

Seasonal Habitat Selection by Resident and Translocated Caribou in Relation to Cougar
Predation Risk

by

Heather Leech
B.Sc., University of Western Ontario, 2008

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

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Supervisory Committee

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Dr. Dennis Jelinski, Department of Geography
Supervisor

Dr. Gerald Kuzyk, Ministry of Forests, Lands and Natural Resource Operations
Departmental Member

Abstract

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Mountain caribou, an arboreal lichen-feeding ecotype of woodland caribou (*Rangifer tarandus caribou*), have been extirpated from much of their historic range. Mountain caribou are federally listed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and red-listed by the BC government. Habitat loss and fragmentation of old growth forest is the ultimate cause for population declines. Yet, predation, linked to apparent competition, is the proximate cause for high rates of mortality. One of the most imperiled populations resides in the Purcell Mountains of BC, which was experimentally augmented in 2012 with 19 northern caribou from northern BC. The caribou-predator literature predominantly focuses on the relationship between caribou and wolves (*Canis lupus*) in northern caribou populations. However, cougars (*Puma concolor*) have been identified as a major predator of Purcell-South (PS) caribou, yet caribou-cougar interactions remain largely unstudied. I evaluated cougar predation risk in space and time on resident and translocated caribou in the Purcell Mountains. To do so, I determined biologically relevant seasons for resident, donor (i.e. not translocated) and translocated caribou, and cougars. I then used these seasons to investigate seasonal patterns of movement and habitat use between the three groups of caribou and cougars. Next I used resource selection functions (RSFs) to estimate habitat based seasonal variation in predation risk. I used these RSFs to compare the seasonal

habitat selection and risk to cougar predation between resident and translocated caribou. Five resident caribou seasons and two cougar seasons were defined. Translocated caribou displayed inconsistent movement behavior with no clear seasonal pattern. Resident caribou remained at high elevations year-round and selected for low risk cougar habitat during the calving season at the home range scale and year-round at the landscape scale. Translocated caribou displayed risky behaviour throughout the study period by traveling to mid to low elevations and habitats selected by cougars. Translocated caribou displayed the same general pattern of elevational movement as their northern conspecifics, spending the majority of their time at lower elevations than resident caribou. Of the 19 translocated caribou, 17 (89%) died during the study, six of which were preyed upon by cougars, two by wolves, and the remainder due to accidents or unknown causes. In summary, translocated caribou did not adopt the predator avoidance or habitat selection strategies of resident caribou. I recommend that future efforts to augment small caribou populations use donor caribou experienced with similar predators and that possess comparable seasonal habitat use to the recipient population. However, because most suitable donor populations are declining, a soft-release of captive-reared mountain caribou might be the best option for mountain caribou recovery efforts.

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Co-Authorship Statement

This thesis is the combination of two scientific manuscripts for which I am the lead author. The initial project structure was provided by Dr. Dennis Jelinski and Dr. Gerald Kuzyk, for which the role of predation risk to the decline of mountain caribou was identified as a key research opportunity. For these two scientific journals, I performed all research, data analysis, initial interpretation of results, and final manuscript preparation. Dr. Mark Boyce provided statistical assistance with developing resource selection functions and interpretation of results. Leo DeGroot provided data and assistance with interpretation of results.

1.0 Introduction

During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain matings and thus realize no reproductive success, but in the long term, the day's shortcomings may have minimal influence on lifetime fitness. Few failures, however, are as unforgiving as the failure to avoid a predator . . .

Lima and Dill

619:1990

1.1 Research context

The global population of mountain caribou (*Rangifer tarandus caribou*), an endangered ecotype of woodland caribou is numbered less than 1500. Of these, at least 98% are found in British Columbia (BC) (Apps and McLellan 2006). They are federally listed as Endangered and red-listed by the BC government (BC Conservation Data Centre 2014, COSEWIC 2014). The ultimate cause for declining mountain caribou populations is habitat loss and fragmentation of old growth forests (Heard and Vagt 1998, Spalding 2000, Apps and McLellan 2006) while the proximate cause is , unsustainable rates of predation (Bergerud and Elliot 1986, Rettie and Messier 1998, Wittmer et al. 2005b). In BC, industrial forestry has created an extensive patchwork of early seral-stage vegetation that supports large populations of mule and white-tailed deer (*Odocoileus hemionus* and *O. virginianus*), elk (*Cervus canadensis*), and moose (*Alces alces*) (Bergerud and Elliot 1986, Wittmer et al. 2005a, 2007). This results in a numerical response of cervid predators (Gibson 2006, DeCesare et al. 2010, Johnson et

al. 2013). Accordingly, higher predator densities increase the probability of encounter and thus potential predation of a secondary, less abundant prey species such as caribou. This indirect interaction between prey populations is commonly termed apparent competition (Holt 1977, Gibson 2006).

To reduce predation risk, mountain caribou spatially and temporally separate themselves from predators and other prey species (Bergerud and Page 1987, Seip 1992, James et al. 2004). For example, during winter, mountain caribou ascend to high elevations to separate from wolves where they can safely feed on arboreal lichen, their preferred winter forage (Seip 1991, Apps et al. 2013). Wolves and cougars typically remain in valley bottoms where there are higher densities of other prey, such as moose (Bergerud and Page 1987, Seip 1992). Thus, the differential selection of habitats by caribou and their main predators decreases predator-prey spatial overlap and therefore predation risk.

The BC Government has recently taken steps to reverse mountain caribou population declines (Integrated Land Management Bureau 2007, Environment Canada 2014). One management technique used is augmenting smaller herds with animals from healthy populations (Letty et al. 2000, 2007). However, nine of the 15 mountain caribou subpopulations have fewer than 50 animals (BC Ministry of Environment 2010, COSEWIC 2014), thus posing a management challenge when selecting suitable donor populations. Accordingly, experimental translocations using donor caribou from a different ecotype was the best option for mountain caribou population recovery. However, it is difficult to predict whether or not the donor caribou will adopt the

effective habitat use and predation avoidance strategies utilized by the resident caribou population.

1.2. Research focus

One of the most imperilled mountain caribou populations resides in the Purcells-South (PS) Mountains of southeastern BC, Canada. The PS mountain caribou herd has been at high risk of extirpation since the mid-1990s (Hatter 2006) and thus identified for translocation in the Mountain Caribou Recovery Implementation Plan (Integrated Land Management Bureau 2007, Kinley 2010). Prior to translocation, a 2011 census confirmed that approximately 15 caribou, distributed into two sub-herds, formed the PS population. In March 2012, the PS herd was experimentally augmented with 19 northern caribou (a different ecotype) from the Level Kawdy (LK) herd in northwestern BC. (A second translocation of an additional 20 caribou was planned for 2013 but was cancelled due to high rates of mortality in the initial translocated group, as discussed later in this thesis.) Northern caribou were used as donor animals because of their relatively large and robust populations. The management objectives were to (1) increase the population of PS caribou; (2) decrease negative effects of genetic, demographic, and environmental stochasticity; and (3) reduce or eliminate Allee effects that cause per capita growth rates to decline as populations decline (Allee et al. 1949, Mclellan et al. 2010).

To evaluate the PS caribou translocation project, cougar predation risk to caribou is examined by comparing seasonal movements and habitat selection patterns between PS resident caribou, translocated caribou, LK donor caribou, and cougars. Wolves and cougars are the principal predators of mountain caribou (Wittmer et al. 2005a, Seip 2008,

Apps et al. 2013), though it is believed that cougar predation may be particularly important to the PS caribou (Kinley and Apps 2000, 2001).

This thesis focuses on predation risk as it is the proximate cause of caribou decline, given that forage quantity and availability is not assumed to be a limiting factor in mountain caribou populations (Wittmer et al. 2005b). Predation risk is defined as the relationship among the rate of encounter between predator and prey, the probability of death given an encounter, and the amount of time prey spend vulnerable to an attack (Lima & Dill 1990). Relative levels of predation risk are represented by the landscape of fear model (Laundré *et al.*, 2001, Laundré *et al.*, 2010), which depicts how fear can alter an animal's space use to reduce risk of predation. For example, in Yellowstone National Park (YNP) reintroduced wolves (*Canis lupus*) changed the landscape of fear for elk (*Cervus canadensis*), causing elk to select safer forest edges rather than previously selected open sagebrush meadows (Laundré et al. 2001). Predation risk also varies temporally (Lima and Bednekoff 1999) and while temporal variability may be stochastic, it may also be regular. Thus, seasonality can have an effect on the landscape of fear, which in turn can affect predator-prey dynamics (Taylor et al. 2013a, 2013b). Seasonal variation in predation risk depends on resource availability, predator numbers, prey preference, and spatial overlap in predator-prey distributions (Lima and Dill 1990, Gervasi et al. 2013). Moreover, prey show seasonal variation in their relative susceptibility to predation. For example, the ability of ungulates to escape predation is hindered by deep snow in the winter, which benefits cursorial predators such as wolves (*Canis lupus*) (Jędrzejewski et al. 2002, Hebblewhite 2005).

1.3. Thesis objective

This research examines cougar predation risk to translocated northern caribou in the PS study area as it changes spatially and temporally. Non-translocated donor and resident caribou are used as control groups for comparison. More specifically, the following overarching objectives will be addressed:

1. Determine biologically relevant caribou and cougar seasons to assess seasonal predation risk to resident, translocated, and non-translocated donor caribou.
2. Estimate the landscape of fear shaped by cougars and compare cougar predation risk between resident and translocated caribou using a resource selection function approach.

Successful long-term management of small mountain caribou populations requires active recovery strategies such as translocation. The ultimate goal of this thesis is to assess the translocation from a predation risk perspective, use the findings to inform future management efforts, and equally, contribute to the larger scientific literature on the concept of predation risk.

References

- Allee, W. C., O. Park, A. E. Emerson, T. Part, and K. P. Schmidt. 1949. Principles of Animal Ecology. Saunders, Philadelphia, USA.
- Apps, C. D., and B. N. McLellan. 2006. Factors influencing the dispersion and fragmentation of endangered mountain caribou populations. *Biological Conservation* 130:84–97.
- Apps, C. D., B. N. McLellan, T. A. Kinley, R. Serrouya, D. R. Seip, and H. U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *Journal of Wildlife Management* 77:1409–1419.
- BC Conservation Data Centre. 2014. Conservation Status Report: *Rangifer tarandus* pop. 1 Caribou (Southern Mountain Population). <http://a100.gov.bc.ca/pub/eswp/>.
- BC Ministry of Environment. 2010. Caribou Distribution in British Columbia by Ecotype. http://www.env.gov.bc.ca/wld/speciesconservation/caribou_by_ecotype.html#_.
- Bergerud, A., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515–1529.
- Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology* 65:1597–1606.
- COSEWIC. 2014. COSEWIC assessment and status report on the Caribou *Rangifer tarandus*, Northern Mountain population, Central Mountain population and Southern Mountain population in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxii + 113 pp.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Environment Canada. 2014. Recovery Strategy for the Woodland Caribou, Southern Mountain population (*Rangifer tarandus caribou*) in Canada [Proposed]. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. viii + 68 pp.

- Gervasi, V., H. Sand, B. Zimmermann, J. Mattisson, P. Wabakken, and J. D. C. Linnell. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications* 23:1722–34.
- Gibson, L. 2006. The role of lethal control in managing the effects of apparent competition on endangered prey species. *Wildlife Society Bulletin* 34:1220–1224.
- Hatter, I. 2006. Mountain Caribou 2006 Survey Results, Subpopulation Trends and Extinction Risks. Proceedings, Multidisciplinary Approaches to Recovering Mountain Caribou in Mountain Ecosystems, May 29–31, 2006, Revelstoke, BC, May 29–31, 2006, Columbia Mountains Institute of Applied Ecology. Pp. 22.
- Heard, D. C., and K. L. Vagt. 1998. Caribou in British Columbia: A 1996 status report. *Rangifer Special Is*:117–123.
- Hebblewhite, M. 2005. Predation by wolves interact with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology* 74:226–233.
- Holt, R. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Integrated Land Management Bureau. 2007. Mountain Caribou Recovery Implementation Plan. Species at Risk Coordination Office, Integrated Land Management Bureau, Victoria, BC
- James, A., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- Jędrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jędrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology* 83:1341–1356.
- Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and V. C. Bleich. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. *Oecologia* 171:295–307.
- Kinley, T. A. 2010. Augmentation plan for the Purcells-South mountain caribou population. BC Ministry of Environment (Ecosystems Branch), Prepared for BC Ministry of Environment (Ecosystems Branch), Victoria, BC.
- Kinley, T. A., and C. D. Apps. 2000. Population Status and Mortality of Mountain Caribou in the Southern Purcell Mountains, British Columbia. Pages 655–661 in L. M. Darling, editor. Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, British Columbia, 15–19 Fe. 1999. Volume 2.

British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College .

- Kinley, T., and C. Apps. 2001. Mortality Patterns in a Subpopulation of Endangered Mountain Caribou. *Wildlife Society Bulletin* 29:158–164.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2010. The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal* 3:1–7.
- Letty, J., S. Marchandea, J. Clobert, and J. Aubineau. 2000. Improving translocation success: an experimental study of anti-stress treatment and release method for wild rabbits. *Animal Conservation* 3:211–219.
- Letty, J., S. Marchandea, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. *Ecoscience* 14:420–431.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. *Ecology* 91:286–292.
- Rettie, W., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology* 76:251–259.
- Seip, D. R. 1991. Predation and caribou populations. *Rangifer* 7:46–52.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494–1503.
- Seip, D. R. 2008. Mountain caribou interactions with wolves and moose in central British Columbia. *ALCES* 44:1–5.
- Spalding, D. J. 2000. The early history of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. BC. Ministry of the Environment. Victoria, BC. Wildlife Bulletin No. B-100.

