

# SCALING UP THE ROLE OF PREDATION IN CARIBOU DECLINES IN WEST-CENTRAL ALBERTA (REDWILLOW, NARRAWAY, REDROCK PRAIRIE CREEK, A LA PÊCHE AND LITTLE SMOKY RANGES)

## Interim Report Deliverables of Year 2011



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## DISCLAIMER

This progress report contains preliminary data from ongoing academic research directed by the University of Calgary and Montana that will form portions of graduate student theses and scientific publications. Results and opinions presented herein are therefore considered preliminary, to be interpreted with caution and are subject to revision.

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## 1.0 INTRODUCTION

*This report relates to accomplishments and deliverables for the Year 2011. This project is designed to last 2 more years. Therefore, other objectives will be addressed in subsequent reports. In addition, due to finalization of the project agreement, our funding started in Spring 2011. Therefore our field activities occurred only for 6 months in 2011.*

Woodland caribou (*Rangifer tarandus caribou*) are classified as threatened in Alberta (under the Alberta Wildlife Act) and nationally (under the Species at Risk Act, COSEWIC 2002), with many local populations in decline throughout their range. This decline is largely attributed to anthropogenic activities that are altering predator-prey dynamics (Alberta Woodland Caribou Recovery Team 2005). In Alberta, woodland caribou are divided into the Boreal and Mountain caribou ecotypes (Alberta Woodland Caribou Recovery Team 2005). Our study supports this division and demonstrates its significance in the greater ecological and evolutionary dynamics of caribou (McDevitt et al. 2009). In the Fall of 2006, an interdisciplinary and multi-university research project led by Mark Hebblewhite and Marco Musiani was initiated to broadly determine causes for declines in threatened woodland caribou populations in west-central Alberta (the mountain ecotype) and east-central British Columbia. Core funding was obtained for the periods 2007-2009 and for 2011 provided by the Petroleum Technology Alliance of Canada in association with the Canadian Association of Petroleum Producers. Additional project funding has included the University of Montana, the University of Calgary, Shell Canada, Weyerhaeuser Company and Parks Canada Agency. Collaborating government agencies include Alberta Sustainable Resource Development – Fish and Wildlife Division, Alberta Community Development and Parks (Willmore Wilderness and Kakwa Wildland Provincial Parks), British Columbia Ministry of Environment, BC Provincial Parks, BC Ministry of Forests and the Foothills Research Institute (formerly Foothills Model Forest). Collaborating researchers include Dr. Fiona Schmiegelow, Dr. Greg McDermid and his lab at the University of Calgary, and Dr. Stefano Mariani at the University of Dublin. This report describes research over the Year 2011 period from.

An agreement with Parks Canada was enacted to support specific research directed to address woodland caribou predator-prey dynamics with relevance towards reintroduction planning for Banff National Park. Our group believes that the principles applied in our research inside Parks also apply out of Parks—our models are currently being modified for use outside parks.

### 1.1 PROJECT OVERVIEW

Our primary goal is to address the relative contributions of forestry and oil and gas production to the decline of caribou populations. This knowledge can then be used to develop appropriate conservation strategies across the range of caribou in west-central Alberta and east-central British Columbia. This Year 2011 report describes findings related to the main knowledge gap stated in our approved PTAC proposal: how does wolf predation affect caribou mortality in the summer and which manageable-by-industry factors contribute to summer predation?

Two competing hypotheses, ‘Forestry Hypothesis’ and ‘Oil and Gas Hypothesis’, are thought to drive caribou decline. The ‘Forestry Hypothesis’ states that improved habitat (due to timber practices) for primary prey of wolves (moose, deer) increases wolf numbers and consequently increases predation on caribou (Weclaw and Hudson 2004, Lessard 2005, Sorenson et al. 2008). Whereas, the ‘Oil and Gas Hypothesis’ states that efficient travel by predators on linear features (roads, seismic lines, trails),

especially during the winter, leads to increased caribou encounters and kills (James and Stuart-Smith 2000, Dyer et al. 2002, Neufeld 2006). Our projects clearly indicated wolf predation pressure on caribou during the summer (see Section 6.0) when the ‘Oil and Gas Hypothesis’ should be weaker because many caribou migrate to less-impacted areas in the mountains. We are quantifying summer predation to reassess the contribution of ‘Oil and Gas’-related features to caribou mortality through predation. In our study area, summer ranges of migratory caribou are largely in undeveloped areas in the mountains where human effects are negligible, thus emphasizing the importance of understanding whether this high summer predation is ‘natural’ or human-induced through forestry or oil and gas. Summer predation by wolves on caribou, on both developed and undeveloped summer ranges, could potentially play a key role in the decline of caribou (see Section 5.0). During winter, wolves are nomadic, whereas during summer they are tied to a den, therefore, the kill-rate estimation methods developed for winter cannot work during summer. We have developed and are continuing to develop mechanistic movement models (see Section 3.0) to answer the summer predation question. We are using these mathematical models to understand the contribution of human factors (e.g., linear features attributable to oil and gas development vs. forestry) to predation of caribou.

With our project, Industry will benefit by improving its environmental performance through more informed planning and implementation. Our research currently benefits industry and the Canadian society at large and will continue to benefit by improving our understanding of the role of predation on caribou declines and the effects of forestry vs. oil and gas development on predation. The results of our research will guide predation-mitigation strategies—wolf control alone may not be the best management option to save caribou. In addition, we have developed and are developing habitat selection models that provide rigorous spatial mitigation strategies for companies operating in the region (see Section 4.0). Our ultimate goal is to assess the relative and cumulative importance of forestry and oil and gas on caribou declines, with implications for mitigation and protection strategies to recover caribou (integrative objective for 2012). We have applied population viability analysis (PVA) to a single meta-population (see Section 7.0) and are currently working towards ‘scaling-up’ our PVA approach to the next level by developing a multi-population matrix projection model for female woodland caribou throughout west-central Alberta.

## **1.2 PROJECT SCHEDULE**

As planned, two PhD projects were completed and relevant results were shared with the PTAC Project Manager, Mark Sherrington as well as with other PTAC members (e.g., Amit Saxena). It is our understanding that Mark and Amit shared our results with PTAC in writing and verbally. The two PhD students are currently writing their final dissertations, and submitting papers for publication in international peer-reviewed journals, some of which were already accepted. Overall, project status reports were sent to PTAC in Mar, Jun, Sep and Dec 2011, and focused on research applications towards the mitigation of human impacts. We thank Mark and Amit for their recent collaborative efforts to clarify some points of our project and refine ideas on tangible products and deliverables needed by Industry.

### *1.2.1 Resource selection and predation risk*

We worked with PTAC contacts in clarifying the terminology used in our project, so that now you can explain our approaches to those outside the wildlife biology field. With regard to this point, we particularly welcomed the opportunity to explain exactly what ‘scaling up’ means in the context of our



project. A paper is accepted (pending final revisions), which is titled: “Transcending scale-dependence in identifying habitat and threats for endangered species”. This paper is thus far well received and is currently In Press; we will send a finalized version when it is officially accepted for publication. Clearly, habitat selection (e.g., avoidance of human features) changes depending on the scale of its investigation. This paper, for the first time, thoroughly presents an approach for integrating scales of resource selection for caribou in west-central Alberta (see Section 4.0 for figures). Now that a number of industries need to be specific at a fine scale and at the same time comprehensive at the regional scale, this approach is ideal. A key point is that our approach is allowing development of habitat selection models that also provide rigorous spatial mitigation strategies for companies operating in the region. Implementation of such mitigation strategies at a regional scale seems especially needed under the Land Use Framework (LUF) of the Alberta Government.

In addition to findings explained in previous reports, our ongoing research into predator-prey dynamics is closing an important information gap regarding predation efficiency. Work conducted in cooperation with Jesse Whittington first identified an important increase in the probability of caribou-wolf encounters in close proximity to linear features within the national parks (Whittington et al. 2011 – *Journal of Applied Ecology*). Our recent follow-up analyses have extended this initial project by: (1) decomposing predation risk into the distinct probabilities of where wolves search for prey and where they successfully kill prey, and (2) compiling data across the entire west-central Alberta caribou range (from Banff to the Narraway/Redwillow). We are assessing how landscape footprint affects the spatial factors driving both wolf search and efficiency rates (Section 6.0). While our search rate analysis corroborates previous evidence that wolves travel disproportionately more on anthropogenic linear features while hunting, their rate of successful predation (i.e., efficiency) does not increase while traveling on these features. Consequently, the mechanism driving increased predation risk for prey on linear features appears to be consistent selection of these features for wolves while hunting, rather than increased efficiency while hunting. From there we spatially integrated these analyses to make a single map depicting predation risk as affected by both components of risk. This is the first mechanistic model of multi-prey predation risk usable for the ecologically unique conditions of west-central Alberta.

The next steps of analysis will include testing the spatial relationships between both our resource selection function models (Section 4.0) and our spatial predation risk model (Section 6.0) and adult female caribou survival. These next steps will test the important potential links between how landscape footprint drives resource selection, predation risk, and ultimately caribou demography and population dynamics.

### *1.2.2 Agent-based modeling of caribou behavioral response to development*

Research efforts also included agent-based modeling of caribou behavioral response to development (Section 3.0). This approach is being used for moving towards future scenario planning to understand caribou responses to industry.

To investigate the impact of forestry and energy activities in the range of the Little Smoky population, we have developed a spatially explicit, agent-based model (ABM) to simulate winter habitat selection and use of woodland caribou, and explore the underlying behavioural mechanisms they are most likely to employ when navigating their landscape. The ABM model is composed of cognitive caribou agents possessing memory and decision-making heuristics that act to optimize tradeoffs between energy acquisition and disturbance. A suite of environmental data layers was used to develop a virtual grid representing the landscape over which caribou move. This grid contains forage-availability, energy-

content, and predation-risk values. The model was calibrated with caribou bio-energetic values acquired from literature sources, and validated using GPS winter activity data from thirteen caribou radio-collars deployed over six months from 2004 to 2005. Simulations were conducted on alternative caribou habitat-selection strategies by assigning different fitness-maximizing goals to agents: energetics-and-predation vs. predation-insensitive vs. predation-hypersensitive strategies. The model outcomes were evaluated by verifying which resultant simulations of caribou movement patterns most closely matched real-world caribou distributions and other patterns extracted from the GPS data. The ‘Energetics and Predation’ scenario, in which the caribou agent must trade off the competing goals of obtaining its daily energy requirement, minimizing reproductive-energy loss, and minimizing predation risk, was the best-fit scenario. Not recognizing industrial features as predation risk (‘Predation-insensitive’ scenario) causes simulated caribou to unrealistically reduce their daily and landscape movements; equally, having predation risk take precedence (‘Predation-hypersensitive’ scenario) results in unrealistic energetic deficits and large-scale movement patterns, unlike those observed in real-world caribou.

These results elucidate the most likely behavioral strategies caribou use to select their habitat, the relative extent to which they perceive industry features as disturbance, and the differential energetic costs associated with each. This provides insight into why caribou choose the habitats they use and can assist future studies of how they may respond to novel changes in their environment related to mitigation and/or continued industrial development.

Other planned activities were also completed including:

*Summer kill-site modeling*

*Resource Selection Function Modeling for Moose (Peters et al., – currently In review)*

*Moose density modeling (Peters et al., - currently In review)*

*Hair gathering from bears, wolves, caribou and moose*

*Hair gathering from rarer species –e.g. snowshoe hare, mountain goats, bighorn sheep, and beaver*

*Stable isotope analyses on hairs to evaluate diet overlap between predators, caribou and other prey (e.g. moose) from isotope data*

*Production of Scientific and Spatial Databases*

*Public communication and dissemination of research results*

*Scientific Publications (6+) and Presentations at Conferences (25+) and at PTAC annual Forum*

## 2.0 ANIMAL CAPTURE AND RADIOCOLLARING

We used the capture and radio-collaring of adult caribou and wolves to monitor movements and survival of individuals across the range of conditions present in the study area. Specifically, we use GPS-enabled collars (Lotek-2200, 3300S, 3300M, 4400S, 4400M, Lotek Wireless, Inc., Newmarket, Ontario, Canada; ATS-G2000, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) to collect location data of high quality and quantity for fine-scale analysis of resource selection, predation and movement patterns.

Winter helicopter net-gunning was used to capture caribou and wolves (Andryk et al. 1983) and we supplemented these efforts with additional summer foot-hold trapping for wolves (Frame and Meier 2007). All animal capture procedures were approved by government and university animal care protocols and permitting processes (Table 2.1). Full details of animal capture protocols are available upon request from any project personnel.

**Table 2.1.** Research and collection permits, Canadian Rockies.

Alberta Sustainable Resource Development: Fish and Wildlife Division

**Collection Licenses: #21803, #27086, #27088, #27090**

**Research Permit: #27085, #27809, #27812**

Alberta Tourism, Parks, and Recreation

**Research and Collection Permits: RC08WC014 & Wilka101-07**



British Columbia Ministry of Environment: Permit and Authorization Service

**Wildlife Act Permit VI08-31411**

**Park Use Permits: 101964**



Parks Canada Agency

**Research and Collection Permit: JNP-2007-952**

**Research and Collection Permit: LL-2010-4392**



University of Montana

**Animal Use Protocol: 056-06MHECS-010207**

**Animal Use Protocol: 059-09MHWB-122109**



University of Calgary

**Animal Use Protocol: BI-2007-57**



## 3.0 DEVELOPMENT OF AN AGENT-BASED MODEL TO ASSESS THE INDUSTRY-INDUCED IMPACTS ON WOODLAND CARIBOU HABITAT SELECTION AND USE IN ALBERTA

The following work in this section is included in a peer-reviewed article currently in review:

Semeniuk, C. A. D., M. Musiani, M. Hebblewhite, S. Grindal, and D. J. Marceau. *In revision*. Incorporating behavioural-ecological strategies in pattern-oriented modelling of caribou habitat use in a highly industrialized landscape. *Ecological Modelling*.

### 3.1 SCOPE

To develop a spatially explicit agent-based model to simulate and recreate the movement behavioural strategies of caribou and to explore how and why caribou select and use their winter habitat.

### 3.2 SCHEDULE

- 2009 Extensive Literature Review for Model Parameterization
- 2010 Gather Spatial Data and Build GIS Database for ABM
- 2010 Build Conceptual Model and Code Agent-Based Model
- 2011 Calibrate Agent-Based Model
- 2011 Run Behavioural Scenarios with the Agent-Based Model
- 2011 Communication of Results (publications, conferences, etc.)
- 2012 Model caribou responses to habitat changes (spatiotemporal and bio-energetic)

### 3.3 INTRODUCTION

An unavoidable challenge in the conservation of endangered species is that their ecologies can sometimes be poorly or only broadly understood, making targeted conservation management particularly difficult. Woodland caribou (*Rangifer tarandus*) are classified as threatened in Canada and Alberta and a local population in the province's Foothills Region, the Little Smoky herd (LSM), is at immediate risk of extirpation due, in part, to anthropogenic activities such as forestry and oil and gas that have altered ecosystem dynamics. While much is known about caribou ecology, the behavioural mechanisms by which resource-extraction industries contribute to caribou population decline are less clear. As such, any management planned for LSM would benefit from (1) an understanding of the mechanisms driving caribou habitat use, and (2) an examination of how caribou respond to future changes in their environment. To address these issues, we have developed a spatially explicit, agent-based model (ABM) to simulate caribou movement behavior in Little Smoky.

### 3.4 METHODS

#### 3.4.1 Description of the study area

The Little Smoky (LSM) herd is located in the foothills of west-central Alberta, east of Grande Cache. Its range covers an approximate area of 3,100 km<sup>2</sup>. The study area is classed into Upper Foothills and Sub-Alpine Natural Subregions (AEP 1992), and contains several major rivers, many small creeks and a few lakes. Elevations range from 850 to 1500 m. The LSM range has the highest level of industrial development of any caribou herd in Canada, with 95% of its range in proximity (500 m buffer) of

anthropogenic activities (Environment Canada 2011a). At present, there is considerable development pressure from all fronts leading to the core of the range and increases in allocations to industrial users within caribou range (Robichaud 2009). The area of interest in this project covers 3,100 km<sup>2</sup> and represents the official political and biological range delineation of the Little Smoky herd by the Alberta Fish and Wildlife Division (ASRD and ACA 2010). Because Little Smoky is such a dynamically changing landscape due to industrial practices, we chose to confine our study to a single time period, and as such, all spatial and caribou data correspond to the winter of 2004-2005.

#### *3.4.2 Computational intelligence tool*

Agent-based models are computational simulation tools with origins in Artificial Intelligence that rely on a bottom-up approach that explicitly considers the components of a system (i.e., individual entities represented as agents), and attempts to understand how the properties of the system emerge from the interactions among these components (Grimm and Railsback 2005). Agents are coded to act independently of any controlling intelligence; they are goal-driven and try to fulfill specific objectives; they are aware of and can respond to changes in their environment; they can move within that environment; and they can be designed to learn and adapt their state and behavior in response to stimuli from other agents and their surroundings. This emphasis on interactions between agents and their environs is what distinguishes agent-based modeling from other systemic, analytic (i.e., statistical) modeling approaches (Tang 2008, Semeniuk et al. 2011).

Over the past fifteen years, ABMs have been applied to address a broad range of issues related to environmental resource management, such as water, forest, and agro-ecosystem management (Bousquet and Le Page 2004). ABMs have also been extensively used in ecology to study species relationships, population dynamics, and to understand how animals perceive, learn and adapt to their environment (Grimm and Railsback 2005). Recently, ABMs have begun being used cross-disciplinarily to address human-wildlife interactions and their management (for a review, see McLane et al. 2011).

The use of an agent-based model for our research is advantageous since dynamic interplay between agents and their environment is readily accommodated, realistic conditions can be approximated (such as movement costs across the landscape), and hypothetical scenarios can be simulated. These models are also amenable to tests of robustness and sensitivity (Grimm and Railsback 2005). The caribou ABM readily incorporates two critical ecological theories involved in habitat selection: animal movement ecology and behavioural ecology, and as such, the model can be used to understand the processes that govern movement, distribution and selection, and therefore predict how animals might respond to habitat loss, industrial features and other environmental change.

The caribou ABM comprises two main components which are described in detail below: (1) landscape representation of Little Smoky, and (2) caribou agents and their decision-making heuristics.

#### *3.4.3 Environmental data collection and preparation*

All geographic datasets used are described in detail in Hebblewhite et al. (2010). These datasets include vector representations of roads, pipelines, seismic lines, and well sites valid to the year 2005, and a raster-based digital elevation model (DEM) and land-cover map both at a spatial resolution of 30 m. The land-cover map is based on Landsat 5TM imagery of 2005 and includes 12 classes that are deemed to be biologically relevant to woodland caribou. For inclusion in the ABM model, all vector layers were rasterized to a resolution of 45 m, with the land-cover map and DEM resampled to the same resolution.

The 45 m resolution chosen represents an optimization of computational performance while reflecting the biologically realistic size of the foraging patch of caribou (Bailey and Provenza 2008). Furthermore, because actual caribou are sensitive to industrial features up to 250 m and 1 km away depending on their type (Dyer et al. 2002), this spatial resolution has no major biasing effect on the caribou agent's ability to perceive them.

For integration with the ABM, four raster maps were generated from the geographic datasets to represent the physical environment where the agents are located: (1) a forage-availability map, (2) an energetic-content map, (3) a predation-risk map, and (4) a digital elevation model. To provide an environment to the agents that allows their movement from one cell to the next cell, a virtual grid was overlaid on these four maps. Each cell in the ABM spatial environment therefore possesses four values: a forage-availability score, an energetic content, a predation-risk score and an elevation (m). Whereas forage-availability and predation-risk scores are fixed (and it is just the agent's willingness to respond to them that varies), the energy content of the cells is depleted (and hence varies) when agents forage.

#### *3.4.4 Caribou data collection and patterns for comparison*

Caribou data used to parameterize and validate the ABM were obtained from a database composed of radio-collared GPS location data of Alberta caribou (Hebblewhite et al. 2010). A total of 5225 location points were obtained for 13 female individuals from Little Smoky during winter (November-April) 2004-2005. Using caribou GPS point samples, the spatiotemporal distribution of each caribou was built and stored within an ArcGIS database as timestamps corresponding to a 4-hour interval. Other sources of biological information necessary for the caribou ABM parameterization and calibration include caribou agents' bio-energetic functions, spatial memory (working and reference), and learned decision-making processes. The values for these variables were either derived or obtained from an extensive literature review.

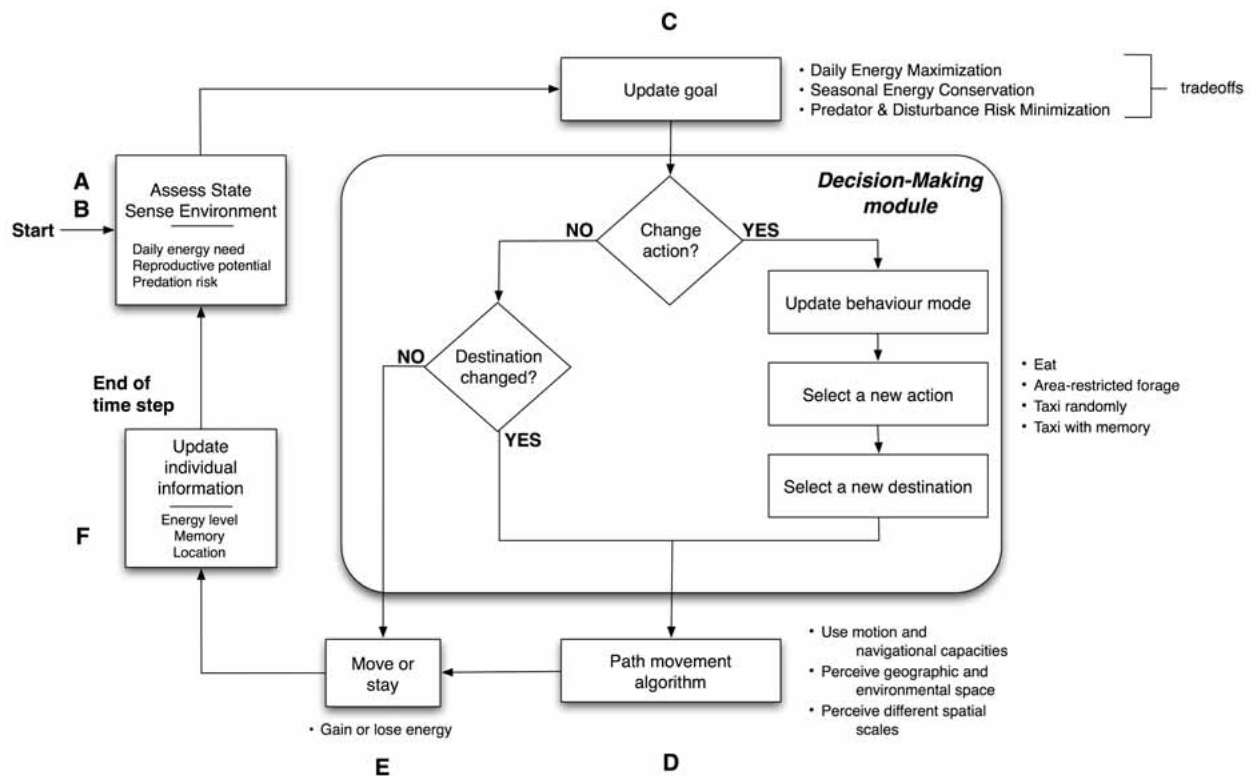
Several metrics were used to compare simulated and observed patterns for validation purposes. These were a combination of (1) spatiotemporal patterns, and (2) spatial distribution patterns at different scales. The spatiotemporal patterns we extracted from the caribou GPS-telemetry data include a description of landcover classes used, differences in use of landcover and elevation in early and late winter, differences in daily step lengths in early and late winter, and the presence of a daily peak in movement activity. The spatial distribution patterns used for comparison comprise: (1) the mean 100% minimum convex polygons (MCPs) for individuals (i.e., individual home range), (2) the total MCP (i.e., for herd range), and (3) the degree of overlap in areal coverage between actual herd MCP and simulated herd MCPs (to compare agreement in space used). These validation metrics were generated from point location data of simulated and real caribou and analyzed for land cover and elevation usage in ArcGIS 9.2. Minimum convex polygons and daily step distributions were calculated using Hawth's Tools in ArcGIS 9.2. All other simulated outputs were generated by NetLogo's (ABM software) reporting mechanism and analyzed in JMP 8.0 (SAS Inc.). For evaluating the different scenarios tested, the patterns were compared to those of actual caribou by a simple, summed ranking of the degree to which patterns were matched.

#### *3.4.5 Model conceptualization and implementation*

The underlying premise of the model is that an individual's internal state influences how it perceives its environment and hence drives its decision-making process (Houston and McNamara 1992). The model consists of one category of agents (the caribou) represented as a cognitive entity. It has a mental

representation of its environment, can plan its activities, and has a memory of profitable and safe patches. Specifically, the caribou agent can balance its needs to satisfy its daily energetic requirements against the need to minimize energetic loss in order to meet its long-term goal of reproductive success. The caribou must also consider its predation risk, for which it must also balance, since relatively safer locations are not always the most profitable.

Figure 3.1 illustrates the sequence of steps involved in the caribou agent's decision making as implemented in the ABM. At each time step, the agent first assesses its energetic state: it determines whether it has reached its daily energetic requirements and by what magnitude, and whether it will have enough energetic reserves (and by what magnitude) to have a successful birth at the end of the season ('A' in Figure 2.1). At this stage it also senses the immediate risk in its environment as well as the forage availability ('B'). It then determines which fitness-maximizing goal is most important to trade off against the others, and does so by assessing which goal has reached a minimum threshold. Based on this decision-making heuristic ('C'), the agent either forages, ruminates, or moves to a new location ('D'). The agent then updates its energy reserves, both gained and lost through its actions ('E'), and commits to memory any profitable or safe locations encountered ('F').



**Figure 3.1.** Steps involved in the caribou agent's decision making (modified from Chion et al. 2011).

Caribou agents forage, rest/ruminate, and travel on a 3,100 km<sup>2</sup> grid surface (1786 x 1619 cells). One time step in the model represents 30 min., which is an appropriate temporal resolution to capture the variability of foraging behaviours characteristic of ungulates at the spatial level of the food patch (Owen-Smith et al. 2010). The model simulates, over a period of 180 days, the span of winter in Alberta.

### 3.4.6 Behavioural-strategy scenarios

Because energy acquisition, energy conservation, and predation-risk minimization are issues which researchers deem important to caribou in winter (e.g., Cameron et al. 1993, Bradshaw et al. 1998, Parker et al. 2005), we have chosen to test these three main behavioural strategies with alternative hypotheses in the caribou ABM, beginning with the full model and then decomposing the framework into biologically-relevant alternative strategies:

- The caribou agent's goal is to find an optimal balance between its daily energetic requirements (**D**), its longer-term reproductive energy requirements (**R**), and its predation-risk minimization (**P**). Known as the 'Energetics and Predation' scenario (**DRP**);
- Industrial features are not deliberately avoided. Known as the 'Predation-insensitive' scenario (**DR**);
- Minimizing risk takes precedence over maximizing daily energy and minimizing reproductive energy loss. Known as the 'Predation-hypersensitive' scenario (**P**).

In the 'Predation-insensitive' scenario, the agent does not perceive industrial features as being any more risky than that of the surrounding environment. Therefore, industrial features take on the predation risk value of their immediate neighbours: a cutblock reverts to a low predation risk score (equivalent to closed conifer forest) but retains its low forage availability and a linear feature (one pixel wide, but many pixels long) takes on the majority value of its eight neighbours). Agent rules remain unchanged. With the 'Predation-hypersensitive' scenario, the agent concerns itself with minimizing predation risk only and assumes that a minimal daily-energy gain is sufficient and that reproductive loss is not an issue. Consequently, the agent is driven to reach its daily minimum energetic requirement only. Once reached, it concerns itself with minimizing risk. However, if the degree of risk is high, the agent will ignore its current energy level (unless it is excessively low).

### 3.4.7 Model calibration

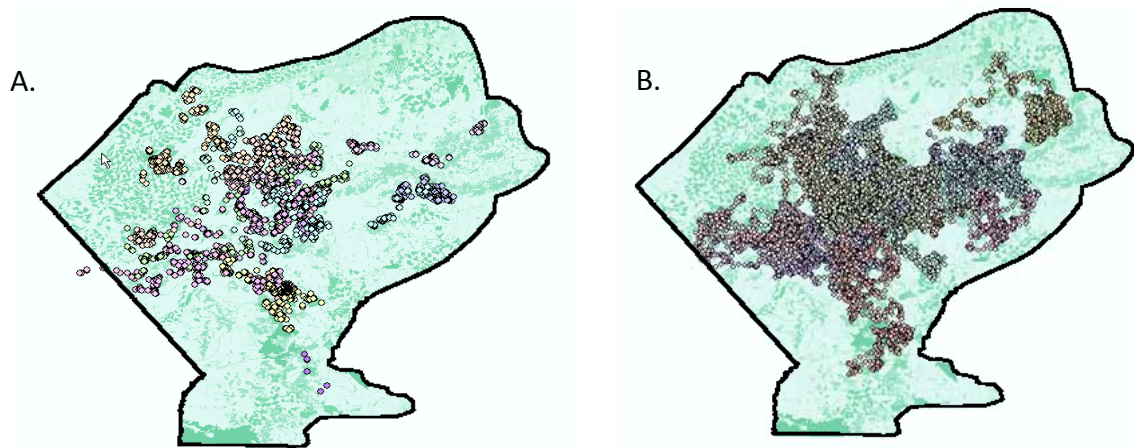
Recognizing that an individual's internal state influences its behaviours is critical to reproducing realistic patterns. Therefore, our model reflected actual bio-energetics of caribou, which was determined through a rigorous calibration process of caribou metabolic rates. The final values chosen for all scenarios in the ABM were based on whether each produced simulated energetic outputs consistent with three criteria: (1) the daily energy gain by agents is within known reported ranges (22-33 MJ day<sup>-1</sup>, McEwan and Whitehead 1970, Boertje 1985); (2) the daily energetic expenditure approaches that which has been reported for free-living *Rangifer tarandus* during winter (28.7 MJ day<sup>-1</sup>; Gotaas et al. 2000); and (3) the proportion of time spent foraging (i.e., ingestion and rumination combined with area-restricted searching) is between 50% and 85% of the agent's daily activity budget (Rominger et al. 1996, Kumpula 2001).

