the fact that home range selection is influenced by territoriality in addition to environmental resources. I maintained this scale of analysis, however, because I constrained predator RSF analyses to the caribou calving season; consequently, predators may show preferential use of areas within their annual home ranges that may not be entirely constrained by territoriality and may be more reflective of seasonal resource selection. To account for the relatively strong territoriality of wolves, I delineated areas used by individual packs using minimum convex polygons, which are likely more reflective of actual home range boundaries for territorial species than UDs (Boyle *et al.* 2009). For black bears, I delineated used areas with 80% UDs as was done for caribou because many of the radio-collared bears had overlapping areas of use during the caribou calving season, indicating a low degree of territoriality. For all second-order predator RSFs, I defined the scale of availability as the distribution of boreal caribou in BC rather than individual caribou ranges because both predators had individuals moving into and out of caribou range. Second-order predator RSFs therefore compared random points generated within pack-level MCPs (wolves) or individual UDs (bears) to random points generated within the distribution of caribou with the number of random points at each scale determined by sensitivity analyses (see *Chapter 4: Appendix 4.1*). Third-order predator RSFs compared the actual GPS locations of individuals to the UD or MCP random points.

I considered a further RSF framework for predators that focused on resources selected by wolves and bears when each predator specifically occurred in caribou range (hereafter, the caribou-range scale). I compared predator GPS locations falling within caribou range to available points drawn within the same range. These analyses may represent a more accurate depiction of predation risk to caribou calves because the majority of calving GPS locations are confined to caribou ranges (>82% based on 2010 range delineations).

To model predator resource selection, I used the same suite of explanatory variables as for caribou and determined the most predictive scale (or grain) of each variable for each predator using repeated univariate logistic regression analyses as detailed in *Chapter 4* (see Appendix 4.3). All predator RSFs were estimated using GLMMs. Because my objective was to generate spatial predictions of habitat suitability and not evaluate predator response to specific covariates *per se*, I used models that specified only random intercepts (Schielzeth & Forstmeier 2009). For wolves, the individual pack was specified as the random intercept for second-order RSFs while third-order and caribou-range RSFs had random intercepts for both packs and individual wolves. Individual bear was specified as the random intercept in all bear RSFs. I evaluated the predictive power of each RSF using *k*-fold cross-validation (Boyce *et al.* 2002), iteratively partitioning the data into five folds. For each iteration, four folds were used for model training then model predictions were tested on the withheld data. For each test, model prediction was evaluated by partitioning the predicted values of 'availability' points into deciles, then comparing the frequency of predicted values of 'used' points falling within a decile to decile rank using Spearman's correlation coefficient ($r_S$). I repeated this process 15 times, calculating a $\bar{r}_S$ for each RSF model.

Using the predator RSFs, I developed maternal selection and exposure metrics of predation risk to be included in calf survival models. For developing both metrics, I used explanatory variables describing either the distance to high quality bear or wolf habitat or the density of high quality bear or wolf habitat. I defined high quality predator habitat as those areas with RSF values > 75th percentile (Gustine *et al.* 2006) and I only used predator RSFs that had $\bar{r}_S$ validation values of > 0.70. To develop selection metrics, I used these predator habitat variables in univariate random-slope GLMMs to estimate selection coefficients for individual female caribou at second- and third-order scales. For variables describing predator habitat density, I evaluated radii from 500-m to 2000-m in 500-m increments to determine the most predictive scale of response. Exposure metrics for predation risk were calculated at the same scales as described in the previous section.

### *Calf Survival Analyses*

I used Cox proportional hazard models to relate variation in either selection or exposure to the probability of calf survival. To account for females calving in multiple years, I used mixed-effects Cox models of the form

$$h_{ij}(t) = h_0(t)\ \exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \ldots\ldots + \beta_k x_{ik} + \Upsilon_j) \qquad \text{(Therneau 2012)}$$

where $h_{ij}(t)$ is the hazard function for individual calf $i$ with female $j$ at time $t$, $h_0(t)$ is an unspecified baseline hazard function, the $x$'s are explanatory covariates and $\Upsilon_j$ is the random effect attributable to female $j$. Cox models are time-to-event analyses and the event in this formulation is calf loss. Positive model coefficients are interpreted as an increasing risk of calf mortality with an increase in the associated covariate. Note that I did not combine different scales of selection or exposure in the same survival models.

To test the four hypotheses relating spatial risk factors to calf survival, I ran the following models:

i. Disturbance hypothesis

Calf survival = distance to well site + distance to early seral + linear feature density

ii. Lake refuge hypothesis

Calf survival = distance to lake

iii. Peatland refuge hypothesis

Calf survival = proportion of poor fen + proportion of treed bog

iv. Predation risk hypotheses

Calf survival = distance to high quality bear habitat

Calf survival = density of high quality bear habitat

Calf survival = distance to high quality wolf habitat

Calf survival = density of high quality wolf habitat

I did not test the lake refuge hypothesis at third-order selection because few calving UD's contained lakes (*n* = 15) and thus this hypothesis was better evaluated at a second-order scale. Similarly, disturbance models at third-order selection consisted of linear feature density only.

I discriminated among models using AIC, first selecting the best model for explaining each hypothesis then selecting a top overall model. Relative model fit was also assessed by comparing AIC values to the value estimated from a null (or random expectation) model. For the top model(s) considered for inference, I tested the assumption of proportional hazards by assessing for linearity and a zero slope of the scaled Schoenfeld residuals (Therneau & Grambsch 2001). I furthered assessed the influence of maternal effects in the top model(s) by computing a chi-squared goodness-of-fit statistic to compare Cox models with and without the random term for individual female. Model prediction was evaluated using Harrell's concordance index, which provides a measure of discriminatory power similar to the area under a receiver operating curve (AUC) used in logistic regression (Harrell *et al.* 1996).

All statistical analyses were performed in R, version 3.0.2 (R Core Team, 2013). I used the R packages 'adehabitatHR' (Calenge 2006) to estimate UDs and 'lme4' (Bates *et al.*, 2013) to estimate GLMMs. Cox proportional hazards models were estimated with the R package 'survival' (Therneau 2014) while the mixed-effects formulations of the Cox model were implemented using the R package 'coxme' (Therneau 2012).