- Taylor, R., J. Sherratt, and A. White. 2013a. Seasonal forcing and multi-year cycles in interacting populations: lessons from a predator-prey model. *Journal of Mathematical Biology* 67:1741-1764.
- Taylor, R., A. White, and J. A. Sherratt. 2013b. How do variations in seasonality affect population cycles? *Proceedings of the Royal Society* 280:20122714.
- Wittmer, H., B. McLellan, D. Seip, and J. Young. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wittmer, H., A. Sinclair, B. McLellan, and R. Sinclair. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Wittmer, H., B. McLellan, R. Serrouya, and C. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* 76:568–79.

2.0 Seasonal differences in predation risk to translocated and resident caribou

2.1 Abstract

Understanding how risk varies seasonally is a major challenge in assessing the spatiotemporal dynamics of predation risk. We evaluated seasonal predation risk from cougars (*Puma concolor*) on resident mountain caribou and translocated northern caribou in the Purcell Mountains of British Columbia (BC). Mountain caribou are an endangered ecotype of woodland caribou (*Rangifer tarandus caribou*) that continue to decline ultimately due to habitat loss and proximately due to predation. The Purcell South mountain caribou herd is one of the most imperilled populations and was experimentally augmented in 2012 with 19 northern caribou from northern BC. We applied a cluster analysis framework using GPS radio-collared animals to determine biologically relevant seasons for resident, donor (i.e., not translocated) and translocated caribou, and cougars. We then assessed seasonal variation in predation risk by comparing seasonal patterns of movement and habitat use among the three groups of caribou. Five resident caribou seasons, two donor caribou seasons, and two cougar seasons were defined. Translocated caribou displayed inconsistent movements and habitat selection, rendering defined seasonal clusters erroneous. Resident caribou remained at high elevations year-round and primarily selected habitats not used by cougars. Translocated caribou occupied habitats used by cougars and displayed similar elevational movements to their northern conspecifics, spending the majority of their time at lower elevations than resident caribou. Additionally, translocated caribou had a significantly higher daily travel rate

than resident caribou (1.93 ± 1.07 km/day and 1.44 ± 0.58 km/day, $p < 0.001$, respectively). We conclude translocated caribou did not adopt the predator avoidance strategies of resident caribou rendering them more vulnerable to cougars.

2.2 Introduction

Most animal populations live in seasonal environments (Fretwell 1972). Animals use a variety of strategies to adapt to multiple and potentially divergent seasonal environmental conditions, such as variation in temperature, snow accumulation, light, forage availability, and predation risk. However, defining what we mean by “season” is problematic. Some studies categorize seasons by the Julian calendar (Bearzi et al. 2008), climate (Owen-Smith 2008), or expert opinion (Mejlgaard et al. 2013). While of heuristic value, these delineations may not correspond to biological reality (Vander Wal and Rodgers 2009, Basille et al. 2012). Species living in seasonal environments have life-history traits controlled by seasonality, such as reproduction and recruitment, growth, dormancy, and migration (Nylin and Gotthard 1998). So, failure to accurately define seasons may lead to inconclusive or inaccurate inferences when examining ecological phenomena in relation to seasons.

One such phenomenon is predation risk. Predator activity may increase at a certain time of day or during a particular season (Lima and Bednekoff 1999). Seasonal variation in predation risk depends on resource availability, predator numbers, prey preference, and spatial overlap in predator-prey distributions (Lima and Dill 1990, Gervasi et al. 2013). Prey may also show seasonal variation in their relative susceptibility to predation. For example, the ability of ungulates to escape predation is hindered by deep snow in the winter, which benefits cursorial predators such as wolves

(*Canis lupus*) (Jędrzejewski et al. 2002, Hebblewhite 2005). Pregnant female ungulates are most vulnerable during gestation because they are less effective at evading predators, and they are especially vulnerable during parturition (Molinari-Jobin et al. 2004). Male ungulates are most vulnerable in autumn when they compete for mates during the rut. At this time they are exposed to injury and isolate themselves from the herd (Fitzgibbon 1990). Additionally, the breeding season is an energetically expensive time, leaving males in a weakened state and hence vulnerable to predators.

Change in seasonal spatial overlap between predator and prey may increase their chance of encounter; predators try to maximize while prey try to minimize spatial overlap. For instance, elk (*Cervus elaphus*) in the Canadian Rockies reduced exposure to wolf predation risk by migrating from winter range to nearby summer range where predation risk was lower (Hebblewhite and Merrill 2009). Similarly, in breeding season, field voles reduced movement and daily-range size in response to predation risk from small mustelids, whereas in the nonbreeding seasons they do not (Borowski and Owadowska 2010).

It remains however, there still may be significant risk of predation even if prey adjust habitat use on a seasonal basis as predators change their tactics to changing prey abundance and distribution (Flaxman and Lou 2009, Gervasi et al. 2013). Furthermore, under certain conditions, animals may choose to use more risky habitats containing essential or more abundant resources (Sih 1984, Lima and Dill 1990, McNamara and Houston 1994). Studies of small mammals, birds, and fishes demonstrate that food deprived animals accept greater risk of predation while feeding (Lima 1998). However, there is a limit to which trade-offs between energy gain and predation risk may be made;

that is, there is a point at which differential use of some resources can significantly affect reproduction, survival, and thus fitness (Sinclair and Arcese 1995, Gaillard et al. 2010).

Woodland caribou (*Rangifer tarandus caribou*) have been decreasing in numbers and range in western North America for many decades (Bergerud 1974, 1996, Seip and Cichowski 1996, Spalding 2000, Wittmer et al. 2005a). Caribou require large, undisturbed areas of old or mature coniferous forest (Heard and Vagt 1998, Kinley et al. 2003, Serrouya et al. 2007) relatively free of direct human disturbance (e.g., snowmobiles) (Kinley et al. 2003, Seip et al. 2007). In British Columbia (BC), caribou are categorized into mountain, northern, and boreal ecotypes – the first two are of concern in this paper. Mountain caribou are red-listed (Endangered), while northern caribou are blue-listed (Special Concern) by the BC provincial government (BC Conservation Data Centre 2014).

The main differences between mountain and northern caribou are in their foraging behaviour, migration patterns, and habitat use (Stevenson and Hatler 1985, Seip and Cichowski 1996). Mountain caribou live at low densities in mountainous environments and forage principally on arboreal lichen in winter (Johnson et al. 2004b). They undergo elevational migrations throughout the year, remaining at high elevations in winter and during calving, and move to lower elevations in summer (Apps et al. 2001, Johnson et al. 2004b). Northern caribou are found in west-central and northern mountainous regions of BC. They use subalpine and alpine habitats during calving and summer seasons, and valley bottoms during winter (Bergerud et al. 1984, Bergerud and Page 1987). During winter, northern caribou primarily forage on terrestrial lichens by cratering through snow (Johnson et al. 2004a). Despite these difference, both mountain and northern caribou are

known to spatially separate from predators and alternate prey to minimize predation risk (Bergerud and Page 1987, Seip 1992, James et al. 2004, Peters et al. 2013). Thus, caribou may increase their chance of survival and persistence by using niche specialization to enable survival in sub-optimal habitats (Bergerud 1974, Bergerud and Page, 1987, Seip 1992).

Habitat loss and fragmentation is the ultimate cause for mountain caribou declines (Bergerud and Mercer 1989, DeCesare et al. 2010, St-Laurent and Dussault 2012); predation has been identified as the proximate cause (Wittmer et al. 2005b, DeCesare et al. 2010, McLellan et al. 2012). Over the past few decades, populations of white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk, and moose (*Alces alces*) have significantly increased in caribou ranges as a function of regenerating early and mid-seral habitat (Bergerud and Elliot 1986, Seip 1991, Latham et al. 2011b). In turn, there has been a numerical response in predators resulting in apparent competition (Holt 1977). These increased predator densities render caribou vulnerable to incidental predation (Wittmer et al. 2005b).

The Purcells-South (PS) mountain caribou herd, located in the Purcell Mountains of southeastern BC, is at high risk of extirpation. In 2011 the PS herd totalled 15, which was further divided into two sub-herds. One management strategy to aid recovery of small wildlife populations is translocation (Seddon et al. 2007, Pérez et al. 2012). Accordingly, the Province of BC utilized translocation as a management lever in the Mountain Caribou Recovery Implementation Plan (Integrated Land Management Bureau 2007). In an effort to increase the PS population, 19 northern caribou from the Level Kawdy (LK) herd were experimentally translocated to the PS herd in March 2012.

The overall conservation objective was to (1) increase the population size of the PS herd, thus decreasing the probability of extirpation; (2) decrease potential negative effects of genetic, demographic, and environmental stochasticity; and (3) reduce or eliminate Allee effects that cause the per capita growth rates to decline as populations decline (Allee et al. 1949, McLellan et al. 2010). Wolves and cougars are the principal predators of mountain caribou (Wittmer et al. 2005b, Seip 2008, Apps et al. 2013), though it is believed that cougar predation may be particularly important to the PS caribou (Kinley and Apps 2000, 2001).

Our study focuses on predation risk to both resident and translocated caribou. We draw on concepts from the emerging field of movement ecology and on general questions similar to those of Nathan et al. (2008) about the interplay between the internal state of an animal in terms of “why move” and the prevailing state of the landscape, or “where to move.” Our specific objectives are twofold. First, we determine biologically relevant seasons for resident PS mountain caribou, donor LK northern caribou, translocated LK northern caribou, and cougars based on patterns of movement and habitat use. Second, to estimate predation risk, we compare spatial separation and seasonal habitat similarity between resident and translocated caribou, and cougars.

2.3 Study area

2.3.1 Capture site – Level Kawdy study area

The 17,000 km² LK study area (57°59'N - 59°53'N and 129°51'W - 132°24'W) was defined by the movements of global positioning system (GPS) radio-collared caribou gathered in northwestern BC (Figure 2.1). The climate, vegetation, and topography is alpine-subalpine with Arctic affinities (Bergerud and Elliot 1986). Mean daily

temperatures range from -22°C in January to 19°C in July, while mean annual precipitation is 426 mm (Government of Canada 2013). Snow depth at the nearest Snow Course (Dease Lake) generally reaches a maximum of 60 cm in March (Ministry of Environment 2013). Elevations range from 470 to 2,240 m asl with moderate slopes and few peaks (Bergerud and Elliot 1986). Between 900 and 1,500 m asl the Spruce-Willow-Birch (SWB) biogeoclimatic (BEC) zone is dominant, and is punctuated by areas of Boreal Altai Fescue Alpine (BAFA) zones at higher elevations. Below the SWB BEC zone lies the Boreal White and Black Spruce (BWBS) zone, dominated by white spruce (*Picea glauca*), black spruce (*Picea mariana*), and lodgepole pine (*Pinus contorta*) (MFLNRO 2013).

Moose, Stone's sheep (*Ovis dalli stonei*), and mountain goats (*Oreamnos americanus*) are the other ungulates in the study area. Large and meso carnivores include wolves, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), and lynx (*Lynx canadensis*).

2.3.2 Release site – Purcells-South study area

The 14,500 km² PS study area (49°04'N - 50°39'N and 115°18'W - 116°50'W) was defined by the movements of GPS radio-collared caribou and female cougars within the Purcell South Mountains (Figure 2.1). Terrain varies in elevation from 535 to 3,040 m asl, but most alpine ridges do not exceed 2,300 m asl (Kinley 2010). Mean daily temperatures range from -12°C in January to 26°C in July, while mean annual precipitation is about 380 mm at the nearest weather station in Cranbrook, BC (930 m asl), in the rain shadow of the Purcell Mountains (Government of Canada 2013). Mean snow depth of 2,100 m asl generally reaches a maximum of 270 cm in April (Powder

Creek Lodge 2013). Both the dry and wet BEC subzones of Engelmann Spruce-Subalpine Fir (ESSF) are at higher elevations, and the Montane Spruce (MS) and Interior Cedar-Hemlock (ICH) zones are at lower elevations (Kinley 2010).

Other ungulates in the region include moose, white-tailed deer, mule deer, mountain goats, and elk. Large and meso carnivores include wolves, coyotes (*Canis latrans*), grizzly bears, black bears, wolverines, bobcats (*Lynx rufus*), lynx, and cougars.

2.4 Methods

2.4.1 Data collection

Four female resident PS caribou (henceforth “resident caribou”), 15 female LK resident caribou (henceforth “donor caribou”), 19 translocated caribou (three male and 16 female) from the LK herd (henceforth “translocated caribou”), and seven female cougars were equipped with GPS radio-collars between February 2011 and February 2013. Caribou were captured using helicopter-based net gunning techniques, whereas cougars were tracked by hounds and sedated using a dart gun. Caribou to be translocated were captured in the LK study area on February 29 and March 1, 2012, then transported approximately 2,100 km by truck to the PS study area and released on March 3, 2012. Animal care followed approved protocols of the University of Victoria and the Province of BC. Caribou were fitted with Advanced Telemetry System G2110E (ATS, Isanti, MN) and cougars with the same or LOTEK TrackM 2D GPS radio-collars (Lotek Engineering, Newmarket, ON). Caribou and cougar GPS positional fixes were taken four times daily, except between December 1 to March 15 and May 1 to August 1 when six daily fixes were taken. We excluded translocated caribou positional data for three days post-translocation because of the potential effects translocation had on animal activity.

Six hours of inactivity triggered a possible mortality signal. Investigation of caribou mortalities were made within 24-48 hours of a mortality notification, except for three mortalities which were assessed four to six days post-mortem due to collar malfunction. Evidence of predation included bleeding, signs of struggle, or bite injuries on the carcass. Carcasses of typical cougar kills were easily recognized because their hair was stripped and remains buried. Additionally, cougar kill sites had evidence of dragging and cashing the carcass, scratch marks, and cougar tracks in the area. Non-predation events were classified as accidents, malnutrition, or unknown causes.