## 3.5 SUMMARY OF RESULTS

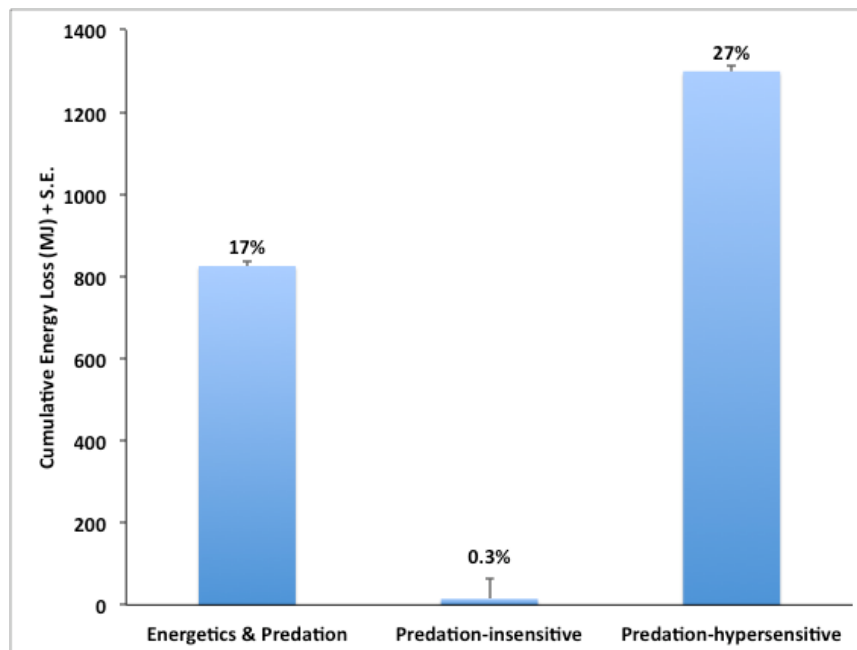
The model outcomes were evaluated by verifying which resultant simulations of caribou movement patterns most closely matched actual LSM caribou distributions and behavioural patterns extracted from the GPS data. The 'Energetics and Predation' scenario, in which the caribou agent must trade off the mutually competing goals of obtaining its daily energy requirement, conserving its reproductive energy and minimizing predation risk, was the best-fit scenario (Figure 3.2, Tables 3.1 and 3.2). Not recognizing industrial features as predation risk ('Predation-insensitive' scenario) causes simulated



caribou to unrealistically conserve energy, and reduce their daily and landscape movements; equally, having predation risk take precedence over maximizing energy acquisition and conservation ('Predation-hypersensitive' scenario) results in unrealistic energetic deficits and large-scale movement patterns, unlike those observed in actual caribou (Figures 3.3 and 3.4).



**Figure 3.2.** A. Spatial distribution of actual LSM caribou, winter 2004-2005. B. Simulated spatial distribution of 13 caribou agents.



**Figure 3.3.** Mean cumulative energy lost over winter for agents in each alternative scenario. Values over bars correspond to percent body mass lost assuming a 132 kg pregnant female.

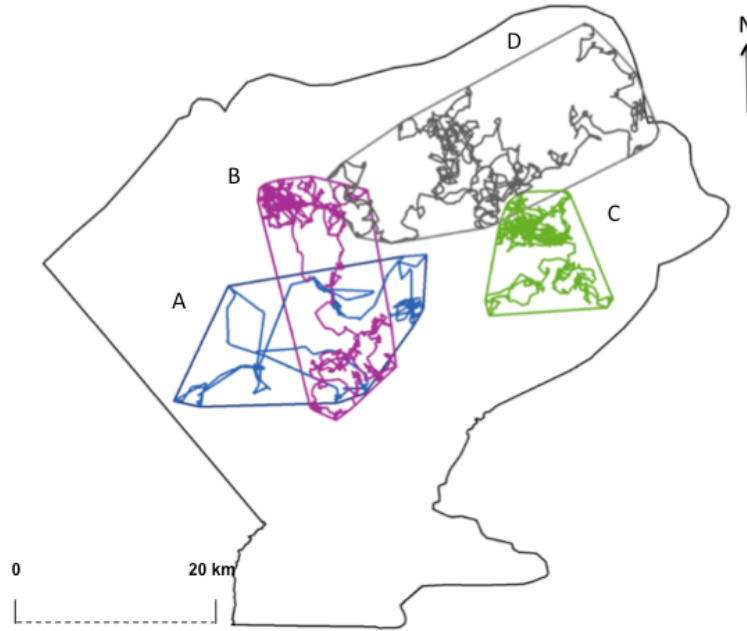
**Table 3.1.** Ranking of spatiotemporal, descriptive patterns by how closely they match patterns of actual caribou in the Little Smoky herd.

Scenario	Spatiotemporal Patterns					Overall Ranking (Total score)
	Landcover Ranking	Change in Landcover Use	Increase Use of Lower Elevation	Decrease in Daily Distance	Peak in Daily Activity	
Energetics & Predation (DRP)	1	2	1	1	1	1 (6)
Predation-insensitive (DR)	2	1	1	3	1	2 (8)
Predation-hyper-sensitive (P)	3	1	1	2	2	3 (9)

**Table 3.2.** Comparison of actual and simulated scenarios of spatial distribution patterns.

Numerical Patterns	Actual	Energetics & Predation (DRP)	Predation-insensitive (DR)	Predation-hypersensitive (P)
Mean Individual MCP* in km <sup>2</sup> (+ S.E.)	271 (38)	297 (37)	153 (19)	458 (57)
Herd MCP* in km <sup>2</sup>	1867	2578	2628	3611
Proportion Spatial Overlap	1	0.715	0.709	0.517
Overall Rank		1	2	3

\*MCP = Minimum Convex Polygon



**Figure 3.4.** Spatial trajectories of an actual female from the Little Smoky herd ('A') and three individual agents ('B', 'C', 'D') from alternate scenarios, each closely representing the mean individual minimum convex polygon. B = Energetics & Predation scenario; C = Predation-insensitive scenario; D = Predation-hypersensitive scenario.

### 3.6 IMPLICATIONS

Our detailed study of caribou movement offered insight into caribou tradeoff processes as the ultimate confluence of individual behaviour, physiological constraints and fine-scale environmental influences (Patterson et al. 2008). Established patterns helped us to develop a model with enough detail to reproduce the system's essential dynamics based in physiological realism yet without excess complexity (Railsback and Johnson 2011). While all three scenarios were calibrated to faithfully reproduce daily caribou bio-energetics coupled with foraging time budgets known from literature sources, there existed enough variation in the alternative scenarios that when we compared how well they satisfied the multiple patterns of actual caribou, we were able to show that one hypothesis was useful for modeling caribou of the Little Smoky herd. The scenario that most consistently produced patterns that coincided with actual caribou data was 'Energetics & Predation'. In this scenario, each of the three behavioural strategies (acquiring energy for daily use, conserving energy for reproductive needs, and minimizing predation) was given consideration whenever the need arose, with energetic needs taking precedence. This outcome sheds light on the underlying motivations of overwintering caribou and can be used in further simulation experiments to investigate responses of caribou to future changes in their environment.

Although critical habitat for LSM caribou has been defined (Environment Canada 2011b), we currently do not have a firm grasp on *why* caribou are using this habitat and in which way caribou may respond to future recovery plans of this environment. By considering the actions of the individual, such information aids in quantifying animal-habitat relationships, describing and predicting differential space use by animals and ultimately identifying habitat that is important to an animal (Beyer et al. 2010). Therefore, our caribou ABM sheds light on caribou behaviours, which can contribute to discussions and assessments of boreal caribou recovery plans. Two broad management strategies proposed for boreal caribou are currently under consideration by the Canadian federal government: (1) to undertake

coordinated and comprehensive landscape-level planning for caribou ranges, and (2) conduct population monitoring (for which our ABM may be particularly informative) to manage both caribou mortality and habitat to meet current and future habitat requirements (Environment Canada 2011b). Our best-fit scenario demonstrates that caribou (in LSM) are sensitive to industrial features on the landscape; features that evoke anti-predator responses and bio-energetic costs even in the absence of any explicit predator models. In essence, mortality tools such as managing predators and alternate prey may help to stabilize population growth rate ( $\lambda$ ), but functional habitat loss (which ensues energetic costs) is still a serious issue.

### **3.7 OUTLOOK: SCENARIO-PLANNING**

With our behavioural baseline now established, it would be of interest to explore how changes to the LSM, in terms of future mitigation or development, would alter the spatiotemporal distribution of caribou as well as their bio-energetics. Because conservation planning of wildlife habitats also involves the analysis of habitat-linked population demographics under various land-use development scenarios, the ABM can be used as a scenario-planning tool. By considering multiple possible future landscapes within a spatially-explicit context and then modeling caribou responses to the changes in their habitat (both spatiotemporal and bio-energetic), scenario planning with ABMs can offer managers a method for creating more resilient conservation policies. This direction is the next phase of our research. ABMs increase understanding of key uncertainties and allow alternative perspectives to be incorporated into conservation planning, which provides greater resilience of decisions to surprise (McLane et al. 2011).

### **3.8 FUTURE DIRECTIONS**

An understanding of the mechanisms driving caribou habitat use allows us to examine how caribou would respond to future changes in their environment. Currently, we are developing future plausible Little Smoky landscapes, projected to the year 2025, where the caribou ABM will explore how changes in landscape development affect caribou habitat, habitat use and caribou fitness.

## 4.0 TRANSCENDING SCALE DEPENDENCE IN IDENTIFYING WOODLAND CARIBOU HABITAT WITH RESOURCE SELECTION FUNCTIONS

The following work in this section is included in a peer-reviewed article currently In Press:

DeCesare, N. J., M. Hebblewhite, F. K. A. Schmiegelow, D. Hervieux, G. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. *In Press*. Transcending scale-dependence in identifying habitat with resource selection functions. *Ecological Applications*.

### 4.1 SCOPE

To assess resource selection of caribou with respect to both natural and anthropogenic features and develop a spatial model of habitat suitability that is integrated across scales of selection.

### 4.2 SCHEDULE

- 1998–2009 GPS radio-collaring and monitoring of caribou by partner agencies
- 2010 Build and compile background GIS layers
- 2010 Compile caribou GPS data
- 2011 Statistical analysis and writing
- 2011 Acceptance to peer-reviewed journal (*Ecological Applications*)
- 2012 Expected publication of article in journal

### 4.3 ABSTRACT

Multi-scale resource selection modeling is used to identify factors that limit species distributions across scales of space and time. This multi-scale nature of habitat suitability complicates the translation of inferences to single, spatial depictions of habitat required for conservation of species. We estimated resource selection functions (RSFs) across three scales for a threatened ungulate, woodland caribou (*Rangifer tarandus caribou*), with the following two objectives: (1) to infer the relative effects of two forms of anthropogenic disturbance (forestry and linear features) on woodland caribou distributions at multiple scales, and (2) to estimate scale-integrated resource selection functions (SRSFs) that synthesize results across scales for management-oriented habitat suitability mapping. We found a previously undocumented scale-specific switch in woodland caribou response to two forms of anthropogenic disturbance. Caribou avoided forestry cut-blocks at broad scales according to first- and second-order RSFs and avoided linear features at fine scales according to third-order RSFs, corroborating predictions developed according to predator-mediated effects of each disturbance type. Additionally, a single SRSF was validated as well as each of three single-scale RSFs when estimating habitat suitability across three different spatial scales of prediction. We demonstrate that a single SRSF can be applied to predict relative habitat suitability at both local and landscape scales in support of critical habitat identification and species recovery.

### 4.4 INTRODUCTION

Ecological patterns result from processes occurring at multiple spatial and temporal scales, yet research is typically scale-specific (Wiens 1989). Different scales of inference may not carry equal weight in driving patterns most relevant to decision-makers (Levin 1992). Thus, applied ecologists require the

elusive ability to focus on ‘the scales that matter’ (Hobbs 2003, p. 233) and ideally to integrate knowledge across scales (Turner et al. 1989). Species-habitat modeling is commonly directed towards applied ecosystem management (Peterson 2006), yet results from such models are necessarily scale-specific (Morris 1987, Hobbs 2003, Boyce 2006). The practical need to generate spatially-explicit estimates of habitat importance for applied management—such as, the designation of ‘critical habitat’ as required by the U.S. Endangered Species Act (ESA) and Canada Species at Risk Act (SARA)—presents significant challenges when interpreting scale-dependent habitat suitability for endangered species (Rosenfeld and Hatfield 2006). Multiple scales of modeling may be required to characterize the full context of habitat relationships (Boyce 2006) and those factors that limit species distributions (Rettie and Messier 2000). However, it remains unclear how to integrate such multi-scale results in applied management, where legal constructs such as critical habitat lack a defined scalar context.

Resource selection has been categorized into an intuitive string of hierarchically nested orders of the behavioral selection process (Johnson 1980, Senft et al. 1987, Meyer and Thuiller 2006). A growing body of research has demonstrated widespread evidence for scale-dependence in resource selection across taxa (Hobbs 2003, Boyce 2006), yet a means of translating multi-scale resource selection into integrated, spatially explicit treatments of habitat suitability is lacking (Wiens 1989, Wheatley and Johnson 2009). Fine-scale resource selection varies according to fine-scale resource availability (Mysterud and Ims 1998), which is in itself the result of broad-scale resource selection. For this reason, spatial extrapolation of fine-scale models alone is not well supported (DeCesare and Pletscher 2006), but broad-scale models can be used to establish the spatial context for their extrapolation (Johnson et al. 2004). Below, we demonstrate that attention to this nested relationship in multi-scale sampling design allows the estimation of resource selection models with nested, conditional probabilities of selection within scales. We then synthesize multi-scale conditional probabilities into a single, scale-integrated function with direct application for habitat management.

Assessment of habitat suitability for species conservation should also include identification of limiting factors (Morrison 2001). The importance of habitat factors likely varies with scale and applied research addressing components of habitat requires cross-scale comparisons of single-scale models to identify the factors that are most limiting (Senft et al. 1987). For example, Rettie and Messier (2000) hypothesized that the fitness consequences of resource selection would decrease at finer spatio-temporal extents. Following this logic, they used multi-scale resource selection analysis to conclude that predation limits populations of a threatened ungulate, woodland caribou (*Rangifer tarandus caribou*, Rettie and Messier 2000, Gustine et al. 2006b), a conclusion further supported by studies of caribou population dynamics (Wittmer et al. 2005b). Woodland caribou (hereafter ‘caribou’) were listed as endangered under the ESA in the contiguous U.S. in 1984 and as threatened (boreal and southern mountain populations) under SARA in Canada in 2002. Federal designation of critical habitat far exceeded legal deadlines in both countries, which may, in some part, be due to complications in delineating spatial boundaries for a species with complex scale-dependent patterns of resource selection (Environment Canada 2008).

The strength of predation in limiting caribou may be enhanced by multiple sources of anthropogenic landscape change to caribou habitat (Wittmer et al. 2007, Courbin et al. 2009). Commercial forestry subsidizes other ungulate prey with preferred early seral-staged forests and facilitates asymmetric predator-mediated apparent competition and caribou declines (Seip 1992, DeCesare et al. 2010). Anthropogenic linear features such as oil/gas seismic exploration lines (James and Stuart-Smith 2000) or trails (Whittington et al. 2011) also promote caribou mortality by facilitating increased predator (e.g., wolf, *Canis lupus*) hunting efficiency and spatial overlap. Generally, the impacts of forestry upon

woodland caribou are mediated by an increase in the numerical response of wolves (Seip 1992), whereas the impacts of linear features are mediated by an increase in the wolf functional response (James and Stuart-Smith 2000, McKenzie 2006). The numerical and functional responses should theoretically act at broad (i.e., inter-generational) and fine (i.e., intra-generational) spatio-temporal scales, respectively (Hassell 1966). If predators indeed limit caribou dynamics, then the scale at which a given disturbance type affects caribou may be a function of the scale at which it affects the predator response. We hypothesized that the mechanisms of predation affected by forestry (numerical response) and linear features (functional response) drive caribou resource selection at broad and fine scales, respectively.

Here we estimate scale-integrated resource selection functions (SRSFs) across 3 orders of selection to guide caribou habitat management and we infer the relative roles of 2 sources of anthropogenic disturbance (forestry and linear features) in limiting caribou distributions. We used hierarchical sampling to allow the integration of conditional relative probabilities of selection across all 3 scales. We then tested whether our SRSF's could translate complex, scale-dependent wildlife-habitat relationships into unified and spatially explicit depictions of habitat quality that could be readily incorporated into endangered species recovery planning.

## 4.5 METHODS

### 4.5.1 Study area

We studied woodland caribou from both the Boreal and Southern Mountain federal designations in 9 spatially distinct populations (Table 4.1; A la Pêche, Banff, Brazeau, Little Smoky, Maligne, Narraway, Redrock-Prairie Creek, Redwillow, and Tonquin) within west-central Alberta and eastern British Columbia, Canada. We defined a greater study area polygon that encompassed the study populations and represented the area historically available to caribou at the broadest scale of selection considered. The study area boundary traced natural bioregion (Natural Regions Committee 2006) and watershed boundaries, while excluding areas occupied by neighboring, unsampled, caribou populations in British Columbia, and was supported by historical observations of caribou in currently unoccupied areas (ASRD and ACA 2010).

The greater study area spanned 73,566 km<sup>2</sup> including: 16,643 km<sup>2</sup> of federally protected areas (National Parks); 7,258 km<sup>2</sup> and 4,813 km<sup>2</sup> of provincially protected areas (Provincial Wildland Parks and Wilderness Areas) in Alberta and British Columbia, respectively; and, 44,854 km<sup>2</sup> of remaining lands primarily managed by provincial governments for multiple uses including forestry, oil, and natural gas industries. Protected areas generally included more high-elevation mountainous terrain compared to multiple-use lands, which were predominately boreal conifer foothills. Forestry cut-blocks (cut since 1950) comprised between 0 and 8.9% of the area within annual caribou ranges, and the average density of non-road linear features (seismic lines and maintained hiking trails) within annual ranges ranged from 0.1 to 3.6 km/km<sup>2</sup> (Table 4.1). The functional footprint of disturbance features extends beyond their immediate location (Dyer et al. 2001), and between 0–22% and 7–87% of the area of each home range was within 250 m of a cut-block and non-road linear feature, respectively (Table 4.1).

**Table 4.1.** Area, percentage of range area covered by cut-blocks, density of linear features (seismic lines and trails), percent of range area within 250 m of cut-blocks or linear features, and number of GPS-collared adult females ( $N_{GPS}$ ) for each of 9 woodland caribou population annual home ranges in west-central Alberta and eastern British Columbia, Canada, 1998–2009.

Population	Area (km <sup>2</sup> )	% Cut-block	% Within 250 m of cut-block	Linear feature density <sup>1</sup> (km/km <sup>2</sup> )	% Within 250 m of linear feature <sup>1</sup>	$N_{GPS}$
A la Pêche <sup>2</sup>	2,867	1.18	3.02	0.786	28.15	26
Banff <sup>2</sup>	157	0	0	0.248	11.60	2
Brazeau <sup>2</sup>	388	0	0	0.140	6.86	10
Little Smoky <sup>3</sup>	1,524	8.94	21.87	3.558	87.04	41
Maligne <sup>2</sup>	419	0	0	0.280	13.92	11
Narraway <sup>2</sup>	2,561	0.95	2.69	0.266	10.89	39
Redrock-Prairie Creek <sup>2</sup>	4,281	1.54	3.74	0.373	16.27	70
Redwillow <sup>2</sup>	1,723	2.63	7.19	0.599	26.16	6
Tonquin <sup>2</sup>	511	0	0	0.203	9.66	15

<sup>1</sup> Linear features in this case included seismic lines and trails and excluded roads.

<sup>2</sup> Federally classified as southern mountain woodland caribou.

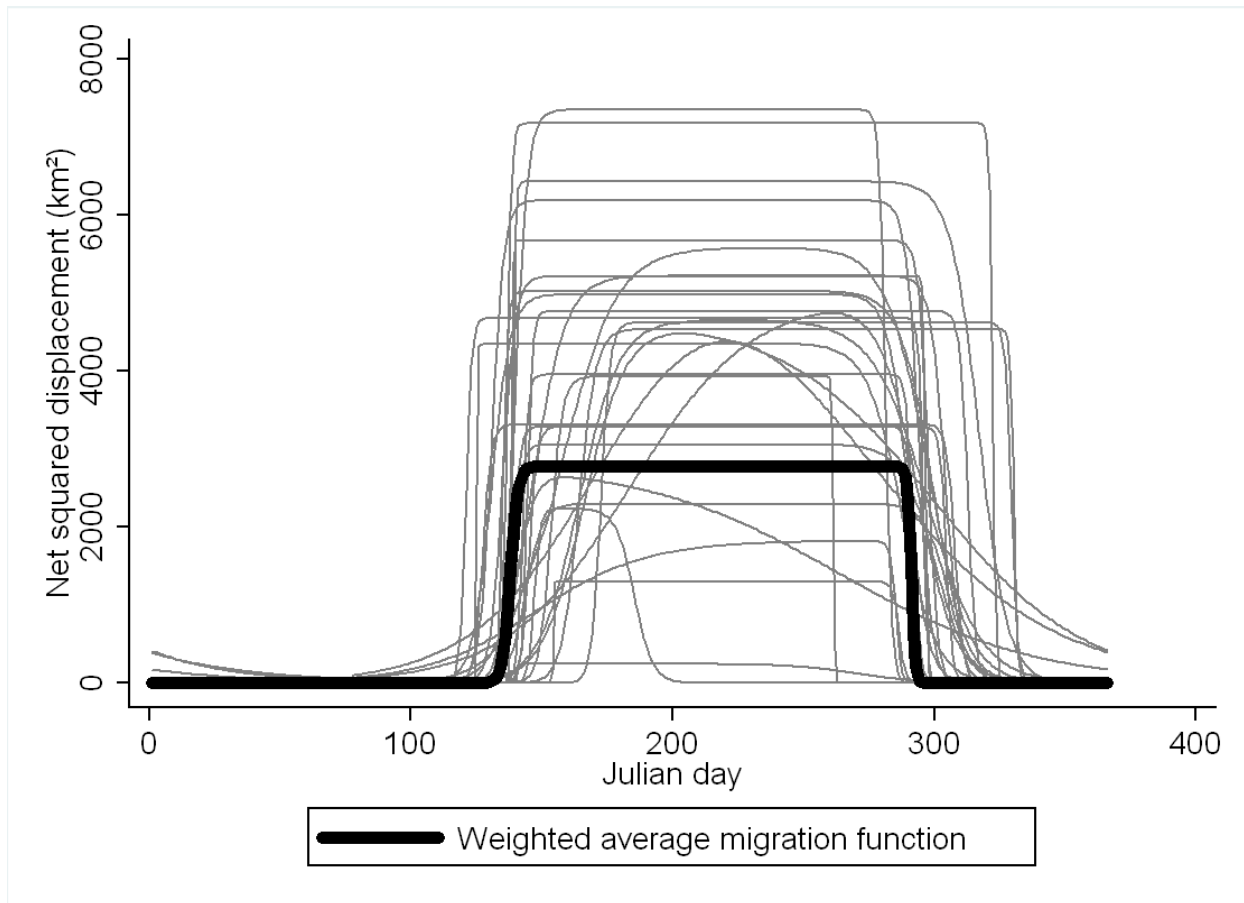
<sup>3</sup> Federally classified as boreal woodland caribou.

#### 4.5.2 Data collection and screening

We deployed global positioning system (GPS) telemetry collars (Lotek GPS 1000, 2000, 2200, 3300, 4400, and 7000 models; Lotek Wireless, Newmarket, Ontario, Canada) during winters of 1998–2009 on 217 female caribou across 9 study populations using helicopter net-gunning (Table 4.1). Capture protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Animal Use Protocol 059-09MHWB-122209), University of Alberta Animal Care Committee (Protocol SCHM-2005-61) and Parks Canada Animal Care Committee (JNP-2009-4052). We targeted adult females for this study and for additional population monitoring objectives, as they represent the segment most responsible for driving overall population dynamics (Eberhardt 2002). Woodland caribou within our study area were partially migratory (McDevitt et al. 2009), and we defined summer (16 May–16 October) and winter (17 October–15 May) seasons for separate analyses according to nonlinear regression analysis of mean migration dates (Figure 4.1; Bunnefeld et al. 2011).

After removing erroneous locations that were beyond the possible range of study animals (D'Eon et al. 2002), we used the methods of Bjørneraas et al. (2010) to remove 270 error-induced spikes from a data set of 661,022 GPS locations. We further filtered and sub-sampled data to include a uniform data set of locations collected at 3- or 4-hour fix intervals for individuals with  $\geq 180$  locations per season, corresponding to at least one month of monitoring. We withheld  $\geq 20\%$  of animals for each population-season from model training for external validation, except for the Banff population ( $N=2$  individuals). After these screening procedures the model training data set used for model construction contained 337,213 locations for 294 animal-seasons from 181 unique individuals, and the testing data set used for validation contained 85,097 locations for 122 withheld animal-seasons. GPS location acquisition success averaged 83% across individuals, low enough for habitat-induced GPS bias to potentially affect habitat





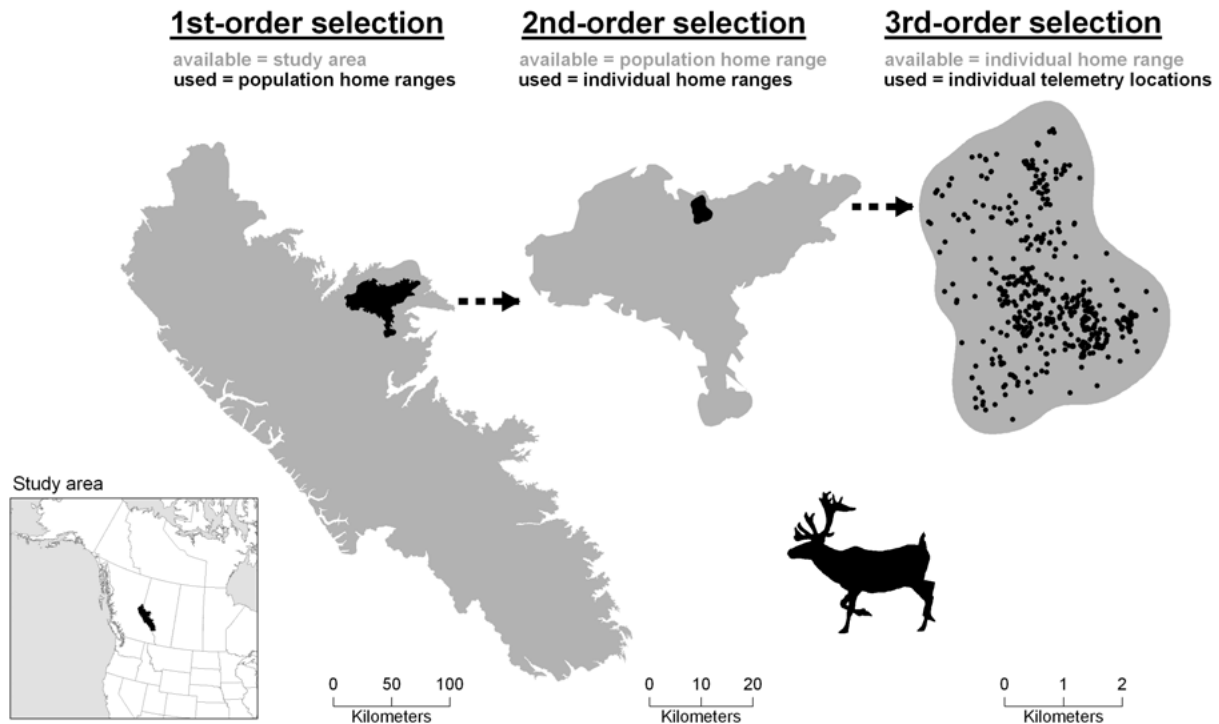
**Figure 4.1.** Nonlinear models of net-squared displacement ( $\text{km}^2$ ) of daily GPS telemetry locations by Julian day for 32 migratory female woodland caribou in west-central Alberta and eastern British Columbia, 1998–2009.

modeling (Frair et al. 2010). We corrected for potential habitat-induced bias of missed fixes using a spatial model of the probability of successfully acquiring a fix ( $P_{fix}$ ) to estimate frequency weights ( $1/P_{fix}$ ) for inclusion in models (Frair et al. 2010). We estimated  $P_{fix}$  using a model developed with test collars in an overlapping study area (Hebblewhite et al. 2007), though we recognize that estimates of  $P_{fix}$  developed with stationary test collars do not account for the interacting role of animal behavior in driving fix acquisition (Augustine et al. 2011).