## RESULTS

Over the three years of data, 26 of 50 calves were predicted to have died prior to four weeks of age. Neonate survival was best predicted by a predation risk model that described the third-order selective response of female caribou to predation risk from bears (Table 5.1). For this model, bear predation risk was represented as the density of high quality bear habitat within a 500-m radius and bear habitat was estimated from RSF models developed at the caribou-range scale. I focus inference on the formulation of this model without random terms as maternal effects were weak ($X^2 = 0.16$, df = 1, $p = 0.68$). Model output suggests that the risk of neonate mortality increases by 59% (95% CI: 28, 98) for every one unit increase in maternal selection of local areas (500-m radius) containing higher proportions of high quality bear habitat. The model's estimated survival function shows that the highest rates of calf mortality occur during the first three weeks of life (Fig. 5.1). Model discriminatory power was good (Harrell's concordance = 0.78) and the assumption of proportional hazards was generally supported as there was no evidence for a non-zero linear trend in the scaled Schoenfeld residuals ($\rho = -0.362$, $X^2 = 1.91$, $p = 0.17$).

The bear predation model had clear separation from all other models considered, being seven AIC units lower than the next best model (Appendix 5.1). Models representing the other three hypotheses performed poorly, having AIC values similar to the null or random expectation model (Table 5.1). In general, models using selection metrics performed better than exposure metrics. For predation risk models, variables describing the density of predator habitat performed better than distance-to variables, particularly those calculated within smaller radii (≤ 1000-m).

Table 5.1: Top-ranked mixed-effect Cox proportional hazard models for each of four hypotheses evaluated for explaining the probability of survival of boreal caribou calves in northeast British Columbia. Analyses were restricted to the neonate period (< 4 weeks old). Models were developed at multiple scales and used two different metrics: selection and exposure (see main text). Models were ranked using Akaike's Information Criterion (AIC) and parameter estimates (β) with their 95% confidence intervals are presented for the top model within each hypothesis.

| **Hypothesis** | **Metric** | **Scale** | **Model Variables** | **β (95% CI)** | **AIC** |
|---|---|---|---|---|---|
| Predation Risk | Selection | 3rd Order | Density of high quality bear habitat [1] | 0.50<br>(0.27, 0.73) | 175 |
| Disturbance | Selection | 2nd Order | Dist. to early seral | 0.09<br>(0.02, 0.16) | 186 |
| | | | Dist. to well | 0.00<br>(-0.06, 0.06) | |
| | | | Line density | -0.10<br>(-0.21, 0.00) | |
| Random Expectation | - | - | Null (intercept –only) model | - | 187 |
| Lake Refuge | Selection | 2nd Order | Dist. to lake | 0.05<br>(-0.02, 0.12) | 188 |
| Peatland Refuge | Exposure | Local | Treed bog [2] | -1.45<br>(-3.14, 0.24) | 188 |
| | | | Poor fen | -0.54<br>(-2.21, 1.13) | |

[1] High quality bear habitat defined as areas with >75% RSF values estimated from a black bear RSF model developed at the caribou-range scale.

[2] Proportion of GPS locations falling within treed bogs or poor fens

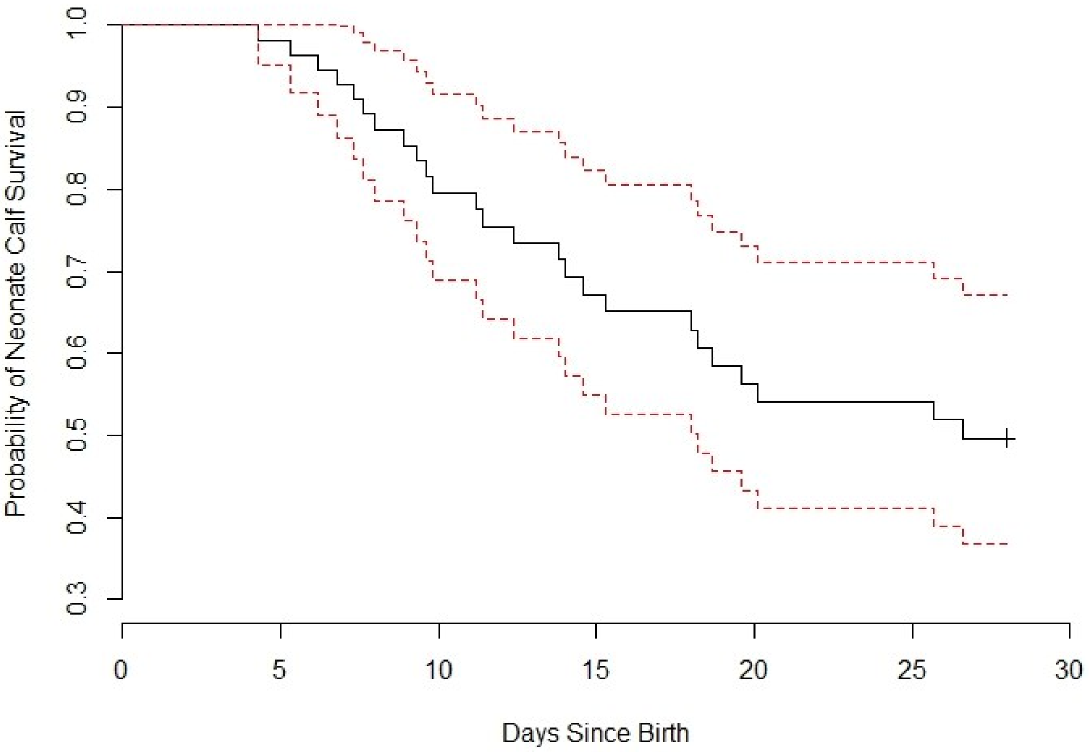

Figure 5.1: Estimated survival function (black line; red dashed lines = 95% confidence interval) of the top-ranked model for predicting survival of boreal caribou calves ≤ 4 weeks old in northeast British Columbia. The model related survival as function of maternal selection of local areas (500-m radius) that varied in the density of high quality black bear habitat.

## DISCUSSION

Assessing habitat quality requires careful consideration of the demographic rate used to measure performance and the potential habitat factors influencing the chosen rate (Johnson 2007). For assessing calving habitat quality of boreal caribou, I evaluated neonate survival and assumed that predation was the primary process affecting survival rates. Of the four predation-oriented hypotheses I evaluated, neonate survival was best predicted by predation risk from black bears. Outputs from this top model were consistent with patterns of black bear predation from other systems; that is, that calf mortality is highest during the first 3-4 weeks of life then lessens as calves gain sufficient mobility to elude bears (Fig. 6; Zager & Beecham 2006). In eastern ranges of boreal caribou, black bears have been identified as the dominant predator of caribou calves (Pinard *et al.* 2012). Moreover, in many multi-predator systems, bear predation is often the primary cause of neonate mortality for many ungulate species (Zager & Beecham 2006; Barber-Meyer *et al.* 2008; White *et al.* 2010; Griffin *et al.* 2011). My results here suggest that black bear predation may play an important role in the low rates of calf survival reported in western ranges of boreal caribou (Stuart-Smith *et al.* 1997; Rettie & Messier 1998; McLoughlin *et al.* 2003; Culling & Cichowski 2010).