2.4.2 Determining temporal clusters

Caribou and cougar seasons were delineated using a cluster analysis framework following Basille et al. (2012), originally developed by Tibshirani et al. (2001) and VanMoorter et al. (2010). We based homogenous space-use behaviour on land cover, elevation, and movement. Land cover types were defined by BEC zones (MFLNRO 2013). BEC zones were grouped according to vegetation density, species composition, and elevation in the donor and recipient areas (Table 2.1 and Table 2.2). Using RESULTS (Reporting Silviculture Updates and Land status Tracking System) silviculture data, we reclassified cut blocks into two age classes (<5 years and 5-20 years) given that after five years or so, the sightability of caribou by predators decreases because of increased shrub and tree height. Land cover classes were rasterized in ArcGIS 10.0 (ESRI, Redlands, CA) at a 25 m resolution grid. Road density (km/km^2) was calculated using a weighted system, giving a weight of one for loose or rough (low volume) logging roads and two for paved (high volume) roads (Chruszcz et al. 2003). Elevation was

estimated using a 25 m resolution digital elevation model (DEM) at the scale of 1:20,000, accurate to within 10 m.

A 15-day moving window was used to characterize the space-use of each caribou and cougar. For each Julian day, the moving window summarized movement and habitat characteristics based on GPS locations seven days before and after a focal day. This smoothed temporal trends by removing fine-grained spatiotemporal variation (such as hourly or unusual daily variation in space-use), and thus offset erroneous (short) seasons (Tibshirani et al. 2001, Van Moorter et al. 2010, Basille et al. 2012).

For each 15-day window we computed: 1) mean travel rate (km/day); 2) tortuosity (turning angle); 3) average elevation (m); 4) average road density (km/km²); and 5) proportion of locations in the moving window located in each habitat. Travel rate and turning angle were used to compare speed and path tortuosity. Travel rate (km/day) was calculated by summing daily Euclidian distances between the current location and the next fixed location. Turning angle, defined as the average difference in direction for two successive moves, was determined between every successive animal location. Measurements were standardized for the entire study period so each variable had the same clustering weight (Steinley 2006). Range standardization (z_i) follows Steinley (2006) defined as:

$$z_i = (x_i - \min(x)) / (\max(x) - \min(x)).$$

The optimal number of clusters (i.e., seasons) was determined using the DD-weighted gap method (Yan and Ye 2007), which is based on the gap statistic (Tibshirani et al. 2001). The gap statistic is defined as:

$$gap_k = E^*\{\log(W_{kb})\} - \log(W_k)$$

where E^* denotes expectation under a sample size of n from the reference distribution and W_k is the pooled within-cluster sum of squares around the cluster mean, based on the sum of the pair-wise distances for all points in a cluster (Tibshirani et al. 2001). The gap statistic sometimes overestimates the “real” number of clusters (k) (Yan and Ye 2007, Basille et al. 2012). Yan and Ye (2007) thus proposed the DDgap method – a multilayer clustering approach ($D_{\text{gap}_k} = \text{gap}_k - \text{gap}_{k-1}$, and $DD_{\text{gap}_k} = D_{\text{gap}_k} - D_{\text{gap}_{k+1}}$) used to estimate the number of clusters when $k > 1$. When k is equal to the true number of clusters, the DD_{gap_k} is maximized (Yan and Ye 2007, Basille et al. 2012).

2.4.3 Defining biological seasons

The number of clusters determined by the DD-weighted gap statistic was used to define the number of seasons. A cluster was defined by the space-use of each group (i.e., resident caribou, donor caribou, translocated caribou, and cougars) at a given day of the year. As such, a cluster may not be continuous in time, but interrupted with a different cluster. Distance decay is the decrease in similarity between objects as the distance between them increases (Tobler 1970), and this concept was used to define temporal space-use trends as neighbouring days are likely to fall into the same space-use state. Therefore, a season is defined as a period of time where species experience the same space-use (Basille et al. 2012).

Bootstrapping was used to evaluate robustness of seasonal delineation using 100 sets of individual year units randomly re-sampled from the original dataset. K -means clustering was used to estimate the number of clusters for the complete dataset. A distribution of daily weights corresponding to the likelihood a given day would start a new season was then estimated within the bootstrap samples following Basille et al.

(2012), whereby days in the top 20% of the weight distribution were retained as the start of a season, and remaining values were removed. The 20% threshold was used because it represented the most likely changes. Seasons less than 10 days were added to the preceding season to facilitate interpretation.

2.4.4 Habitat selection

We used 90% kernel density estimations (KDEs) for each animal group following the notion of Johnson's (1980) second-order selection. Availability was assumed using one random location within the KDE for each used location (Marcum and Loftsgaarden 1980, Johnson et al. 2006, Latham et al. 2011a, 2013). Habitat use within KDEs was then estimated using Jacobs' index, calculated as:

$$D = (r - p) / (r + p - 2rp)$$

where r is the proportion of habitat used and p is the proportion available (Jacobs 1974, Kauhala and Auttila 2010). D ranges from -1 (strong avoidance) to +1 (strong preference), and near zero values indicate habitat used in proportion to its availability (Jacobs 1974, Kauhala and Auttila 2010). Chi-square goodness-of-fit tests determined whether habitat selection was independent of availability ($\alpha < 0.05$) (Jelinski 1991).

2.4.5 Habitat similarities between animal groups

Jaccard's index (Birks 1987, Real and Vargas 1996) was used to estimate overlap of habitat used by each group. Travel rate and turning angle were also compared between the resident, translocated, and donor caribou. Similarity was measured as the intersection between any two groups divided by the size of the union based on minimum and maximum values of each variable such that:

$$J(A,B) = \frac{\min[\max(A), \max(B)] - \max[\min(A), \min(B)]}{\max[\max(A), \max(B)] - \min[\min(A), \min(B)]}$$

$$\max(A, B) - \min(A, B)$$

The index ranges from 0 (no similarity) to 1 (total similarity), where negative values are set to zero. All indices were averaged for each variable to determine overall habitat similarity, as well as by resident caribou season for the resident caribou, translocated caribou, and cougars.

Cougar harvest data from hunters and problem kills from conservation officers in the Kootenay Region (which envelopes the study area) were obtained to estimate cougar population trends from 1976 to 2013 (Forest, Lands and Natural Resource Operations (FLNRO), unpublished data). One-way ANOVAs with Tukey's HSD post hoc tests were used to compare all metrics, except habitat similarity, between seasons for resident, translocated, and donor caribou, and cougars. For statistical analyses we used R 2.15.3 (R Core Team 2014) with the R packages: *aspace* (Bui et al. 2013) for determining turning angles; *seasonality* (Basille 2013) for calculating cluster statistics and biological seasons; and *adehabitatHR* (Calenge 2013) for establishing KDEs.

2.5 Results

No resident caribou, one donor caribou, and one cougar (trapped as a problem cougar) died during this study. Harvest data shows a peak in cougar kills between 1996 and 1998, as well as an increasing trend from 2005 to 2013 (Figure 2.2). Of the 19 translocated caribou, eight died due to predation (six by cougars and two by wolves), and an additional nine died of accidental or unknown causes (three by falling or injury, and six by unknown causes) within the first 13 months following translocation. These deaths decreased the *n* value and increased the contribution that remaining translocated caribou

had to the statistical analysis; for this reason, we did not estimate seasons for translocated caribou.

2.5.1 Defining seasonality

Resident caribou

The DD-weighted gap statistic for resident caribou clustered into three groups (DD-gap = 0.268) and corresponded to five seasons. A nine-day cluster between July 2 and July 11 was added to the preceding season as it was less than 10 days. Start dates of the five seasons were May 5, June 10, July 11, September 19, and December 17 (Figure 2.3). The September 19 breakpoint was not within the top 20% of the weight distribution, but was retained because resident caribou generally change their movement patterns at that time (Miller 2006). Resident caribou had the highest annual travel rate (2.66 ± 2.83 km/day) in spring (May 5 - June 9), and the lowest rate (1.14 ± 1.35 km/day, $p < 0.001$) in calving season (June 10 - July 10). In calving season, resident caribou moved to higher elevations ($2,090 \pm 115$ m) and increased use of ESSF Woodland zones. In summer (July 11 - September 18), they made extensive use of Other ESSF zones and travelled to lower elevations ($1,960 \pm 117$ m). In the early winter season (September 19 - December 16), they moved to higher elevations ($2,072 \pm 111$ m) and reduced use of Other ESSF zones, while use of ESSF Woodland and Parkland zones increased. In late winter (December 17 - May 4), they reduced travel rates (1.15 ± 1.46 km/day) and use of higher elevations ($2,161 \pm 81$ m) and increased use of ESSF Woodland and Parkland zones.

Donor caribou

Data from donor caribou clustered into two seasons (DD-gap = 0.648). Both were strongly weighted with start dates of May 12 and December 19 (Figure 2.3). Season 1 (May 12 - December 18) corresponded to caribou moving quickly (3.52 ± 4.50 km/day, $p < 0.001$) at high elevations ($1,427 \pm 213$ m, $p < 0.001$). In Season 2 (December 19 - May 11) they reduced speed (2.33 ± 5.50 km/day, $p < 0.001$), and used subalpine and mid-elevation habitats (912 ± 127 m, $p < 0.001$).

Translocated caribou

Data from translocated caribou were clustered into two groups (DD-gap = 0.634) with breakpoints within the top 20% of the weight distribution delineated by March 6 and October 26 (Figure 2.3). The first breakpoint occurred on March 6, the day data collection began (three days post-translocation). At this time translocated caribou had high travel rates (3.02 ± 5.09 km/day, $p < 0.001$), and used high elevations ($1,618 \pm 443$ m, $p < 0.001$) and areas of high road density (1.21 ± 0.93 km/km², $p < 0.001$) relative to the second break point. Additionally, they used ESSF Woodland zones and Other ESSF zones during the first break point. The second break point occurred on October 26 and was characterized by lower travel rates (1.04 ± 1.81 km/day, $p < 0.001$), and use of lower elevations ($1,171 \pm 386$ m, $p < 0.001$) and areas of lower road density (0.71 ± 0.36 km/km², $p < 0.001$). They also made extensive use of ICH zones at this time.

Cougars

Cougar data clustered into two groups (DD-gap = 0.135) beginning July 11 and October 5 (Figure 2.3). From July 11 to October 4, the birthing season, cougars used higher elevations ($1,546 \pm 351$ m, $p < 0.001$) and areas with lower road density (2.23 ± 0.94 km/km², $p < 0.001$) than the other season. At this time, cougars primarily used ESSF

Woodland zones, Other ESSF zones, and cut blocks less than five years of age. From October 5 to July 10, the non-birthing season, cougars used lower elevations ($1,164 \pm 233$ m, $p < 0.001$) and areas with higher road density (2.79 ± 0.85 km/km², $p < 0.001$) as well as ICH and IDF zones. Cougar travel rates between birthing and non-birthing seasons were comparable (3.77 ± 3.38 and 3.44 ± 3.18 km/day, respectively, $p = 0.2239$).

2.5.2 Habitat selection

Resident caribou selected ESSF Woodland zones (Jacobs index of 0.628, χ^2 test, $p < 0.001$), and did not show selection or avoidance of ESSF Parkland zones, but rather used it in proportion to its availability (Jacobs index of -0.010, χ^2 test, $p < 0.637$) (Table 2.3, Figure 2.4). They strongly avoided ICH zones and both categories of cut blocks (Jacobs index of -0.985, -0.836, and -0.780, respectively, χ^2 test, $p < 0.001$) (Table 2.3, Figure 2.4). Conversely, translocated caribou selected ESSF Woodland zones and Other ESSF zones (Jacobs index of 0.301 and 0.088, respectively, χ^2 test, $p < 0.001$) and had no strong selection for other habitat types (Table 2.3, Figure 2.4). The donor caribou strongly selected alpine habitat, followed by mid-elevations (Jacobs index of 0.148 and 0.153, respectively, χ^2 test, $p < 0.001$) (Table 2.4, Figure 2.5), and avoided subalpine habitat relative to its abundance (Jacobs index of -0.191, χ^2 test, $p < 0.001$) (Table 2.4, Figure 2.5).

Cougars selected ICH zones, which resident caribou avoided. Additionally, cougars avoided all types of ESSF zones, and cut blocks less than five years old (Jacobs index of -0.628, -0.560, -0.578, and -0.553, respectively, χ^2 test, $p < 0.001$) (Table 2.3, Figure 2.4).

2.5.3 Habitat similarities between animal groups

Caribou and cougars

There was little habitat similarity between resident caribou and cougars (Table 2.5), with the highest degree associated with use of Other ESSF zones (similarity index (SI) = 0.309, Table 2.5), and some similarity in cut blocks less than five years old (SI = 0.072, Table 2.5) and cut blocks 5-20 years old (SI = 0.208, Table 2.5). Conversely, habitat similarity was greater between translocated caribou and cougars, except in Other ESSF zones (Table 2.5). When comparing resident caribou and cougars to translocated caribou and cougars, the greatest difference in habitat similarity was found in ICH zones (difference of 0.786, Table 2.5). In these zones, resident caribou and cougars had no similarity, while translocated caribou and cougars had high similarity (SI = 0.000 and SI=0.786, respectively, Table 2.5). Translocated caribou and cougars also experienced a high degree of elevational similarity (SI = 0.386, Table 2.5).