#### 4.5.3 Sampling framework

Analysis of resource selection involves modeling the response (used resources) to spatial heterogeneity (available resources), where the scale of selection is a function of sampling design. We adopt Meyer and Thuiller's (2006) update to Johnson's (1980) terminology and consider three orders of selection:  $S_1$ =first-order population-level selection of seasonal home ranges within the species range,  $S_2$ =second-order individual-level of selection of seasonal home ranges within population home ranges, and  $S_3$ =third-order individual-level selection of locations within seasonal individual home ranges (Figure 4.2). These three orders of selection are conditionally nested (Meyer and Thuiller 2006, Schaefer and Mahoney 2007),

though rarely do ecologists take advantage of these nested relationships to integrate inferences across scales.



**Figure 4.2.** Schematic of the hierarchically nested sampling design followed for modeling woodland caribou resource selection at three scales of selection in west-central Alberta and eastern British Columbia, 1998–2009, with a case example for a single season (summer), population (Little Smoky) and individual (F555). For each scale, used and available locations were randomly drawn within black and gray polygons, respectively, except for the 3<sup>rd</sup> order scale of selection where GPS telemetry locations (shown in black) defined used locations.

We used RSFs to translate environmental patterns of resource selection into spatial predicted values proportional to the probability of use for each order of selection (Hirzel and LeLay 2008). Theoretically, any unit of geographic space (30 x 30 m pixel) within the study area has distinct probabilities of being within the population-level home ranges occupied by caribou ( $P[S_1]$ ), being within an individual's home range given that it is within a population home range ( $P[S_2 | P[S_1]]$ ), and being used by a caribou given that it is within an individual's home range ( $P[S_3 | P[S_2]]$ ). Models estimated for multiple scales have been multiplied together as a form of model weighting (Johnson et al. 2004), but the conditional relationship of selection across scales has not been explicitly addressed by integrating models. We sampled used and available locations in a hierarchically nested manner (Figure 4.2), which exploited the conditional relationships of selection among scales such that  $S_2 = P(S_2 | S_1)$  and  $S_3 = P(S_3 | S_2)$ . This allowed the estimation of an integrated relative probability of use for a given pixel ( $w_{SRSF}$ ) as:

$$w_{SRSF} = P(S_1 \& S_2 \& S_3) = P(S_1) * P(S_2 | S_1) * P(S_3 | S_2) = P(S_1) \times P(S_2) \times P(S_3). \text{ (Equation 4.1)}$$

We sampled  $S_1$  selection with a used-unused design (Manly et al. 2002) by drawing a set of random locations within our study area polygon equal in number to the mean number of telemetry locations collected per season ( $N=187,928$ , Figure 4.2). We then designated locations as used or unused distinctly for each of 9 caribou populations and 2 seasons according to whether they fell inside or outside seasonal population home ranges. We considered population home ranges to be a complete depiction of broad-scale caribou use based on  $\geq 20$  years of intensive caribou monitoring in this region, which justified our choice of a used-unused sampling framework at the  $S_1$  scale. For  $S_2$  and  $S_3$  selection analyses, we treated individuals as samples of use and applied used-available sampling (Manly et al. 2002, Johnson et al. 2006). We quantified  $S_2$  selection by treating population seasonal home ranges as available for comparison with used individual seasonal home ranges (Figure 4.2). For each population-season, we drew an equal number of random locations within both used (individual) and available (population) home ranges, and we calculated the number of random locations as the mean number of seasonal GPS locations collected per individual. We evaluated  $S_3$  selection with a used-available design by treating random locations within each individual seasonal home range as available for comparison with GPS telemetry-based used locations (Figure 2.2). Within available (individual) home ranges we drew sets of random points equal to the number of caribou GPS locations per individual-season.

We estimated population home ranges by buffering GPS-based movement paths (Ostro et al. 1999) with the across-population mean step length (SL) between consecutive 3- or 4-hour locations during winter (mean SL=511 m) and summer (mean SL=625 m). To remove the effect of outlying locations, we then defined the population home range as the intersection of a polygon outlining all buffered movement paths and a 95% fixed-kernel isopleth (calculated with the reference bandwidth, Worton 1989; Figure 4.2). For population-level home ranges, we included unused areas enclosed by movement paths as part of the home range polygon (*sensu* Ostro et al. 1999); these unused lacunae represented a mean of 8.0% of the total polygon areas. We estimated seasonal individual home ranges similarly by clipping buffered GPS-based movement paths with both population- and individual-level 95% kernel estimators (Figure 4.2). Because clipped home ranges excluded 5% of caribou locations, we removed those same locations from the  $S_3$  analyses to maintain comparable extents of use and availability.

#### 4.5.4 Resource variables

The RSF models included a suite of topographic (elevation, slope, aspect, topographic position, and distance to water), climatic (percent snow cover and distance to treeline) and vegetative (land cover type and normalized difference vegetation index [NDVI]) explanatory variables. These variables have been found to be important predictors of caribou occurrence in previous caribou ecology research (see Appendix B in DeCesare et al. [In press] for details of resource variables; Johnson et al. 2004, Apps and McLellan 2006) and may be considered as surrogates to mechanistic conditions driving caribou space use such as forage quantity and quality, thermal microclimates, and safety from predation (Mitchell and Hebblewhite 2012). We created a base model for each order of resource selection using scale-specific combinations of resource variables (Appendix B in DeCesare et al. [In press]).

We then compared the base models to global models which included both the base resource variables and variables characterizing anthropogenic disturbance, estimated using densities of forestry cut-blocks and linear features (seismic lines and maintained hiking trails; Appendix B in DeCesare et al. [In press]). Notably, we did not include roads in the layer of linear features for two reasons: (1) available spatial roads data were digitized with different precision across the provincial boundary, such that much spatial variation in road density was an artifact of data origin, and (2) roads and cut-blocks aligned closely in principal components analysis of disturbance vectors (N. DeCesare, unpublished data), suggesting that

the addition of roads captured relatively little additional spatial heterogeneity in overall disturbance patterns. We calculated densities for cut-blocks (proportionate area) and linear features (km/km<sup>2</sup>) using circular neighborhoods surrounding each raster pixel. We conducted preliminary analyses using density estimates measured at varying radii to identify the most predictive radius at each order of selection (Apps et al. 2001). We pooled the seasonal use-availability data for each order of selection and then estimated a suite of logistic regression models containing both cut-block and linear feature density predictors measured at concentric radii from 1,000 to 20,000 m at 1,000 m increments for first- and second-order selection and from 30 to 5000 m at 10 and 100 m increments for third-order selection. We adjusted for unequal sample sizes in the logistic regression models by weighting individuals equally and populations according to their relative area (Table 4.1). We selected the most predictive radius according to the model with the minimum Akaike Information Criterion (AIC<sub>c</sub>, Burnham and Anderson 2002), and this radius was then used to characterize both feature densities for subsequent analyses within a given order of selection.

#### 4.5.5 Data analysis

We used logistic regression to compare resources of used and unused (or available) locations for each order of selection. We included quadratic terms to allow for non-linear relationships between resource variables and the logit for  $S_1$  analysis of selection across the greater study area. Quadratic terms were not consistently supported in univariate evaluations of continuous variables at finer scales of selection so we restricted parameterization of continuous variables to linear terms for  $S_2$  and  $S_3$  analyses to facilitate averaging coefficients across individuals (Murtaugh 2007). We included only those resource variables with predicted biological relevance at each order of selection (Appendix B in DeCesare et al. [In press]) and did not include correlated ( $|r| > 0.7$ ) variables or those with variation inflation factors  $>10$  (Montgomery and Peck 1992). When models included the set of land cover type indicator variables we set the most abundant land cover type (closed conifer forest) as the reference category, pooled with any other cover types that represented an average of  $<1\%$  of available points per population-season. For  $S_3$  analysis involving telemetry locations, we used frequency weights of  $1/P_{fix}$  to account for habitat-induced biases in GPS fix success (Frair et al. 2010).

We treated resource selection as population-specific, such that we estimated season- and population-specific RSFs for each order, and we did not estimate statistical models of data pooled across populations. For each population ( $S_1$ ) and individual ( $S_2$  and  $S_3$ ) data set we fit two models: (1) a base model including all topographic, climatic, and vegetative predictor variables and (2) a global model adding anthropogenic predictor variables to the base model. We used AIC<sub>c</sub> to assess the relative support for models including and excluding the effects of anthropogenic features. We averaged AIC weights ( $w_{AIC}$ ) for models with and without anthropogenic effects for each population-season and removed individuals with no measurable coefficients for either disturbance variable (i.e., individuals with cut-block and linear feature densities fixed at 0 within used or available samples) from these averages. For  $S_2$  and  $S_3$  orders of selection we then estimated two-stage, population-averaged global models (Marzluff et al. 2004, Fieberg et al. 2010) using Equations 4.2–4.4 to estimate inverse variance weighted mean coefficients (Murtaugh 2007) averaged across individuals  $i$  within populations  $j$  for each parameter  $k$  and season  $s$ :

$$\hat{\beta}_{jks} = \sum_{i=1}^N w_{ijks} \hat{\beta}_{ijks}, \text{ (Equation 4.2)}$$

where  $w_{ijks}$ =seasonal individual parameter weights estimated as:

$$w_{ijks} = \frac{1/\left[\text{SE}\left(\hat{\beta}_{ijks}\right)\right]^2}{\sum_{i=1}^N \left(1/\left[\text{SE}\left(\hat{\beta}_{ijks}\right)\right]^2\right)}. \text{ (Equation 4.3)}$$

and standard errors estimated as:

$$\text{SE}\left(\hat{\beta}_{jks}\right) = \sqrt{\frac{\sum_{i=1}^N w_{ijks} \left(\hat{\beta}_{ijks} - \hat{\beta}_{jks}\right)^2}{N-1}}. \text{ (Equation 4.4)}$$

Standardized coefficients offer one means of comparing the relative effect of predictor variables but their interpretation is complicated when using logistic regression (Menard 2004). Wald statistics (the unstandardized coefficients divided by their estimated standard errors) offer another means for standardized comparison of the relative strength of selection among variables (Goodman 1972) but are sensitive to sample size (Hosmer and Lemeshow 2000). We estimated ‘standardized Wald statistics,’  $z_{stdz}$ , for cut-block and linear feature densities by dividing the Wald statistic for each by the average of the absolute values of all Wald statistics estimated for all predictor variables included in global population-season models. These standardized Wald statistics facilitated the comparison of the direction and strength of selection for anthropogenic features across orders of selection where models differed in sample units, sample sizes, and non-anthropogenic resource variables. Positive or negative values of  $z_{stdz}$  indicated selection for increasing or decreasing values in the predictor variable, respectively, while values  $>1$  or  $<-1$  indicated above average selective response to a given resource variable relative to others in the model. We re-estimated  $S_1$  models similar to  $S_2$  and  $S_3$  models—using only linear (no quadratic) terms for continuous variables—for this comparison.

#### 4.5.6 Integrated habitat mapping

We generated population-level RSFs across 3 orders of selection, 2 seasons and 9 populations. More specifically, the used-unused design of  $S_1$  selection models generated resource selection probability functions (RSPFs) that estimated the probability of use, whereas the used-available designs of  $S_2$  and  $S_3$  models generated RSFs that are proportional to the probabilities of use (Manly et al. 2002). We spatially mapped the per-pixel predicted values ( $w_{js}$ ) for population-level RSPFs and RSFs across the study area at a 30 x 30 m resolution. We capped resource values according to the minimum and maximum values sampled for each model to avoid extrapolating predictions beyond the extent of sampled data. We estimated  $S_1$  RSPF predicted values following Manly et al. (2002), as

$$w_{js}(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)}{(1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k))}. \text{ (Equation 4.5)}$$

We estimated  $S_2$  and  $S_3$  RSF predicted values as

$$w_{js}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k), \text{ (Equation 4.6)}$$

and used a linear stretch to re-scale RSF predicted values between 0 and 1 (Johnson et al. 2004):

$$\hat{w}_{js} = \left( \frac{w_{js}(x) - w_{min}}{w_{max} - w_{min}} \right). \text{ (Equation 4.7)}$$

For each population-season, we estimated scale-integrated Resource Selection Functions (SRSFs), which integrated selection across orders into a single relative probability, as the product of the conditional relative probabilities using Equation 4.1. We stretched SRSFs to range between 0 and 1 according to Equation 4.7 and we generated study area-wide weighted average SRSF maps for each season by weighting the predicted values of SRSFs for each population according to the relative proximity between population home ranges and each pixel. Areas within a population's home range were predicted by that population's SRSFs, whereas areas outside of home ranges were estimated with a distance-weighted average across populations. Thus, the net contribution of each population's SRSF model to the averaged maps was a function of both the area of that population and its proximity to other populations.

#### 4.5.7 Multi-scale model validation

We used validation procedures to assess how well single-scale and scale-integrated resource selection models predicted woodland caribou habitat use across different spatial scales. Specifically, we evaluated the spatial predictions of all three single-scale models within both the scales for which they were developed and the remaining two scales, and we assessed the spatial predictions of SRSFs across all scales. First, we spatially extrapolated all  $S_1$ ,  $S_2$ ,  $S_3$ , and SRSF models for each population and season across all three scales of availability: (1)  $S_1$  study area, (2)  $S_2$  seasonal population home ranges, and (3)  $S_3$  seasonal individual home ranges. We sampled predicted values of 50,000 random locations within the study area, 10,000 random locations within each population home range and 1,000 random locations within each individual home range to characterize the distributions of available predicted values at each spatial scale. We then reclassified each model's predicted values into 10 ordinal, categorical ranks (1–10) of equal area using the percentiles of predicted values for each scale of availability (Boyce et al. 2002). We measured woodland caribou use for each scale identically as sampled for model development, using population home ranges, individual home ranges, and individual telemetry locations to represent use for  $S_1$ ,  $S_2$ , and  $S_3$  scales, respectively.

We validated models by comparing the relative frequencies of woodland caribou use within each category of model predicted values to the ranks of those categories using Spearman rank correlations ( $r_s$ ), following Boyce et al. (2002). We initially validated models at all three scales internally by using the same use-availability data that were used for model training. We also validated  $S_2$  and  $S_3$  models (excluding the Banff population) externally by using animals completely withheld from model training ( $\geq 20\%$  of individuals per population, as described above) as a means of robust, external validation with independent data (Fielding and Bell 1997). Lastly, we used a paired t-test comparing  $r_s$  among scale-specific and scale-integrated models for each population-season to test whether scale-specific models for each scale validated better than scale-integrated models.

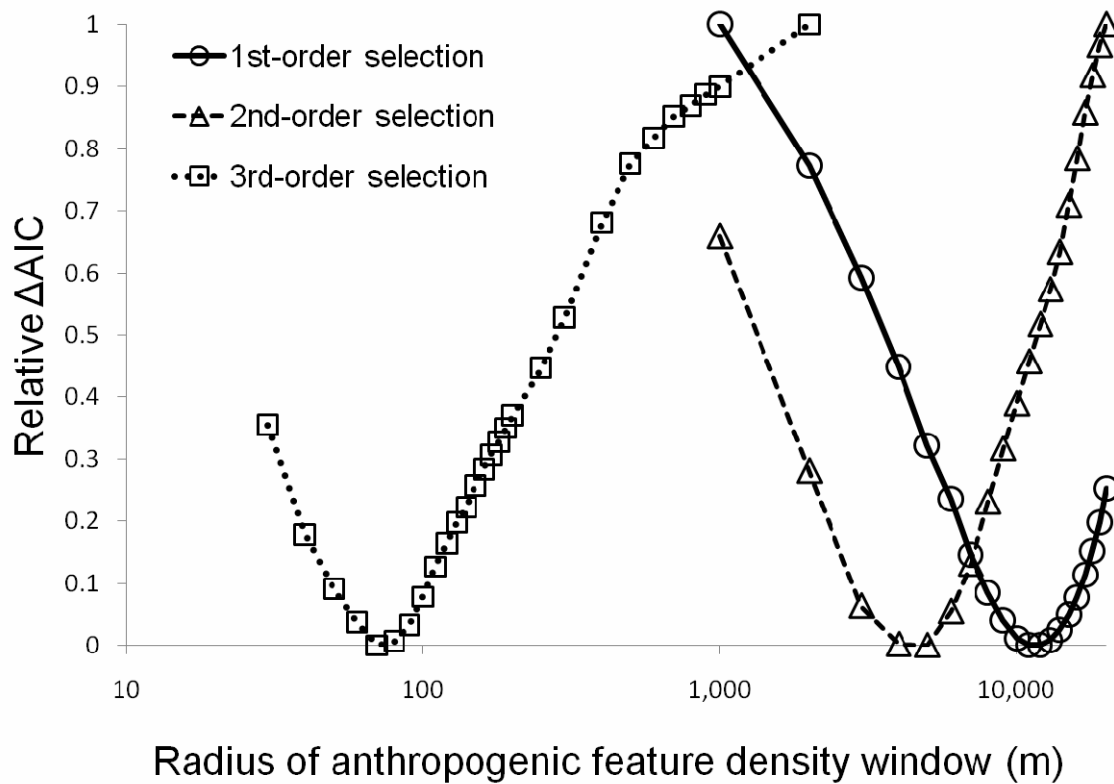
## 4.6 RESULTS

Caribou selection response to anthropogenic features was strongest when feature densities were measured within radii of 12,000 m, 5,000 m, and 70 m for first-, second-, and third-order selection, respectively (Figure 4.3). Model weights ( $w_{AIC}$ ) comparing the strength of evidence between our base

models and global models suggested a ubiquitous effect of anthropogenic features on caribou resource selection across all 3 scales of selection (Table 4.2). The average  $w_{AIC}$  for models, including anthropogenic disturbance across individuals and populations, declined from 1.00 to 0.908 to 0.801 for first-, second-, and third-order selection, respectively, indicating that responses to human disturbance were clearest at broader scales.

**Table 4.2.** Average  $AIC_c$  model weights,  $w_{AIC}$ , of global woodland caribou resource selection models including variables characterizing anthropogenic feature densities (cut-blocks and linear features) when compared to base models excluding anthropogenic features ( $1 - w_{AIC}$ ) across two seasons, nine populations, and three orders of selection, Alberta and British Columbia, 1998–2009.

Population	1 <sup>st</sup> -order	$w_{AIC}$ 2 <sup>nd</sup> -order	3 <sup>rd</sup> -order
<u>Winter</u>			
A la Pêche	1.00	0.926	0.865
Banff	1.00	0.707	0.281
Brazeau	1.00	0.898	0.832
Little Smoky	1.00	1.000	0.835
Maligne	1.00	0.766	0.750
Narraway	1.00	0.955	0.751
Redrock-Prairie Creek	1.00	0.978	0.620
Redwillow	1.00	0.662	1.000
Tonquin	1.00	0.929	0.837
Average (Winter)	1.00	0.869	0.752
<u>Summer</u>			
A la Pêche	1.00	1.000	0.934
Banff	1.00	0.846	1.000
Brazeau	1.00	0.818	0.986
Little Smoky	1.00	1.00	0.991
Maligne	1.00	0.998	0.951
Narraway	1.00	0.987	0.620
Redrock-Prairie Creek	1.00	0.919	0.626
Redwillow	1.00	1.00	0.720
Tonquin	1.00	1.00	0.873
Average (Summer)	1.00	0.952	0.856
Average (Total)	1.00	0.908	0.801

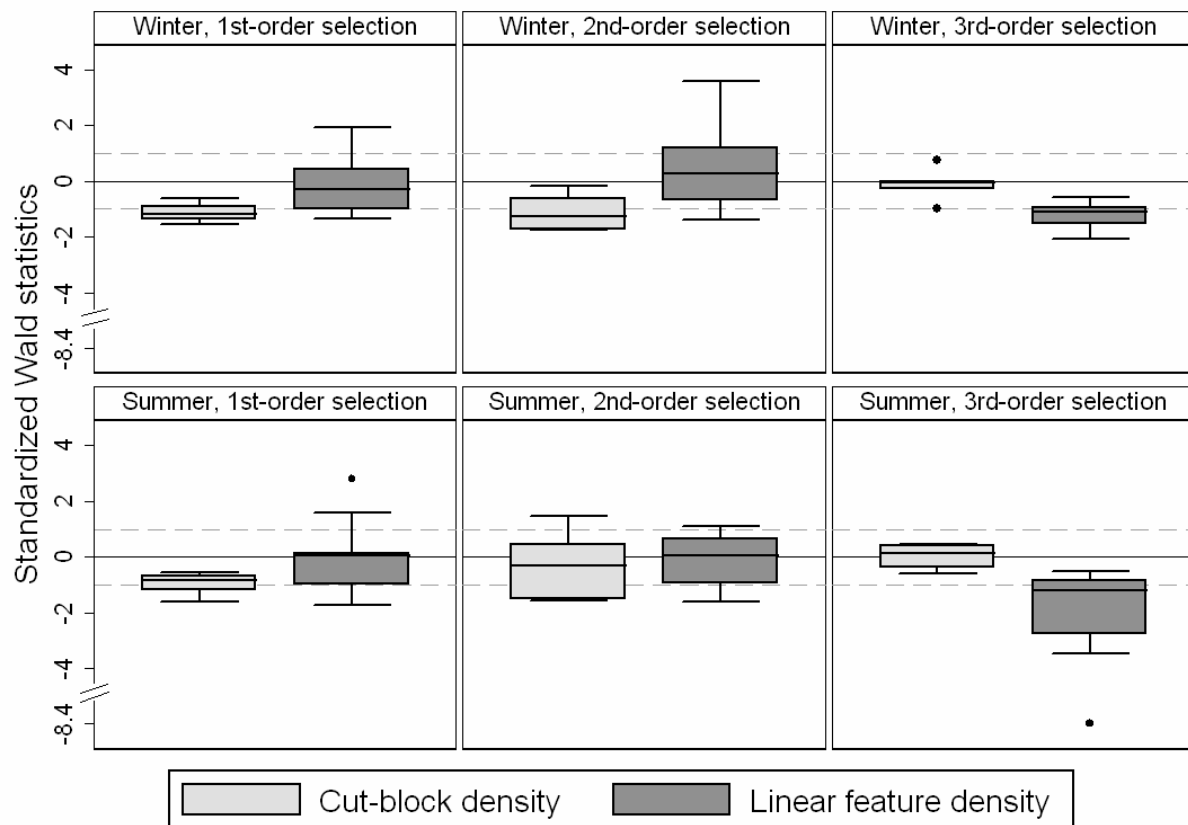


**Figure 4.3.** Relative  $\Delta AIC$  ( $\Delta AIC/\Delta AIC_{max}$ ) of logistic regression models within three orders of selection assessing the relationship between forestry and linear feature densities upon woodland caribou resource selection patterns pooled across populations and seasons within west-central Alberta and eastern British Columbia, 1998–2009.

The relative strength of response to cut-block and linear feature densities within models also varied across orders of selection (Table 4.3, Figure 4.4; see Appendix C in DeCesare et al. [*In press*] for full sets of coefficients for all RSFs). Population-averaged linear coefficients for cut-block density were negative and stronger than other model coefficients at the broadest scale of first-order selection of population ranges (Figure 4.4). Second-order selection of individual home ranges showed weaker but similarly overall negative coefficients for cut-block density, and third-order selection within home ranges was inconsistent and weak relative to cut-block density (Figure 4.4). Selection of linear feature density showed the opposite effect, being relatively weak and inconsistent at the broader two orders of selection, but consistently negative for third-order selection of locations within home ranges (Figure 4.4). Thus, at broad scales ( $S_1$  and  $S_2$ ) caribou avoided areas of high cut-block density and responded inconsistently to linear features, whereas at fine scales ( $S_3$ ) caribou avoided areas of high linear feature density and responded weakly to cut-blocks.



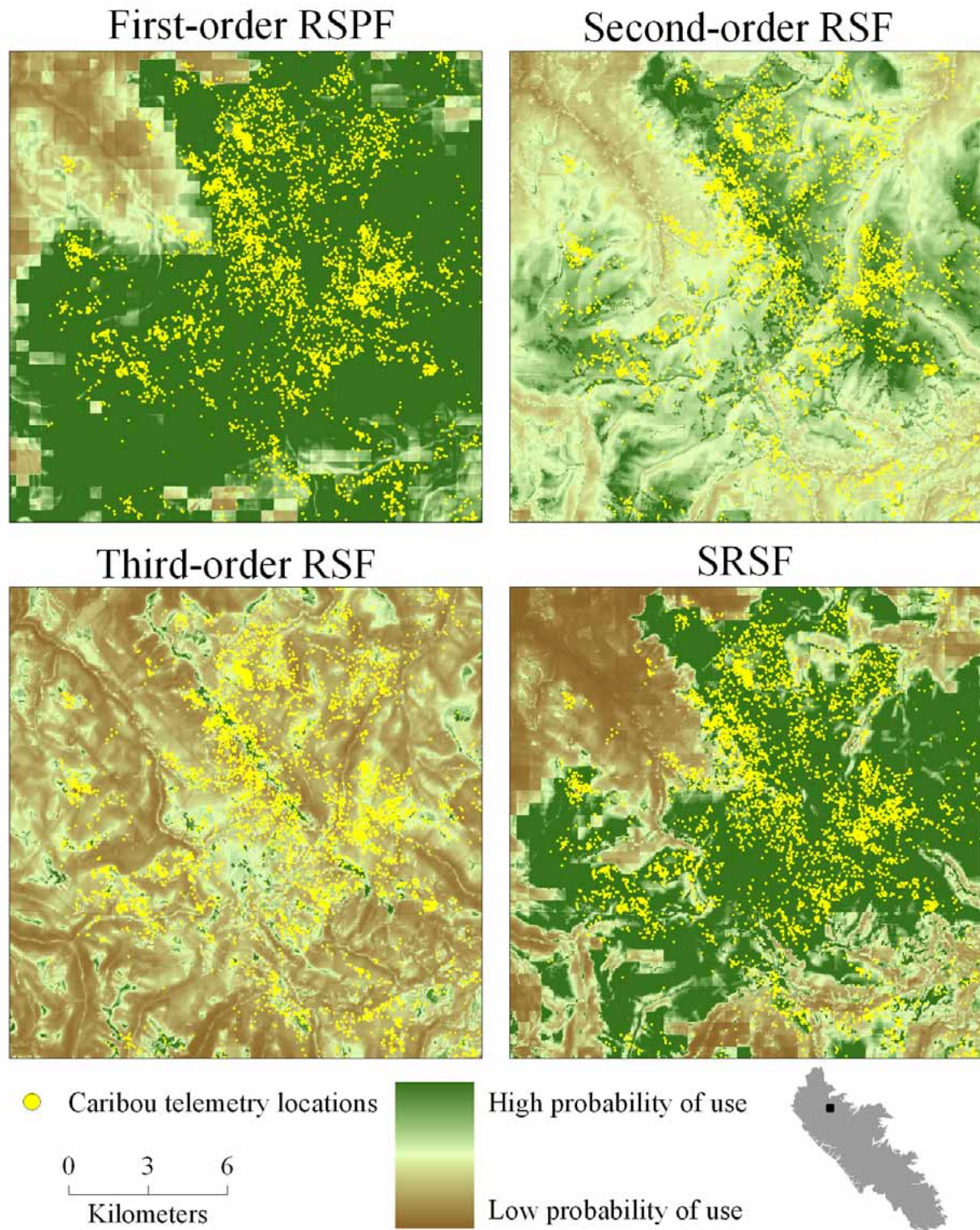
Scale-integrated RSFs performed well across all three scales according to validation with used telemetry locations. Internal validation of models using re-substituted training data indicated strong predictive capacity when single-scale models were spatially applied to extents for which they were developed ( $\bar{r}_s = 0.908$ , Table 4.4). However, extrapolation of single-scale models to other extents revealed inconsistent and relatively poor cross-scale predictive ability of single-scale models ( $\bar{r}_s = 0.450$ , Table 4.4). On the other hand, scale-integrated resource selection functions (SRSFs, Figure 4.5) validated well across all 3 extents ( $\bar{r}_s = 0.900$ , Table 4.4, Figure 4.6; Appendices D and E in DeCesare et al. [*In press*]). External validation of  $S_2$  and  $S_3$  models with an independent data set of withheld animals showed similar patterns, but slightly poorer fit of both scale-specific ( $\bar{r}_s = 0.674$ , Table 4.5) and scale-integrated models ( $\bar{r}_s = 0.723$ , Table 4.5) to external data. As a final test of SRSFs, we found no significant difference in the predictive capacity of SRSFs and the relevant scale-specific RSFs at each scale of selection according to paired t-tests comparing Spearman rank statistics using both internal ( $t_{53} = 0.345$ ,  $P = 0.366$ ) and external ( $t_{53} = -0.684$ ,  $P = 0.751$ ) validation data.



**Figure 4.4.** Box plots of scale- and season-specific standardized Wald statistics ( $z_{stdz}$ ) for predictor variables describing cut-block and linear feature (seismic lines and trails) densities within global logistic regression models for 3 scales of resource selection by 9 woodland caribou populations in west-central Alberta and eastern British Columbia, 1998–2009.

**Table 4.3.** Population- and season-averaged partial logistic regression coefficients ( $\beta$ ), standard errors (SE), and standardized Wald statistics ( $z_{stdz}$ ) for a subset of predictor variables describing cut-block and linear feature (seismic lines and trails) densities for three scales of resource selection by woodland caribou in west-central Alberta and eastern British Columbia, 1998–2009.