The relatively strong influence of bear predation risk on neonate survival, however, should be viewed cautiously given my analytical framework. I modelled predation risk for wolves and bears using the top 25% of values from predator-specific RSF models. This framework only considers habitat and does not take into account differences in search rate, search radius and abundances between the two species. These three factors would necessarily influence the relative risk that each species represents to caribou (Lima & Dill 1990;

Hebblewhite & Merrill 2007). Thus, a pixel with a 75th percentile value from an RSF developed for bears may not equate to the same predation risk as a pixel with a 75th percentile value from a wolf RSF. Given this limitation, I caution that my results should not be construed as evidence discounting the predation risk of wolves. Indeed, a model describing predation risk from wolves was second-ranked overall for explaining neonate survival (Appendix 5.1, Table A5.4). Nevertheless, the clear separation of the top-ranked bear model from others suggests that bear predation is a significant factor in rates of neonate mortality and, similar to conclusions drawn from eastern caribou ranges, this finding may be driven by high bear densities (Bastille-Rousseau *et al.* 2011; Pinard *et al.* 2012).

Predation risk from bears occurred at relatively small spatial scales, which was perhaps counter to expectations. Rettie & Messier (2000) suggested that large-scale patterns of habitat selection should reflect the primary limiting factor(s) of animal populations, which for caribou is predation (Bergerud 1988). Variation in large-scale habitat selection or exposure patterns should therefore equate to variation in predation rates, as reflected by rates of caribou survival (e.g. Wittmer *et al*. 2007; Sorensen *et al*. 2008). At the largest scale of analysis, I detected no differences among caribou ranges in rates of neonate survival. Similarly, variation in female selection of calving areas within ranges did not correlate to variation in neonate survival. Combined with the realized high rates of neonate mortality, these findings suggest that (*i*) spatial factors thought to influence the predation process have exceeded thresholds where variation in predation of neonates is detectable, at least at large scales; and, (ii) that female caribou cannot effectively space away from predators within northeast BC landscapes. Apps *et al*. (2013) reported similar results for mountain caribou where landscape disturbance indices had minimal effect on adult female survival. They suggested, however, that their scale of analysis was not sufficiently broad to encompass highly disturbed areas outside of caribou range, a factor likely to be unimportant in my study area given the wide distribution of disturbance within and outside of boreal caribou ranges in northeast BC (Thiessen 2009).

I found little support for the other three hypotheses linking spatial factors to the probability of neonate survival. Unlike the predation risk hypothesis which was tested using predator-specific RSF models encompassing multiple spatial factors, the disturbance, lake refuge and peatland refuge hypotheses were specified as univariate or bivariate models representing specific landscape attributes. My results suggest that no specific landscape feature contributes disproportionately to the high mortality rates of neonate calves in northeast BC. A number of explanations may account for the lack of findings. First, neonate mortality may be driven more by predator density (i.e. the numeric response) than by variation in spatial factors potentially influencing the predation process (i.e. the functional response; Holling 1959). Predator density is thought to be driven by increased densities of other ungulate species (e.g. moose [*Alces alces*]), which respond favourably to the early seral conditions that follow disturbance (Schwartz & Franzmann 1991; Seip 1992; Festa-Bianchet *et al.* 2011). This relationship, however, may not hold across northeast BC caribou ranges. For example, in the Calendar range calf recruitment has been higher (~35 calves: 100 females) than in other ranges (all < 28 calves: 100 females) despite high levels of landscape disturbance (Culling & Culling 2013). In this case, predator densities – and thus calf mortality rates – may be unrelated to landscape disturbance because moose density is also low in Calendar (Thiessen 2010). Predator densities may further explain why there was no support for the peatland refuge hypothesis.

Historically, peatlands are thought to have provided caribou a spatial refuge from predators (McLoughlin *et al.* 2005) and my results from *Chapter 4* suggest that caribou are selecting peatland-dominated areas for calving. Caribou calves, however, are still incurring high rates of mortality within these refugia. This lack of a refuge effect is consistent with one potential outcome of apparent competition where increasing predator densities will result in higher numbers of predators “spilling over” into the spatial refugia of the victim prey (Holt 1984; Jeffries & Lawton 1984).

Specific to the disturbance hypothesis, my lack of findings may indicate that the degree of disturbance within caribou range has exceeded thresholds where differences in neonate survival may be detected. McCutchen (2007) suggested that any enhancement to wolf hunting efficiency (i.e. the functional response) provided by linear features asymptotes at a line density of 1 km/km$^2$. When measured on a per kilometre basis, this threshold is exceeded in large portions of my study area (mean = 3.6 km/km$^{2,}$ range: 0 - 22.73; see Thiessen 2009); however, it is unclear over what spatial scale that such a threshold might apply. Previous research linking disturbance levels to caribou demographic performance has been integral to informing management strategies for sustaining and/or recovering caribou populations in multi-use landscapes (Courtois *et al*. 2007; Wittmer *et al*. 2007; Environment Canada 2008; Sorensen *et al.* 2008). From the standpoint of the federal recovery strategy, disturbance is measured at the range scale yet caribou ranges can differ in size by an order of magnitude (Environment Canada 2012). I did not detect disturbance effects at the range scale, perhaps due to my small sample size of ranges (*n* = 6), their relatively high levels of disturbance and the small variation among them (57-83%; Thiessen 2009; Environment Canada 2012). I also did not detect disturbance effects at small spatial scales (< 6 km radii), despite 13 females having calving areas with line densities < 1 km/km$^2$. This finding indicates that caribou calving habitat cannot be managed by disturbance indices at small spatial scales. Nagy (2011) suggests that caribou require 500 km$^2$ of intact space (0% disturbance) to effectively reduce predation risk although his observational findings were limited by a small sample size ($n$ = 6) and did not explicitly test the interaction between disturbance levels and the space over which they are measured. In my study, I could not test Nagy's (2011) hypothesis because this level of intactness is rare to non-existent. Testing this space-disturbance interaction, however, will be critical to understanding the spatial requirements of caribou and ultimately inform management strategies for sustaining caribou populations in multi-use landscapes.