Annual habitat similarities between caribou and cougars

Habitat similarity between translocated caribou and cougars was high year-round, except during spring season. Conversely, habitat similarity between resident caribou and cougars was low year-round (Figure 2.6). Differences in habitat similarity between both resident and translocated caribou and cougars were greatest in summer, late winter, and early winter seasons, while differences were lowest during spring and calving seasons (Figure 2.6).

Resident caribou and cougars had the greatest degree of habitat similarity in spring and early winter seasons, with no habitat similarity during summer season (Figure 2.6). Habitat similarity between translocated caribou and cougars was greatest in winter

season and lowest during spring season. There was a comparable trend in habitat similarity between both resident and translocated caribou and cougars throughout the year, where higher similarity occurred during the winter months and lower habitat similarity in calving and summer seasons (Figure 2.6).

2.5.4 Habitat similarities in resident, translocated and donor caribou

Habitat similarity between resident and translocated caribou was generally low year-round (Table 2.6), with the greatest similarity associated with ESSF Parkland zones, Other ESSF zones, and 5-20 year old cut blocks; no habitat similarity was associated with the ICH and IDF zones (Table 2.6). There was little habitat similarity among all the other variables (Table 2.6). We found high similarity between the travel rate and tortuosity variables (Table 2.6), indicating that translocated and resident caribou had similar movement patterns on an annual basis.

Translocated and donor caribou used elevations more similarly than translocated and resident caribou (Table 2.6), despite translocated and resident caribou residing in the same landscape. There was low to no similarity of road density use between all caribou comparisons (i.e., resident-translocated, donor-translocated, and donor-resident). Resident and translocated caribou had the highest habitat similarity in ESSF Parkland zones and zero similarity in their use of ICH and IDF zones. Travel rate and tortuosity were most similar between resident and translocated caribou and least similar between donor and resident caribou (Table 2.6).

2.6 Discussion

For effective conservation of small populations remedial action is often required to minimize the probability of extinction due to demographic, environmental, and genetic stochasticity (Caughley 1994). In our study, the endangered PS caribou herd was experimentally augmented with 19 caribou of a different ecotype; a second translocation of 20 caribou planned for the following year was cancelled. To gauge success of this experiment we examined risk of predation from cougars in relation to habitat use and patterns of movement. We hypothesized resident and translocated caribou would spatially separate from cougars and there would be seasonal differences in habitat use between caribou and cougars resulting in temporal variation in predation risk. We found resident caribou were successful at spatially separating from cougars by remaining at high elevations year-round, while translocated caribou traversed habitats selected by cougars and were therefore subject to greater predation risk.

2.6.1 Seasonality

Fretwell (1972) maintained that seasonality is essential to understanding the role of a regularly varying environment in affecting life history strategies. A major aspect of seasonality in prey is variation in the ability to exploit resources under predation risk, thus seasonality affects density-independent mortality (Cody 1966, King and Anderson 1971, Roughgarden 1971, Boyce et al. 1999). For example, Boyce et al. (1999) have shown that seasonal density dependence is the mechanism behind compensatory mortality and natality, and that predation or human harvest may not influence spring breeding or pre-harvest season densities in a variety of species.

Five resident caribou seasons were established. According to the spatial separation hypothesis, mountain caribou migrate to higher altitudes to mitigate predation risk. Highest elevations were reached during calving season, when adult females are most vulnerable during late stages of gestation due to reduced mobility and agility, as well as when they have a calf at heel (Magnhagen 1991, Pavlová et al. 2010). Similarly, in late winter, mountain caribou travelled to high elevations to separate from alternate prey, such as white-tailed deer, which congregate at lower elevations in winter (Pauley et al. 1993). Also, the snowpack is sufficiently deep at high elevations in winter to provide a supportive base to reach arboreal lichen, a critical winter food for mountain caribou (Stevenson et al. 2001). Slightly lower elevations were used in spring and early winter seasons, and the lowest elevations were used in summer. Correspondingly, Kinley and Apps (2000, 2001) found predation by cougars and other predators in the PS caribou herd was highest in summer and fall suggesting lower elevations used by resident caribou in these seasons increase their risk to cougar predation. During the caribou rut, which generally occurs in fall from September to early October (Miller 2006) males may be at greater risk to predation due to their lack of group security and high energy expenditures (Fitzgibbon 1990, Magnhagen 1991).

The forage maturation hypothesis proposes that ungulate migration is driven by the selection of high quality forage (McNaughton 1985, Fryxell 1991, Hebblewhite et al. 2008). Thus, it is possible that mountain caribou undergo seasonal migrations to track phenology. However, our analysis did not measure forage quality or availability because it is not assumed to be a limiting factor in mountain caribou populations (Wittmer et al. 2005a).

The donor caribou moved to alpine areas from May 12 to December 18, and to lower elevations between December 19 and May 11. They followed a migration pattern similar to that described by Johnson et al. (2004a) for caribou in the Wolverine northern caribou herd, approximately 300 km from the donor population. Northern caribou migrate to subalpine and alpine habitats during calving and summer to avoid predation by wolves (Bergerud et al. 1984, Bergerud Page 1987, Johnson et al. 2004a). In winter they use low elevation pine forests and forage on terrestrial lichens by cratering (Bergerud et al. 1984, Bergerud and Page 1987). Wolves are the primary predator of northern caribou (Bergerud and Elliot 1986, Bergerud and Elliott 1998) and tend to select low elevation habitat such as patches of spruce, pine, wetlands, lakes, and rivers (Johnson et al. 2004a). Northern caribou may trade-off forage abundance at lower elevations in favour of forage accessibility (windswept ridges with terrestrial lichen) and lower predation risk by selecting alpine habitats (Seip 1992). Although translocated caribou data clustered into two groups, we believe this is a statistical artefact consistent with the date of translocation and has no biological meaning.

The two cougar seasons, birthing and non-birthing, are consistent with the female cougar birth pulse from July to September in North America (Pierce and Bleich 2003, Laundre and Hernandez 2007). After kittens are born, female cougars exploit predation opportunities to meet the demands of the dependent litter (Ross and Jalkotzy 1996, Knopff et al. 2010). Knopff et al. (2010) found cougars in west-central Alberta killed primarily female ungulates around the birthing period (April to June), juvenile ungulates in spring, and males before and during the rut (September to November). This follows a

central tenet of predation theory that cougars select vulnerable individuals (Pierce and Bleich 2003, Knopff et al. 2010), and prey vulnerability fluctuates on an annual basis.

2.6.2 Habitat selection and predation risk

Habitat selection is a hierarchical process involving a series of innate and behavioural decisions (Johnson 1980, Orians and Wittenberger 1991, Rettie and Messier 2000). In caribou, this involves a trade-off between forage quantity and quality, and risk of predation (Bergerud et al. 1984, Rettie and Messier 2000, Barten et al. 2001, Gustine et al. 2006). DeCesare et al. (2014) found adding predation risk to resource selection function (RSF) models strongly improved the explanation power of adult caribou spatial patterns. We included predation risk from cougars when assessing caribou habitat selection and found resident caribou minimized habitat similarity with cougars, which is consistent with the spatial separation hypothesis (Bergerud and Elliot 1986, James et al. 2004, Robinson et al. 2010). However, most research on this hypothesis examines the relationship between wolves and caribou (Bergerud et al. 1984, Seip 1992, Bergerud and Elliott 1998, James et al. 2004, Ferguson and Elkie 2004, Stotyn et al. 2007, Whittington et al. 2011). There were wolves in our study area, so caribou may have reduced predation risk from both wolves and cougars. Yet, cougars often use different habitat types than wolves due to their different hunting strategies (Woodruff 2006, Bartnick et al. 2013). For example, Woodruff (2006) found wolves use open areas with less topographic relief, while cougars use structurally complex habitats on rugged terrain. Therefore, refugia from cougars may be different than from wolves.

Resident caribou and cougars had the greatest habitat similarity in Other ESSF zones, making it a zone of high cougar predation risk. This zone, characterized by

continuous conifer forest of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), is generally at lower elevations than ESSF Woodland and Parkland zones. From late May to mid-October 2012, three cougars in our study made forays to potential resident caribou habitat with elevations greater than 2,000 m, increasing their chance of encounter with resident caribou. Likewise, Steenweg (2011) found although wolves rarely went to high elevation caribou habitat, the absolute amount of time spent there was enough to kill caribou.

Somewhat paradoxically, resident caribou and cougars had some habitat similarity in their use of both age categories of cut blocks. We believe resident caribou may use cut blocks simply due to their high proportion in the landscape and adjacency to preferred habitats (Hins et al. 2009, Beauchesne et al. 2014). Numerous studies show predators select cut blocks due to their availability of ungulates (Kuzyk et al. 2004, Courbin et al. 2009, Roever et al. 2010); including cougars during summer (Goh 2000). Our results suggest resident caribou remained at low risk of cougar predation for most of the year by residing in ESSF Woodland and ESSF Parkland zones, which were avoided by cougars.

Low to no similarity was found between donor and resident caribou in terms of elevational usage and movement patterns, indicating they had different movement strategies throughout the year. Warren et al. (1996) found patterns of habitat use, movement, and dispersal of translocated northern and translocated mountain caribou appeared to be related to their traditional habitat use and movement patterns learned prior to translocation. That is, northern and mountain caribou have different movement patterns throughout the year. Yet, in this study, translocated caribou were more similar in their movement patterns to resident caribou than to donor caribou. Previous studies of

ungulates in North America have shown that movement rates change in response to weather (Parker et al. 1984, Beier and McCullough 1990, Webb et al. 2010, Beest et al. 2013, Avgar et al. 2013) and forage availability (Wickstrom et al. 1984, Ager et al. 2003, Avgar et al. 2013). Therefore, experiencing the same environmental changes, in combination with traversing similar terrain in the PS study area, may explain why translocated caribou were more similar to resident caribou in their movement patterns than to donor caribou.

Translocated caribou displayed risky behaviour by residing in habitats used by cougars and travelling at higher rates than resident caribou. They showed no systematic pattern in terms of elevation use and at lower elevations they were subject to greater cougar predation risk, resulting in six cougar-related mortalities. Wide ranging movements of translocated animals is a major concern for translocation efforts (Letty et al. 2007). Dispersal decreases numbers in the desired resident population, and increases the potential for higher mortality risk and energy depletion (Yoder et al. 2004, Letty et al. 2007, Dickens et al. 2010). Large movements by translocated caribou may be, in part, due to their inexperience with the landscape or an attempt to reach their native home range (Stamps and Swaisgood 2007, Scillitani et al. 2013). Translocated Alpine ibexes (*Capra ibex ibex*), in the eastern Italian Alps, had larger home range sizes than residents until they became familiar with their new habitat and settled into spatial patterns similar to residents one to two years post-translocation (Scillitani et al. 2012). Similarly, elk translocated from Alberta to Ontario dispersed over a 27,000 km² area, with the majority of elk travelling 20-140 km from the release site (Rosatte et al. 2007).

Cougar harvest data showed an increasing trend in cougar numbers at the time of translocation (FLNRO, unpublished data), so it is possible that high predation rates on translocated caribou is partly due to increased cougar abundance. Kinley and Apps (2001) found the PS caribou herd declined from 78 to 18 between 1995 and 2000, which corresponds to a peak in cougar population (FLNRO, unpublished data).

In our study, translocated caribou were exposed to cougars, a novel predator. Prey with little or no experience with a predator may fail to use appropriate avoidance behaviours to reduce predation risk (Atwood et al. 2007). Wolves are the main predator of the donor caribou herd (Bergerud and Elliot 1986), while cougars are the main predator of PS caribou (Kinley and Apps 2000, 2001). Wolves hunt in open habitats (Mech 1970), whereas cougars are more successful when hunting prey along forest edges (Hornocker 1970). In the LK study area, forestry and road development is much less intensive than in the PS study area, reducing the amount of artificial forest edges. Therefore, translocated caribou are unlikely to know that residing in or travelling near forest edges increases their risk of cougar predation. The inexperience of translocated caribou with cougars likely led to riskier behaviour in terms of habitat use. Atwood et al. (2007) have found elk can learn about new predation risk within one year. Specifically, elk in the northern Madison Range, Montana, shifted their habitat selection from simple grassland habitats to structurally complex refugia in attempts to lessen the predation risk from recolonizing wolves, a novel predator (Atwood et al. 2007). In our study, translocated caribou did not aggregate with resident caribou and many died before it was possible to learn cougar avoidance strategies.

Had resident and translocated caribou coalesced, translocated caribou should have benefited from herd formation which reduces predator search efficiency by creating void spaces across the landscape that would otherwise be filled by asocial prey (Fryxell et al. 2007). Grouping behaviour also dilutes predation risk and reduces individual vigilance needed to detect predators (Hamilton 1971, Dehn 1990, Hebblewhite and Pletscher 2002). Additionally, social animals learn from each other allowing an individual to exploit the expertise of others (Russon 1997, Choleris and Kavaliers 1999). For example, bighorn sheep learn movement patterns by virtue of being gregarious (Geist 1971). Learning essential skills from others, such as appropriate food source selection or locating refugia from predators, would give an individual a survival advantage (Curio 1988, Mineka and Cook 1988, Choleris and Kavaliers 1999). Thus, it is also possible that failure of the translocated caribou to join resident caribou compromised any potential opportunity to learn PS specific predator avoidance strategies. It remains, however, that spatial separation may be an innate behavioural strategy.