Population	First-order selection						Second-order selection						Third-order selection					
	Cut-block density			Linear Feature density			Cut-block density			Linear Feature density			Cut-block density			Linear Feature density		
	$\beta$	SE	$z_{stdz}$	$\beta$	SE	$z_{stdz}$	$\beta$	SE	$z_{stdz}$	$\beta$	SE	$z_{stdz}$	$\beta$	SE	$z_{stdz}$	$\beta$	SE	$z_{stdz}$
Winter																		
A la Pêche	-17.52	0.59	-1.40	0.59	0.02	1.54	-15.46	4.56	-1.73	-0.52	0.38	-0.70	0.67	0.26	0.75	-0.03	0.01	-1.26
Banff				0.15	0.27	0.06				0.86	0.94	0.75				0.03		
Brazeau				-3.03	0.30	-1.32				-4.54	4.02	-0.74				-0.18	0.05	-1.23
Little Smoky	-4.98	0.30	-0.61	0.82	0.02	1.95	-5.82	1.55	-1.74	-0.47	0.16	-1.38	-0.01	0.22	-0.01	-0.02	0.00	-1.86
Maligne				0.47	0.09	0.44				1.83	0.54	3.61				-0.09	0.02	-2.09
Narraway	-41.61	1.21	-1.53	-0.56	0.04	-0.60	-7.29	3.07	-1.27	1.06	0.20	2.84	-0.24	0.67	-0.07	-0.03	0.01	-0.94
Redrock-Prairie Creek	-16.78	0.52	-1.20	-0.82	0.03	-1.03	-1.28	2.06	-0.18	0.20	0.22	0.26	-0.33	0.20	-0.30	-0.02	0.01	-0.57
Redwillow	-17.33	0.81	-0.91	-2.11	0.07	-1.34	-1.45	1.05	-0.63	-0.76	0.48	-0.71	-1.54	0.64	-0.98	-0.04	0.02	-0.94
Tonquin				-0.20	0.10	-0.27				3.34	2.02	1.21				-0.07	0.04	-1.01
Summer																		
A la Pêche	-24.79	0.80	-1.62	0.59	0.02	1.58	-21.74	10.55	-1.56	-0.30	0.48	-0.47	-0.31	0.57	-0.17	-0.08	0.01	-3.46
Banff				0.24	0.25	0.11				-0.98						-0.37		
Brazeau				-3.41	0.24	-1.01				1.17	3.02	0.48				-0.29	0.04	-2.68
Little Smoky	-8.37	0.31	-1.23	0.89	0.01	2.79	-4.30	1.73	-1.54	-0.65	0.27	-1.46	-0.52	0.23	-0.59	-0.07	0.01	-2.80
Maligne				0.22	0.14	0.13				1.91	1.00	1.11				-0.13	0.00	-8.44
Narraway	-14.26	0.66	-0.84	-1.98	0.08	-0.91	2.85	3.59	0.47	0.43	0.30	0.84	0.73	0.47	0.44	-0.05	0.03	-0.53
Redrock-Prairie Creek	-9.72	0.64	-0.70	-1.40	0.06	-1.03	-1.66	4.22	-0.33	-0.78	0.41	-1.60	0.40	0.30	0.41	-0.08	0.02	-0.98
Redwillow	-4.62	0.70	-0.54	-2.11	0.10	-1.75	1.28	1.17	1.45	-0.24	3.55	-0.09	1.35			-0.03	0.01	-1.19
Tonquin				0.06	0.13	0.05				0.43	1.11	0.16				-0.09	0.04	-0.85



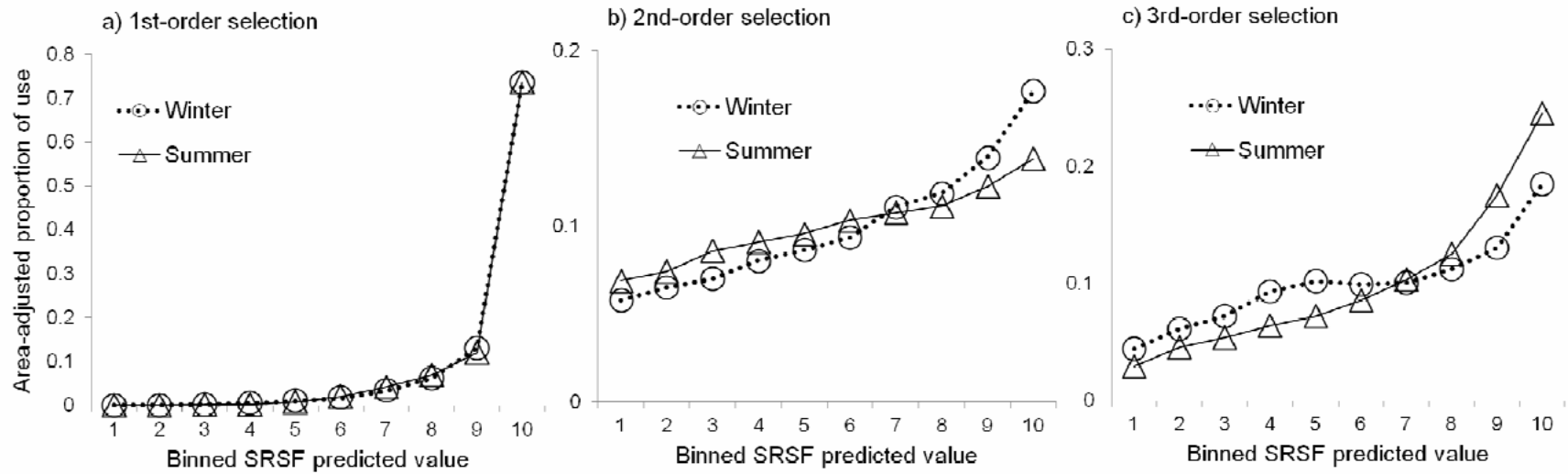
**Figure 4.5.** Sample maps showing predicted values for winter woodland caribou resource selection functions (RSFs) estimated at 3 scales of selection, a scale-integrated resource selection function (SRSF), and GPS-based telemetry locations for woodland caribou within the Redrock-Prairie Creek population in west-central Alberta, 1998–2009.

**Table 4.4.** Spearman rank correlations ( $r_s$ ) and associated P-values correlating woodland caribou resource selection function model predictions and observed frequencies of use using internal, re-substituted training data for validation in west-central Alberta and eastern British Columbia, 1998–2009. Italic values indicate results for models being tested at the extents for which they were developed and **bold** values indicate results for scale-integrated models.

Model	Study area	$r_s$ (P)	
		Population home range	Individual home range
Winter			
First-order RSPF	<i>0.907 (0.005)</i>	0.768 (0.065)	0.270 (0.204)
Second-order RSF	0.268 (0.179)	<i>0.922 (0.001)</i>	0.196 (0.236)
Third-order RSF	0.483 (0.070)	0.669 (0.184)	<i>0.958 (&lt;0.001)</i>
SRSF	<b>0.906 (0.005)</b>	<b>0.934 (0.004)</b>	<b>0.838 (0.025)</b>
Summer			
First-order RSPF	<i>0.889 (0.006)</i>	0.618 (0.166)	0.484 (0.202)
Second-order RSF	0.328 (0.143)	<i>0.790 (0.069)</i>	0.705 (0.169)
Third-order RSF	0.075 (0.288)	0.542 (0.230)	<i>0.981 (&lt;0.001)</i>
SRSF	<b>0.907 (0.004)</b>	<b>0.849 (0.040)</b>	<b>0.966 (&lt;0.001)</b>

**Table 4.5.** Spearman rank correlations ( $r_s$ ) and associated P-values correlating woodland caribou resource selection function model predictions and observed frequencies of use using external, withheld testing data for validation in west-central Alberta and eastern British Columbia, 1998–2009. Italic values indicate results for models being tested at the extents for which they were developed and **bold** values indicate results for scale-integrated models.

Model	$r_s$ (P)	
	Population home range	Individual home range
Winter		
First-order RSPF	0.776 (0.124)	0.212 (0.326)
Second-order RSF	<i>0.566 (0.093)</i>	0.476 (0.273)
Third-order RSF	0.648 (0.079)	<i>0.933 (0.001)</i>
SRSF	<b>0.903 (0.016)</b>	<b>0.795 (0.072)</b>
Summer		
First-order RSPF	0.223 (0.264)	0.062 (0.224)
Second-order RSF	<i>0.344 (0.331)</i>	0.456 (0.295)
Third-order RSF	0.397 (0.011)	<i>0.853 (0.015)</i>
SRSF	<b>0.438 (0.087)</b>	<b>0.755 (0.070)</b>



**Figure 4.6.** Area-adjusted proportions of internal validation used locations within each ordinal bin of SRSF predicted values, averaged across nine populations for winter and summer seasonal models depicting woodland caribou resource selection at a) first-order ( $S_1$ ), b) second-order ( $S_2$ ), and c) third-order ( $S_3$ ) scales of selection in west-central Alberta and eastern British Columbia, 1998–2009.

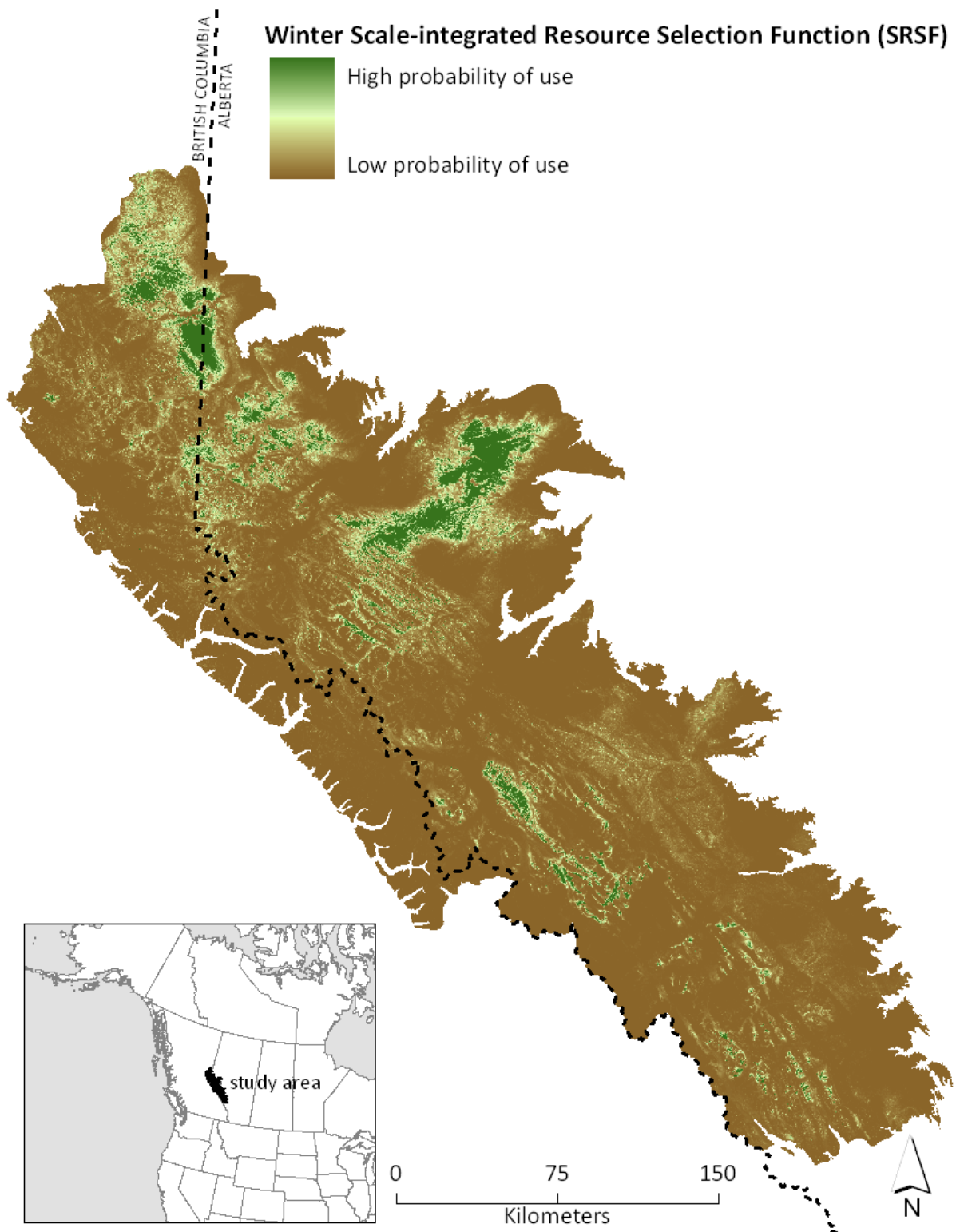
## 4.7 DISCUSSION

### 4.7.1 Scale-dependent effects of anthropogenic disturbance

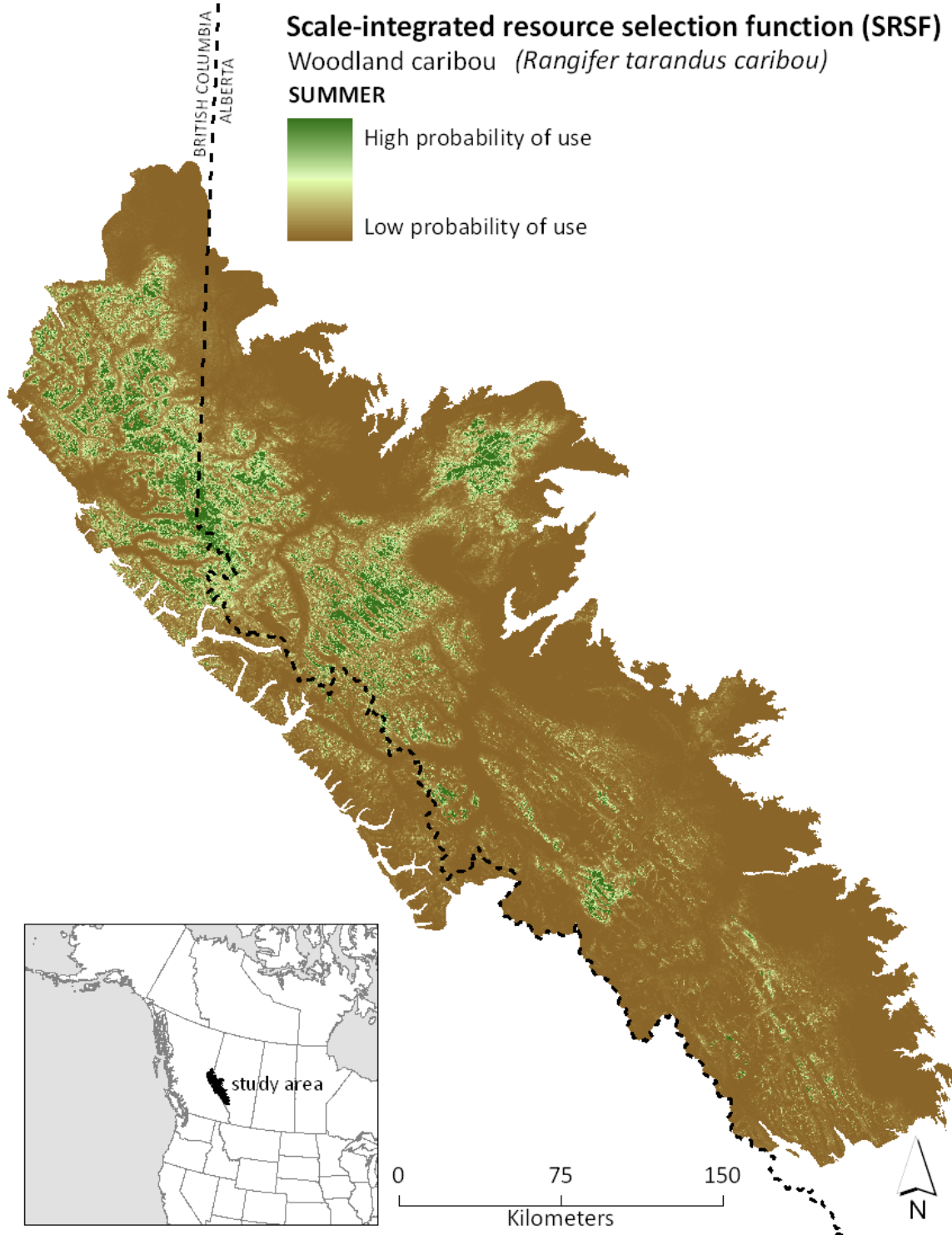
We found support for our hypothesis whereby anthropogenic disturbance previously linked to predator numerical responses (forestry cut-blocks, Latham et al. 2011) drove first- and second-order caribou resource selection and disturbance linked to predator functional responses (linear features, McKenzie 2006) drove third-order caribou resource selection. Predator functional and numerical responses have also been described as intra-generation and inter-generation responses, respectively (Hassell 1966), which suggests a scale-specific nature of predation paralleling that of prey resource selection. Thus, our results support a predator-mediated link between anthropogenic disturbance and woodland caribou distributions across spatio-temporal extents. Corroborating our results, scale-specific effects of predation risk have been found in studies of resource selection by ungulate prey (Gustine et al. 2006b, Kittle et al. 2008). Additionally, and with important implications for population dynamics, our results also shed light on the initial findings of Vors et al. (2007), who found two-decade (i.e., inter-generational) time lags between forestry activity and caribou extirpations in Ontario.

We show a scale-dependent trade-off, such that avoidance of forestry cut-blocks must be achieved before fine-scale avoidance of linear features becomes predictive of caribou distribution. Theoretically, we suggest that forestry disturbance presents a relatively greater limitation to woodland caribou (*sensu* Rettie and Messier 2000). Animals may exhibit resource selection that conveys poor fitness consequences, particularly in recently human-altered systems (Battin 2004). However, for woodland caribou, fitness costs of anthropogenic disturbance are evident. Two independent meta-analyses found the combined footprint of all anthropogenic and natural (fire) disturbances to explain 69% of the among-population variation in calf recruitment (Environment Canada 2011) and 96% of the among-population variation in annual population growth rates (Sorensen et al. 2008). Fitness costs have been associated with proximity to (James and Stuart-Smith et al. 2000, Whittington et al. 2011) and density of linear features (McKenzie 2006), and linear features also may factor into the numerical response (Lee and Boutin 2006). However, the ultimate costs to caribou habitat suitability appear relatively less for linear feature-induced changes to the predator functional response (predator kill rate) than forestry-induced changes to the predator numerical responses (predator density, Vucetich et al. 2011).

Vors et al. (2007) observed an extinction debt, or lag time between habitat loss and extirpation, for woodland caribou in Ontario, and they recommended that buffers of intact habitat should surround current population ranges to ensure persistence. Our broad-scale ( $S_1$ ) selection results support their suggestion that caribou spatial persistence is a function of habitat factors beyond range boundaries and that habitat protection, such as critical habitat designation, should extend beyond range boundaries themselves. We found broad-scale caribou distribution to be most strongly affected by cut-block density measured within 12 km radii. This 12 km distance is of the same order of magnitude as previously recommended tolerance distances between caribou and cut-blocks of 9.2 km (Schaefer and Mahoney 2007), 11.1 km (Smith et al. 2000) and 13 km (Vors et al. 2007). However, the area-weighted average ages of cut-blocks within our greater study area and within population home ranges were 13 and 7 years, respectively, relative to our average date of animal capture. Thus, additional time-lagged effects on predator-prey dynamics and caribou demography may be yet underway, and caribou habitat may take decades to recover.



**Figure 4.7.** Winter scale-integrated resource selection function (SRSF) using inverse proximity weighting to average among the predicted values of nine populations' global models (including both natural and anthropogenic covariate effects) across three scales of selection for woodland caribou in west-central Alberta and eastern British Columbia, 1998–2009.



**Figure 4.8.** Summer scale-integrated resource selection function (SRSF) using inverse proximity weighting to average among the predicted values of nine populations' global models (including both natural and anthropogenic covariate effects) across three scales of selection for woodland caribou in west-central Alberta and eastern British Columbia, 1998–2009.



At the finest scale of selection, we found caribou distribution was most strongly affected by linear feature density measured within 70 m radii, which seemingly contradicts distances commonly used to represent the zone of influence of linear features upon woodland caribou, such as 250 (Dyer et al. 2001, Sorensen et al. 2008) or 500 m (Environment Canada 2011). We attribute this to two methodological differences between our and previous studies: (1) we aimed to find the distance at which the predictive capacity of a linear feature density variable was maximized, rather than the maximum distance at which avoidance could still be detected (*sensu* Dyer et al. 2001), and (2) we characterized linear features as seismic lines and maintained trails but excluded roads (for reasons described above), which can affect caribou differently than seismic lines (Dyer et al. 2002). The most predictive radii for measuring feature density at each scale of selection were not consistent when analyses were restricted to particular population-seasons (N. DeCesare, unpublished data), suggesting the realized zone of influence of anthropogenic features may vary by population, season and type of disturbance (Dyer et al. 2001, Polfus et al. 2011).

#### 4.7.2 Integrating resource selection functions across scales

Resource selection functions and other species distribution models serve an applied role of converting ecological niche relationships in environmental space into gradients of predicted habitat suitability across geographic space (Hirzel and LeLay 2008). A wide range of species distribution modeling techniques are available (Elith & Leathwick 2009) and in some applied cases generalized linear models may be outperformed by other techniques (Cianfrani et al. 2010). However, scale-dependency is prevalent across all techniques (Hobbs 2003, Barve et al. 2011) and complicates their translation for applied purposes. Scale-specific models yield scale-specific predictions whereas land managers and conservation biologists often require scale-independent maps of habitat (Turner et al. 1989). Though examples of consistent selection patterns across scales do exist (Schaefer and Messier 1995), we use woodland caribou resource selection functions to demonstrate that single-scale models cannot be reliably extrapolated across scales. As a solution, we encourage hierarchically nested sampling and analysis of use-availability data across scales as a means of transcending scale-dependence in habitat modeling. Importantly, the product of the resultant conditional probabilities yields a relative probability of use that is integrated across all sampled scales, or an SRSF. Rather than requiring the application of different models to guide conservation efforts directed at different scales, scale-integrated models such as SRSFs provide a single model with predictive capacity across local and landscape scales.

Scale-dependent habitat selection patterns have been well documented for other species of conservation concern, including capercaillie (*Tetrao urogallus*, Storch 2003), cutthroat trout (*Oncorhynchus clarki*, Harig and Fausch 2002), Canada lynx (*Lynx canadensis*, Fuller and Harrison 2010), greater sage-grouse (*Centrocercus urophasianus*, Walker et al. 2007), and grizzly bears (*Ursus arctos*, Ciarniello et al. 2007). Spatial quantification of habitat suitability for such species is a common step in recovery planning and approaches that integrate selection across scales into single spatial depictions of habitat may best facilitate conservation (Storch 2003). Other researchers wishing to integrate multi-scaled selection models need not follow our exact sampling approach, but must ensure the conditionality of model predicted values. For example, for two models to be hierarchically nested, the predicted values of the broader-scaled model must represent both the probability of being used at the broad scale and the probability of being available at the fine scale. In other words, treating what is available at fine scales as what is used at broad scales ensures a hierarchically nested design (Figure 4.2). Designs where the same set of telemetry locations is repeatedly treated as a used sample for comparison with different samples of availability (e.g., Apps et al. 2001, Gustine et al. 2006b) will not

allow conditional predictions because the used and available locations for each scale are not hierarchically nested. On average, our patterns for natural covariates were similar to those found in other studies (Appendix C in DeCesare et al. [*In press*]), including broad-scale selection for intermediate elevations and slopes (Johnson et al. 2004), and varying degrees of fine-scale selection for gentle slopes and conifer, shrub and alpine vegetated land cover types and avoidance of deciduous and rock/ice land cover types depending upon population and season (Johnson et al. 2004, Apps and McLellan 2006, Gustine et al. 2006b). We used a proximity-weighted average of the spatial predictions of population-specific SRSFs to estimate multi-population RSFs for each season (Figure 4.7, 4.8). We did not account for within-population heterogeneity in selection that may occur with partial migration (Hebblewhite and Merrill 2009), and differences in the proportion of migratory individuals between training and testing data sets may explain some instances of poor fit (Appendices D, E in DeCesare et al. [*In press*]; N. DeCesare, unpublished data). Furthermore, distinct selection patterns during potentially important life history states such as calving (Gustine and Parker 2008) or migration (Sawyer and Kauffman 2011) may be muted by the relatively brief proportionate time during which they occurred.

The implications of our SRSF analysis for recovery planning of this species are indicative of generally wide-ranging benefits of scale-integrated habitat assessment for species conservation. Specifically, our predictive SRSF maps (Figure 4.7, 4.8) may be used for directing broad-scale conservation efforts such as protected area strategy and buffer-based area management (Woodroffe and Ginsberg 1998) as well as for fine-scale management of resource extraction practices such as spatial alignment of linear features or forestry cut-blocks. Our models offer a multi-scaled and predictive form of environmental impact assessment, wherein the zone of influence of different anthropogenic disturbances (Polfus et al. 2011) can be explored relative to multiple scales of caribou response. These models may also be used to directly estimate the scale-integrated changes in habitat suitability for future extraction or restoration management proposals. Lastly, given the biological, social, and legal complexities of critical habitat designation as a component of protection under the ESA and SARA, the spatial predictions of our scale-integrated habitat suitability model offer a biological and objective means of delineating explicit boundaries of critical habitat.

Resource selection functions represent habitat suitability as a continuous gradient and ascribe to a niche-based definition of habitat (Gaillard et al. 2010). However, other treatments of spatial habitat suitability, such as legal boundaries of critical habitat or fragmentation models of patch vs. matrix habitat, require Boolean categorization of suitability into habitat and non-habitat. Such ecological boundaries are arguably over-simplified (Strayer et al. 2003, Hirzel and LeLay 2008), although various techniques are available to estimate threshold predicted values that discretize this gradient (Liu et al. 2005). Meaningful categorization may require more than 2 states of suitability (Hirzel et al. 2006), and thresholds in resource selection may be more evident for some spatial scales than others (Figure 4.6). Potential thresholds in habitat suitability may be best determined or validated with fitness-based measures of response (Gaillard et al. 2010). In our study system, further evaluation of the relationship between SRSF predicted values and realized woodland caribou survival and recruitment would best synthesize resource selection, fitness, and persistence measures inherent in the definition of what is critical. Overall, we encourage the incorporation of predictive RSF and SRSF maps within an adaptive conservation framework (Johnson et al. 2004) to be refined with attention to site-specific variation and habitat-demography relationships.

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## 5.0 ESTIMATING WOODLAND CARIBOU RECRUITMENT AND GROWTH RATES USING AGE RATIOS

The following work in this section is included in a published peer-reviewed article:

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

### 5.1 SCOPE

To review and develop techniques for incorporating commonly collected monitoring data (calf/cow ratios) into models of recruitment and population growth rates.

### 5.2 SCHEDULE

- 1998–2009 Monitoring of calf/cow ratios by partner agencies
- 2010 Idea development, simulation, and statistical analysis
- 2010 Writing and article submission
- 2011 Acceptance to peer-reviewed journal
- 2012 Publication of article (*Journal of Wildlife Management* 76:144–153)

### 5.3 ABSTRACT

Trends in population growth can be monitored with data for key vital rates without knowledge of abundance. Although adult female survival has the highest elasticity for ungulate population dynamics, the more variable recruitment rates are commonly monitored to track local variation in growth rates. Specifically, recruitment is often measured using late winter young:adult age ratios, though these age ratios are difficult to reliably interpret given the contribution of multiple vital rates to annual ratios. We show that the supplementation of age ratio data with concurrent radio-telemetry monitoring of adult female survival allows both retrospective estimation of empirical population growth rates and the decomposition of recruitment-specific vital rates. We demonstrate the estimation of recruitment and population growth rates for 1 woodland caribou population using these methods, including elasticity and life-stage simulation analysis of the relative contribution of adult female survival and recruitment rates to variation in population growth. We show, for this woodland caribou population, that adult female survival and recruitment rates were nearly equivalent drivers of population growth. We recommend the concurrent monitoring of adult female survival to reliably interpret age ratios when managing caribou and other ungulates.

### 5.4 INTRODUCTION

Monitoring population trends is fundamental to species conservation. Abundance estimates are ideal for monitoring population dynamics but are often challenging to reliably obtain for species that are difficult to count due to rarity, uneven distributions or poor detectability. Because knowledge of population trend may be as valuable for conservation as abundance per se, and estimates of trend do not necessarily require estimates of abundance, trend estimates are a common surrogate for abundance in conservation planning. Demographic models allow the estimation of population growth rates using vital rates without requiring knowledge of abundance and, in closed populations, key vital rates can reduce

to survival and recruitment (Hatter & Bergerud 1991, Danchin et al. 1995, White and Bartmann 1998, Caswell 2001).

Recruitment is commonly monitored with young:adult age ratios derived from harvest and survey data, particularly for populations of birds (Kaminski & Gluesing 1987, Menu et al. 2002) and ungulates (Roseberry and Woolf 1991, Monello et al. 2001, White et al. 2001, Bright and Hervert 2005, Hegel et al. 2010). Several authors have cautioned that age ratios alone are not sufficient for population monitoring (Caughley 1974, McCullough 1994, White and Bartmann 1998), though they are positively correlated with population growth rates for elk under some conditions (Harris et al. 2008). We consider age ratios collected near the end of the biological year (e.g., late winter for ungulates that birth in spring), when juveniles are considered as recruited to the adult population. These ratios are difficult to interpret with specific reference to population growth or vital rates given that they can be influenced by multiple contributing vital rates. The numerator, or number of young at the time of survey, is the product of the age-specific fecundity of adult females (which is itself the product of pregnancy rate, fetal survival, and litter size) and the survival of young to the time of survey, whereas the denominator, or number of adults at the time of survey, is affected by the age-specific survival rates of adults since the birth pulse. The interpretation of ungulate recruitment rates using age ratios is further complicated by an unknown age structure of breeding- and non-breeding-aged adults, given a minimum age of first reproduction of 2-years-old. Trained observers may not be able to reliably differentiate non-breeding yearlings (1–2-year-olds) and breeding-aged adults ( $\geq 2$ -year-olds) in the total count of adult females, especially during aerial surveys (Smith and McDonald 2002).