### *Management Implications*

Hypotheses for population declines in the western distribution of boreal caribou have primarily focused on the role of wolf predation and its link to landscape disturbance (Rettie & Messier 1998; McLoughlin *et al.* 2003; Hervieux *et al.* 2013, 2014). For woodland caribou, calf recruitment is a key demographic rate affecting population growth (DeCesare *et al.* 2012) and my results here suggest that black bear predation may be an important factor in the low rates of calf recruitment currently being documented in many western ranges of boreal caribou. The degree to which bear predation influences population growth rates of caribou, however, remains unclear. Moreover, mechanistic hypotheses linking bear predation to caribou population declines are not well developed. Black bears have been shown to favour early seral vegetation following disturbance (Mosnier *et al.* 2008; Brodeur *et al.* 2008; Latham *et al.* 2011a) but it is uncertain as to whether disturbance facilitates a sufficient increase in bear abundance (but see Schwartz & Franzmann 1991) to in turn increase bear predation rates of calves above pre-disturbance levels. The role of disturbance in facilitating caribou-bear spatial overlap and enhancing bear movement rates also requires further investigation, particularly given recent research suggesting relatively high use of seismic lines by black bears in northeast BC (Tigner *et al.* 2014). For these reasons, I echo the recommendation of Latham *et al*. (2011a) that future research and management actions for conserving caribou should consider the entire suite of predators potentially affecting caribou population declines.

## LITERATURE CITED

Aldridge, C.L. & Boyce, M.S. (2008). Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. *Israel Journal of Ecology & Evolution*, **54**, 389–419.

Apps, C.D., Mclellan, B.N., Kinley, T.A., Serrouya, R., Seip, D.R. & Wittmer, H.U. (2013). Spatial factors related to mortality and population decline of endangered mountain caribou. *The Journal of Wildlife Management*, **77**, 1409–1419.

Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008). Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs*, **169**, 1–30.

Bastille-Rousseau, G., Fortin, D., Dussault, C., Courtois, R. & Ouellet, J.-P. (2011). Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography*, **34**, 588–596.

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2013). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5. http://CRAN.R-project.org/package=lme4

Battin, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, **18**, 1482–1491.

Bergerud, A.T. (1985). Antipredator strategies of caribou: dispersion along shorelines. *Canadian Journal of Zoology*, **63**, 1324–1329.

Bergerud, A.T. (1988). Caribou, wolves and man. *Trends in Ecology & Evolution*, **3**, 68–72.

Bock, C.E. & Jones, Z.F. (2004). Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment*, **2**, 403.

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

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

Brodeur, V., Ouellet, J.-P., Courtois, R. & Fortin, D. (2008). Habitat selection by black bears in an intensively logged boreal forest. *Canadian Journal of Zoology*, **86**, 1307–1316.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516-519.

Carr, N.L., Rodgers, A.R., Kingston, S.R. & Lowman, D.J. (2011). Use of island and mainland shorelines by woodland caribou during the nursery period in two northern Ontario parks. *Rangifer*, **31**, 49–61.

Chalfoun, A.D. & Martin, T.E. (2007). Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, **44**, 983–992.

Chalfoun, A.D. & Schmidt, K.A. (2012). Adaptive breeding-habitat selection: Is it for the birds? *The Auk*, **129**, 589–599.

Courtois, R., Ouellet, J.-P., Breton, L., Gingras, A. & Dussault, C. (2007). Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*, **14**, 491–498.

Culling, D.E. & Cichowski, D. (2010). *Scientific update for the boreal caribou (Rangifer tarandus caribou) in British Columbia, 2010*. British Columbia Ministry of Environment, Victoria, BC.

Culling, D.E. & Culling, B.A. (2013). *BC boreal caribou implementation plan: 2012-13 collar deployment and late winter recruitment survey*. Diversified Environmental Services, Fort St. John, BC.

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

DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K.G., Hervieux, D. & Neufeld, L. (2012). Estimating ungulate recruitment and growth rates using age ratios. *The Journal of Wildlife Management*, **76**, 144–153.

Dussault, C., Pinard, V., Ouellet, J.-P., Courtois, R. & Fortin, D. (2012). Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4481–4488.

Environment Canada. (2012). *Recovery strategy for the woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa, ON. xi + 138pp.

Environment Canada. (2008). *Scientific review for the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Environment Canada, Ottawa, ON. 72 pp. plus 180 pp. Appendices.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D. & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology*, **89**, 419–434.

Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2187–2200.

Franklin, A.B., Anderson, D.R., Gutiérrez, R.J. & Burnham, K.P. (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*, **70**, 539–590.

Fretwell, S.D. & Lucas, H.J. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **14**, 16–36.

Griffin, K.A., Hebblewhite, M., Robinson, H.S., Zager, P., Barber-Meyer, S.M., Christianson, D., Creel, S., Harris, N.C., Hurley, M.A., Jackson, D.H., Johnson, B.K., Myers, W.L., Raithel, J.D., Schlegel, M., Smith, B.L., White, C. & White, P.J. (2011). Neonatal mortality of elk driven by climate, predator phenology and predator community composition: Neonate elk calf survival across the north-western USA. *Journal of Animal Ecology*, **80**, 1246–1257.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P. & Buckley, Y.M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424–1435.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.

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

Harrell, F.E., Lee, K.L. & Mark, D.B. (1996). Tutorial in biostatistics multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. *Statistics in Medicine*, **15**, 361–387.

Hebblewhite, M. & Merrill, E.H. (2007). Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia*, **152**, 377–387.

Heinrichs, J.A., Bender, D.J., Gummer, D.L. & Schumaker, N.H. (2010). Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence. *Biological Conservation*, **143**, 2229–2237.

Hervieux, D., Hebblewhite, M., DeCesare, N.J., Russell, M., Smith, K., Robertson, S. & Boutin, S. (2013). Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology*, **91**, 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. *Canadian Journal of Zoology*, **92**, 1029–1037.

Holling, C.S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**, 293–320.

Holt, R.D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *The American Naturalist*, **124**, 377–406.

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

Jeffries, M.J. & Lawton, J.H. (1984). Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.

Johnson, M.D. (2007). Measuring habitat quality: a review. *The Condor*, **109**, 489–504.,

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

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

Leclerc, M., Dussault, C. & St-Laurent, M.-H. (2014). Behavioural strategies towards human disturbances explain individual performance in woodland caribou. *Oecologia*, **176**, 297–306.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Manly, B.F.J., McDonald, L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*, 2nd ed. Kluwere Academic Publishers, New York, NY. 221 pp.

McCutchen, N.A. (2007). *Factors affecting caribou survival in northern Alberta: the role of wolves, moose, and linear features*. Ph.D. thesis, University of Alberta, Edmonton, AB.

McLoughlin, P.D., Dunford, J.S. & Boutin, S. (2005). Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology*, **74**, 701–707.

McLoughlin, P.D., Dzus, E., Wynes, B.O.B. & Boutin, S. (2003). Declines in populations of woodland caribou. *The Journal of Wildlife Management*, **67**, 755–761.