2.7 Conclusions

Small populations have an increased risk of extinction due to factors such as inbreeding, demographic stochasticity, and loss of cooperative interactions with conspecifics, causing the per capita rate of increase to decrease as populations reach small sizes or low densities (Courchamp et al. 1999, Stephens and Sutherland 1999). These factors produce an inverse density-dependant decline or Allee effect (Allee et al. 1949) and populations may decline to extinction below a threshold density (Dennis 2002). This threshold of the number of individuals to ensure (at some acceptable level of risk) a population will persist in a viable state for a given interval of time is deemed

minimum viable population (MVP; Shaffer 1981, Rai 2003). MVPs have not been found to differ significantly among taxa and estimates exceed a few thousand (Reed et al. 2003, Brook et al. 2006, Traill et al. 2007), with Trail et al. (2010) suggesting to manage for biologically relevant MVPs of at least 5,000 adult individuals. Currently, the meta-population of mountain caribou is less than 1,500 individuals, with nine of the 15 fragmented subpopulations less than 50. These subpopulations are no longer viable because of an increasing isolation from other larger subpopulations which prevents natural immigration, limiting possible heterozygosity, especially towards the meta-population's southern extremity. Consequently, increasing the meta-population of mountain caribou to their MVP is not likely in the near-term; however, translocations may prevent small subpopulations from becoming extirpated in the near future.

Pérez et al. (2012) provide a comprehensive review of why translocations can fail and appropriate criteria to follow. Likely solutions for increasing the success of translocations would involve removing or diminishing limiting factors to the resident population (Pérez et al. 2012) and using a suitable source population that is experienced with the release site's mortality risks (Warren et al. 1996, Frair et al. 2007). Further, juveniles are known to be more behaviourally plastic than sub-adults and adults (Letty et al. 2007). Therefore, it is possible that translocating northern calves in late winter or rearing calves in the PS Mountains would increase site fidelity and the potential for young caribou to learn resident caribou behaviours and predator avoidance strategies. Our findings suggest, to encourage herd amalgamation and reduction in predation risk, translocated caribou should have experience with the same predators occurring at the release site and possess seasonal habitat use comparable to the recipient population.

References

- Ager, A., B. Johnson, J. Kern, and J. Kie. 2003. Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. *Journal of Mammalogy* 84:1076–1088.
- Allee, W. C., O. Park, A. E. Emerson, T. Part, and K. P. Schmidt. 1949. *Principles of Animal Ecology*. Saunders, Philadelphia, USA.
- Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *Journal of Wildlife Management* 65:65–77.
- Apps, C. D., B. N. McLellan, T. A. Kinley, R. Serrouya, D. R. Seip, and H. U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *Journal of Wildlife Management* 77:1409–1419.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2007. Comparative Patterns of Predation by Cougars and Recolonizing Wolves in Montana’s Madison Range. *Journal of Wildlife Management* 71:1098–1106.
- Avgar, T., A. Mosser, G. S. Brown, and J. M. Fryxell. 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology* 82:96–106.
- Barten, N. L., T. R. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. *Journal of Wildlife Management* 65:77–92.
- Bartnick, T. D., T. R. Van Deelen, H. B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology* 91:82–93.
- Basille, M. 2013. R package “seasonality”. R package version 1.0. <<http://ase-research.org/basille/seasonality>>.
- Basille, M., D. Fortin, C. Dussault, J.P. Ouellet, and R. Courtois. 2012. Ecologically based definition of seasons clarifies predator-prey interactions. *Ecography* 35:1–10.
- BC Conservation Data Centre. 2014. Conservation Status Report: *Rangifer tarandus* pop. 1 Caribou (Southern Mountain Population). <http://a100.gov.bc.ca/pub/eswp/>.
- Bearzi, G., A. Azzellino, E. Politi, M. Costa, and M. Bastianini. 2008. Influence of seasonal forcing on habitat use by bottlenose dolphins *Tursiops truncatus* in the northern Adriatic Sea. *Ocean Science Journal* 43:175–182.

- Beauchesne, D., J. Jaeger, and M. St-Laurent. 2014. Thresholds in the capacity of boreal caribou to cope with cumulative disturbances: Evidence from space use patterns. *Biological Conservation* 172:190–199.
- Beest, F., E. Vander Wal, A. Stronen, and R. Brook. 2013. Factors driving variation in movement rate and seasonality of sympatric ungulates. *Journal of Mammalogy* 94:691–701.
- Beier, P., and D. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:5–51.
- Bergerud, A., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515–1529.
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38:757–770.
- Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer* 16:95–116.
- Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566–1575.
- Bergerud, A. T., and J. P. Elliott. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology* 76:1551–1569.
- Bergerud, A. T., and W. E. Mercer. 1989. Caribou Introductions in Eastern North America. *Wildlife Society Bulletin* 17:111–120.
- Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology* 65:1597–1606.
- Birks, H. J. B. 1987. Recent methodological developments in quantitative descriptive biogeography. *Annales Zoologici Fennici* 24:165–177.
- Borowski, Z., and E. Owadowska. 2010. Field vole (*Microtus agrestis*) seasonal spacing behavior: the effect of predation risk by mustelids. *Naturwissenschaften* 97:487–93.
- Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal Compensation of Predation and Harvesting. *Oikos* 87:419–426.
- Brook, B. W., L. W. Traill, and C. J. A. Bradshaw. 2006. Minimum viable population size and global extinction risk are unrelated. *Ecology Letters* 9:375–382.
- Bui, R., R. Buliung, and T. Rimmel. 2013. R package “aspace”. R package version 3.2. <<http://cran.r-project.org/web/packages/aspace/aspace.pdf>>.

- Calenge, C. 2013. R package “adehabitatHR”. R package version 0.4.10. < <http://cran.r-project.org/web/packages/adehabitatHR/adehabitatHR.pdf>>.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Choleris, E., and M. Kavaliers. 1999. Social learning in animals: sex differences and neurobiological analysis. *Pharmacology, biochemistry, and behavior* 64:767–76.
- Chruszcz, B., A. P. Clevenger, K. E. Gunson, and M. L. Gibeau. 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81:1378–1391.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* 20:174–184.
- Courbin, N., D. Fortin, C. Dussault, and R. Courtois. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landscape Ecology* 24:1375–1388.
- Courchamp, F., T. Clutton-Brock, B. Grenfell. 1999. Inverse density-dependence and the Allee effect. *Trends in Ecology & Evolution* 14:405–410.
- Curio, E. 1988. Cultural transmission of enemy recognition by birds. Pages 75–97 in T. R. Zentall and B. G. Galief, editors. *Social learning: Psychobiological and biological perspectives*. Lawrence Erlbaum Associates, Hillsdale, NJ.
- DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. 2014. Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology* 83:343–352.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology* 26:337–342.
- Dennis, B. 2002. Allee effects in stochastic populations. *Oikos* 96:389–401.
- Dickens, M. J., D. J. Delehanty, and L. M. Romero. 2010. Stress: An inevitable component of animal translocation. *Biological Conservation* 143:1329–1341.
- Ferguson, S. H., and P. C. Elkie. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology* 262:125–134.

- Fitzgibbon, C. 1990. Why do hunting cheetahs prefer male gazelles? *Animal Behaviour* 40:837–845.
- Flaxman, S., and Y. Lou. 2009. Tracking prey or tracking the prey's resource? *Journal of Theoretical Biology* 256:187–200.
- Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management* 71:541–554.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138:478–498.
- Fryxell, J. M., A. Mosser, A. R. E. Sinclair, and C. Packer. 2007. Group formation stabilizes predator-prey dynamics. *Nature* 449:1041–1043.
- Gaillard, J., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 365:2255–65.
- Geist, V. 1971. *Mountain sheep: a study in behavior and evolution*. University of Chicago Press, Chicago, Illinois, USA.
- Gervasi, V., H. Sand, B. Zimmermann, J. Mattisson, P. Wabakken, and J. D. C. Linnell. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications* 23:1722–34.
- Goh, K. 2000. *Macrohabitat Selection by Vancouver Island Cougar*. M.S. thesis, University of British Columbia, Vancouver, BC.
- Government of Canada. 2013. *Canadian Climate Normals 1971-2000 Station Data*. http://climate.weather.gc.ca/climate_normals/index_e.html#1971.
- Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* 165:1–32.
- Hamilton, W. D. 1971. Geometry for the selfish group. *Journal of Theoretical Biology* 31:295–311.
- Heard, D. C., and K. L. Vagt. 1998. Caribou in British Columbia: A 1996 status report. *Rangifer Special Is*:117–123.

- Hebblewhite, M. 2005. Predation by wolves interact with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology* 74:226–233.
- Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–54.
- Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A Multi-Scale Test of the Forage Maturation Hypothesis in a Partially Migratory Ungulate Population. *Ecological Monographs* 78:141–166.
- Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800–809.
- Hins, C., J.P. Ouellet, C. Dussault, and M.H. St-Laurent. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: Evidence of a landscape configuration effect. *Forest Ecology and Management* 257:636–643.
- Holt, R. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Hornocker, M. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 21:3–39.
- Integrated Land Management Bureau. 2007. Mountain Caribou Recovery Implementation Plan. Species at Risk Coordination Office, Integrated Land Management Bureau, Victoria, BC.
- Jacobs, J. 1974. Quantitative measurement of food selection: A modification of the forage ratio and Ivlev's Electivity Index. *Oecologia* 14:413–417.
- James, A., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- Jędrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jędrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill Rates and Predation by Wolves on Ungulate Populations in Białowieża Primeval Forest (Poland). *Ecology* 83:1341–1356.
- Jelinski, D. E. 1991. On the use of chi-square analyses in studies of resource utilization. *Canadian Journal of Forest Research* 21:58–65.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347–357.

- Johnson, C. J., K. L. Parker, D. C. Heard, and D. R. Seip. 2004a. Movements, foraging habits, and habitat use strategies of northern woodland caribou during winter: Implications for forest practices in British Columbia. *BC Journal of Ecosystems and Management* 5:22–35.
- Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004b. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41:238–251.
- Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61:65–71.
- Kauhala, K., and M. Auttila. 2010. Estimating habitat selection of badgers – a test between different methods. *Folia Zoologica* 59:16–25.
- King, C. E., and W. W. Anderson. 1971. Age-specific selection. II. The interaction between r and K during population growth. *American Naturalist* 105:137–156.
- Kinley, T. A., and C. D. Apps. 2000. Population Status and Mortality of Mountain Caribou in the Southern Purcell Mountains, British Columbia. Pages 655–661 in L. M. Darling, editor. Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, British Columbia, 15-19 Fe. 1999. Volume 2. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College.
- Kinley, T. A., J. Bergenske, J. A. Davies, and D. Quinn. 2003. Characteristics of early-winter caribou, *Rangifer tarandus caribou*, feeding sites in the southern Purcell Mountains, British Columbia. *Canadian Field Naturalist* 117:352–359.
- Kinley, T., and C. Apps. 2001. Mortality Patterns in a Subpopulation of Endangered Mountain Caribou. *Wildlife Society Bulletin* 29:158–164.
- Kinley, T. A. 2010. Augmentation plan for the Purcells-South mountain caribou population. BC Ministry of Environment (Ecosystems Branch), Prepared for BC Ministry of Environment (Ecosystems Branch), Victoria, BC.
- Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar Kill Rate and Prey Composition in a Multiprey System. *Journal of Wildlife Management* 74:1435–1447.
- Kuzyk, G., J. Kneteman, and F. Schmiegelow. 2004. Winter habitat use by wolves, *Canis lupus*, in relation to forest harvesting in west-central Alberta. *Canadian Field Naturalist* 118:368–375.
- Latham, A. D., C. Latham, M. S. Boyce, and S. Boutin. 2013. Spatial relationships of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) with woodland caribou

- (*Rangifer tarandus caribou*) during the calving season in a human-modified boreal landscape. *Wildlife Research* 40:250–260.
- Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011a. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. *Canadian Journal of Zoology* 89:267–277.
- Latham, A., M. Latham, N. Mccutchen, and S. Boutin. 2011b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *Journal of Wildlife Management* 75:204–212.
- Laundre, J. W., and L. Hernandez. 2007. Do female pumas (*Puma concolor*) exhibit a birth pulse? *Journal of Mammalogy* 88:1300–1304.
- Letty, J., S. Marchandea, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. *Ecoscience* 14:420–431.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology & Evolution* 6:183–186.
- Marcum, C., and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. *Journal of Wildlife Management* 44:963–968.
- McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. *Ecology* 91:286–292.
- McLellan, M. L., R. Serrouya, B. N. McLellan, K. Furk, D. C. Heard, and H. U. Wittmer. 2012. Implications of body condition on the unsustainable predation rates of endangered mountain caribou. *Oecologia* 169:853–60.
- McNamara, J. M., and A. I. Houston. 1994. The effect of a change in foraging options on intake rate and predation rate. *American Naturalist* 144:978–1000.
- McNaughton, S. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259–294.

- Mech, D. L. 1970. The wolf: ecology and behavior of an endangered species. Natural History Press, Doubleday, N.Y.
- Mejlgaard, T., L. E. Loe, J. Odden, J. D. C. Linnell, and E. B. Nilsen. 2013. Lynx prey selection for age and sex classes of roe deer varies with season. *Journal of Zoology* 289:222–228.
- Miller, F. L. 2006. Caribou (*Rangifer tarandus*). Pages 965–997 in G. Feldhamer, B. Thompson, and J. Chapman, editors. *Wild Mammals of North America*. 2nd ed. The John Hopkins University Press, Baltimore.
- Mineka, S., and M. Cook. 1988. Social learning and the acquisition of snake fear in monkeys. Pages 51–73 in T. R. Zentall and B. G. Galef, editors. *Social learning: Psychobiological and biological perspectives*. Lawrence Erlbaum Associates, Hillsdale, NJ.
- Ministry of Environment. 2013. Historic snow survey data for British Columbia: 4C03 Dease Lake. <http://a100.gov.bc.ca/pub/mss/stationdata.do?station=4C03>.
- Ministry of Forest Lands and Natural Resource Operations (MFLNRO). 2013. Biogeoclimatic Ecosystem Classification Program. <http://www.for.gov.bc.ca/hre/becweb/>.
- Molinari-Jobin, P., P. Molinari, A. Loison, and U. Breitenmoser. 2004. Life Cycle Period and Activity of Prey Influence Their Susceptibility to Predators. *Ecography* 27:323–329.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105:19052–19059.
- Nylin, S., and K. Gotthard. 1998. Plasticity in Life-History Traits. *Annual Review of Entomology* 43:63–83.
- Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29–S49.
- Owen-Smith, N. 2008. Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos* 117:602–610.
- Parker, K., C. Robins, and T. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474–488.
- Pauley, G. R., J. M. Peek, and P. Zager. 1993. Predicting White-Tailed Deer Habitat Use in Northern Idaho. *Journal of Wildlife Management* 57:904–913.