Despite these complications in interpreting age ratios, Harris et al. (2008) found that 96% of the variation in simulated age ratios for elk (*Cervus elaphus*) was explained by variation in a single vital rate, calf survival. Consequently, in populations where calf survival is the vital rate most predictive of population growth rates (Gaillard et al. 2000, Raithel et al. 2007), age ratios alone may be suitable for monitoring population trends. For long-lived, iteroparous species such as ungulates, the elasticity of population growth rates is typically highest in adult female survival (Gaillard et al. 2000), but variation in this important vital rate is expected to be minimized by evolutionary adaptation (Pfister 1998, Gaillard and Yoccoz 2003). The survival, or recruitment, of young generally has higher variance than that of adults (Gaillard et al. 1998), which affords this vital rate subsequently greater correlation to realized population growth rates (Gaillard et al. 2000, Raithel et al. 2007). However, additional demographic analyses have revealed that the variance of vital rates and their resultant importance to population growth rates can vary across populations within species and across time or space within populations (Albon et al. 2000, Morrison and Hik 2007, Ezard et al. 2008, Nilsen et al. 2009, Johnson et al. 2010). Furthermore, the importance of adult survival in explaining ungulate population growth rates may be accentuated in declining or endangered populations experiencing patterns of adult survival that are lower or more variable than would have been evolutionarily stable (Owen-Smith and Mason 2005, Nilsen et al. 2009, Johnson et al. 2010), which highlights the potential importance of monitoring both recruitment and adult survival for complete depiction of population trend. We show that concurrent monitoring of adult survival using radio-telemetry supplements age ratio data sufficiently to alleviate the initial concerns of Caughley (1974) and McCullough (1994) and allow the estimation of both recruitment and population growth rates.

Annual population estimates of a threatened ungulate, woodland caribou (*Rangifer tarandus caribou*), would inform recovery planning under Canada's Species at Risk Act (SARA) but monitoring of woodland caribou abundance is difficult due to their low density, small group sizes, and low sightability in densely forested habitat. In Alberta and other jurisdictions, monitoring of woodland caribou has focused on the

monitoring of adult female survival and age ratios from which population growth rates have been estimated (McLoughlin et al. 2003). We use monitoring data, from a population of woodland caribou in Alberta, as a case study for developing demographic models of population growth with adult female survival and age ratio data. We demonstrate the estimation of population growth with 2 methods, Hatter and Bergerud's (1991) R/M equation and matrix population models. For use with matrix models, we show the proper adjustment of age ratio data to isolate adult female recruitment rates. Lastly, we use adult survival, age ratio, and age of first reproduction data to conduct a life-stage simulation analysis (LSA, Wisdom et al. 2000), assessing the relative importance of each vital rate to population growth for a single woodland caribou population.

## 5.5 METHODS

### 5.5.1 Study area

We studied vital rates and population growth for the A la Pêche woodland caribou population in the Rocky Mountains of west-central Alberta. The A la Pêche population traditionally migrates between an alpine summer range in protected areas (Jasper National Park and the Willmore Wilderness Area) and a forested foothill winter range east of park boundaries, though individuals can exhibit sedentary behavior in both winter and summer ranges (McDevitt et al. 2009). The eastern portion of the range has been modified by industrial land use such that 59% of the population's range outside of protected areas is within 500 m of an anthropogenic feature (e.g., road, seismic line, or forest harvest unit; ASRD and ACA 2010). Wolf (*Canis lupus*) population control was conducted to benefit a neighboring caribou population in an area overlapping the eastern boundary of the A la Pêche winter range during 2006–2009 (ASRD and ACA 2010). Caribou are protected from hunting within the national parks and licensed hunting of the A la Pêche population, when outside of the park, was discontinued in 1981. Forested habitats included upland lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.) and aspen (*Populus tremuloides*) mixed forests and lowland black spruce (*Picea mariana*) muskegs.

### 5.5.2 The R/M equation

Hatter and Bergerud (1991) derived the following equation (the R/M equation) as a means of retrospectively estimating population growth ( $\lambda$ ), recruitment ( $R$ ), or either mortality ( $M$ ) or survival ( $S=1-M$ ) rates for a given year when at least 2 of these 3 rates are known:

$$\lambda = \frac{(1 - M)}{(1 - R)} = \frac{S}{(1 - R)}. \text{ (Equation 5.1)}$$

The R/M equation was originally proposed as a complementary means for estimating growth rates in concert with surveys of abundance (e.g., Patterson et al. 2002) but has since been applied to monitor populations lacking abundance data. It has been used to estimate population trends for deer (*Odocoileus* spp., Patterson et al. 2002), elk (Kunkel and Pletscher 1999), moose (*Alces alces*, Hayes et al. 2000) and caribou (McLoughlin et al. 2003, Hebblewhite et al. 2007, Sorensen et al. 2008) and is a cornerstone of Alberta's caribou monitoring and recovery plan (ASRD and ACA 2010). Although Hatter and Bergerud (1991) specified both male- and female-based models, we focus specifically on female-only models.

This model is conveniently designed to estimate the recruitment rate,  $R_{RM}$ , using age ratio data collected at the end of a biological year when the survival of juveniles is assumed to become equal to that of

adults (Hatter and Bergerud 1991). The age ratio,  $X$ , is commonly estimated as the number of juveniles,  $n_j$ , per adult female,  $n_{af}$ , observed at the end of a measurement year, such that

$$X = \frac{n_j}{n_{af}}, \text{ and } X/2 = \frac{n_{jf}}{n_{af}}, \text{ (Equation 5.2)}$$

where  $X/2$  estimates number of female juveniles,  $n_{jf}$ , per adult female assuming a 50:50 sex ratio. Although studies of caribou population trend have occasionally treated  $X/2$  and  $R_{RM}$  as equal (McLoughlin et al. 2003, Hebblewhite et al. 2007), proper adjustment of  $X/2$  to a juveniles/(juveniles + adults) ratio is necessary, according to

$$R_{RM} = \frac{n_{jf}}{n_f} = \frac{(X/2)}{1 + (X/2)}, \text{ (Equation 5.3)}$$

where  $n_f = n_{jf} + n_{af}$ , or the total number of females of all age classes, including juveniles counted at the end of the measurement year. Failure to make this adjustment has resulted in overestimates of recruitment and optimistic estimates of population growth.

Additionally, for ungulates, the count  $n_{af}$  includes both breeding adult females and non-breeding yearlings and sub-adults given that the age of first reproduction is  $\geq 2$ -years old. The R/M model does not require knowledge of age structure or age-specific fecundity and instead growth rates are estimated treating recruitment as the simple proportion of recruits in the total population of females (Equation 5.3). Thus, the inclusion of non-breeding-aged adults in the recruitment denominator is appropriate for this model. However, this inclusion of both breeding-aged and non-breeding-aged adults in the denominator of age ratios complicates estimation of stage-specific recruitment rates necessary for using structured demographic models such as stage- or age-based matrix population models.

### 5.5.3 Matrix population models

We also estimated population growth rates using matrix models, which can project age- or stage-structured female-only populations using survival and recruitment vital rates (Caswell 2001). If we assume, as we do when using the R/M equation, that survival is equal across all non-juvenile age classes, then the appropriate dimensions of a stage-based matrix for ungulates are a function of age-specific fecundity or more simply, the age of first reproduction. Though yearling pregnancy in caribou can approach 100% under optimal conditions (Ouellet et al. 1997), caribou on average may have an older age of first reproduction than typical of other ungulates. Studies of both woodland and tundra-dwelling caribou have found 3-years old to be the most common age of first reproduction (range 2–6; Parker 1981, Messier et al. 1988, Fancy et al. 1994, Adams and Dale 1998).

For simplicity of presentation we treat age of first reproduction as 2-years-old and begin with a 2-stage, pre-birth pulse, female-only matrix model  $A$  for a given time step,  $t$ , and a stage-structured population vector,  $n(t)$ . We estimate caribou population growth according to

$$\lambda(t) = \frac{A(t) \times n(t)}{n(t)}, \text{ (Equation 5.4)}$$

$$A(t) = \begin{bmatrix} 0 & F_a p_f S_j \\ S_y & S_a \end{bmatrix} = \begin{bmatrix} 0 & R_{2-stage} \\ S_a & S_a \end{bmatrix}, \text{ (Equation 5.5)}$$

and

$$n(t) = \begin{bmatrix} p_y(t) \\ p_a(t) \end{bmatrix} = \begin{bmatrix} p_y(t) \\ 1 - p_y(t) \end{bmatrix}, \text{ (Equation 5.6)}$$

where the survival of yearlings,  $S_y$ , is assumed to be equal to adult survival,  $S_a$ ; the recruitment of 12-month-old females to the population,  $R_{2-stage}$ , is the product of adult female fecundity  $F_a$ ; the proportion of juveniles that are female,  $p_f$ , and the first-year survival of juveniles,  $S_j$ , and the age structure of the population  $n(t)$  is a function of the proportion of the population entering the time step as non-breeding yearlings,  $p_y(t)$ , and breeding adults,  $p_a(t)$ . For retrospective assessment of population growth with matrix models given a set of empirical vital rates, Equation 5.4 is preferable to estimating the dominant eigenvalue of a given projection matrix because it specifies a transient population age structure rather than assuming an asymptotic stable age structure (Fox and Gurevitch 2000).

DeCesare et al. (2011) showed that  $R$  for matrix models should be estimated as the number of juveniles at the end of the time step per breeding adult present at the beginning of the time step. They decreased the numerator of caribou age ratios to account for a 50:50 sex ratio and the survival of juveniles from the time of survey to the completion of the time step, and they increased the denominator using the survival rate of adults from the beginning of the time step to the time of survey. Assuming, as we did above for the R/M equation, that survival of all age classes is equivalent to adult survival for the remainder of the biological year after the time of survey, this adjustment reduced to  $\hat{R} = (X/2) \times \hat{S}_a$  (DeCesare et al. 2011). However, although DeCesare et al. (2011) attempted to identify and exclude yearlings in the collection of their age ratio data, the denominator in most ungulate age ratio data includes yearling females in the count of adults (Smith and McDonald 2002), which were incapable of giving birth at the beginning of the time step. Although suitable for estimating recruitment when using the R/M equation, the inclusion of yearlings is inappropriate for our matrix model (Equation 5.5), which specifically requires an estimate of the per-capita contribution to recruitment of breeding females. Thus, an additional adjustment is required to remove the proportion of yearlings or perceived adults, which have not reached the age of first reproduction, to estimate the appropriate recruitment rate of breeding-age adults as

$$\hat{R}_{2-stage} = \frac{(X/2)}{(1 - p_y) / \hat{S}_a}. \text{ (Equation 5.7)}$$

The proportion of yearlings entering a given time step,  $t$ , can be estimated using the adjusted age ratio of the previous time step,  $t-1$ , where

$$p_y(t) = \frac{(X_{t-1}/2)}{1 + (X_{t-1}/2)}. \text{ (Equation 5.8)}$$

Thus, an adjusted recruitment term for use in matrix models,  $R_{2-stage}$ , is estimable for all years when the age ratio is available for both the year of interest and the previous year.

With the assumption that survival is equal across non-juvenile age classes (i.e.,  $S_y=S_a$ ), as held in Equation 5.5, all age structure ( $p_y[t]$ ) terms cancel out when estimating  $\lambda$ , and Equation 5.4 becomes numerically equivalent to Equation 5.1, the R/M equation. In other words, population growth rate estimates from Equations 5.4–5.7 are insensitive to age structure when the included matrix population model lacks age-specific differences in vital rates. For each pair of annual estimates of  $S_a(t)$  and  $X(t)$ , equivalent estimates of  $\lambda$  can be achieved using either Equation 5.1 or Equation 5.4 (substituting any value for  $p_y[t]$ ). However, the recruitment term itself,  $R_{2-stage}$ , which varies according to  $p_y(t)$ , will not be interpretable without consecutive years of age ratio data to properly estimate  $p_y(t)$  using Equation 5.8. Interpretable estimates of  $R_{2-stage}$  will be necessary if the user wishes to isolate the contribution of recruitment parameters from those of age structure and  $S_a$  to age ratios or to specifically estimate means or process variances of recruitment parameters.

To treat age of first reproduction as 3-years-old, these methods can be extended to a 3-stage matrix model by adding an additional non-breeding sub-adult stage, such that

$$A = \begin{bmatrix} 0 & 0 & R_{3-stage} \\ S_a & 0 & 0 \\ 0 & S_a & S_a \end{bmatrix}, \text{ (Equation 5.9)}$$

$$n(t) = \begin{bmatrix} p_y(t) \\ p_s(t) \\ 1 - p_y(t) - p_s(t) \end{bmatrix}, \text{ (Equation 5.10)}$$

$$\hat{R}_{3-stage} = \frac{(X/2)}{(1 - p_y - p_s) / \hat{S}_a}, \text{ (Equation 5.11)}$$

and,

$$p_s(t) = \frac{P_{y,t-1}}{1 + (X_{t-1}/2)}, \text{ (Equation 5.12)}$$

where  $p_y(t)$  is estimated using Equation 5.8, and the proportion of sub-adults that entered the time step,  $p_s(t)$ , is estimated using the age ratio and estimate of  $p_y(t-1)$ . In total, estimation of an interpretable value of  $R_{3-stage}$  requires 3 consecutive years of data, though population growth rates can still be estimated with vital rates for a single year using Equations 5.4 and 5.9–11. Annual population growth rates estimated with the 2-stage (Equations 5.4–7) or 3-stage (Equations 5.4 and 5.9–11) models will be equivalent, but recruitment rates will vary according to the proportion of the perceived adult population assumed to be of actual breeding age.

#### 5.5.4 Case study: Estimating $\lambda$ for woodland caribou



*Empirical vital rates and growth rates.* — We monitored the survival and recruitment of the A la Pêche woodland caribou population during 1998–2009. We monitored survival of  $\geq 1.5$ -year-old females by capturing animals using helicopter net-gunning and fitting captured animals with very high frequency and global positioning system telemetry collars (ASRD and ACA 2010). Animal use protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Animal Use Protocol 059-09MHWB-122209). We monitored recruitment with late winter helicopter surveys documenting calf/cow age ratios with the counts of cows including both yearling and adult females (Smith and McDonald 2002, ASRD and ACA 2010). Recruitment surveys targeted caribou groups containing at least 1 radio-collared adult female and included an average of 99.7 (SD=26.0) individuals in 14.2 (SD=4.0) groups per year.

We estimated annual adult female survival rates,  $S_a(t)$ , for each biological year (1 May to 30 April) using Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model. We estimated caribou age ratios according to Equation 5.2 and estimated recruitment for use with the R/M equation and matrix models according to Equations 5.3 ( $R_{RM}$ ), 3.7 ( $R_{2-stage}$ ), and 3.11 ( $R_{3-stage}$ ). For 2 years (1998 and 1999) when only late fall survey data were available, we reduced calf counts by an additional 15% as estimated by comparing years with both late fall and late winter survey data (Smith 2004). When adults counted during surveys were not classified according to sex (due to dense forested cover and low sexual dimorphism, Geist and Bayer 1988), we partitioned unclassified adults as 65% female and 35% male following Smith (2004). Linear regression revealed no significant bias in annual age ratio estimates caused by annual variation in the proportion of unclassified adults ( $\beta = -0.057$ ,  $P = 0.34$ ). We estimated annual population growth rates using each demographic model and used the geometric mean of annual growth rates to estimate the overall average annual growth rate. In addition to estimating empirical growth rates for the A la Pêche population, we also simulated a range of survival and recruitment values observed in other woodland caribou populations in Alberta (ASRD and ACA 2010) to visually depict the potential range of transient population growth rates given input vital rates.

*Elasticity and life-stage simulation analyses.* — We calculated analytical elasticities of adult survival and recruitment vital rates using a 2-stage matrix model (Equation 5.5) parameterized with the geometric mean survival and recruitment values of the A la Pêche woodland caribou population. We conducted elasticity analysis using the MATLAB (The MathWorks, Natick, MA) code `vitalsens.m`, provided by Morris and Doak (2002). We used life-stage simulation analysis (LSA) to incorporate empirical measures of vital rate variation into the assessment of vital rate importance (Wisdom et al. 2000). We used LSA to estimate the relative contribution of adult survival, recruitment and age of first reproduction to deterministic or asymptotic population growth rates.

Stochastic simulations of vital rates, as conducted with LSA, should simulate the variation of vital rates according to the process or environmental variance after excluding the contribution of sampling error to raw estimates of variance (White 2000). We isolated the process variance of adult survival among years using program `Kendall.m` in MATLAB v.7.9.0 (Kendall 1998, Morris and Doak 2002). To account for censoring in our survival data, we first estimated the within-year means and variances of adult female survival using non-parametric methods (Greenwood 1926, Pollock et al. 1989) and we then adjusted the input annual sample sizes of animals and survival events to produce equivalent mean and variance estimates using a binomial variance estimator (Morris and Doak 2002). We tested sets of 2,500 possible means and variances with each run of `Kendall.m`, and we iteratively re-ran the program manually refining the limits on means and variances until we reached a consistent best estimate. To estimate the within-year variance of recruitment, we treated each group of animals observed during an annual survey as the sample unit (Bowden et al. 1984). We then removed the effect of adult survival and age structure

from age ratio data by adjusting the numerators and denominators of the calf/cow ratios of each group observed during annual surveys to group-specific estimates of  $R_{2-stage}$  according to Equation 5.7. We then used the variance of ratios estimator (Cochran 1977, Krebs 1989) to estimate the variance of the recruitment term,  $R_{2-stage}$ , per year as

$$Var(R) = \frac{(1-f)}{n_g \bar{n}_{af}^2} \times \frac{\left(\sum n_{jf}^2\right) - 2\hat{R}_{2-stage} \left(\sum n_{jf} n_{af}\right) + \hat{R}_{2-stage}^2 \left(\sum n_{af}^2\right)}{n_g - 1}, \text{ (Equation 5.13)}$$

where  $n_{jf}$  and  $n_{af}$  are counts of juveniles and adult females per group,  $n_g$  = the number of groups surveyed and  $f = n_g/N_g$  or the sampling fraction of the number of groups surveyed divided by the total number of groups in the population. For each annual estimate of  $f$  we calculated  $N_g$  by dividing a reported population estimate of 150 individuals in the A la Pêche population (ASRD and ACA 2010) by the mean number of animals per group for a given year. For 1 year (2002) when per-group age ratio data were unavailable we estimated within-year variance using the mean value of all other years. We then isolated the process variance of  $R_{2-stage}$  according to White (2000) using program White.m in MATLAB v.7.9.0, as provided by Morris and Doak (2002).

We created beta distributions for adult survival and recruitment with mean and process variance estimates and drew a set of 100,000 stochastic vital rate combinations using program MATLAB (Morris and Doak 2002). We used previously published data (Adams and Dale 1998) to estimate the frequency of age of first reproduction values of 2- (22.5%), 3- (58.3%), 4- (14.8%), 5- (3.0%), and 6-years old (1.5%) for female caribou after accounting for animals that did not breed before either death or the end of the study. We estimated asymptotic population growth rates ( $\lambda_1$ , Morris and Doak 2002) from the set of 100,000 stochastic  $S_a$  and  $R_{2-stage}$  values by inserting them into 2-, 3-, 4-, 5-, and 6-stage matrix models, with respective matrix model frequencies according to this distribution in age of first reproduction. For each matrix model, recruitment was set to zero for all age classes except the oldest one, for which we parameterized recruitment by stochastic values of  $R_{2-stage}$ . Our distribution of  $R_{2-stage}$  recruitment values specifically estimated the contribution of breeding-aged adults to annual recruitment assuming an age of first reproduction of 2-years old, but we applied stochastic  $R_{2-stage}$  values to 2–6-stage matrices to assess the effect of age of first reproduction given equal distributions of recruitment per breeding-aged adult. This method created a data set of population growth rates accounting for empirical estimates of environmental variance in all 3 vital rates. We then used linear regression to assess the coefficient of determination,  $r^2$ , for 3 models predicting simulated population growth rates as a function 3 vital rates (adult survival, recruitment and a set of indicator variables for the age of first reproduction) to assess the percentage of variability in population growth rates explained by each vital rate (Wisdom et al. 2000).

## 5.6 RESULTS

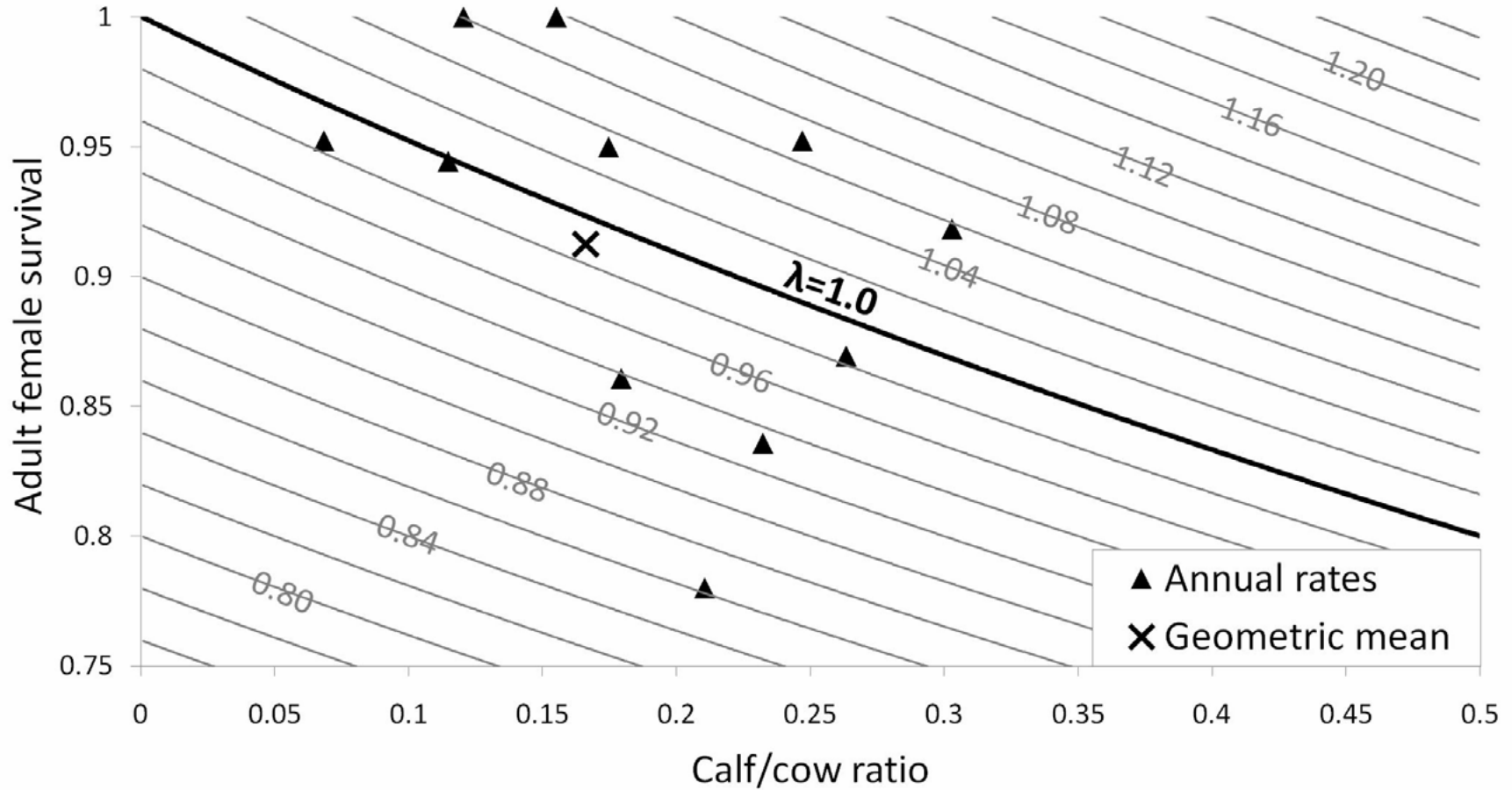
We documented 19 mortalities of 87 captured individuals and monitored an average of 23 adult female woodland caribou per year (range 18–32) during 1998–2009. The geometric mean of annual survival rates was 0.912 and 11% of the total variance ( $Var[S_a] = 0.00488$ ) was attributed to process variance ( $V_c[S_a] = 0.000526$ ). Late winter composition surveys included an average of 100 individuals of all sex and age classes, with a geometric mean calf/cow ratio of 0.166 either-sex calves per cow (range 0.068–0.303). Calf/cow ratio data resulted in 3 different geometric mean estimates of recruitment depending on the demographic model used ( $R_{RM} = 0.0796$ ,  $R_{2-stage} = 0.0867$ , and  $R_{3-stage} = 0.0898$ , Table 5.1). We attributed 73% of the total variance ( $Var[R_{2-stage}] = 0.00109$ ) in recruitment rates to process variance

( $V_c[R_{2-stage}] = 0.000795$ ). Population growth rates using each method were equivalent (Table 5.1), with a geometric mean annual growth rate of 0.998 (range 0.862–1.078). The distribution of potential transient growth rates varied according to both vital rates (Figure 5.1).

Elasticities of recruitment and adult survival for the 2-stage matrix model were 0.0744 and 0.926, respectively. Coefficients of determination ( $r^2$ ) from our life-stage simulation analysis revealed that 54.0% of the variation in deterministic growth rates was explained by the adult survival rate, followed by 43.3% explained by the recruitment rate and 1.7% explained by the age of first reproduction.

**Table 5.1.** Geometric means of adult female survival ( $S_a$ ) and March calf/cow ratios ( $X$ ), the proportion of yearlings ( $p[y]$ ) and subadults ( $p[s]$ ) in the female population, and recruitment rates ( $R$ ) and transient population growth rates ( $\lambda$ ) estimated over a single time step using Hatter and Bergerud's (1991) R/M equation and 2- and 3-stage matrix population models for the A la Pêche woodland caribou population in west-central Alberta, 1998–2009.

Years	$S_a$	$X$	$p(y)$	$p(s)$	$R_{RM}$	$R_{2-stage}$	$R_{3-stage}$	$\lambda_{RM}$	$\lambda_{2-stage}$	$\lambda_{3-stage}$
1998		0.100			0.048					
1999	0.918	0.303	0.048		0.132	0.146		1.057	1.057	1.057
2000	0.870	0.263	0.132	0.041	0.116	0.132	0.138	0.984	0.984	0.984
2001	0.950	0.175	0.116	0.116	0.080	0.094	0.108	1.033	1.033	1.033
2002	0.952	0.247	0.080	0.107	0.110	0.128	0.145	1.070	1.070	1.070
2003	0.861	0.179	0.110	0.071	0.082	0.087	0.094	0.938	0.938	0.938
2004	1.000	0.155	0.082	0.101	0.072	0.085	0.095	1.078	1.078	1.078
2005	0.952	0.068	0.072	0.076	0.033	0.035	0.038	0.985	0.985	0.985
2006	0.836	0.232	0.033	0.070	0.104	0.100	0.108	0.933	0.933	0.933
2007	0.944	0.115	0.104	0.030	0.054	0.060	0.063	0.999	0.999	0.999
2008	0.780	0.211	0.054	0.098	0.095	0.087	0.097	0.862	0.862	0.862
2009	1.000	0.120	0.095	0.049	0.057	0.067	0.070	1.060	1.060	1.060



**Figure 5.1.** Contour plot depicting the range of possible transient population growth rates ( $\lambda$ ) and empirical annual estimates for the A la Pêche woodland caribou population according to the paired values of adult female survival and late winter calf/cow ratios as estimated equivalently by both Hatter and Bergerud’s (1991) R/M equation and the projection of 2- and 3-stage population matrix models over a single time step, Alberta, Canada, 1998–2009.

## 5.7 DISCUSSION

We demonstrated that age ratios can be used to retrospectively estimate empirical population growth rates using Hatter and Bergerud's (1991) R/M equation and 2- and 3-stage matrix population models when combined with estimates of adult female survival. Age ratios result from the combination of multiple vital rates, including the proportion of yearlings in the population, the survival of adults and those rates affecting recruitment of juveniles. Concurrent monitoring of adult survival allowed us to remove its effect in age ratio data and consecutive years of age ratio data allowed us to estimate and remove the effects of age structure. In these cases, we were able to isolate the portions of age ratios relevant for recruitment alone and estimate the mean and variance of the recruitment term in matrix models. This method allowed the estimation of process variance of recruitment from age ratio data for use in stochastic matrix model projections and a life-stage simulation analysis.

Our results supported previous findings that adult female survival has the highest elasticity for population growth in ungulates (Gaillard et al. 1998). Previous research has also shown that annual differences in population growth of ungulates can be better explained by more variable recruitment or juvenile survival rates despite their low elasticity (Hatter and Janz 1994, Gaillard et al. 2000, Raithel et al. 2007). In our study, a life-stage simulation analysis suggested that high variation in recruitment caused it to explain a greater percentage of population growth rates (43%) than might be expected from its low elasticity (0.07). However, adult female survival still explained comparatively more of the variation (54%) in annual estimates of  $\lambda$  than has been shown in other ungulate populations (Gaillard et al. 2000, Raithel et al. 2007). This may suggest an effect of recent disturbances to caribou demography (e.g., Sorensen et al. 2008) because vital rates that are both highly elastic and variable would not have been sustainable over evolutionary time (Pfister 1998, Johnson et al. 2010). Further analysis across multiple caribou populations may be necessary to fully describe the relationships between human disturbance, vital rate variance and caribou population growth. Age of first reproduction can vary among species (Cole 1954), populations (Langvatn et al. 1996), cohorts (Langvatn et al. 1996) and individuals within a population (Festa-Bianchet et al. 1995) and has been theoretically described as the key vital rate underlying maximum growth rates achievable by species (Hone et al. 2010). Simulations of caribou population growth accounting for a level of variation in age of first reproduction observed in barren-ground caribou (*R. t. granti*, Adams and Dale 1998) revealed that this vital rate explained a relatively small percentage (1.7%) of the variation in population growth estimates, similar to results from other woodland caribou population simulations (Wittmer et al. 2010).