Mech, L.D. & Boitani, L. (2003). *Wolves: behavior, ecology, and conservation*. The University of Chicago Press, Chicago, IL. 448 pp.

Morellet, N., Verheyden, H., Angibault, J.-M., Cargnelutti, B., Lourtet, B. & Hewison, M.A.J. (2009). The effect of capture on ranging behaviour and activity of the European roe deer (*Capreolus capreolus*). *Wildlife Biology*, **15**, 278–287.

Morris, D.W. (1989). Density-dependent habitat selection: testing the theory with fitness data. *Evolutionary Ecology*, **3**, 80–94.

Morris, D.W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13.

Mosnier, A., Boisjoly, D., Courtois, R. & Ouellet, J.-P. (2008). Extensive predator space use can limit the efficacy of a control program. *The Journal of Wildlife Management*, **72**, 483–491.

Mysterud, A. & Ims, R.A. (1998). Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*, **79**, 1435–1441.

Nagy, J.A. (2011). *Use of space by caribou in northern Canada*. Ph.D thesis. University of Alberta, Edmonton, AB.

Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, **130**, 217–229.

Olson, G.S., Glenn, E.M., Anthony, R.G., Forsman, E.D., Reid, J.A., Loschl, P.J. & Ripple, W.J. (2004). Modelling demographic performance of northern spotted owls relative to forest habitat in Oregon. *The Journal of Wildlife Management*, **68**, 1039–1053.

Peters, W., Hebblewhite, M., DeCesare, N., Cagnacci, F. & Musiani, M. (2013). Resource separation analysis with moose indicates threats to caribou in human altered landscapes. *Ecography*, **36**, 487–498

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D. & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, **76**, 189–199.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rettie, W.J. & Messier, F. (1998). Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology*, **76**, 251–259.

Rettie, W.J. & Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.

Robertson, B.A. & Hutto, R.L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, **87**, 1075–1085.

Schielzeth, H. & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, **20**, 416–420.

Schwartz, C.C. & Franzmann, A.W. (1991). Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife Monographs*, **113**, 3–58.

Seip, D.R. (1992). Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology*, **70**, 1494–1503.

Sih, A., Ferrari, M.C.O. & Harris, D.J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**, 367–387.

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B. & Boutin, S. (2008). Determining sustainable levels of cumulative effects for boreal caribou. *The Journal of Wildlife Management*, **72**, 900–905.

Stuart-Smith, K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M. & Rippin, A.B. (1997). Woodland caribou relative to landscape patterns in northeastern Alberta. *The Journal of Wildlife Management*, **61**, 622–633.

Therneau, T. (2012). *coxme: Mixed-effect cox models*. Retrieved from http://CRAN.R-project.org/package=coxme

Therneau, T. (2014). A package for survival analysis in S. R package version 2.37-7, <URL http://CRAN.R-project.org/package=survival>.

Therneau, T.M. & Grambsch, P.M. (2001). *Modeling survival data: Extending the Cox Model*. Springer, New York, NY. 350 pp.

Thiessen, C. (2010). *Horn River Basin moose inventory January / February 2010*. BC Ministry of Environment, Fort St. John, BC.

Thiessen, C. (2009). *Peace region boreal caribou monitoring: annual report 2008-09*. British Columbia Ministry of Environment, Fort St. John, BC.

Tigner, J., Bayne, E.M. & Boutin, S. (2014). Black bear use of seismic lines in Northern Canada. *The Journal of Wildlife Management*, **78**, 282–292.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, **47**, 893–901.

White, C.G., Zager, P. & Gratson, M.W. (2010). Influence of Predator Harvest, Biological Factors, and Landscape on Elk Calf Survival in Idaho. *The Journal of Wildlife Management*, **74**, 355–369.

Wiens, J.A. (1989). *The ecology of bird communities*. Vol. 1. Cambridge University Press, Cambridge, UK. 560 pp.

Wirsing, A.J. & Heithaus, M.R. (2014). Accounting for individual behavioural variation in studies of habitat selection. *Journal of Animal Ecology*, **83**, 319–321.

Wittmer, H.U., Mclellan, B.N., Serrouya, R. & Apps, C.D. (2007). Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology*, **76**, 568–579.

Zager, P. & Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus*, **17**, 95–108.

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

Zuur, A.F., Ieno, E., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York, NY. 574 pp.

## APPENDIX 5.1: MODEL SELECTION RESULTS

I tested four hypotheses relating spatial factors to the survival probability of neonate calves (< 4 weeks old). Within each hypothesis, I evaluated a suite of models that described either (*a*) variation in maternal selection of resources at second- and third-order scales; or (*b*) exposure, defined as the mean value of explanatory covariates calculated at multiple spatial scales. I discriminated among models using Akaike's Information Criterion (AIC).

Table A5. 1: Model selection results for the disturbance hypothesis. Distance-to variables (early seral and well) were used only in second-order selection and local exposure analyses.

| Metric | Scale | Model Variables | AIC |
|---|---|---|---|
| Selection | 2nd order | early seral + well + line density | 186 |
| Exposure | Local | early seral + well + line density | 189 |
| Exposure | Buffer 2000m | line density | 189 |
| Exposure | Buffer 1500m | line density | 189 |
| Exposure | Calving Area | line density | 189 |
| Exposure | Buffer 1000m | line density | 189 |
| Selection | 3rd order | line density | 189 |
| Exposure | Buffer 500m | line density | 189 |
| Exposure | Range | line density | 189 |

Table A5. 2: Model selection results for the peatland refuge hypothesis. For exposure analyses, the proportion of treed bog and nutrient-poor fen was calculated within each scale. For second-order selection, the proportion of treed bog and nutrient-poor fen was calculated in a 1500-m radius, the most predictive scale for land cover type in resource selection function analyses (see Appendix 7). Third-order selection maintained treed bog and nutrient-poor fen at the pixel scale (30-m).

| Metric | Scale | Model Variables | AIC |
|---|---|---|---|
| Exposure | Local | treed bog + poor fen | 188 |
| Selection | 2nd order | treed bog + poor fen | 189 |
| Exposure | Buffer 500m | treed bog + poor fen | 189 |
| Exposure | Buffer 1000m | treed bog + poor fen | 190 |
| Exposure | Buffer 1500m | treed bog + poor fen | 190 |
| Exposure | Buffer 2000m | treed bog + poor fen | 190 |
| Selection | 3rd order | treed bog + poor fen | 190 |
| Exposure | Calving Area | treed bog + poor fen | 191 |
| Exposure | Range | treed bog + poor fen | 191 |

Table A5. 3: Model selection results for the lake refuge hypothesis. Third-order selection analyses were not considered as few calving areas contained lakes.