- Pavlová, V., L. Berec, and D. S. Boukal. 2010. Caught between two Allee effects: trade-off between reproduction and predation risk. *Journal of theoretical biology* 264:787–98.
- Pérez, I., J. D. Anadón, M. Díaz, G. G. Nicola, J. L. Tella, and A. Giménez. 2012. What is wrong with current translocations? A review and a decision-making proposal. *Frontiers in Ecology and the Environment* 10:494–501.
- Peters, W., M. Hebblewhite, N. DeCesare, F. Cagnacci, and M. Musiani. 2013. Resource separation analysis with moose indicates threats to caribou in human altered landscapes. *Ecography* 35:487–498.
- Pierce, B., and V. Bleich. 2003. Mountain Lion (*Puma concolor*). Pages 744–757 in G. Feldhamer, B. Thompson, and J. Chapman, editors. *Wild Mammals of North America*. 2nd ed. The John Hopkins University Press, Baltimore.
- Powder Creek Lodge. 2013. Snow Report. <http://powdercreeklodge.com/>.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rai, U.K. 2003. Minimum sizes for viable populations and conservation biology. *Our Nature* 1:3-9.
- Real, R., and J. M. Vargas. 1996. The probabilistic basis of Jaccard's Index of Similarity. *Systematic Biology* 45:380–385.
- Reed, D. H., J. J. O'Grady, B. W. Brook, J. D. Ballou, and R. Frankham. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113:23-34.
- Rettie, W. J., and F. Messier. 2000. Hierarchical Habitat Selection by Woodland Caribou: Its Relationship to Limiting Factors. *Ecography* 23:466–478.
- Robinson, H. S., M. Hebblewhite, N. J. DeCesare, J. Whittington, L. Neufeld, M. Bradley, and M. Musiani. 2010. The effect of fire on spatial separation between wolves and caribou. *Rangifer* 20:277–294.
- Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. *Ecography* 33:1113–1122.
- Rosatte, R., J. Hamr, J. Young, I. Filion, and H. Smith. 2007. The Restoration of Elk (*Cervus elaphus*) in Ontario, Canada: 1998 – 2005. *Restoration Ecology* 15:34–43.

- Ross, P. I., and M. G. Jalkotzy. 1996. Cougar Predation on Moose in Southwestern Alberta. *ALCES* 32:1–8.
- Roughgarden, J. 1971. Density-dependent natural selection. *Ecology* 52:453–468.
- Russon, A. E. 1997. Exploiting the expertise of others. Pages 174–231 in A. Whiten and R. W. Byrne, editors. *Machiavellian intelligence II, extension and evaluations*. Cambridge University Press, New York, USA.
- Scillitani, L., G. Darmon, A. Monaco, G. Cocca, E. Sturaro, L. Rossi, and M. Ramanzin. 2013. Habitat selection in translocated gregarious ungulate species: An interplay between sociality and ecological requirements. *Journal of Wildlife Management* 77:761–769.
- Scillitani, L., E. Sturaro, A. Menzano, L. Rossi, C. Viale, and M. Ramanzin. 2012. Post-release spatial and social behaviour of translocated male Alpine ibexes (*Capra ibex ibex*) in the eastern Italian Alps. *European Journal of Wildlife Research* 58:461–472.
- Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. *Conservation Biology* 21:303–312.
- Seip, D. R. 1991. Predation and caribou populations. *Rangifer* 7:46–52.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494–1503.
- Seip, D. R. 2008. Mountain caribou interactions with wolves and moose in central British Columbia. *ALCES* 44:1–5.
- Seip, D. R., and D. B. Cichowski. 1996. Population Ecology of Caribou in British Columbia. *Rangifer Special Issue No. 9*:73–80.
- Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. *Journal of Wildlife Management* 71:1539–1544.
- Serrouya, R., B. N. McLellan, and J. P. Flaa. 2007. Scale-dependent microhabitat selection by threatened mountain caribou (*Rangifer tarandus caribou*) in cedar–hemlock forests during winter. *Canadian Journal of Forest Research* 37:1082–1092.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- Sih, A. 1984. The behavioral response race between predator and prey. *American Naturalist* 123:143–150.

- Sinclair, A. R. E., and P. Arcese. 1995. Population Consequences of Predation-Sensitive Foraging: The Serengeti Wildebeest. *Ecology* 76:882–891.
- Spalding, D. J. 2000. The early history of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. Wildlife Bulletin No. B-100. BC. Ministry of the Environment. Victoria, BC.
- Stamps, J., and R. Swaisgood. 2007. Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392–409.
- Steenweg, R. W. 2011. Interactions of wolves, mountain caribou and an increased moose-hunting quota – Primary-prey management as an approach to caribou recovery. M.S. thesis, University of Northern British Columbia, Prince George, BC.
- Steinley, D. 2006. K-means clustering: a half-century synthesis. *British Journal of Mathematical and Statistical Psychology* 59:1–34.
- Stephens, P.A., and W.J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution* 14:39-42.
- Stevenson, S. K., H.M. Armleder, M.J. Jull, D.G. King, B.N. McLellan, D.S. Coxson. 2001. Mountain Caribou in Managed Forests: Recommendations for Managers. Second Edition. 58pp.
- Stevenson, S. K., and D. F. Hatler. 1985. Woodland caribou and their habitat in southern and central British Columbia. British Columbia Ministry of Forests Land Management Report 23. Volume 2. Victoria, Canada.
- St-Laurent, M., and C. Dussault. 2012. The reintroduction of boreal caribou as a conservation strategy: A long-term assessment at the southern range limit. *Rangifer Special Issue No. 20*:127-138.
- Stotyn, S. A., B. N. McLellan, and R. Serrouya. 2007. Mortality sources and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia. Pages 1–55. Prepared for Columbia Basin Fish and Wildlife Compensation Program, Nelson, BC.
- Tibshirani, R., G. Walther, and T. Hastie. 2001. Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society: Series B* 63:411–423.
- Tobler, W. R. 1970. A computer movie simulating urban growth in the Detroit region. *Economic Geography* 46:234–240.
- Trall, L. W., C. J. A. Bradshaw, and B. W. Brook. 2007. Minimum viable population

- size: A meta-analysis of 30 years of published estimates. *Biological Conservation* 139:159-166.
- Trails, L.W., B.W. Brook, R.R. Frankham, C.J.A. Bradshaw. 2010. Pragmatic population viability targets in a rapidly changing world. *Biological Conservation* 143:28-34.
- Vander Wal, E., and A. R. Rodgers. 2009. Designating seasonality using rate of movement. *Journal of Wildlife Management* 73:1189–1196.
- VanMoorter, B., D. R. Visscher, C. L. Jerde, J. L. Frair, and E. H. Merrill. 2010. Identifying movement states from location data using cluster analysis. *Journal of Wildlife Management* 74:588–594.
- Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. *Conservation Biology* 10:547–553.
- Webb, S., K. Gee, B. Strickland, S. Demarais, and R. DeYoung. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. *International Journal of Ecology* 459610.
- 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.
- Wickstrom, M., C. Robbins, T. Hanley, D. Spalinger, and S. Parish. 1984. Food-intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285–1301.
- Wittmer, H., B. McLellan, D. Seip, and J. Young. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wittmer, H., A. Sinclair, B. McLellan, and R. Sinclair. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Woodruff, S. 2006. Characteristics of wolf and cougar kill sites in the Southern Yellowstone Ecosystem. M.S. thesis, Prescott College, Prescott, Arizona.
- Yan, M., and K. Ye. 2007. Determining the number of clusters using the weighted gap statistic. *Biometrics* 63:1031–7.
- Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* 15:469–476.

Table 2.1 Purcell South Biogeoclimatic Ecosystem Classification (BEC) zone descriptions based on vegetation structure relevant to resident caribou.

Vegetation Type	Description
ESSF Parkland Zones	<p>Subalpine parkland at upper elevations. Clumps of trees occur together in areas of heath, meadow, and grasslands. Includes krummholz.</p> <p>Typical species include Sitka valerian (<i>Valeriana sitchensis</i>), Indian hellebore (<i>Veratrum viride</i>), arrow leaved groundsel (<i>Senecio triangularis</i>), western meadowrue (<i>Thalictrum occidentale</i>), bracted lousewort (<i>Pedicularis bracteosa</i>), common red paintbrush (<i>Castilleja miniata</i>), and various heather species (<i>Cassiope sp.</i> and <i>Phyllodoce sp.</i>)</p> <p>Elevation range: 1850 to 3500</p>
ESSF Woodland Zones	<p>Open and continuous, upper elevation forest dominated by Engelmann spruce (<i>Picea englemannii</i>) and subalpine fir (<i>Abies lasiocarpa</i>)</p> <p>Elevation range: 1650 to 2650m</p>
Other ESSF Zones	<p>Engelmann spruce and subalpine fir dominate wetter areas, with lodgepole pine (<i>Pinus contorta</i>) as a pioneer after disturbance and mountain hemlock (<i>Tsuga mertensiana</i>) in higher snowfall areas. Whitebark pine (<i>Pinus albicaulis</i>) and limber pine (<i>P. flexilis</i>) occur on drier sites. White rhododendron (<i>Rhododendron albiflorum</i>) and false azalea (<i>Menziesia ferruginea</i>) are common understory plants.</p> <p>Elevation range: 720 to 2600</p>
ICH Zones	<p>Upland coniferous forests with high diversity of tree species. Western red cedar (<i>Thuja plicata</i>) and western hemlock (<i>Tsuga heterophylla</i>) dominate mature climax forests. Grand fir (<i>Abies grandis</i>) is common. Steeply sloping, mountainous terrain.</p> <p>Elevation range: 300 to 1980</p>
IDF Zones	<p>Open to closed, mature forests containing Douglas-fir (<i>Pseudotsuga menziesii</i>) and lodgepole pine. Ponderosa pine (<i>Pinus ponderosa</i>) occurs at lower elevations.</p> <p>Elevation range: 440 to 1500</p>
<5 year cut blocks	<p>High proportion of woody shrubs and herbaceous species (Pypker and Fredeen 2003).</p> <p>Elevation range: 440 to 2200 m</p>
5-20 year cut blocks	<p>Woody shrubs with many conifer seedlings (Pypker and Fredeen 2003).</p> <p>Elevation range: 436 to 2400 m</p>

Table 2.2 Level Kawdy Biogeoclimatic Ecosystem Classification (BEC) zone descriptions based on vegetation structure relevant to donor caribou.

Vegetation Type	Description
Alpine	High elevations. Temperatures are cold throughout the year, lowering the tree line by heavy and prolonged snow cover. Much of the land is covered by vegetated tundra, glaciers, or recently exposed bare rock. Elevation range: 1,025 to 2,745 m
Subalpine	Higher elevation valleys and mountain slopes. White spruce (<i>Picea glauca</i>) and subalpine fir (<i>Abies lasiocarpa</i>) are the most common species. Engelmann spruce (<i>Picea engelmannii</i>) and lodgepole pine (<i>Pinus contorta</i>) are also found. Stands are often sparsely treed due to extensive cold temperatures. Subalpine forbs, grasses, sedges, and some heath vegetation cover the ground. Elevation range: 800 to 1,880 m
Mid-elevation	Common tree species include: white spruce, trembling aspen (<i>Populus tremuloides</i>), lodgepole pine, black spruce (<i>Picea mariana</i>), balsam poplar (<i>Populus balsamifera</i>), tamarack (<i>Larix laricina</i>), common paper birch (<i>Betula papyrifera</i>), and Alaska paper birch (<i>Betula neoalaskana</i>). At higher elevations Engelmann spruce and subalpine fir are also found. Grassland and scrub communities occur in small pocks on steep slopes. Elevation range: 600 to 1,415 m
Low-elevation	Extensive old growth forests dominated by western and mountain hemlock forests (<i>Tsuga heterophylla</i> and <i>T. mertensiana</i> , respectively). Some white spruce, yellow cedar (<i>Chamaecyparis nootkatensis</i>), subalpine fir, and Western red cedar (<i>Thuja plicata</i>) are also found. Younger forest dominated by lodgepole pine, trembling aspen, and paper birch. Most of this zone consists of moist, cool climate. Elevation range: 100 to 1,200 m
5-20 year cut blocks	Woody shrubs with many conifer seedlings (Pypker and Fredeen 2003). Elevation range: 300 to 1,460 m

Table 2.3 Use of land cover types by resident caribou, translocated caribou, and cougars in the Purcell Mountains by number of GPS points and percent of points in each category from February 2011 to February 2013.

Land Cover Type	Resident Caribou <i>n</i> = 4		Translocated Caribou <i>n</i> = 19		Cougars <i>n</i> = 7	
	Number of GPS Locations	Percent (%)	Number of GPS Locations	Percent (%)	Number of GPS Locations	Percent (%)
ESSF Woodland	7187	65.8	2872	22.2	62	0.8
ESSF Parkland	1289	11.8	344	2.7	21	0.3
Other ESSF	2277	20.9	3854	29.7	314	4.2
ICH Zone	5	0.0	4142	32.0	3514	46.9
IDF Zone	0	0.0	890	6.9	2639	35.3
Cut block <5yrs	8	0.1	223	1.7	43	0.6
Cut block 5-20yrs	153	1.4	633	4.9	892	11.9
Total	10919	100	12958	100	7485	100

Table 2.4 Relative use of land cover types by Level Kawdy donor caribou in native habitat.