Asymptotic projections of vital rates can be used to estimate long-term deterministic growth rates given a set of vital rates, but these methods assume stable age distributions and may be less appropriate for recovery monitoring (Fox and Gurevitch 2000, Yearsley 2004). We have shown that transient population growth rates for a single time step can be estimated consistently without knowledge of the age of first reproduction, but these ad hoc rates are not necessarily representative of long-term trends due to a simplified treatment of age structure and age of first reproduction (Danchin et al. 1995). Future projections of vital rates to estimate long-term trends may best be conducted using stochastic matrix models (Boyce et al. 2006). Specifically, projections should simulate the variation of vital rates according to empirical estimates of their means and environmental variances and be parameterized to account for population age structure and age-specific vital rate variation (Gaillard et al. 1994, Ezard et al. 2010). Stochastic population projections should also address the potential for within- and among-year correlation of vital rates, which can affect realized growth rates (Coulson et al. 2005). Our equations are based on 2- and 3-stage population models and incorporation of age-specific vital rates into age-based matrix models offer an alternative when data are available (Raithel et al. 2007). We recommend our

methods for retrospective interpretation of monitoring data, but encourage the use of stochastic, age-structured models for predicting future trends for caribou (e.g., Walsh et al. 1995, Wittmer et al. 2010, DeCesare et al. 2011) and other species.

Ungulate population monitoring designs exist on a continuum from trend monitoring with composition counts alone (McCullough 1994) to individual-based studies of sex- and age-specific vital rates (Coulson et al. 2001, Nussey et al. 2009). Our methods reduce ungulate population dynamics to 2 key parameters and reflect a trade-off between what is commonly measurable given the costs and extent of monitoring ungulate populations and what is necessary for baseline estimates of population trend (Bowden et al. 2000). Specifically in the case of woodland caribou, recovery planning faces the challenge of monitoring a threatened subspecies that occurs in >164 populations across 9 jurisdictions (Thomas and Gray 2002) and our methods reflect those recently adopted for broad-scale monitoring of population trends in Alberta (Alberta Woodland Caribou Recovery Team 2005). We reiterate Hatter and Bergerud's (1991) caution that the reliability of trend estimates using our methods depends strongly on the precision of input survival and recruitment vital rate estimates. For example, the precision of adult female survival estimates incorporated into these models is dependent on both the sample size of radio-collared individuals and the process mean of the adult survival vital rate (White and Bartmann 1998). We recommend incorporation of estimates of precision about vital rates into our equations by estimating growth using both vital rate means and confidence limits or using Monte Carlo simulation of vital rates and growth estimates (Patterson et al. 2002).

When collected in tandem with adult female survival rates, age ratio data may provide a suitable alternative for managers interested in documenting recruitment and growth rates. However, further study of the component vital rates of recruitment (pregnancy, litter size and fetal and juvenile survival) may be necessary to understand mechanistic relationships between factors such as density dependence, climate, predation and net recruitment rates. The majority of variation in age ratios for primiparous species such as elk or woodland caribou is often attributed to juvenile survival (Harris et al. 2008) given fixed litter sizes and relatively invariable pregnancy rates (Wittmer et al. 2005b, Raithel et al. 2007). Studies of juvenile woodland caribou survival using radio-collared calves are rare (Gustine et al. 2006a), yet such studies would be beneficial for conservation by assessing cause-specific juvenile mortality and the link between recruitment and anthropogenic disturbance. For multiparous ungulates, age ratios contain added variation in litter size, which further complicates the interpretation of age ratio-based recruitment rates with specific reference to component vital rates.

Age ratio data can suffer from other potential sources of error, such as misclassification of female juvenile and adult age classes (Smith and McDonald 2002) as well as the potential misidentification of sex during adult female counts. This latter problem may be especially relevant for caribou, given the capacity of both females and young males to carry antlers into late winter. Although female caribou and reindeer typically carry antlers until parturition (Espmark 1971), antlerless females can also be common, particularly within woodland caribou populations and those in poor condition (Reimers 1993). Consistent errors in identifying the sex of adults may lead to biases in recruitment estimates either by the inclusion of males in the female count, which would bias estimates of low recruitment low, or the exclusion of antlerless females from the female count, which would bias estimates of recruitment high.

Monitoring vital rates allows managers to estimate trends in population growth as well as study mechanistic relationships between environmental factors and specific components of population demography not possible with estimates of abundance alone (Todd and Rothermel 2006). However, estimates of actual abundances may be necessary to compare risk among populations (e.g., Wittmer et

al. 2010), assess recovery goals (Gerber and Hatch 2002) and to validate trends measured with vital rates alone (McCullough 1994). For woodland caribou, traditional aerial survey methods can be used successfully when counting caribou in open alpine or shrubland habitats (Seip 1990, Mahoney et al. 1998, Wittmer et al. 2005b). However, the application of such methods to monitor caribou in dense boreal forest habitats suffers due to low sightability and grouping behavior (Stuart-Smith et al. 1997). Hierarchical, 2-tier approaches may provide an effective but expensive alternative (Courtois et al. 2003). Genetic monitoring may provide another means of estimating woodland caribou population abundance (Hettinga 2010), though the feasibility of applying genetic techniques to monitor caribou populations over provincial or federal scales is uncertain. A quantitative assessment of the costs and power of monitoring strategies (*sensu* Bowden et al. 2000) for woodland caribou including all forms of abundance and vital rate estimation would benefit recovery planning for this and other endangered species.

In addition to methodological implications of our results, we also portray a stable trend for the A la Pêche population of woodland caribou over the past decade. Woodland caribou are federally classified as threatened in Canada as a component of woodland caribou occurring within the Southern Mountain National Ecological Area (Committee on the Status of Endangered Wildlife in Canada 2002). As most woodland caribou populations are in decline in Alberta (Schneider et al. 2010), conservation of the A la Pêche population may be particularly important for the species' persistence at the provincial or even national scale. A recovery strategy for woodland caribou should include collection of survival and recruitment data similar to those used in our analyses as important components of population monitoring.

## 5.8 MANAGEMENT IMPLICATIONS

The value of age ratios for population monitoring has been both questioned (Caughley 1974, McCullough 1994) and supported (Harris et al. 2008) in previous research. We show how concurrent monitoring of adult female survival and age ratios allows both retrospective estimation of empirical population growth rates and the decomposition of recruitment-specific vital rates. We also use the A la Pêche woodland caribou population as an example population for which adult survival and recruitment parameters have contributed nearly equally to population growth rates over the past decade. White and Bartmann (1998) recommended that monitoring schemes for ungulates include both fawn survival and adult survival data. Similarly, we recommend the concurrent monitoring of adult female survival to complement age ratio data when managing caribou and other ungulates. This recommendation is partially due to the potential role of both vital rates in driving ungulate population growth rates and additionally due to the important ability to isolate relevant recruitment terms from age ratios for stochastic modeling of future dynamics.

## 6.0 DETERMINE THE RELATIVE IMPORTANCE OF WOLF-CARIBOU SPATIAL OVERLAP AND WOLF DENSITIES ON CARIBOU-WOLF ENCOUNTER RATES AND CARIBOU SURVIVAL

The following work in this section is included in a published peer-reviewed article:

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

### 6.1 SCOPE

We examined the role of wolf-caribou spatial overlap, wolf pack characteristics and anthropogenic features on the rates at which caribou encountered wolves. We further compared spatio-temporal patterns of encounter rates to those of wolf resource selection and caribou mortality.

### 6.2 SUMMARY OF FINDINGS

1. Caribou, *Rangifer tarandus*, across North America and Scandinavia are declining in part from wolf (*Canis lupus*) mediated apparent competition with more abundant ungulate prey species. While caribou generally persist in areas with low wolf density, wolf packs that overlap caribou ranges could trigger caribou declines. Moreover, anthropogenic linear features such as roads, trails, and seismic lines are hypothesized to increase predation risk for caribou, yet few studies have examined the mechanistic effects of these factors on wolf-caribou encounter rates and predation risk.
2. We used (a) time-to-event models of wolf-caribou encounters estimated from concurrent GPS radio-collar data from wolves and caribou, and (b) wolf resource selection models of travel locations, to determine the potential influence of wolf-caribou spatial overlap, linear features, elevation and season on encounter rates.
3. Wolf-caribou encounter rates increased with high wolf-caribou overlap, proximity to linear features, and lower elevations. Wolves strongly selected low elevations, especially during winter and spring. Selection for linear features as travel routes increased with elevation.
4. Caribou risk of encounter was highest during the summer and fall when wolves spent the most time at high elevations. Most wolf-caused mortalities (n=12) occurred during spring and summer.
5. Synthesis and applications: The presence of anthropogenic linear features and the amount of time wolves spend in caribou range could be equally important as wolf density when prioritizing caribou recovery actions such as wolf or primary prey reductions or reintroductions. Our use of GPS locations and time-to-event modeling offer a powerful tool for evaluating factors affecting predation risk.

### 6.3 INTRODUCTION

Predation risk affects the distribution, behaviour and trophic interactions amongst species (Brown et al. 1999, Creel et al. 2007). Predation risk is the combined function of the ability of predators to find prey (encounter rates) and the conditional ability to kill prey given an encounter (attack rates) (Holling 1959a,



1959b, Lima and Dill 1990, Hebblewhite et al. 2005). Encounter rates have traditionally been measured using visual observations (Scheel 1993, MacNulty et al. 2007), snow tracking (Hebblewhite et al. 2005, Sand et al. 2006) or using theoretical models of predator-prey densities, group size and movement strategies (Fryxell et al. 2007, Mitchell 2009). The increasing use of global positioning system (GPS) radio-collars to collect fine-scale movement data on both predators and prey (Cagnacci et al. 2010), however, has great potential to provide insights into the mechanisms of predation risk by allowing further examination of factors affecting both encounter and mortality rates (Merrill et al. 2010). Eriksen et al. (2008) examined observed and expected distances between wolf and moose, *Alces alces*, GPS locations to test whether or not wolves actively searched for moose. We build upon their approach here by using time-to-event modeling to examine factors affecting encounter rates between wolves, and their endangered prey, woodland caribou.

Caribou populations are declining through much of their range in North America and Scandinavia (Vors and Boyce 2009, Nellemann et al. 2010) and woodland caribou within the Southern Canadian Rockies are listed as threatened under Canada's Species At Risk Act (COSEWIC 2002). Many of the declines are thought to be driven by anthropogenic changes to landscapes resulting in wolf-mediated apparent competition between caribou and more abundant ungulate prey (Wittmer et al. 2005a, DeCesare et al. 2010). There are two proposed mechanisms affecting wolf-mediated apparent competition for caribou. First, conversion of old forests into early seral stage forests increase habitat quality for primary prey such as moose (Serrouya et al. 2011) possibly resulting in increased wolf densities and lower caribou survival rates (James et al. 2004, Sorensen et al. 2008). Second, anthropogenic linear features such as roads or seismic exploration lines provide wolves with efficient travel routes into caribou range (James and Stuart-Smith 2000). Caribou counter predation risk near these features by avoiding roads and seismic lines (Dyer et al. 2001, Nellemann et al. 2001), yet still have lower population growth rates in areas with high densities of linear features (Sorensen et al. 2008). Despite the links between linear features and population-level declines, few studies have directly examined the mechanisms underlying how anthropogenic features, predator density, and predator-prey overlap affect predation risk and prey mortality (James and Stuart-Smith 2000). Understanding mechanisms of anthropogenically enhanced predation risk is of vital conservation importance given the widespread declines in woodland caribou across their entire range.

Wolves are a dynamic and resilient species that have high growth potential but are also subject to high levels of human-caused mortality (Weaver et al. 1996, Fuller et al. 2003). Consequently, the density of wolves and their spatio-temporal overlap with caribou can vary greatly over time. While caribou have poor survival and recruitment rates in areas with high wolf density (Bergerud and Elliot 1986), it is not quantitatively clear how wolf-caribou overlap and variability in that overlap affects caribou demographic rates. This information is important for predicting likelihood of caribou persistence (Hebblewhite et al. 2007, DeCesare et al. 2011) and for prioritizing recovery actions within caribou populations (McLellan et al. 2010, Schneider et al. 2010). For instance, translocation-based management has been considered as a means to recover declining or extirpated woodland caribou populations (DeCesare et al. 2011), but we still need to assess how the amount of wolf-caribou overlap and interactions with primary prey would influence likelihood of persistence (Hebblewhite et al. 2007).

Prey species reduce their risk of predation from learning predators by moving (Mitchell and Lima 2002, Alonzo et al. 2003, Mitchell 2009) and by occurring in areas with low probability of attack success (Creel et al. 2005, Laundré 2010). Woodland caribou reduce predation risk by occurring in low densities and in areas with few other prey species (Wittmer et al. 2005a) but little is known about how these caribou, in the face of increasing wolf overlap, would fare in the predator-prey shell game (Mitchell and Lima 2002).

Here, we used time-to-event models (Cox-proportional hazards) to determine the effects of wolf-caribou overlap, roads, trails and elevation on encounter rates—important components of predation risk (Hebblewhite et al. 2005). We defined encounters as the spatio-temporal overlap between caribou and wolf GPS locations (Eriksen et al. 2008). We further tested the hypothesis that caribou avoid encounters with wolves by comparing encounter rates of concurrent wolf and caribou locations to a null model of encounter rates.

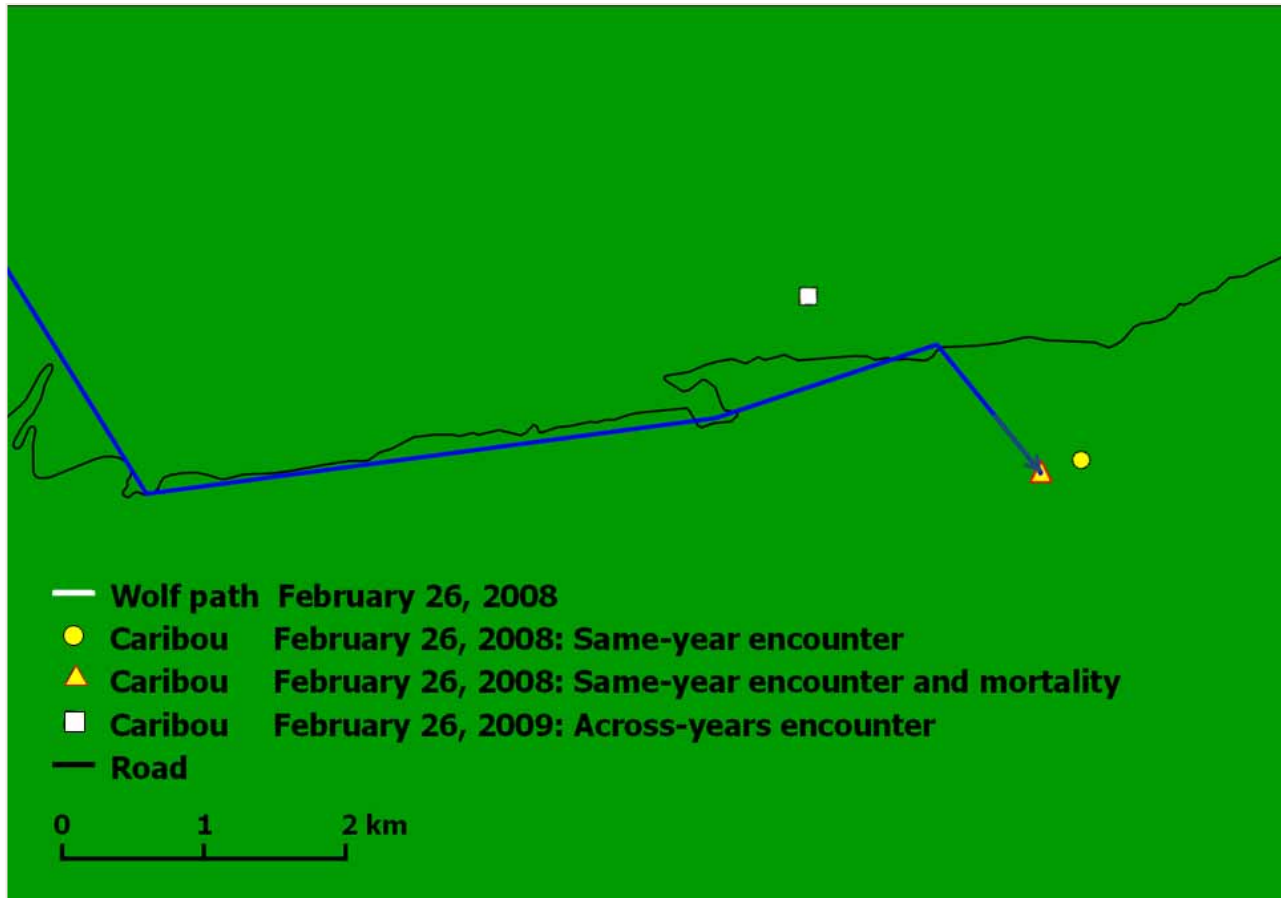
We also examined how the association between wolf travel routes and linear features (roads and trails) changed with elevation and season using resource selection analyses of wolf travel routes. Wolves clearly select linear features as travel routes (James and Stuart-Smith 2000, Whittington et al. 2005) and are more likely to kill ungulate prey near linear features (James and Stuart-Smith 2000). However it is unclear how wolf selection for linear features and caribou predation risk are affected by rugged topography associated with higher elevations and deep snow depths during winter (Seip 1992). Therefore, we also assessed how wolves varied their selection for linear features, which is important for determining when and where linear features increase caribou predation risk. Together, our encounter rate and wolf movement resource selection analyses enabled us to better understand the fine-scale mechanisms affecting wolf-caribou encounters and potentially predation risk.

## 6.4 MATERIALS AND METHODS

We collected GPS radio-collar (LOTEK, Aurora, ON, brands 3300, 4400) data from 35 adult female caribou and 37 male and female wolves from 11 packs from 2002 until 2010. Radio-collared wolves were greater than 8 months old. Caribou were captured using helicopter net-gun during winter, and wolves were captured using helicopter net-gun and darting in winter and foot-hold trapping in summer according to Parks Canada and University of Montana approved animal capture protocols (Animal Use Protocol 059–09MHWB-122209). GPS fix schedules ranged from fixes every 15 minutes to every 6 hours. Data were collected from four caribou subpopulations including the Tonquin, Maligne and Brazeau in Jasper National Park and Banff in the northern portion of Banff National Park.

### 6.4.1 Wolf-caribou encounter rates

We first examined the effects of wolves, linear features, elevation, and differences in caribou subpopulations on wolf-caribou encounter rates using Cox-proportional hazard models (Harrell 2001). Encounters occurred when a wolf travelled within 1.285 km (median 6-hour wolf step length) of a caribou location on the same year and calendar day (same-year encounter) or a different year and same calendar day (across-years encounter; analysis conducted to test hypotheses explained below) (Figure 6.1). Our detection distance was likely within a wolf's sensory detection range (Mech and Boitani 2003) and is similar to a detection distance of 1.5 km for wolves in other studies (Laporte et al. 2010, Muhly et al. 2010). Furthermore, the effects of the distance threshold did not strongly affect univariate model coefficients (see Appendix A). Some wolves encountered caribou on successive days but to ensure independence, we only classified the first day as an encounter.



**Figure 6.1.** Examples of wolf-caribou encounters showing a wolf movement path and caribou locations resulting in a same-year encounter with no caribou mortality, same-year encounter resulting in mortality, and an across-years encounter (same calendar day but different year).

We addressed encounter rates from the caribou's perspective using a temporal resolution of one caribou location per day. For each location we determined whether or not an encounter occurred and calculated distance to nearest linear feature (road or trail; km), elevation (km), late winter wolf pack size, whether or not the wolf pack was transient and a wolf-caribou utilization distribution overlap index (UDOI) (Fieberg and Kochanny 2005). We considered wolf packs that formed for 1 to 3 years and then dispersed as transient wolf packs (Fuller et al. 2003). These wolf packs could have disproportionately large effects on caribou because they often occur in lower quality wolf habitats, which include higher elevation caribou ranges (Kauffman et al. 2007). When calculating the UDOI, we sub-sampled GPS data to a 6-hour fix rate so that all animals had the same fix frequency. We calculated separate UDOI's for each season (summer=June - August; fall=September - November; winter=December - February; spring=March - May). We limited the encounter analyses to GPS-collared wolves and caribou with a UDOI > 0.001 to include only animals that had a non-zero probability of encounter. We centered the explanatory variables on their median value (Harrell 2001) and performed univariate analyses to remove correlated and uninformative variables. We compared competing models with all combinations of the remaining variables using Akaike Information Criterion (AIC), selected the top ranked models with  $\Delta AIC$

< 4, and averaged model coefficients and standard errors over the top ranked models (Burnham and Anderson 2002).

We used Cox-proportional hazard models to determine how wolves and linear features (roads and trails) affected caribou encounter rates. We used June 1st as a recurrent time of origin (Fieberg and DelGiudice 2009) because it is the start of a biological year when caribou are born and because the seasonal baseline hazard was not correlated with most annually changing explanatory variables of interest (unpublished data). We estimated the effects of wolves, linear features and topography on encounter rates using a generalized linear mixed model (GLMM) formulation of the Cox model (Whitehead 1980, Fieberg and DelGiudice 2009) with a Poisson distribution and a random intercept for each caribou (Yau 2001, Donohue and Xu 2010). We used natural splines with four fixed knots at the 0.05, 0.35, 0.65 and 0.95 quantiles of days since June 1st (Harrell 2001) to estimate the underlying baseline hazard.

The analyses used both same-year and across-years encounters. The across-years encounters provided a null model that allowed us to test the hypothesis that caribou evade wolf encounters. For this approach, we compared models with and without the covariate same-year (versus across-year) and its interaction with UDOI. The across-years encounters assumed that within their home ranges, caribou did not change their movements on a yearly time-scale to avoid wolf predation and that wolves did not change their movements on a yearly scale to search for caribou. However, if those assumptions did not hold and caribou adapted to real-time changes in wolf distribution, then we expected encounter rates for the same-year data to be lower than encounter rates for across-years data and that  $\beta$  coefficients for the wolf-caribou overlap index would be lower for same-year analysis. Conversely, if wolves actively searched for caribou, then we expected encounter rates for the same-year data to be higher and  $\beta$  coefficients for the wolf-caribou overlap index to be higher than in the across-years data. Furthermore, the interaction between same-year and UDOI allowed us to examine the effects of increasing overlap on predator-prey behavioural dynamics.

#### *6.4.2 Caribou mortality*

We determined the cause of caribou mortalities by conducting aerial telemetry on a total of 53 caribou fitted with VHF or GPS radio-collars every four to six weeks. When radio-collars emitted a mortality signal, we investigated the mortality site and determined cause of death by looking for evidence of predation. We classified mortalities as wolf-caused or other based on signs of chase sequences, hematomas, carcass disarticulation, wolf tracks and wolf GPS data. We then assessed how season affected caribou vulnerability to predation by comparing the baseline hazards of encounter rates and wolf-caused caribou mortalities. We graphically compared the hazards because our limited number of wolf-caused mortalities prohibited rigorous statistical comparisons.

#### *6.4.3 Wolf travel resource selection*

We tested how wolf selection for linear features varied with elevation and season using resource selection function (RSF) models of wolf travel routes (Manly et al. 2002). We considered that wolves searched for prey while travelling (MacNulty et al. 2007) and thus, discriminated wolf travel from other states (resting, feeding on kills). We first rarefied the data into 2-hour fix intervals and removed resting or feeding locations where wolves spent > six hours within a 300 m radius over four days (Webb et al. 2008). To test for selection of linear features, we compared attributes of wolf travel locations to an equal number of random locations within each individual wolf's home range estimated with a 95% adaptive kernel home range. We then developed a base RSF model with the explanatory variables known to strongly influence wolf movements (Whittington et al. 2005, Hebblewhite and Merrill 2008) and compared five a priori models with interactions between linear features (on or off a trail or road),

elevation and season. Explanatory variables used in the baseline RSF model were: elevation (km), slope (degrees), southern aspects ( $-1 * \cosine[\text{aspect}]$ ), land cover (Hebblewhite and Merrill 2008) and distance to nearest edge (km). We defined edge as the border between forests and open land cover classes (herbaceous, shrubs, deciduous, rock, water) and we used a decay term for distance ( $1 - \exp(-2 * \text{distance})$ ) that has been used for grizzly bears (Nielsen et al. 2009). We used GLMM's with a logit link and a random intercept for each wolf and we centered explanatory variables on their median value to improve model convergence. We generated models using data from 30 randomly selected wolves of a total of 37 and validated the models with the remaining 7 wolves using the area under the receiving operating characteristic curve (ROC) and the Spearman rank correlation coefficients between bin rank and area adjusted frequencies of used locations (Boyce et al. 2002). All analyses were conducted using R 2.12.0 (R Development Core Team 2010) with the *adehabitat* (Calenge 2006), *sp* (Bivand et al. 2008), *survival* (Therneau and Lumley 2009) and *lme4* (Bates and Maechler 2010) packages.

## 6.5 RESULTS

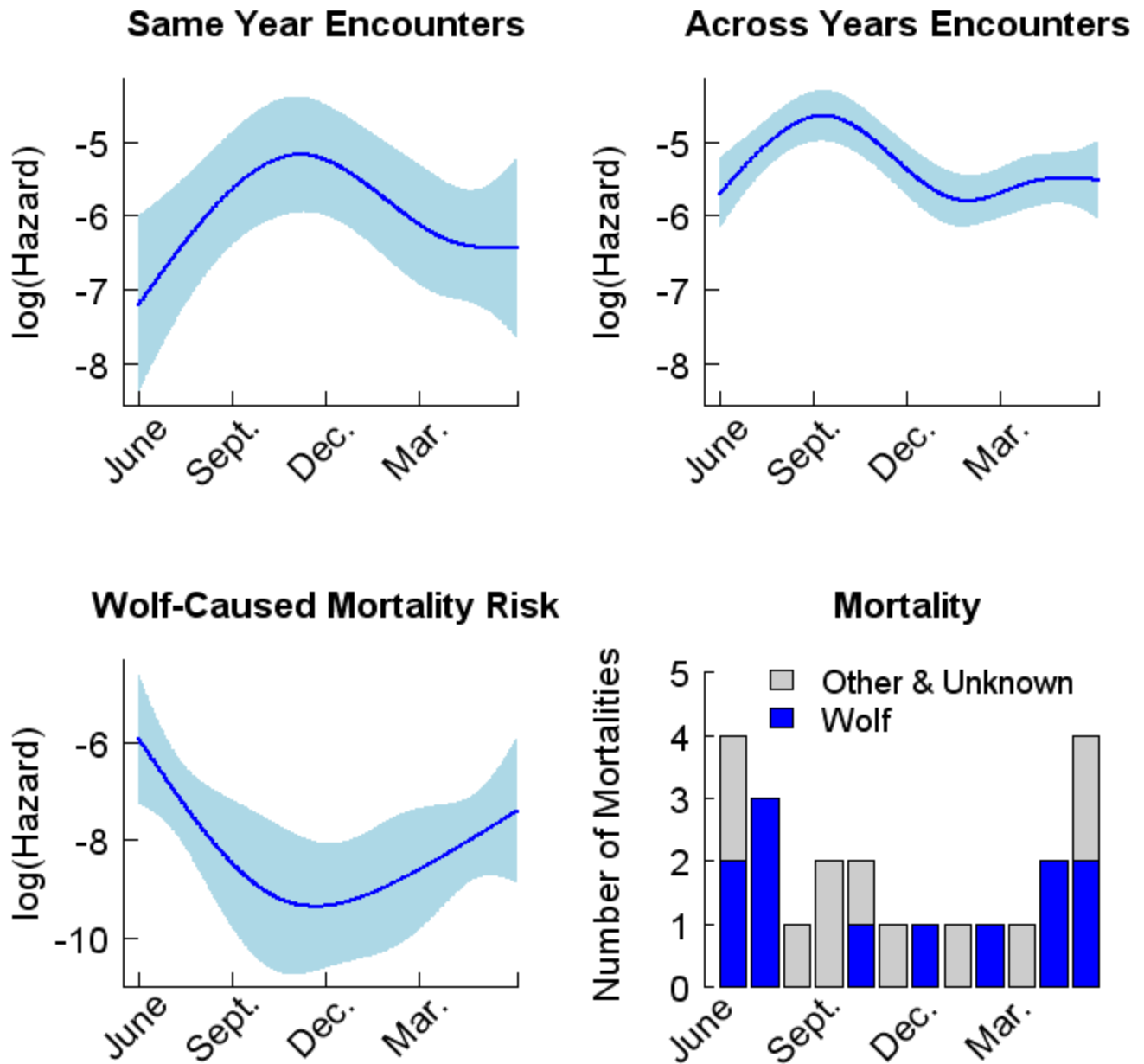
### 6.5.1 Wolf-caribou encounter rates

Twenty-eight of the 37 wolves had home ranges that overlapped with caribou home ranges. We recorded 58 independent same-year encounters out of 9695 wolf-caribou days and 365 across-years encounters out of 67,209 caribou wolf days. This resulted in daily same-year encounter rates of 0.6% (Banff = 1.8%, Brazeau = 1.0%, Maligne = 0.4% and Tonquin = 0.5%) and daily across-years encounter rates of 0.5% (Banff = 1.8%, Brazeau = 1.1%, Maligne = 0.4% and Tonquin = 0.5%). Forty-four percent of the 35 caribou encountered a GPS collared wolf and the number of encounters per caribou ranged from 0 to 9. Most wolf-caribou encounters occurred during the summer and fall (Figure 6.2a,b).