| Metric | Scale | Model Variables | AIC |
|---|---|---|---|
| Selection | 2nd order | distance to lake | 188 |
| Exposure | Local | distance to lake | 189 |

Table A5. 4: Model selection results for the predation risk hypothesis. For each metric and scale, I used the most predictive explanatory variable for each predator (wolves and black bears; see Appendix 7). Predator habitat was defined as areas having resource selection function (RSF) values >75 percentile from predator-specific RSF models. For all model variables, the RSF analysis used to derive predator habitat predictions is listed and for selection analyses the radius at which the variable was calculated is shown, where appropriate (in brackets).

| Metric | Scale | Model Variables | AIC |
|---|---|---|---|
| Selection | 3rd order | Density of Bear Habitat (500m; Caribou Range RSF) | 175 |
| Selection | 2nd order | Density of Wolf Habitat (1000m) | 183 |
| Selection | 3rd order | Density of Wolf Habitat (500m) | 186 |
| Selection | 2nd order | Density of Bear Habitat (500m; Caribou Range RSF) | 186 |
| Exposure | Local | Distance to Bear Habitat (2nd Order RSF) | 188 |
| Exposure | Buffer 1000m | Density of Bear Habitat (Caribou Range RSF) | 189 |
| Exposure | Buffer 500m | Density of Bear Habitat (Caribou Range RSF) | 189 |
| Exposure | Buffer 1500m | Density of Bear Habitat (Caribou Range RSF) | 189 |
| Exposure | Buffer 2000m | Density of Wolf Habitat | 189 |
| Exposure | Calving Area | Density of Bear Habitat (2nd Order RSF) | 189 |
| Exposure | Range | Density of Bear Habitat (2nd Order RSF) | 189 |
| Exposure | Buffer 2000m | Density of Bear Habitat (Caribou Range RSF) | 189 |
| Exposure | Buffer 500m | Density of Bear Habitat (2nd Order RSF) | 189 |
| Exposure | Buffer 1000m | Density of Wolf Habitat | 189 |
| Exposure | Buffer 1500m | Density of Wolf Habitat | 189 |
| Exposure | Buffer 1000m | Density of Bear Habitat (2nd Order RSF) | 189 |
| Exposure | Buffer 1500m | Density of Bear Habitat (2nd Order RSF) | 189 |
| Exposure | Range | Density of Wolf Habitat | 189 |
| Exposure | Buffer 2000m | Density of Bear Habitat (2nd Order RSF) | 189 |
| Exposure | Local | Distance to Wolf Habitat | 189 |
| Exposure | Calving Area | Density of Wolf Habitat | 189 |
| Exposure | Local | Distance to Bear Habitat (Caribou Range RSF) | 189 |
| Exposure | Buffer 500m | Density of Wolf Habitat | 189 |

# CHAPTER 6

## GENERAL CONCLUSIONS AND RECOMMENDATIONS

Predation exerts a strong selective pressure on animal morphology and behaviour, resulting in a multitude of life history strategies in prey species for reducing predation effects (Dawkins & Krebs 1979; Lima & Dill 1990; Creel & Christianson 2008). In North American ungulates, such life history strategies generally fall on a continuum between those that allow spatial coexistence with predators (e.g. wolves [*Canis lupus*], mountain lions [*Puma concolor*], and bears [*Ursus* spp.]) and those that spatially separate predator and prey. For the former strategy, adaptations such as large size (e.g. moose [*Alces alces*], Haber 1977) and high escape speed (e.g. white-tailed deer [*Odocoileus hemionus*], Sweeney *et al.* 1971) can reduce the probability of death on predator encounter while high reproductive rates can offset predation losses (Pimlott 1959; Ghalambor & Martin 2001). For species that spatially separate, physiological adaptations allow them to subsist in environments that are less conducive to other ungulates, which reduces predator encounters because predators track other, more abundant ungulate prey (Huggard 1993; James *et al.* 2004).

Spatial separation is central to the life history strategy of boreal caribou (Rettie & Messier 2000; Bergerud *et al.* 2008) and results of this thesis demonstrate that the importance of space and habitat selection – key components of spatial separation – intensifies during the calving season. Just prior to the onset of calving, parturient females disperse widely on the landscape, effectively using increased space among conspecifics to reduce predation risk to vulnerable neonate calves (*Chapter 3*; Bergerud & Page 1987). I evaluated potential evolutionary drivers of this spacing behaviour in *Chapter 3*, finding that spatial dispersion increased individual fitness because it eliminated the possibility of multiple calves being killed on predator encounter if caribou were to remain grouped. Notably, I did not explicitly evaluate how this dispersion strategy is affected in multi-use landscapes undergoing human-induced rapid environmental change (*sensu* Sih *et al.* 2011). My results, however, suggest that if environmental change causes females to become increasingly clumped, then rates of calf survival may be negatively affected, a mechanism that could be contributing to the current low rates of calf recruitment reported in many declining populations (Environment Canada 2008). Such clumping could occur from behavioural responses to disturbance (e.g. avoidance of cut blocks; Fortin *et al.* 2013) or if permanent landscape structures restrict pre-calving migratory-type movements (e.g. permanent above-ground pipelines; Muhly *et al.* 2015, *in review)*.

Within this dispersion strategy, results from *Chapter 4* indicate that females selected calving areas to increase spatial separation from other ungulates and predators. Females with neonates showed increased avoidance of uplands compared to other seasonal periods, a response indicative of a strengthening of spatial separation from areas selected by moose (James *et al.* 2004; McLoughlin *et al.* 2011). Moreover, females selected landscapes dominated by large peatland complexes, a habitat-type relatively avoided by moose (James *et al.* 2004; McLoughlin *et al.* 2011). Females with neonates also showed stronger avoidance of disturbed areas, presumably because these areas are selected by predators (Latham *et al.* 2011b; Courbin *et al.* 2013; Tigner *et al.* 2014).

Yet, despite these predation-sensitive behaviours, the spatial strategies of maternal female caribou clearly have reduced effectiveness in highly modified landscapes, as evidenced by high rates of neonate mortality in many populations (Stuart-Smith *et al.* 1997; Pinard *et al.* 2012; DeMars & Boutin 2014). In *Chapter 5*, I investigated how spatial scale might influence the effectiveness of calving habitat use and selection strategies as reflected by the probability of neonate survival. Surprisingly, I found no direct effects from disturbance features (e.g. linear features, well sites) across the scales assessed; rather, neonate survival was best explained by a relatively fine-scale model (within-calving area) representing predation risk from black bears. This result, however, does not preclude the influence of landscape disturbance on neonate predation rates. Landscape disturbance may indirectly influence predator numbers by facilitating an increase in alternative prey or resources (e.g. forbs and grasses for bears; Mosnier *et al.* 2008b) and high predator numbers may swamp any effect of spatial pattern on predation rates (McCutchen 2007). Understanding the interacting effects of space and disturbance density – and their resultant effect on predator numbers – will be key to understanding how much space is needed by caribou to effectively reduce predation risk.