Land Cover Type	Donor Caribou	
	# GPS Points	Percent (%)
Alpine	837	11.1
Subalpine	4388	58.1
Mid-elevation	2330	30.8
Low-elevation	0	0.0
Cut block 5-20yrs	0	0.0
Total	7555	100.0

Table 2.5 Measure of habitat similarity (Jaccard's index) between resident caribou, translocated caribou, and cougars based on use of habitat attributes in the Purcell Mountains.

Variable	Resident-Cougar	Translocated-Cougar	Difference
Elevation	0.000	0.386	0.386
Road Density	0.000	0.337	0.337
ESSF Woodland	0.000	0.001	0.001
ESSF Parkland	0.000	0.000	0.000
Other ESSF	0.309	0.213	-0.096
ICH Zone	0.000	0.786	0.786
IDF Zone	0.000	0.370	0.370
Cut blocks <5 yrs	0.072	0.220	0.148
Cut blocks 5-20 yrs	0.208	0.303	0.095

Table 2.6 Measure of habitat similarity (Jaccard's index) between resident and translocated caribou based on their use of habitat attributes in the Purcell Mountains and a similarity measure of movement (travel rate and tortuosity) between resident, translocated, and donor caribou.

Variable	Resident- Translocated	Donor- Translocated	Donor- Resident
Elevation	0.112	0.245	0.000
Road Density	0.093	0.000	0.000
ESSF Woodland	0.014	-	-
ESSF Parkland	0.823	-	-
Other ESSF	0.691	-	-
ICH Zone	0.000	-	-
IDF Zone	0.000	-	-
Cut blocks <5 yrs	0.016	-	-
Cut blocks 5-20 yrs	0.685	-	-
Travel Rate	0.650	0.450	0.304
Tortuosity	0.770	0.449	0.384



Figure 2.1 Locations of the Level Kawdy and Purcells-South study areas, British Columbia, Canada.

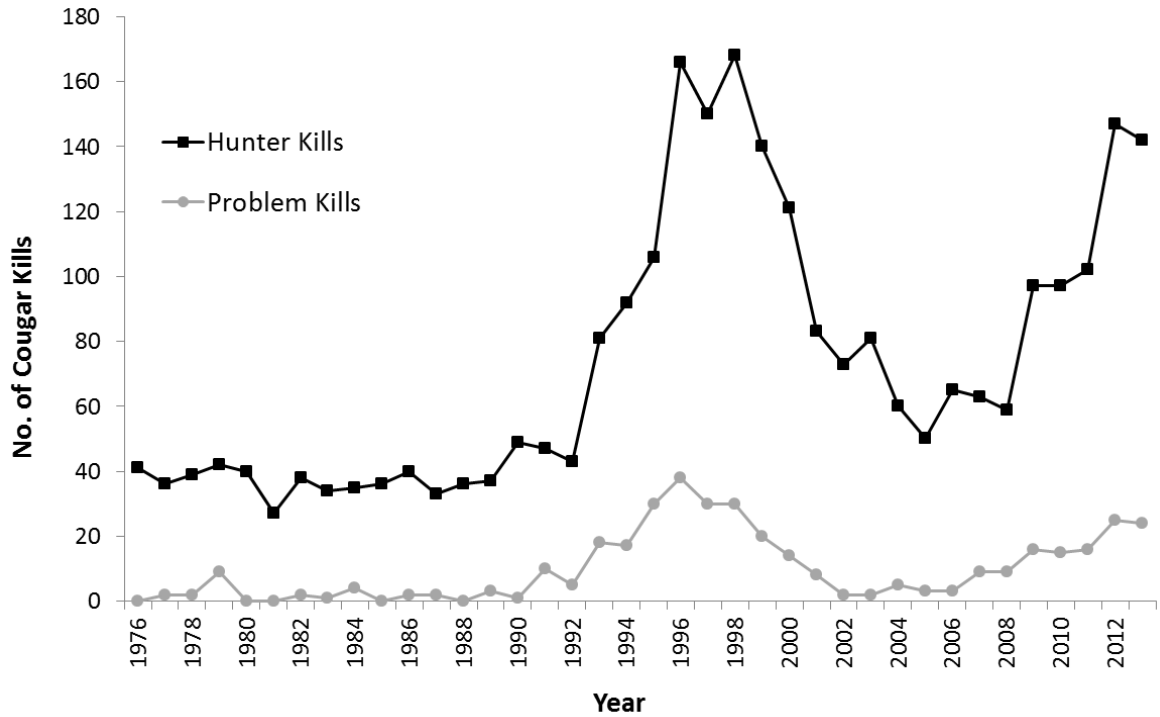


Figure 2.2 Cougar harvest data for hunter kills (black square) and problem kills by conservation officers (grey circle) in the Kootenay Region, British Columbia, Canada from 1976 to 2013. Data obtained from BC Ministry compulsory inspection reports, required for all cougars killed in the Kootenay Region (Forests, Lands and Natural Resource Operations, unpublished data).

Resident Caribou	LW			Sp	Clv	Sum			EW		LW	
Donor Caribou	Sea2				Sea1							
Translocated Caribou	Clu1		Clu2						Clu1			
Cougars	NB					B			NB			
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec

Figure 2.3 Representation of the biological seasons for resident caribou and female cougars in the Purcell South Mountains in southeastern BC, and donor caribou from the Level Kawdy herd in northern BC. Translocated clusters are depicted, although these are likely a statistical artefact consistent with the date of translocation. Abbreviations symbolize: LW – late winter, Sp – spring, Clv – calving, Sum – summer, EW – early winter, Sea1 – season 1, Sea2 – season 2, Clu1 – cluster 1, Clu2 – cluster 2, NB – non-birthing, B – birthing, W – winter.

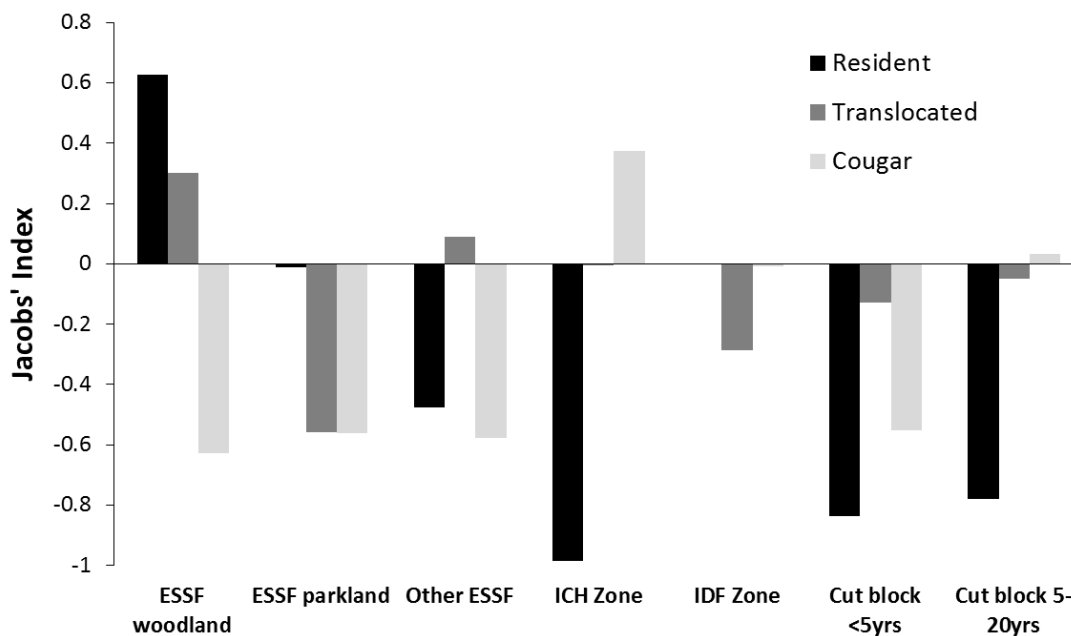


Figure 2.4 Selection for land cover types by resident caribou, translocated caribou, and cougars in the Purcell South Mountains, BC as shown by the Jacobs Index.

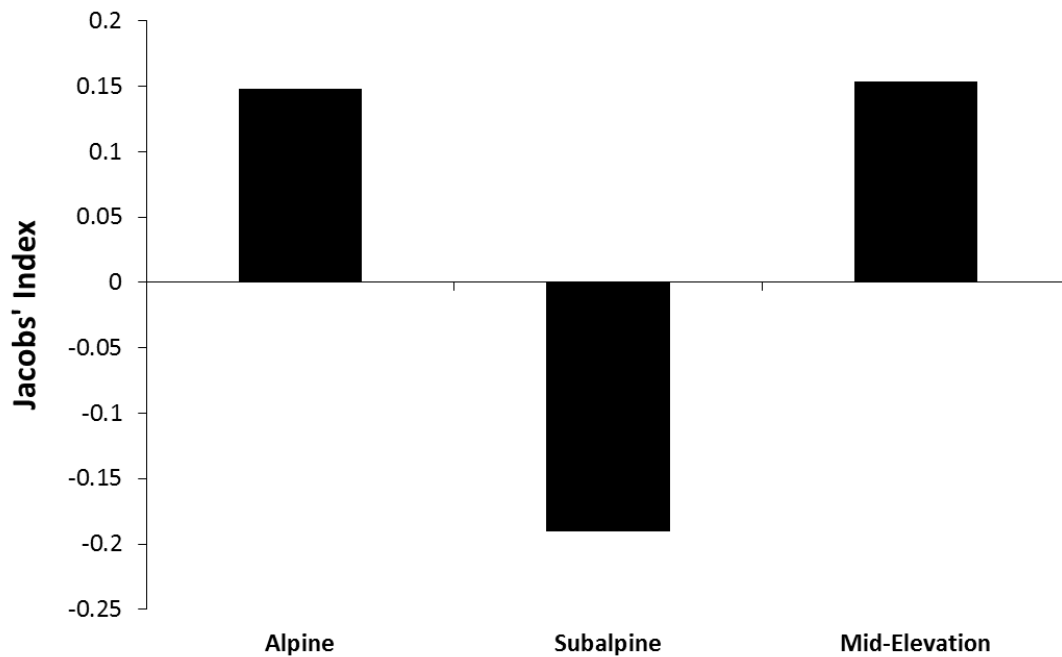


Figure 2.5 Selection for land cover types by donor caribou in the Level Kawdy study area as shown by the Jacobs Index.

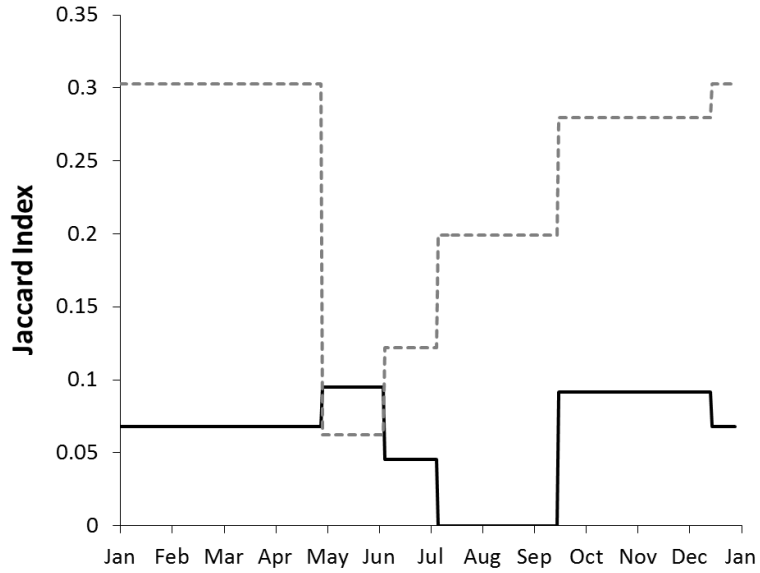


Figure 2.6 Seasonal changes in habitat similarity between cougars and resident caribou (solid black line), and between cougars and translocated caribou (dashed grey line) based on temporal patterns of habitat use including average elevation, average road density, and proportions of time spend in selected Biogeoclimatic Ecosystem Classification zones.

3.0 Habitat selection by resident and translocated caribou in relation to cougar predation risk

3.1 Abstract

Predation is a selective pressure affecting prey populations through lethal effects, where prey is consumed, or through non-lethal (non-consumptive) effects, where prey perform behaviours to avoid predation risk. Non-lethal effects influence prey habitat selection by altering mortality risk in available habitats and is central to the landscape of fear model. Mountain caribou (*Rangifer tarandus caribou*), an endangered ecotype of woodland caribou, reduce predation risk by spatially separating from predators through differential habitat use. However, predation remains the proximate cause for high rates of mountain caribou mortality, likely linked to apparent competition. Cougars (*Puma concolor*) have been identified as a major predator of mountain caribou, but non-lethal effects from cougars remains unclear. In 2012, an imperilled mountain caribou herd in the Purcell Mountains of British Columbia was experimentally augmented with 19 northern caribou, a different ecotype inexperienced with cougars. We estimated resident caribou, translocated caribou, and cougar resource selection functions (RSFs) in five mountain caribou seasons to assess seasonal habitat selection and caribou risk to cougar predation. Model coefficients and RSF maps indicted that resident caribou selected low risk cougar habitat during the calving season at the home range scale and year-round at the landscape scale. Translocated caribou displayed risky behaviour year-round. They occupied mid to low elevations and traversed habitats highly selected by cougars. Translocated caribou exhibited typical elevational patterns of northern caribou by

selecting mid elevations in spring, calving, and summer and lower elevations in late and early winter seasons. Of the 19 translocated caribou, 17 (89%) died during the 30 month study period (six by cougar predation). Translocated caribou, being naïve to non-lethal cougar effects, did not exhibit the spatial separation strategy characteristic of resident caribou and thus were subject to greater cougar predation risk.