Encounter rates increased with increasing UDOI and transient wolf packs (Table 6.1 and 6.2). Encounter rates also increased when caribou travelled to lower elevations and areas near linear features (Figure 6.3). The Banff and Brazeau subpopulations had higher across-years encounter rates than the Tonquin. The interaction between same-year data and UDOI suggested that as UDOI increased, encounter rates for same-year data were higher than for across-years data. Model coefficients estimated using the same-year subset of encounters data were similar in direction but had wider confidence intervals, likely due to a smaller sample size, than coefficients estimated with both same-year and across-years data.

### 6.5.2 Caribou mortality patterns

We recorded 23 mortalities from radio-collared caribou of which at least 12 were caused by wolves. Wolf-caused caribou mortalities occurred throughout the year and most mortality occurred from April through July (Figure 6.2c,d). Conversely, most encounters occurred during the late summer and fall. Thus, the risk of mortality for adult female caribou was not directly proportional to their risk of encounter.



**Figure 6.2.** Seasonal distributions of (a) same-year encounters ( $n=58$ ), (b) across-years encounters ( $n=365$ ), (c) wolf caused mortality risk ( $n=12$ ), and (d) caribou mortalities ( $n=23$ ). June 1st was used as the time of origin in the Cox-proportional hazards encounters analysis. Seasonal hazards were estimated using natural splines within a GLMM. Shaded areas indicate 95% confidence intervals of the seasonal hazards.

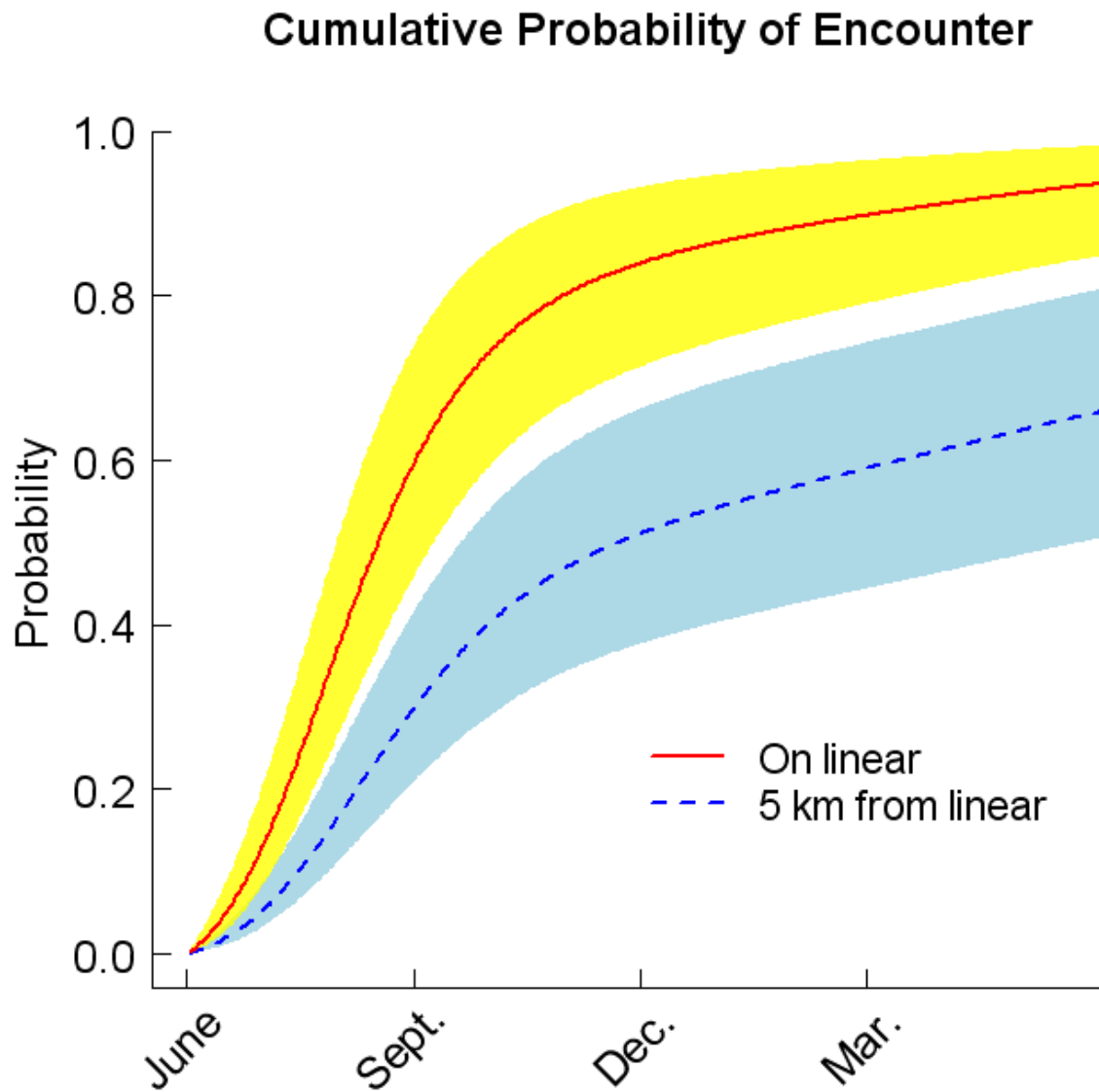
**Table 6.1.** Top ranking models and Akaike weights ( $w_{AIC}$ ) for same-year and across-years wolf-caribou encounter rates (Cox proportional hazards) and for wolf travel resource selection. Top ranking models were models with  $\Delta AIC < 4.0$  from the model with the lowest AIC value.

Rank	Model	df	$\Delta AIC$	$w_{AIC}$
<i>Encounters</i> <i>423 encounters (58 same-year and 365 across-years) out of 76904 wolf-caribou days</i>				
1	UDOI + region + transient + elev + dlinear	8	0.0	0.451
2	UDOI + same-year + region + transient + elev + dlinear +	10	0.3	0.389
3	UDOI + same-year + region + transient + elev + dlinear	9	2.1	0.161
<i>Wolf travel</i> <i>30 wolves and 29638 locations; Validate 7 wolves and 2224 locations</i>				
1	elevation + slope + aspect-s + landcover + dist.edge + linear*elevation*season	35	0	1

\*UDOI = utilization distribution overlap index; dlinear= distance to nearest linear feature (km), dist.edge =  $1 - \exp^{(-2 * \text{distance to nearest edge})}$  (km); aspect-s =  $-1 * \cos(\text{aspect})$ ; linear = on or off linear feature.

**Table 6.2.** Model averaged coefficients and standard errors for top ranked models of wolf-caribou encounters from Table 6.1. Model estimates for the intercept and splines are not shown for the encounter results.

Variable	B	SE	$B \cdot SE^{-1}$	P
dlinear	-0.154	0.040	-3.8	< 0.001
elevation	-1.279	0.278	-4.6	< 0.001
region: Banff vs Tonquin	1.376	0.387	3.6	< 0.001
region: Brazeau vs Tonquin	0.819	0.243	3.4	0.001
region: Maligne vs Tonquin	-0.028	0.235	-0.1	0.907
transient	0.698	0.178	3.9	< 0.001
UDOI	0.656	0.115	5.7	< 0.001
same-year	0.004	0.086	-0.1	0.960
UDOI:same-year	0.208	0.101	-2.0	0.040



**Figure 6.3.** Cumulative probability of a wolf-caribou encounter with 95% confidence intervals for caribou on and 5 km from linear features. 95% of caribou locations occurred within 5.3 km from roads and trails.

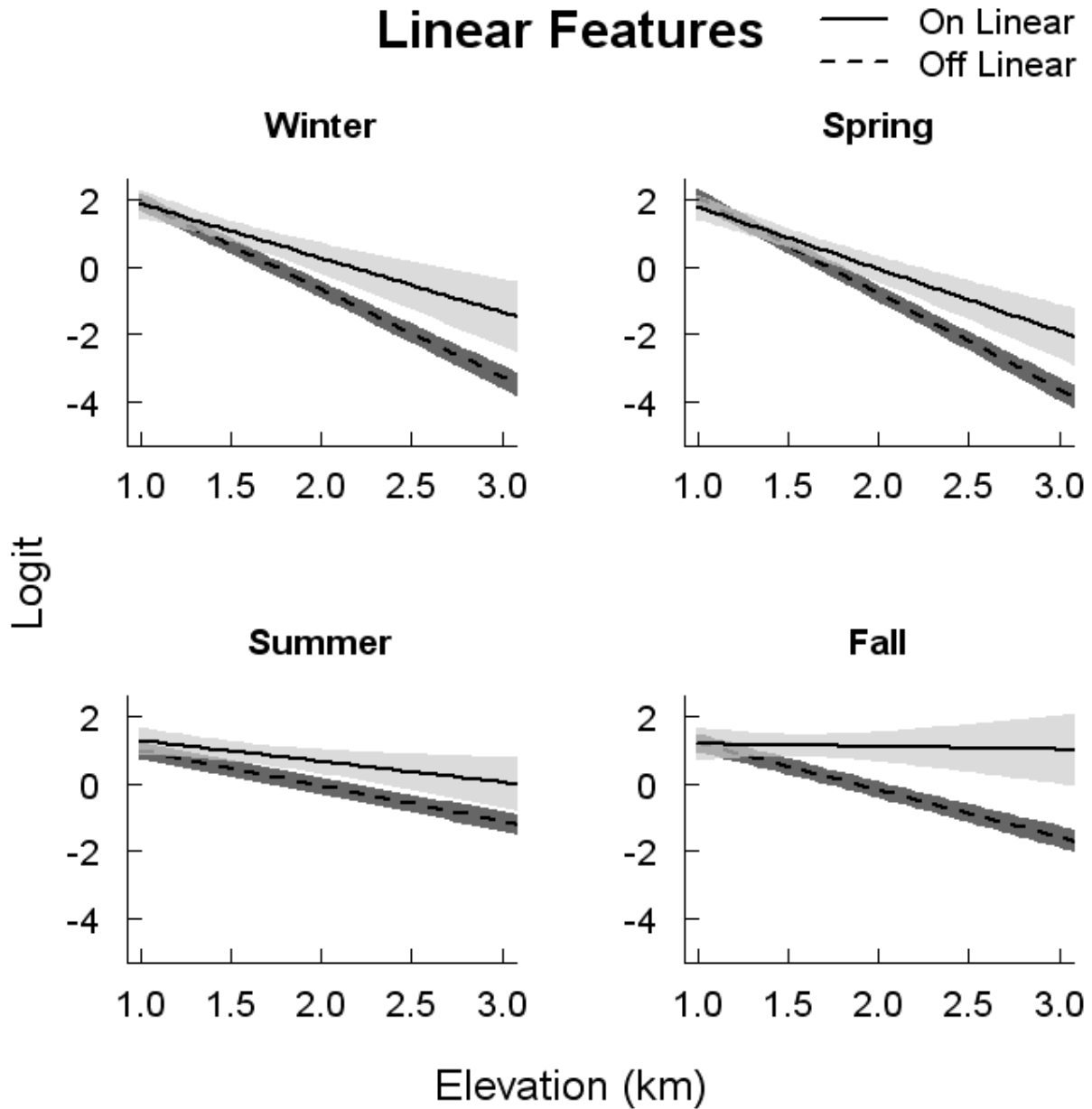


### 6.5.3 Wolf travel resource selection

The top-ranked RSF model for wolf travel included a strong three-way interaction between being on or off linear features, elevation, and season (Table 6.1). Wolf selection for trails and roads increased with increasing elevation, especially during fall, winter and spring (Table 6.3, Figure 6.4). The wolves strongly selected lower elevations during winter and spring and used higher elevations more during summer and fall, which was also when caribou had the highest risk of wolf encounter. The RSF model differentiated between the used and random locations well for both the model training (ROC = 0.80, Spearman rank correlation coefficient = 0.98) and withheld validation (ROC = 0.73, Spearman rank correlation coefficient = 0.91) data sets.

**Table 6.3.** Top ranked RSF model results for wolf travel locations.

Variable	B	SE	B·SE <sup>-1</sup>	P
elevation	-1.039	0.075	-14.0	< 0.001
aspect-south	0.095	0.021	4.5	< 0.001
slope	-0.050	0.002	-29.7	< 0.001
dedge	-1.209	0.062	-19.6	< 0.001
landcover: reference conifer-closed				
barren	0.262	0.053	5.0	< 0.001
conifer-open	0.159	0.045	3.6	< 0.001
herb-high elevation	1.229	0.072	17.2	< 0.001
herb-low elevation	0.752	0.101	7.5	< 0.001
mixed deciduous	0.448	0.107	4.2	< 0.001
shrub	0.773	0.060	12.9	< 0.001
water-rock	0.155	0.075	2.1	0.039
season: reference summer				
fall	-0.003	0.045	-0.1	0.940
spring	-0.190	0.041	-4.6	< 0.001
winter	-0.144	0.047	-3.1	0.002
linear	0.600	0.101	5.9	< 0.001
linear * elevation	0.424	0.247	1.7	0.086
linear * fall	0.281	0.166	1.7	0.091
linear * spring	-0.170	0.149	-1.1	0.254
linear * winter	0.039	0.166	0.2	0.816
elevation * fall	-0.352	0.100	-3.5	< 0.001
elevation * spring	-1.795	0.097	-18.5	< 0.001
elevation * winter	-1.552	0.105	-14.8	< 0.001
linear * elevation * fall	0.886	0.417	2.1	0.034
linear * elevation * spring	0.570	0.354	1.6	0.107
linear * elevation * winter	0.563	0.404	1.4	0.163



**Figure 6.4.** The influence of season and elevation on wolf resource selection for linear features (roads and trails) as travel routes. Shaded areas indicate 95% confidence intervals. Wolf selection for low elevations was strongest during winter and spring. Wolf selection for linear features increased with elevation, especially during fall, winter and spring.

## 6.6. DISCUSSION

Woodland caribou populations are thought to persist in areas with large-scale wolf densities lower than six wolves per 1000 km<sup>2</sup> (Bergerud and Elliot 1986). We found that encounter rates were driven by spatial-temporal overlap between wolves and caribou but not late winter wolf pack size. Moreover, the effect of overlap was stronger for the same-year data compared to our null model of across-years data. This suggests that during periods of high overlap, wolves win the predator-prey shell game and that caribou are unable to avoid encounters with wolves. In another system with more abundant prey, wolves also actively searched for moose (Eriksen et al. 2008). Our metric for pack size (a fine-scale estimate of wolf density) was estimated during late winter, which could be poorly correlated with pack sizes during the rest of the year. Large wolf packs could have larger effects on caribou compared to smaller packs given that large wolf packs have higher prey predation rates (Hayes et al. 2000). However, attack success, especially on smaller bodied prey, does not always increase with pack size (Mech and Boitani 2003) and may instead depend on the oldest male in the pack (Sand et al. 2006). Thus, small packs with high overlap could have large consequences for small prey populations (McLellan et al. 2010) contrary to broad-scale predictions of the general threshold put forth by Bergerud and Elliot (1986).

Encounter rates with wolves increased when caribou moved near linear features and wolves showed strong selection for linear features, especially at high elevations near caribou range. The two results suggest that the addition of linear features into caribou range would likely increase encounter rates and predation risk. Snow compaction of linear features in caribou range could have an especially large effect in mid-winter when deep unconsolidated snow normally restricts wolves to the valley bottoms (Paquet et al. 2010). Our results support other studies where caribou face increased risk of predation near linear features (James and Stuart-Smith 2000) and have lower demographic rates in areas with a high density of linear features (Sorensen et al. 2008).

Our subpopulation-specific encounter rates ranked similarly to estimates of subpopulation specific survival rates (DeCesare et al. 2011). Banff, which historically had the smallest but now extirpated subpopulation (Hebblewhite et al. 2010), had the highest encounter rates. They were three times higher than the Tonquin, which had the highest survival rates and the largest number of caribou. Thus, predicted survival rates for Banff translocation scenarios may be optimistic (DeCesare et al. 2011). The Brazeau also had higher encounter rates and lower survival rates than the Tonquin and now has less than 20 caribou remaining. The Maligne had surprisingly similar encounter rates to the Tonquin given that it has lower survival rates and less than 10 animals remain.

Transient wolf packs encountered caribou more frequently than stable wolf packs. Transient packs have higher predation rates on caribou (Kojola et al. 2004) and we speculate that the Maligne and Brazeau subpopulations declined because of predation by transient wolf packs. Translocation success of caribou into Idaho also appeared to depend on regional and temporally varying predator use of caribou range (Compton et al. 1995). Similarly, populations of other species such as bighorn sheep also appear to be driven by transient predators and stochastic predation events (Festa-Bianchet et al. 2006). Thus, transient predators could have large effects on recovery actions for small populations.

Despite the importance of wolf overlap and resource selection for increasing encounter rates, the seasonal distribution of encounter rates did not mirror the seasonal distribution of our limited sample of adult female mortalities. Most wolf-caribou encounters occurred during the summer and fall, which is when wolves also showed the strongest selection for high elevations, whereas most wolf-caused mortality occurred during the spring and summer. Several biological mechanisms that mediate the risk

of death given an encounter could explain the apparent discrepancy between risk of encounter and mortality. Annual variation in prey group size could reduce risk (Hebblewhite and Merrill 2011), caribou could be in better body condition and better able to reduce predation risk during summer or wolf encounters with caribou could be incidental to wolf selection for sympatric and more abundant elk or moose during summer (Robinson et al. [In press]). Similarly, caribou in our study could be more susceptible to predation given an encounter during late winter when snow crusts sometimes enable wolves to more easily prey upon caribou. Finally, other cohorts of the population, such as calves, may be more susceptible to predation given an encounter (Gustine et al. 2006a). The seasonal distributions of caribou mortality in other studies were similar to our distributions of encounter rates and wolf-caused mortality. Most wolf-caused caribou predation occurred during summer in Alberta (McLoughlin et al. 2003), Saskatchewan (Rettie and Messier 1998) and British Columbia (Kinley and Apps 2001, Wittmer et al. 2005a). In Norway, wolf predation on reindeer occurred during summer, fall and early winter but rarely in late winter (Kojola et al. 2004).

Our results suggest that when evaluating population persistence (Wittmer et al. 2010), ranking caribou populations for recovery (Schneider et al. 2010) or considering translocations to augment existing populations (DeCesare et al. 2011), wildlife managers need to consider not just the density of predators but also the distribution of linear features, trends in wolf density, trends in wolf-caribou overlap and methods of mitigation for transient predators. Moreover, as in other studies (James and Stuart-Smith 2000, Sorensen et al. 2008), the creation of linear features in caribou range would increase caribou risks of encounters and predation from wolves and potentially displace caribou from high quality habitat (Nellemann et al. 2001, Vistnes and Nellemann 2008, Nellemann et al. 2010).

Predation risk, the combined effects of encounter risk and attack success (Lima and Dill 1990, Hebblewhite et al. 2005) affects prey resource selection (Creel et al. 2005, Mao et al. 2005), reproduction (Creel et al. 2007), migration (Hebblewhite and Merrill 2009) and grouping behaviour (Hebblewhite and Pletscher 2002, Creel and Winnie 2005, Fryxell et al. 2007). Predators counter these prey defence strategies with their own hunting strategy, such as focusing on large groups (Hebblewhite and Pletscher 2002) or selecting resources that increase their probability of predation success (Hebblewhite et al. 2005, Merrill et al. 2010). Our approach for estimating encounter rates could have wide applicability to other systems given that GPS technology is being collected on a wide variety of species (Cagnacci et al. 2010) and similar encounter rate analyses could be even more powerful for systems with higher encounter rates between predators and primary prey with concurrent mortality data.

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## 7.0 THE ROLE OF TRANSLOCATION IN RECOVERY OF WOODLAND POPULATIONS

The following work in this section is included in a published peer-reviewed article:

DeCesare, N.J., J. Whittington, H. Robinson, M. Hebblewhite, M. Bradley, L. Neufeld, and M. Musiani. 2011. The role of translocation in recovery of Woodland caribou populations. *Conservation Biology* 25:365–373.

### 7.1 SCOPE

We used population viability analysis (PVA) of 4 populations of woodland caribou to assess relative need for, and the efficacy of, translocation-based recovery among caribou populations.

### 7.2 ABSTRACT

Maintenance of viable populations of many endangered species will require conservation action in perpetuity. Efforts to conserve these species are more likely to be successful if their reliance on conservation actions is assessed at the population level. Woodland caribou (*Rangifer tarandus caribou*) were extirpated recently from Banff National Park, Canada and translocations of caribou to Banff and neighboring Jasper National Park are being considered. We used population viability analysis to assess relative need for and benefits from translocation among caribou populations. We measured stochastic growth rates and the probability of quasi-extinction of 4 populations of woodland caribou with and without translocation. We used 2 vital rates in our analysis: mean adult female survival and calf-female proportion-based estimates of mean fecundity, with process variance isolated for each. Our results suggested the Tonquin caribou population in Jasper is likely to remain viable without translocation, but that translocation is probably insufficient to prevent eventual extirpation of the 2 other populations in Jasper. Simulated reintroductions of caribou into Banff resulted in a 53–98% probability of >8 females remaining after 20 years, which suggests translocation may be an effective recovery tool for some caribou populations.

### 7.3 INTRODUCTION

The long-term conservation of many endangered species may require sustained conservation effort, and most likely these species will never recover to the point where they can be delisted (Doremus and Page 2001, Scott et al. 2010). Such species have been called conservation reliant (Scott et al. 2005). Scott et al. (2005) hypothesized that the level of recovery attainable for different species varies as a function of the level of effort needed to ensure the species' persistence. The extent to which populations of a given species that differ in size or level of exposure to threats are conservation reliant and also may vary. Quantification of the level of conservation reliance among populations could provide information on the likely efficiency of proposed recovery actions (Bottrill et al. 2008, McDonald-Madden et al. 2008).

One common recovery tactic is the translocation of animals to either reintroduce populations or to increase the number of individuals in extant populations (Scott et al. 2005, Armstrong and Seddon 2008). Translocations of endangered species rarely are successful (Fischer and Lindenmayer 2000), although many translocations have not considered species' population ecology in detail (Seddon et al. 2007). Retrospective analyses have been used to assess the demographic outcomes of past translocation programs (Van Houtan et al. 2010) and population viability analyses (PVA) allow the a priori comparison of population persistence given different translocation scenarios (Morris and Doak

2002). Given that few individuals typically are translocated, demographic stochasticity and Allee effects may affect whether translocations increase the probability of species recovery (Deredec and Courchamp 2007, Van Houtan et al. 2010). Population viability analysis can be used to quantify the extent to which populations of endangered species are reliant on translocation or other conservation interventions by allowing the comparison of projected population outcomes under different scenarios.

Woodland caribou (*Rangifer tarandus caribou*) are listed as endangered in the United States and listed as threatened across most of their range in Canada. Evidence that populations of woodland caribou are conservation-reliant is mounting along the southern edge of the species' range (Schaefer 2003), where translocation (Compton et al. 1995), habitat protection (Mosnier et al. 2003) and predator control (Gross 2008) have been used to maintain extant populations. Extirpations of populations of woodland caribou occurred recently in British Columbia (Wittmer et al. 2010) and several other southern populations have high probabilities of extirpation in the near future (Boisjoly et al. 2010, Schneider et al. 2010, Wittmer et al. 2010). Anthropogenic land use is hypothesized to be the primary driver of the decline of woodland caribou. Human activities have caused habitat loss (Schaefer 2003) and have indirectly caused asymmetry in wolf- (*Canis lupus*) mediated apparent competition (DeCesare et al. 2010) between caribou and primary prey species such as moose (*Alces alces*), which increase in abundance in areas of anthropogenic land use (Wittmer et al. 2007). In addition, at low population densities caribou may be susceptible to Allee effects (Wittmer et al. 2005b, McLellan et al. 2010).

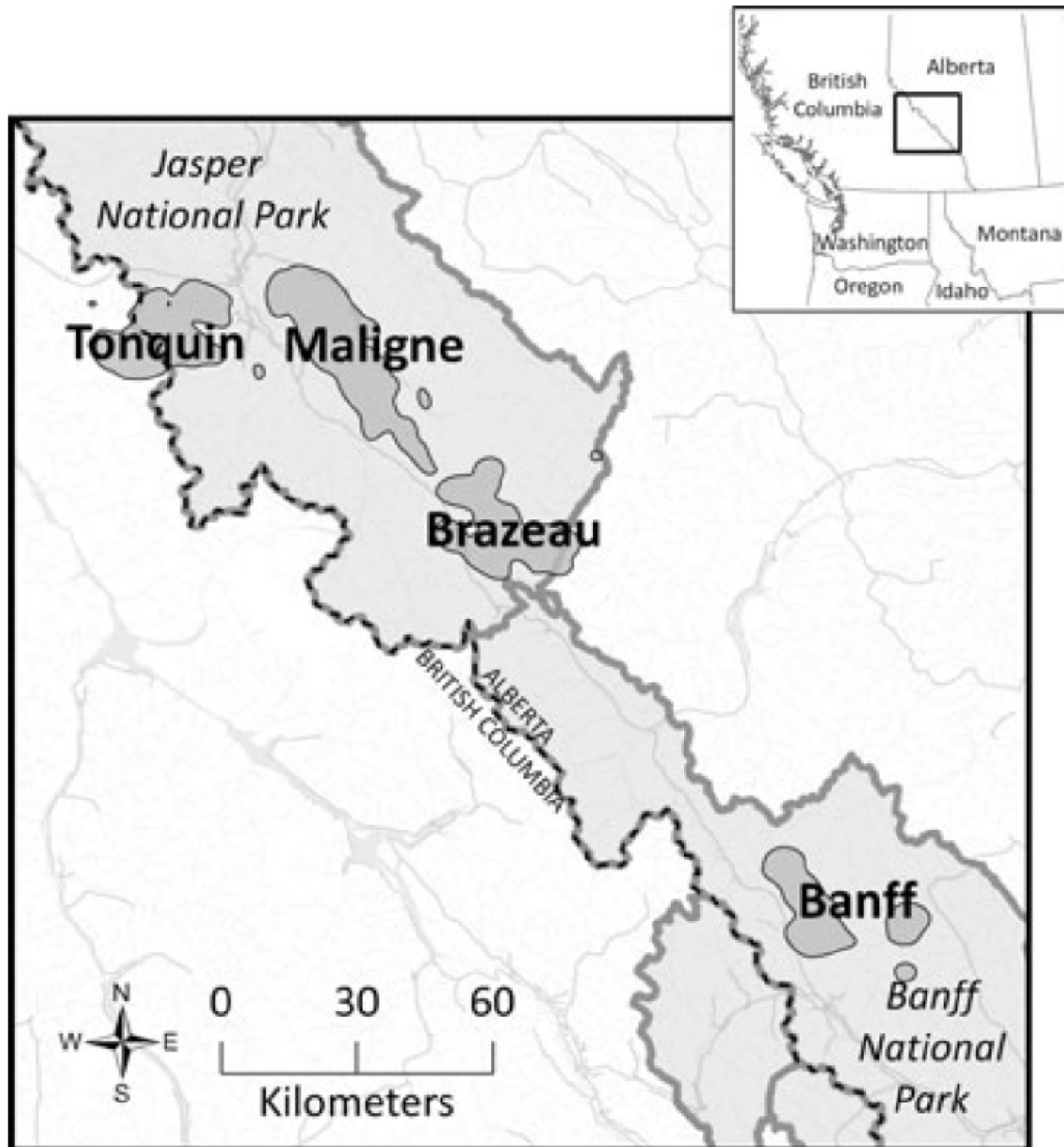
Protected areas alone may not be sufficient to conserve caribou (Brashares 2010), as evidenced in Banff and Jasper National Parks where one population was extirpated in 2009 (Hebblewhite et al. 2010) and 2 of 4 remaining populations have declined to  $\leq 10$  individuals. Hebblewhite et al. (2010) and Serrouya and Wittmer (2010) argue that caribou conservation in Canada's national parks was ineffective because there were episodically high levels of wolf predation, delays in production and implementation of a recovery plan, a lack of political will to conserve the taxon and disagreements about the roles of passive and active recovery strategies. However, similar arguments also applies to caribou conservation outside of parks, thus highlighting the importance of studying the application of conservation strategies (e.g., translocations) using approaches that can be applied to any caribou populations. Translocation may be the most aggressive approach available to caribou conservation given lack of societal support for predator control (Garrott et al. 1993, Bruskotter et al. 2009). We conducted PVAs of 4 populations of woodland caribou in Banff and Jasper National Parks to assess the efficacy of translocation-based recovery. Although we focused on caribou within national parks, our approach is broadly applicable. Our models can be modified to take into account variations in environmental characteristics (e.g., anthropogenic disturbance) that are different from those observed within parks. In fact, we are currently developing PVA models for use outside of parks.