### *Management Implications and Future Research*

Results from this thesis have direct implications for managing population of boreal caribou. The methods developed in *Chapter 2* have particular relevance for monitoring caribou demography. I used these movement-based methods to identify calving events and predict neonate survival, primarily to isolate GPS locations of females accompanied by neonate calves. These methods, however, could be used to assess and monitor trends in parturition and neonate survival. GPS radio-collars are frequently deployed on samples of female caribou for other management objectives; for example, to monitor survival (Hervieux *et al.* 2013), understand space use (Nagy 2011), and identify habitat requirements (this thesis; DeCesare *et* *al.* 2012). The methods in *Chapter 2* provide an avenue for increasing the amount of information that could potentially be extracted from GPS collar data. Monitoring changes in parturition could yield insights into changing forage quality (Parker *et al.* 2009) or identify potential outbreaks of disease or parasites (Schwantje *et al.* 2014), though such effects are unlikely to be significant factors in current caribou declines (Festa-Bianchet *et al.* 2011; McLellan *et al.* 2012). Moreover, comparing rates of neonate survival with annual recruitment surveys could indicate which seasonal periods have the highest influence on juvenile recruitment.

Results from *Chapters 3* through *5* have direct relevance for managing calving habitat for boreal caribou in multi-use landscapes. Importantly, they highlight a number of challenges. First and foremost is the issue of spatial scale. Management actions aimed at improving the quality of calving habitat will need to be conducted at large spatial scales because (*i*) compared to other seasons, boreal caribou are at their most dispersed during calving; and (*ii*) management actions employed at small spatial scales (e.g. the calving area scale) will be ineffective at improving rates of neonate survival. Because many female caribou migrate to landscape mosaics dominated by nutrient-poor fens, I suggest that potential management actions are best targeted toward large fen complexes. While providing specific recommendations on the most appropriate spatial scale for management actions remains difficult, such scales may need to exceed 100 km$^2$ – the approximate size of the largest calving area my study – and that larger scales are likely better.

The link of caribou population declines to landscape disturbance dictates that management actions will need to address habitat restoration (Environment Canada 2012).

Such actions, however, are necessarily long-term; for example, seismic lines in lowland black spruce (*Picea mariana*) forests can take > 50 years to recover (Lee & Boutin 2006; van Rensen *et al.* 2015). For some caribou herds, current population trends point to extirpation before the effects of habitat restoration are realized (Schneider *et al*. 2010). For such herds where calf recruitment is a limiting factor, short-term actions such as maternal penning (Chisana Caribou Recovery Team 2010) or predator control (Mosnier *et al.* 2008a; White *et al.* 2010; Hervieux *et al.* 2014) may be necessary to augment habitat restoration. For the latter option, my results highlight the need to understand the specific predator(s) contributing disproportionately to calf mortality rates. In addition to these options, ongoing initiatives assessing line de-activation techniques (e.g. fencing, coarse woody debris) may hold promise but their efficacy in reducing predation rates is currently unknown.

Collectively, my findings from this thesis provide a basis for understanding the habitat requirements of boreal caribou during the calving season. To build upon the results of my research, I suggest the following avenues for further investigation:

1. Effectively managing for caribou calving habitat requires understanding the full continuum of calving behaviour. To that end, I recommend:
    a. An assessment of female fidelity to calving areas, particularly if potential management actions include the protection of predicted calving areas within caribou range. Research into site fidelity has been equivocal, partly because of differences in the way fidelity has been measured (Schaefer *et al.* 2000; Rettie & Messier 2001; Faille *et al.* 2010). I was unable to assess site fidelity due to the limited number of radio-collared females calving in multiple seasons. Movement

patterns of these animals, however, are suggestive of fidelity as most travelled along similar routes from winter ranges to calving areas in successive years (*personal observation*).

   b. Identifying attributes of movement corridors used by females travelling from winter ranges to calving areas.

2. The role of bear predation in population declines of boreal caribou in western ranges requires further investigation.

   Results from *Chapter 5* suggested that predation risk from black bears had a strong influence on mortality rates of neonate calves. Black bear predation has been identified as a limiting factor in many ungulate populations (Zager & Beecham 2006; White *et al.* 2010) including caribou (Ballard 1994) although for boreal caribou much of the focus on black bear – caribou dynamics has been restricted to eastern populations (Mosnier *et al.* 2008a; Bastille-Rousseau *et al.* 2011; Pinard *et al.* 2012 but see Latham *et al.* 2011a). For western populations, understanding the influence of black bear predation on caribou demography should be a priority to inform effective caribou management strategies (see also *Management Implications* in *Chapter 5* for further discussion).

3. Understanding the interacting effects of space, disturbance and predator numbers on caribou predation rates.

   As mentioned above, these three parameters likely govern the effectiveness of spatial separation as a strategy for reducing predation risk. Individually, estimates correlating with caribou population stability exist for all three parameters but each is accompanied by uncertainties. For predators, Bergerud & Elliot (1986) suggested that caribou populations decline when wolf numbers exceed 6.5/1000 km$^2$. This estimate, however, does not account for the potential influence of disturbance, which may enhance the functional response of predators (McKenzie *et al.* 2012), leading to a possible lowering of this threshold. For disturbance, estimates of thresholds have been identified in the federal *Recovery Strategy*, which suggests caribou populations are stable when disturbance impacts are limited to ≤ 35% of a population's range (Environment Canada 2012). Range sizes for caribou, however, differ by an order of magnitude and for small ranges in particular, it is unknown whether meeting this threshold would result in population stability if the surrounding landscape remained highly impacted (Wiersma *et al.* 2004). In terms of space, Nagy (2011) suggested that caribou populations are stable when intact patch sizes are > 500 km$^2$. As noted in *Chapter 5*, this analysis was affected by a small sample size and a north-south latitudinal gradient (i.e. northern populations were more stable). Moreover, patch size is likely correlated with the density of disturbance (Fahrig 2003), making it difficult to disentangle these two effects. Isolating such effects is difficult in an empirical setting, requiring either *i*) experimental manipulation or replication of disturbance densities over large spatial areas, or *ii*) contrasting similarly sized and positioned caribou ranges with sufficient variation in disturbance density, a requirement that would severely limit sample size. Because of these logistical challenges, I suggest that insights into the spatial requirements of boreal caribou may be gained through simulation analyses similar to those in *Chapter 3* or in McCutchen (2007) where the relative effects of each parameter can be controlled.