## 7.4 METHODS

### 7.4.1 Study area and caribou populations

Our study area included portions of the Canadian Rockies within Banff and Jasper national parks (Banff and Jasper hereafter) in Alberta, Canada (Figure 7.1; 52°N, 117°W). Banff and Jasper combine with adjacent federal and provincial protected areas to form one of the largest protected landscapes (>20,000 km<sup>2</sup>) in North America. Elevations in Banff and Jasper range from 1000 to 3500 m and the mean slope is 20°. Winters are long and cold and summers are short. Most precipitation occurs in spring.

Caribou populations within the national parks in the Canadian Rockies are federally classified as components of caribou within the Southern Mountain National Ecological Area. There are 4 extant populations of caribou in Jasper: A la Pêche (northern Jasper), Brazeau, Maligne and Tonquin. In 2009, estimated sizes of these populations were 150, 10, 4 and 74 individuals, respectively (M. B. and L. N., unpublished data). Nuclear DNA of caribou in the Canadian Rockies shows that the caribou in Banff and Jasper are distinct from neighboring populations (McDevitt et al. 2009). We did not consider the A la Pêche caribou because they generally migrate outside the national parks in winter. We focused our PVA on reintroduction of the Banff population and on translocations to re-stock the Brazeau, Maligne and Tonquin populations in Jasper (Figure 7.1).



**Figure 7.1.** Home ranges (shaded) of woodland caribou in 3 extant populations in Jasper National Park and the recently extirpated population in Banff National Park, Alberta, 2001–2009.

### 7.4.2 PVA scenarios

To parameterize population viability analyses, we summarized the means and process variances of survival and fecundity of adult females of the caribou populations in Banff and Jasper from 2001 through 2009. We used these vital rates to project persistence of the populations for 20 years. We selected a projection time of 20 years because it is a feasible horizon for management and recovery planning and action in the parks. We conducted 4 sets of population viability analyses. In the first set, we used the fixed-mean survival rate for each population as the stochastic survival rate. In the second set of simulations, we evaluated the effects on persistence of positive density-dependent survival (i.e., an Allee effect) (Wittmer et al. 2005b, McLellan et al. 2010). We assumed the small populations in our study area remained below carrying capacity and did not model negative density dependence in vital rates. In our third and fourth sets of analyses, we considered different translocation scenarios (described below) with both fixed and density-dependent mean survival.

### 7.4.3 Estimating vital rates

#### 7.4.3.1 Adult survival

We fitted satellite or radio collars (Lotek Engineering, Aurora, Ontario) on female caribou ( $\geq 1.5$  years old) in the Banff ( $n=2$ ) (before extirpation), Brazeau ( $n=13$ ), Maligne ( $n=10$ ) and Tonquin ( $n=22$ ) populations. We used helicopter net guns to capture animals (protocols approved by Parks Canada and University of Montana; Animal Use Protocol 059-09MHWB-122209).

For each of the Jasper populations, we used a staggered-entry Kaplan-Meier procedure (Pollock et al. 1989) in program Stata 10 (StataCorp 2007) to estimate population-specific mean annual survival from 1 June through 31 May (a biological year) for each year of the study. Sample size for the Banff population was insufficient to estimate a herd-specific survival rate. Thus, we considered 2 scenarios of mean survival in Banff: one was based on pooled data from all collared individuals and one was based on data from the Tonquin population in Jasper. Survival rates in the former scenario were lower than in the latter. We assumed that survival rates of reintroduced adult female caribou in Banff would remain at or above the pooled mean over 20 years. Probability of caribou persistence in the Canadian Rockies can be theoretically estimated solely as a function of wolf density and densities of the wolves' primary prey (Hebblewhite et al. 2007). We based our assumption of female survival in Banff on the 75% decline in primary prey (elk) populations and subsequent and equivalent declines in wolf density (Hebblewhite 2006, Hebblewhite et al. 2010).

We quantified positive density dependence in survival rates by regressing annual survival rates and  $\ln(\text{number of females})$  for all population years (*sensu* Wittmer et al. 2005b; DeCesare et al. 2011, Supporting Information). Annual survival ( $S$ ) increases linearly as  $\ln(\text{number of females } [N_f])$  increases,

$$S = 0.724 + 0.0488 * \ln(N_f). \text{ (Equation 7.1)}$$

Although the relation was not statistically significant ( $R^2=0.10$ ,  $F_{1,16}=1.85$ ,  $P=0.19$ ), it was similar to previously documented positive density dependence in woodland caribou populations (DeCesare et al. 2011, Supporting Information; Wittmer et al. 2005b, McLellan et al. 2010).

Variance estimation for stochastic modeling should isolate process from sampling variance (White 2000), which is possible when estimates of both within- and among-year variances are available (Morris



and Doak 2002). We calculated within-year variance of annual survival estimates pooled among all populations according to Greenwood (1926) and then used White's (2000) method to isolate process variance ( $V_c$ ).

#### 7.4.3.2 Fecundity

Fecundity ( $\hat{F}$ ) in female-based, pre-birth pulse, matrix models is the product of multiple vital rates, including pregnancy fetal survival, fetal sex ratio and calf survival through the first year. Although survival of woodland caribou calves is poorly studied, recruitment is commonly monitored with spring aerial surveys that quantify the proportion of calves per breeding-aged female ( $\hat{R}$ ; McLoughlin et al. 2003). Calf-female proportions can be adapted for use in pre-birth matrix models by combining multiple vital rates into a single matrix element that parameterizes the contribution of 1-year-old calves at the end of each time step per adult that entered the time step. From 2004 through 2009, we conducted aerial counts of calves and females in March and used data pooled across Jasper populations to estimate the mean and process variance of fecundity. We estimated within-year mean proportions from survey counts per year ( $i$ ) as

$$\hat{R}_i = \frac{\sum y_i}{\sum c_i}, \text{ (Equation 7.2)}$$

where  $y_i$  and  $c_i$  are the numbers of calves and females aged  $\geq 1.5$  years old detected during an annual survey, respectively. We estimated within-year variance of calf-female proportion estimates with a binomial estimator (Thompson 1992):

$$\text{var}(\hat{R}_i) = \left( \frac{C_i - c_i}{C_i} \right) \frac{\hat{R}_i(1 - \hat{R}_i)}{c_i - 1}, \text{ (Equation 7.3)}$$

where  $C_i$  is the estimated number of females in the population on the basis of population-wide surveys. We used White's (2000) method to estimate process variance of  $\hat{R}$  across all years of monitoring.

March calf-female proportions did not correspond directly to  $\hat{F}$  for matrix projections, so we adjusted stochastically derived values of  $\hat{R}$  in 3 ways. First, we divided the denominator of Equation 2 by a concurrent stochastic value for 10-month adult survival ( $\hat{S}_i^{10/12}$ ), which converted the number of females detected each March to an estimate of number of females that entered the time step the previous June. Second, we multiplied the numerator by the same stochastic value for adult survival adjusted to 2-month survival, which converted the number of calves detected each March to an estimate of number of calves surviving to the end of the time step the following May (assuming calf survival = adult survival in April–May). Third, we multiplied the numerator by 0.5 to account for an estimated sex ratio of 1:1. Thus, we estimated fecundity as

$$\hat{F}_i = \hat{R}_i \times \frac{\hat{S}_i^{2/12} \times 0.5}{1 / \hat{S}_i^{10/12}}, \text{ (Equation 7.4)}$$

which reduces to

$$\hat{F}_i = \hat{R}_i \times \hat{S}_i \times 0.5 \text{ . (Equation 7.5)}$$

#### 7.4.4 Current viability

We constructed a stochastic, female-based, age-structured, pre-birth pulse, Leslie matrix to model caribou life history and population growth for each of our four study populations (Leslie 1945). We did not model senescence in survival or fecundity. Instead, we assumed survival and fecundity estimates were representative of the entire age distribution across all breeding age classes. We used code adapted from Morris and Doak (2002) to conduct stochastic simulations in both programs MATLAB (version R2009a, The MathWorks, Natick, Massachusetts) and R (version 2.11.1, R Development Core Team 2010). We based initial simulations on fixed, population-specific, mean survival rates by drawing random values of adult survival and March calf-female proportions (adjusted to fecundity with Equation 7.5) from beta distributions with estimated means and process variances. Simulations in which survival was density dependent were similar, except that stochastic survival rates were generated from beta distributions with a density-dependent mean survival rate derived from Equation 7.1.

In all simulations we explicitly modeled demographic stochasticity so as to treat vital rates as probabilistic individual outcomes rather than population-level averages (Morris and Doak 2002). We projected abundances of all populations 20 years into the future and ran 10,000 simulations of each scenario. Because we only observed one movement of a radio-collared individual among populations, we treated populations as demographically isolated. We reduced extant populations to female-only vectors by distributing minimum number of adult females detected in 2009 into a stable age distribution according to the right eigenvector of the mean matrix and by assuming a 1:1 sex ratio of calves. Correlations between survival and fecundity within- and among-years were not statistically significant, and the parameterization of correlated vital rates in simulations had minimal effects on results. Thus, we report simulation results assuming no within- or among-year vital-rate correlation.

Small populations may be affected by stochasticity (e.g., inbreeding depression or susceptibility to catastrophic events) that increases the probability of extirpation when abundance is below a quasi-extinction threshold (Ginzberg et al. 1982, Gilpin and Soulé 1986). We incorporated a quasi-extinction threshold in the interpretation of PVA results equal to our maximum observed group size to account for the increased probability of extirpation when all females are in a single group. During winter population surveys from 2003–2008, female caribou group size in Jasper ranged from 1–8 ( $\bar{x}$  =3.1,  $n$ =81 groups), which is similar to the size of summer groups in British Columbia ( $\bar{x}$  =3.8,  $n$ =2099 groups, McLellan et al. 2010). Therefore, we used a threshold of 8 females as the quasi-extinction threshold, which also represents the minimum population size at which recovery efforts are feasible in other populations of woodland caribou (Compton et al. 1995, Stronen et al. 2007). We summarized the results of all simulations with the cumulative probability of quasi extinction ( $n \leq 8$  females at any point in time) over 20 years and the stochastic population growth rate ( $\lambda_s$ ), estimated as a geometric mean across simulations.

#### 7.4.5 Viability with translocation

We used similar methods to simulate scenarios in which caribou were translocated into each of the 4 populations. Caribou translocations typically involve the introduction of 30–60 caribou over 1-3 years (e.g., Stronen et al. 2007). Thus, we simulated the translocation of 15 caribou per year over 1, 2 and 3

years, respectively, which represented the translocation of 15, 30 and 45 females or 20, 40 or 60 total caribou, respectively, assuming the inclusion of males in translocations at a sex ratio of 3 females:1 male. We also assumed translocated caribou fit the stable age distribution. Translocated animals can have lower probabilities of apparent survival than residents due to mortality and emigration, although survival probabilities can increase gradually to equal resident survival (Warren et al. 1996). We modeled 3 years of post-translocation survival depression, with 30%, 20% and 10% decreases in annual adult survival probabilities for the first 3 years when projecting populations of translocated individuals, and we assessed the effect of post-translocation survival depression by simulating all scenarios with and without survival depression.

## 7.5 RESULTS

### 7.5.1 Current viability

Pooled mean annual survival of adult female woodland caribou ( $S$ ) was 0.874 during the study period; raw variance ( $s^2$ ) was 0.00985 and isolated process variance ( $V_c[S]$ ) was 0.00693. Mean population-specific, annual survival differed among extant populations within Jasper (Table 7.1), although 95% CIs overlapped among all populations. The pooled mean calf-female proportion ( $R$ ) was 0.284, raw variance was 0.01230 and process variance ( $V_c[R]$ ) was 0.01030. Simulations of extant population sizes in which mean vital rates were either fixed or density-dependent generated a high probability of quasi extinction ( $\text{pr}[n_f \leq 8] = 1.0$ ) for the Brazeau and Maligne populations. The Banff population was extirpated in 2009, and the Brazeau and Maligne populations had low initial population sizes (Brazeau  $n_{f,t=0} = 6$ , Maligne  $n_{f,t=0} = 3$ ) and low adult female survival (Brazeau  $S = 0.806$ , Maligne  $S = 0.842$ ), which resulted in declining stochastic growth rates (Brazeau  $\lambda_{S,FMS} = 0.874$ ,  $\lambda_{S,DDS} = 0.851$ ; Maligne  $\lambda_{S,FMS} = 0.916$ ,  $\lambda_{S,DDS} = 0.845$ ). The median times to extirpation ( $n_f = 0$ ) for both the Brazeau and Maligne populations were 14 and 8 years, assuming fixed mean and density dependent survival, respectively.

After 20 years only the Tonquin population was extant (Table 7.2 and Figure 7.2). Projections of population size for the Tonquin population were considerably more responsive than those for other populations to whether mean survival values were fixed or positively density dependent. When mean survival was fixed, abundance was stable to increasing over 20 years ( $\lambda_{S,FMS} = 1.040$ ;  $\text{pr}[n_f \leq 8] = 0.008$ ). Because the estimated population size for 2009 was low relative to recent years ( $n_{f,t=0} = 33$ ), density-dependent survival led to a decrease in population size and possible quasi extinction in 20 years ( $\lambda_{S,DDS} = 0.962$ ;  $\text{pr}[n_f \leq 8] = 0.286$ ).

### 7.5.2 Viability with translocation

The effect of translocation on population viability depended on whether survival was fixed or density-dependent. When mean survival was fixed, translocations increased population sizes and minimally increased stochastic growth rates (Table 7.2). When survival was positively density dependent, translocations increased both initial population sizes and stochastic growth rates (Table 7.2 and Figure 7.2). Although positive density dependence accelerated population declines of the Brazeau and Maligne populations when no individuals were translocated, it led to increased survival when individuals were translocated. Stochastic growth rates of 0.966 and 0.955 in the Brazeau and Maligne, respectively, resulted from translocation alone (Table 7.2).

Stable to positive growth rates were generated by translocation in the Tonquin population under all scenarios ( $\lambda_S = 0.992 - 1.043$ ), whereas in Banff, stable to positive growth rates were achieved only when

survival rates were fixed and high ( $\lambda_s=1.038-1.042$ ). Simulations in which 45 females (60 total) were translocated to Banff resulted in a 53–98% probability of the population containing >8 females in 20 years and the stochastic population growth rates were 0.938–1.043. We assumed 3 years of post-translocation survival depression in all simulations, which resulted in an average 40% decrease in the median number of females after 20 years.

**Table 7.1.** Population-level annual survival of adult females ( $S$ ), pooled mean March calf-female proportion ( $R$ ), and pooled process variance ( $V_c$ ) estimates for woodland caribou in Banff and Jasper national parks, Alberta, Canada, 2001–2009.\*

Population	$n_{monitored}$	$n_{mortalities}$	days	$S$	Adult female survival		March calf-female proportions	
					95% CI	$V_c(S)$	$R$	$V_c(R)$
Banff	2	2	1996	.	.	.	.	.
Brazeau	13	7	2425	0.806	0.670-0.916	.	.	.
Maligne	10	5	2792	0.842	0.605-0.925	.	.	.
Tonquin	22	5	2425	0.944	0.871-0.976	.	.	.
Pooled	47	19	2792	0.874	0.808-0.919	0.0069	0.284	0.0103

\*Key:  $n_{monitored}$ , number of females monitored;  $n_{mortalities}$ , number of mortalities; days, length of survival monitoring period in days.

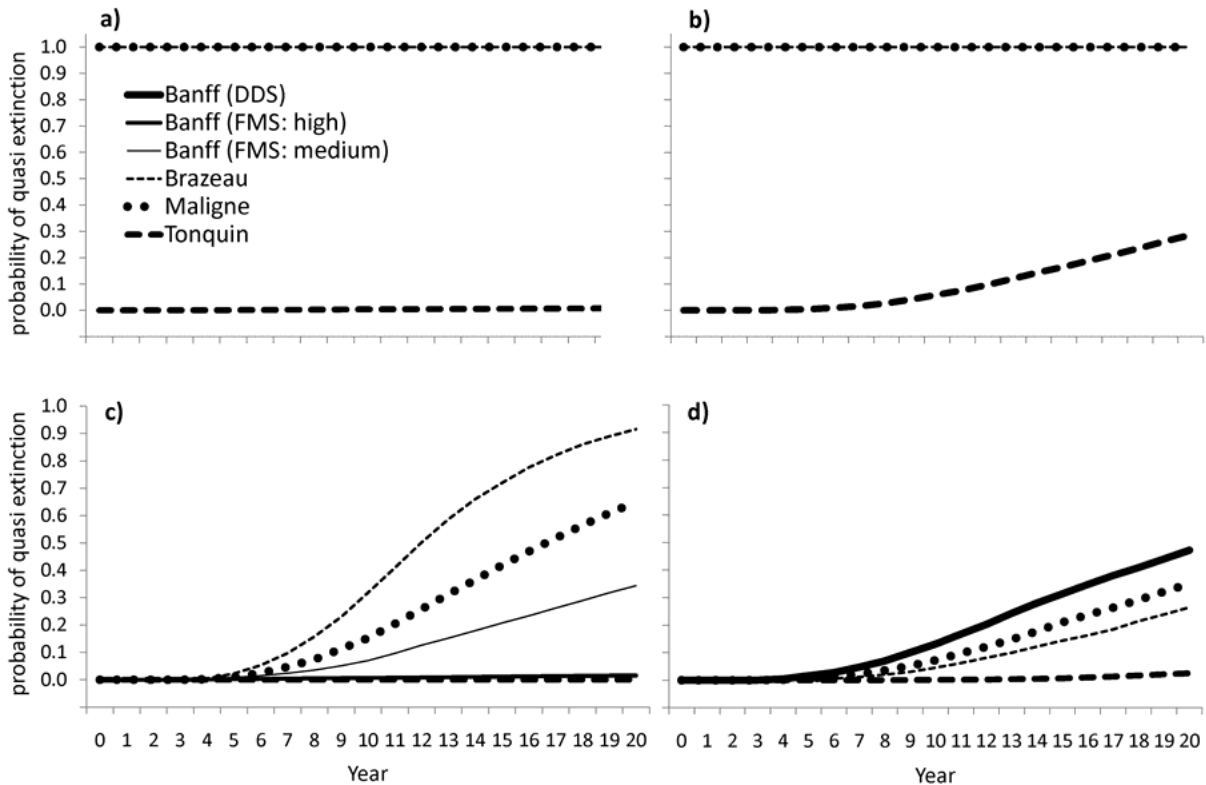
**Table 7.2.** Probability of quasi extinction ( $\text{pr}[n_f \leq 8]$ ), geometric mean stochastic growth rates ( $\lambda_s$ ) and starting number of females without translocation ( $n_f$ ) for the Banff, Brazeau, Maligne and Tonquin populations of woodland caribou under different translocation scenarios.<sup>a</sup>

Number of translocated females <sup>b</sup>	$\text{pr}(n_f \leq 8)$									$\lambda_s^c$								
	<u>Brazeau</u> ( $n_f=6$ )		<u>Maligne</u> ( $n_f=3$ )		<u>Tonquin</u> ( $n_f=33$ )		<u>Banff</u> ( $n_f=0$ )			<u>Brazeau</u> ( $n_f=6$ )		<u>Maligne</u> ( $n_f=3$ )		<u>Tonquin</u> ( $n_f=33$ )		<u>Banff</u> ( $n_f=0$ )		
	FMS	DDS	FMS	DDS	FMS	DDS	FMS med	FMS high	DDS	FMS	DDS	FMS	DDS	FMS	DDS	FMS med	FMS high	DDS
0	1.000	1.000	1.000	1.000	0.008	0.286	.	.	.	0.874	0.851	0.916	0.845	1.040	0.962	.	.	.
15	0.993	0.855	0.969	0.936	0.003	0.118	0.937	0.550	0.986	0.873	0.894	0.913	0.877	1.041	0.992	0.949	1.038	0.859
30	0.965	0.528	0.830	0.670	0.002	0.052	0.606	0.073	0.796	0.873	0.935	0.916	0.917	1.042	1.012	0.956	1.042	0.898
45	0.916	0.265	0.650	0.351	0.001	0.025	0.344	0.016	0.472	0.875	0.966	0.920	0.955	1.043	1.027	0.960	1.043	0.938

<sup>a</sup> Scenarios included different numbers of translocated females and either fixed (FMS) or density-dependent (DDS) survival. Results were generated from population viability analyses with translocation as the mode of reintroduction (Banff) or re-stocking (Brazeau, Maligne, Tonquin) of caribou in Banff and Jasper national parks, Alberta, Canada.

<sup>b</sup> Translocated animals were subject to 30%, 20%, and 10% decreases in survival probability for the first 3 years after translocation.

<sup>c</sup> Years during which population sizes were affected by animals added to the population through translocation and survival depression after translocation were excluded from the estimation of stochastic growth rates ( $\lambda_s$ ).



**Figure 7.2.** Probability of quasi-extinction ( $n_t \leq 8$ ) over time in 10,000 population-projection simulations of 4 scenarios for the Banff, Brazeau, Maligne and Tonquin populations of woodland caribou. Data used in simulations were collected during 2001–2009 in Banff and Jasper National Parks, Alberta. The 4 scenarios are (a) 2009 female population size and population-specific, fixed-mean, survival rates (FMS), (b) 2009 female population size and density-dependent survival rates (DDS), (c) translocation of 15 females/year for 3 years to each population and fixed mean survival rates, and (d) translocation of 15 females/year for 3 years to each population and density-dependent survival rates.

## 7.6 DISCUSSION

Our results suggest there is variation in the extent to which persistence of different woodland caribou populations in Banff and Jasper rely on translocation. The Brazeau and Maligne populations are likely to be extirpated in <20 years without translocation. Although translocation efforts may reduce the short-term probability of these populations' extirpation, translocation does not appear sufficient to reverse declines in abundance. The Tonquin population appears viable without translocation. If caribou are reintroduced into Banff, the population may be viable without further translocation if high survival probabilities are realized. Thus, managers of conservation-reliant populations must differentially prioritize recovery actions, such as translocation, among populations of endangered species.

In a recent review of reintroduction biology, Armstrong and Seddon (2008) identify an information gap relative to the relation between population establishment and the number of individuals that are translocated. We believe populations respond to number of translocated individuals in 3 ways. First, translocations increase population size regardless of trends in abundance, which decreases the short-term probability of extirpation. Second, translocations can decrease the negative effects of demographic stochasticity by leading to small increases in stochastic population growth rates ( $\lambda_{S,FMS}$  in Table 7.2) (Morris and Doak 2002). Third, in populations with positive density dependence, translocations may reduce the intensity of Allee effects by increasing both population sizes and subsequent population growth rates ( $\lambda_{S,DDS}$  in Table 7.2). Translocations have been correlated with increased means and reduced variances in population growth rates for ungulates (Komers and Curman 2000, Van Houtan et al. 2010). However, the effects of translocations observed during past research may not be independent of other concurrent recovery actions (Van Houtan et al. 2010). In our work, when survival was density dependent, a threshold between positive and negative stochastic population growth occurred when the number of female caribou was approximately 50 (Table 7.2), although this number may be higher for populations outside protected areas (DeCesare et al. 2011, Supporting Information; Wittmer et al. 2010).

The International Union for Conservation of Nature (IUCN) recommends that individuals only should be translocated when threats have been removed and sufficient habitat is available (IUCN 1987). Our results suggest translocation alone will not lead to recovery of the Brazeau and Maligne populations unless underlying vital rates are improved naturally or through additional conservation actions. Current probabilities of persistence may be driven by wolf-mediated apparent competition among caribou and abundant primary prey species such as moose (Seip 1992), elk (*Cervus elaphus*, Hebblewhite et al. 2007), and deer (*Odocoileus* spp., Latham 2009). Thus, translocation of caribou may increase probabilities of persistence of the Brazeau or Maligne populations if primary prey and wolf densities were to decline substantially. Direct community manipulation of predators or primary prey species may be effective short-term recovery actions for endangered secondary prey species (Courchamp et al. 2003, Lessard et al. 2005), particularly in combination with translocations (Van Houtan et al. 2010). While directives for managing hyper-abundant species are in place within Parks Canada (Prior 2010), achieving consensus on these forms of active management for endangered species recovery is challenging inside and outside of the national parks (Hebblewhite et al. 2010, Serrouya and Wittmer 2010). Additionally, conservation tactics such as predator control are often short-term and proximate solutions to asymmetric dynamics driven by long-term and ultimate causes (Musiani et al. 2005, DeCesare et al. 2010) and may come with additional social (Garrott et al. 1993, Bruskotter et al. 2009) and ecological (Wallach et al. 2010) costs.

It is difficult to measure the success of translocation projects because such projects often lack explicit goals and completion times (Fischer and Lindenmayer 2000). Many translocation programs do not



distinguish between phases of initial population establishment and long-term persistence (Armstrong and Seddon 2008). To account for increased mortality and emigration during population establishment, our analysis assumed survival rates for 3 years following translocation would be reduced (Warren et al. 1996). We assumed that environmental conditions during the next 20 years will be similar to those of the past 8 years. Twenty years is a relatively short time frame for population projections, but the potential for changing climate (Post et al. 2009), anthropogenic land use (Wittmer et al. 2010) and predator-prey community (Hebblewhite et al. 2007) conditions make longer-term projections challenging. Woodland caribou and other species that have locally adapted behaviors are difficult to translocate successfully.

Most endangered species occur in multiple populations (Wilcove et al. 1993) and these populations vary in the extent to which they depend on conservation actions. We used PVA to quantify the probability of extinction and to predict the probability of recovery of populations of woodland caribou with and without translocation. Recovery efforts may be aimed at preventing the loss of a single population (Chauvenet et al. 2010) or at prioritizing populations for conservation (Bottrill et al. 2008, McDonald-Madden et al. 2008). In either case, explicit recovery priorities are needed to set quantitative recovery criteria, determine probability of extinction and identify efficient conservation strategies.

## PRESENTATIONS, PUBLICATIONS AND WORKSHOPS

### Publications

- Semeniuk, C. A. D., M. Musiani, M. Hebblewhite, S. Grindal, and D. J. Marceau. *In review*. Incorporating behavioural-ecological strategies in pattern-oriented modelling of caribou habitat use in a highly industrialized landscape. *Ecological Modelling*.
- DeCesare, N. J., M. Hebblewhite, F. K. A. Schmiegelow, D. Hervieux, G. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. *In press*. Transcending scale-dependence in identifying habitat with resource selection functions. *Ecological Applications*.
- DeCesare, N. J., M. Hebblewhite, M. Bradley, K. Smith, D. Hervieux, and L. Neufeld. 2012. Estimating ungulate recruitment and growth rates using age ratios. *Journal of Wildlife Management* 76:144–153.
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- Semeniuk, C.A.D., M. Musiani, and D. J. Marceau. 2011. Integrating Spatial Behavioral Ecology in Agent-based Models for Species Conservation. In: G. Venora, O. Grillo, and J Lopez-Pujol (eds). *Biodiversity*. InTech. 24 pp. Available from: <http://www.intechopen.com/articles/show/title/integrating-spatial-behavioral-ecology-in-agent-based-models-for-species-conservation>
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### Presentations at Scientific Conferences with Refereed Conference Proceedings

- Semeniuk, C.A.D., M. Musiani, M. Hebblewhite, S. Grindal, and D. J. Marceau. *In press*. Evaluating the impacts of industrial features on woodland caribou habitat-selection strategies in west central Alberta using agent-based modelling. *Procedia Environmental Sciences* for the 18<sup>th</sup> Biennial Conference of International Society for Ecological Modelling, Beijing Normal University, Beijing, China. September 20-23, 2011.
- Semeniuk, C.A.D., M. Musiani, M. Hebblewhite, S. Grindal, and D. J. Marceau. 2011. Evaluating risk effects of industrial features on woodland caribou habitat selection in west central Alberta using agent-based modeling. *Proceedings of the 4<sup>th</sup> International Cartographic Association Workshop on Geospatial Analysis and Modeling* Simon Fraser University, Vancouver, Canada. August 10-12, 2011.
- Semeniuk, C.A.D., M. Musiani, M. Hebblewhite, S. Grindal, and D. J. Marceau. 2011. An agent-based model of woodland caribou habitat selection in west central Alberta: A behavioural and ecological approach. *Proceedings of the 11th International Conference on GeoComputation* University College London, London, England. July 20-22, 2011.

### Presentations at Scientific Conferences

- Semeniuk, C.A.D., M. Musiani, G. McDermid, M. Hebblewhite, S. Grindal, D. Birkigt, and D. J. Marceau. 2012. A scenario planning-model to forecast the impact of different degrees of land-use development on Albertan woodland caribou. Alberta Chapter of the Wildlife Society, Annual Meeting. Medicine Hat, Alberta. March 16-18, 2012.
- DeCesare, N. J., M. Hebblewhite, F. K. A. Schmiegelow, D. Hervieux, G. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani (2011). Transcending scale-dependence in identifying habitat for endangered species. Montana Chapter of the Society for Conservation Biology, Annual Meeting. Missoula, Montana.
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### Workshops

- Semeniuk, C.A.D., M. Musiani, G. McDermid, M. Hebblewhite, S. Grindal, D. Birkigt, D. J. Marceau. 2012. Moving towards scenario planning to understand caribou responses to industry in the future. Foothills Research Institute Caribou Workshop, January 12-13, 2012.
- DeCesare, N. J., and M. Hebblewhite. 2010. Banff-Jasper population viability analysis: what is the likelihood of caribou persistence in Banff and Jasper under several translocation scenarios? Banff Caribou Translocation Technical Meeting, Banff National Park, Alberta, Canada.
- Whittington, J., N. DeCesare, H. Robinson, M. Bradley, L. Neufeld, M. Musiani, and M. Hebblewhite. 2010. Caribou translocations to Banff National Park: are conditions right for success? 13<sup>th</sup> North American Caribou Workshop, Winnipeg, Manitoba, Canada.

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