## LITERATURE CITED

Ballard, W.B. (1994). Effects of black bear predation on caribou - a review. *Alces*, **30**, 25–35.

Bastille-Rousseau, G., Fortin, D., Dussault, C., Courtois, R. & Ouellet, J.-P. (2011). Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography*, **34**, 588–596.

Bergerud, A.T. & Elliot, J.P. (1986). Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology*, **64**, 1515–1529.

Bergerud, A.T., Luttich, S.N. & Camps, L. (2008). *The return of caribou to Ungava*. McGill-Queen's University Press. 586 pp.

Bergerud, A.T. & Page, R.E. (1987). Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology*, **65**, 1597–1606.

Chisana Caribou Recovery Team. (2010). *Recovery of the Chisana caribou herd in the Alaska / Yukon borderlands: captive-rearing trials*. Yukon Fish and Wildlife Branch.

Courbin, N., Fortin, D., Dussault, C., Fargeot, V. & Courtois, R. (2013). Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey (J. Newman, Ed.). *Journal of Animal Ecology*, **82**, 1062–1071.

Creel, S. & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.

Dawkins, R. & Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **205**, 489–511.

DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., Bradley, M., Whittington, J., Smith, K.G. & Morgantini, L.E. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, **22**, 1068–1083.

DeMars, C.A. & Boutin, S. (2014). *Assessing spatial factors affecting predation risk to boreal caribou calves: implications for management. Final report.* Report prepared for the Science, Community and Environmental Knowledge fund, Victoria, BC.

Environment Canada. (2012). *Recovery strategy for the woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa, ON. xi + 138pp.

Environment Canada. (2008). *Scientific review for the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal population, in Canada*. Environment Canada, Ottawa, ON. 72 pp. plus 180 pp. Appendices.

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

Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H. & Dussault, C. (2010). Range fidelity: The missing link between caribou decline and habitat alteration? *Biological Conservation*, **143**, 2840–2850.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D. & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology*, **89**, 419–434.

Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Tye Gingras, C., Moorcroft, P.R., Courtois, R. & Dussault, C. (2013). Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. *The American Naturalist*, **181**, 827–836.

Ghalambor, C.K. & Martin, T.E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, **292**, 494–497.

Haber, G.C. (1977). *Socio-ecological dynamics of wolves and prey in a subarctic ecosystem*. Ph.D. dissertation. University of British Columbia, Vancouver, BC.

Hervieux, D., Hebblewhite, M., DeCesare, N.J., Russell, M., Smith, K., Robertson, S. & Boutin, S. (2013). Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology*, **91**, 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. *Canadian Journal of Zoology*, **92**, 1029–1037.

Huggard, D.J. (1993). Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology*, **71**, 130–139.

James, A.R., Boutin, S., Hebert, D.M. & Rippin, A.B. (2004). Spatial separation of caribou from moose and its relation to predation by wolves. *The Journal of Wildlife Management*, **68**, 799–809.

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

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

Lee, P. & Boutin, S. (2006). Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. *Journal of Environmental Management*, **78**, 240–250.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

McCutchen, N.A. (2007). *Factors affecting caribou survival in northern Alberta: the role of wolves, moose, and linear features*. Ph.D. thesis, University of Alberta, Edmonton, AB.

McKenzie, H.W., Merrill, E.H., Spiteri, R.J. & Lewis, M.A. (2012). How linear features alter predator movement and the functional response. *Interface Focus*, **2**, 205–216.

McLellan, M.L., Serrouya, R., McLellan, B.N., Furk, K., Heard, D.C. & Wittmer, H.U. (2012). Implications of body condition on the unsustainable predation rates of endangered mountain caribou. *Oecologia*, **169**, 853–860.

McLoughlin, P.D., Wal, E.V., Lowe, S.J., Patterson, B.R. & Murray, D.L. (2011). Seasonal shifts in habitat selection of a large herbivore and the influence of human activity. *Basic and Applied Ecology*, **12**, 654–663.

Mosnier, A., Boisjoly, D., Courtois, R. & Ouellet, J.-P. (2008a). Extensive predator space use can limit the efficacy of a control program. *Journal of Wildlife Management*, **72**, 483–491.

Mosnier, A., Ouellet, J.-P. & Courtois, R. (2008b). Black bear adaptation to low productivity in the boreal forest. *Ecoscience*, **15**, 485–497.

Muhly, T., Serrouya, R., Neilson, E., Li, H. & Boutin, S. (2015). Influence of in-situ oil sands development on caribou (Rangifer tarandus) movement. *PLoS ONE*, *in review*.

Nagy, J.A. (2011). *Use of space by caribou in northern Canada*. Ph.D. thesis. University of Alberta, Edmonton, AB.

Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.

Pimlott, D.H. (1959). Reproduction and productivity of Newfoundland moose. *The Journal of Wildlife Management*, **23**, 381.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D. & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, **76**, 189–199.

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. *Biological Conservation*, **184**, 127–135.

Rettie, W.J. & Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.

Rettie, W.J. & Messier, F. (2001). Range use and movement rates of woodland caribou in Saskatchewan. *Canadian Journal of Zoology*, **79**, 1933–1940.

Schaefer, J.A., Bergman, C.M. & Luttich, S.N. (2000). Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology*, **15**, 731–739.

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

Schwantje, H., Macbeth, B.J., Kutz, S. & Elkin, B. (2014). *British Columbia boreal caribou health program progress report: year 1 (November 1, 2013 - December 31, 2014)*. Report prepared for the Science, Community and Environmental Knowledge fund, Victoria, BC.

Sih, A., Ferrari, M.C.O. & Harris, D.J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**, 367–387.

Stuart-Smith, K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M. & Rippin, A.B. (1997). Woodland caribou relative to landscape patterns in northeastern Alberta. *The Journal of Wildlife Management*, **61**, 622–633.

Sweeney, J.R., Marchinton, R.L. & Sweeney, J.M. (1971). Responses of radio-monitored white-tailed deer chased by hunting dogs. *The Journal of Wildlife Management*, **35**, 707.

Tigner, J., Bayne, E.M. & Boutin, S. (2014). Black bear use of seismic lines in Northern Canada. *The Journal of Wildlife Management*, **78**, 282–292.

White, C.G., Zager, P. & Gratson, M.W. (2010). Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *Journal of Wildlife Management*, **74**, 355–369.

Wiersma, Y.F., Nudds, T.D. & Rivard, D.H. (2004). Models to distinguish effects of landscape patterns and human population pressures associated with species loss in Canadian national parks. *Landscape Ecology*, **19**, 773–786.

Zager, P. & Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus*, **17**, 95–108.