3.2 Introduction

Predation is a selective pressure influencing prey behaviour so prey become more difficult to capture, detect, or encounter (Lima and Dill 1990, Lima 1998). Predation has both lethal and non-lethal (behaviourally-mediated) effects on prey. Lethal effects result in mortality from a successful predation event, whereas non-lethal effects cause prey to change their behaviour to reduce predation risk (Lima 1998, Cresswell 2008, Cresswell and Quinn 2013). In recent years, it has been suggested that non-lethal effects may be just as, or more important, than lethal effects because of associated fitness consequences such as reduced foraging rates, lower reproductive rates, and slower growth rates (Schmitz et al. 1997, Cresswell 2008). To this end, non-lethal effects result in prey avoiding habitats where they are more likely to be predated.

Spatial variation in predation risk plays an important role in non-lethal effects (Cresswell and Quinn 2013) due to the limitations predation risk puts on foraging behaviour (Lima and Dill 1990). That is, prey will select habitats in which predation risk is low, even at the expense of reducing foraging opportunities (Lima and Dill 1990). Although the distribution and density of resources are useful predictors of an animals' habitat selection, animals modify their selection of habitats based on their perceived

distribution of predation risk (Lima and Dill 1990, Brown and Kotler 2004, Cresswell 2008).

The spatial variation of non-lethal risk effects has been conceptualised by the landscape of fear model (Laundré et al. 2001, Tolon et al. 2009), which is built on the premise that predation risk varies in a measureable manner over space and time.

Specifically, the landscape of fear topography is established by the level of predation risk prey will encounter in different types of habitats (Hernández and Laundré 2005).

Animals then alter their behaviour and time allocation patterns based on variable levels of fear they experience from predation risk (Laundré et al. 2010). For example, the presence of re-introduced wolves (*Canis lupus*) in Yellowstone National Park (YNP) changed the landscape of fear causing elk (*Cervus canadensis*) to shift their habitat use from high risk open sagebrush meadows to safer forested habitats (Hernández and Laundré 2005). The concept of a landscape of fear may also have a seasonal component where prey must adapt to seasonal variation in their landscape of fear to reduce predation risk. For instance, Festa-Bianchet (1988) found pregnant bighorn sheep (*Ovis canadensis*) isolate themselves from predators by lambing at high elevations in spring. Similarly, during winter, moose (*Alces alces*) (Kunkel and Pletscher 2000) and elk (*Cervus elaphus*) (Fortin et al. 2005) move to dense conifer forest which, in part, effects the search efficiency of wolves.

Predators are typically inefficient, allowing prey to adapt strategies to avoid capture (Vermeij 1982). These antipredator strategies have been grouped into two categories (predator avoidance mechanisms and antipredator mechanisms) based on whether they function before or after a predator detects its prey (Sih 1987, Brodie et al.

1991). Predator avoidance mechanisms enable prey to avoid an attack by spatially and/or temporally avoiding an encounter, while antipredator mechanisms increase the probability of survival once detected (Sih 1987, Brodie et al. 1991, Barshaw et al. 2003). When a prey species evolves either predator avoidance mechanisms or antipredator mechanisms, the selective pressure on the other is reduced (Brodie et al. 1991). So, a prey inapt to fight off a predator would be well adapted to avoid an encounter. One behavioural predator avoidance mechanism ungulates have evolved is selecting for safe habitats (a hiding strategy; Geist 1974, Ruckstuhl and Neuhaus 2000). For example, ungulate species in Africa, including wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and giraffe (*Giraffa camelopardalis*), avoid risky habitats associated with large predators, lion (*Panthera leo*) and leopard (*P. pardus*) (Thaker et al. 2011). By virtue of unsuccessful predator attacks, a prey can evolutionarily 'learn' from a predator's failure and adapt accordingly (Vermeij 2002). In the case of ungulates, they have adapted to select for areas where their predators are absent.

Mountain caribou (*Rangifer tarandus caribou*) are an arboreal lichen-feeding ecotype of woodland caribou that are imperilled throughout British Columbia (BC). Nine of 15 subpopulations have been reduced to fewer than 50 animals and their prospects for long-term persistence are slim (BC Ministry of Environment 2010). The decline of mountain caribou has been attributed to anthropogenic habitat change that creates fragmented habitats and large areas of early seral vegetation communities (Rettie and Messier 1998, Schaefer 2003, Wittmer et al. 2005a). These early seral communities have resulted in increases in ungulates such as white-tailed deer (*Odocoileus virginianus*), moose, and elk which support higher densities of predators, such as wolves and cougars

(*Puma concolor*) (Bergerud and Elliot 1986, Seip 1991, Latham et al. 2011, Apps et al. 2013). This increase in predator density renders caribou vulnerable to incidental predation (Wittmer et al. 2005b). Thus, the abundance of one prey species (e.g. moose) negatively affects the abundance of another (e.g. caribou) through a shared predator, a relationship referred to as apparent competition (Holt 1977). In such a system, the secondary prey (i.e. caribou) are vulnerable to extirpation if they fail to spatially separate themselves from predators and densely populated primary prey (Bergerud et al. 1984, James et al. 2004, Wittmer et al. 2007).

The Purcells-South (PS) mountain caribou subpopulation, numbered 15 in 2012, has been facing imminent extirpation since the mid-1990s (Hatter 2006). The main predators that have contributed to the PS caribou decline are wolves and cougars, although cougars are thought to be a particularly important predator in this subpopulation (Kinley and Apps 2000, 2001). In 2007, the Province of British Columbia adopted the Mountain Caribou Recovery Implementation Plan (BC Ministry of Environment 2013), which called for augmenting select mountain caribou herds with fewer than 50 animals. The PS herd was selected to be augmented with 20 caribou per year in 2012 and 2013 with the goal of growing the population to 100 animals by 2026. Since most mountain caribou herds are too small to be translocation donors, the Province experimentally translocated 19 northern caribou from the Level Kawdy (LK) herd to the PS mountain caribou herd in 2012. The working assumption was that translocated northern caribou would join resident caribou and thus benefit from the latter's habitat selection and predator avoidance strategies. The specific management objectives were to increase the population size of the PS herd, thus decreasing the probability of extirpation; decrease

potential negative effects of genetic, demographic, and environmental stochasticity; and increase population growth (Kinley 2010).

We examine the extent to which resident and translocated caribou respond to non-lethal effects of cougar predation risk in the PS Mountains by assessing seasonal habitat use by caribou and cougars, and identifying habitats of low cougar predation risk. First we estimate the cougar-influenced landscape of fear using resource selection functions (RSFs) in five biologically defined mountain caribou seasons (see Chapter Two). We then use RSFs to compare the seasonal selection of habitat and risk to cougar predation between resident and translocated caribou. Under the spatial separation hypothesis, we predict resident caribou will exploit the cougar influenced landscape of fear to reduce predation risk by selecting habitats with a low probability of cougar use. Furthermore, we predict translocated caribou, which have no experience with stalk and ambush predators such as cougars, will ultimately become more adept at selecting low cougar risk areas across the landscape by learning from resident caribou.

3.3 Study area

The study area (14,500 km²) was defined by movements of global positioning system (GPS) radio-collared caribou and cougars within the Purcell South Mountains in southeastern BC (49°04'N - 50°39'N and 115°18'W - 116°50'W; Figure 3.1). Terrain varies in elevation from 535 to 3,040 m asl, with most alpine ridges below 2,300 m asl (Kinley 2010). Precipitation typically increases from northeast to southwest, and from lower to higher elevations (Kinley et al. 2003). At the lowest elevations, climax forest consists of hybrid white spruce (*Picea glauca x engelmannii*) or western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). Forests at higher elevations consist

of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). At even higher elevations these forests become woodland and parkland areas with stands of whitebark pine (*Pinus albicaulis*), subalpine fir, and alpine larch (*Larix lyallii*). Alpine tundra vegetation occurs at the highest elevations (Kinley and Apps 2001, Kinley et al. 2003). Timber harvesting is prevalent throughout the study area, except in the Purcell Wilderness Conservancy Provincial Park. Core caribou habitat has been off-limits to further timber harvesting since 2009.

Other ungulates in the region include moose, white-tailed deer, mule deer (*Odocoileus hemionus*), mountain goat (*Oreamnos americanus*), and elk. Large and meso carnivores include wolves, coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), bobcats (*Lynx rufus*), lynx (*Lynx canadensis*), and cougars.

3.4 Methods

3.4.1 Data collection

Nineteen adult northern caribou (three male and 16 female) from the LK herd in northwestern BC (57°59'N - 59°53'N and 129°51'W - 132°24'W) were captured by net-gun, radio-collared, and translocated approximately 2,100 km in a cattle liner to the PS study area between February 29 and March 3, 2012 (Figure 3.1). Five adult resident caribou (one male and four female) and 12 cougars (four male and eight female) located in the PS study area were radio-collared between February 2011 and 2013. Resident caribou were captured via helicopter net-gunning. Cougars were tracked by hounds and once treed, immobilized with telazol. We deployed Advanced Telemetry System G2110E radio-collars (ATS, Isanti, MN) on caribou, and the same ATS system or

LOTEK TrackM 2D (Lotek Engineering, Newmarket, ON) Iridium GPS radio-collars on cougars. Both caribou and cougar positional fixes were taken four times daily, except from December 1 to March 15 and May 1 to August 1 when six daily fixes were taken.

Six hours of inactivity triggered a possible mortality signal, which was investigated as soon as possible. The cause of mortality was determined from evidence found at the site. When possible a necropsy was performed and samples of the carcass were taken, including: lung, heart, liver, spleen, kidney, stomach, intestine, muscle, head, rumen content, feces, long bone, skin, skull, and lower jaw. Predation was apparent when there was evidence of bleeding, a struggle, or bite injuries. A predation event was more obvious in winter when snow was on the ground, but less so during the summer. Carcasses of typical cougar kills were easily recognized because their hair was stripped and remains buried. Additionally, typical cougar kill sites had evidence of dragging and cashing the carcass, scratch marks, and cougar tracks. Deaths not attributed to predation were classified as accidents, malnutrition, or unknown causes.

3.4.2 Data preparation

Following Johnson's (1980) third-order habitat selection criteria at the temporal scale of seasons, we determined habitat selection by resident and translocated caribou using logistic regressions in resource selection functions (RSFs) (Johnson et al. 2006, Manly et al. 2010). Seasonal ranges were utilized because habitat selection and predation risk are known to change among seasons (DeCesare 2012, DeCesare et al. 2014). This is also the scale typically used in making wildlife management decisions (Walker et al. 2007).

We divided resident and translocated caribou GPS data into the five caribou seasons defined in Chapter Two (spring: May 5 - June 9; calving: June 10 - July 10; summer: July 11 - September 18; early winter: September 19 - December 16; and late winter: December 17 - May 4). Data for resident caribou were pooled across years to maximize the number of locations. Translocated caribou data were not pooled because: (1) 12 of 19 translocated caribou died within five months of translocation (Figure 3.2), (2) only three translocated caribou were available to pool across years, and (3) we sought to assess their change in selection patterns from release to death or end of the 30 month study period. Therefore two late winter models were developed for translocated caribou (end of late winter (December 17 to December 31) of 2012 and late winter of 2012/2013). A 95% fixed-kernel estimate (Seaman and Powell 1996) was calculated using least-squares cross-validation as a smoothing parameter to delineate each caribou's seasonal home range. Within each individual's seasonal home range, five random locations were generated for each used location to estimate the difference between used and available sites (Baasch et al. 2010).

3.4.3 Model selection and validation

To identify characteristics influencing caribou habitat selection we used RSFs of the exponential form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i),$$

where $w(x)$ is the RSF, x_i are the predictor variables, and β_i are the coefficients estimated using logistic regression software.

We developed a set of 12 *a priori* candidate models for caribou (Table 3.1). Each candidate model corresponds to a set of similar variables or combination of variables

(Burnham and Anderson 2002) that we hypothesized to be ecologically meaningful based on previous studies of caribou habitat selection (Apps et al. 2001, Gustine et al. 2006, Jones et al. 2007, Seip et al. 2007, Chapter Two). We excluded habitats that were not available within an individual caribou's seasonal home range and those available but used less than 2% of the time to avoid estimating perfect predictors (Burnham and Anderson 2002). Predictor variables were tested for collinearity using Pearson's correlation coefficient (r). Correlated variables with $|r| > 0.7$ were not used in the same model (Hosmer and Lemeshow 2002).

Because covariates within the models were on different scales, raw coefficient values (β_i) could not convey which variables were most important in a model based on their magnitude. Therefore, values were scaled to have a mean of zero and a standard deviation of one to interpret the relative influence of specific variables using:

$$x_i^* = \frac{x_i - \bar{x}}{sd}$$

where x_i^* is the standardized form of a given variable in the i^{th} location, x_i is the original value in the i^{th} location, \bar{x} is the mean of all x_i , and sd is the standard deviation of all x_i .

Standardized coefficients indicated the amount of change in a RSF that accompanied one standard deviation change in the raw covariate score, meaning a standardized coefficient's magnitude indicated its effect size (Knopff 2011).

For each caribou in each season we evaluated model selection using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002). We used AIC_c for selection instead of AIC to correct for small sample size because the ratio of caribou locations to the number of model parameters was less than 40 (Burnham and Anderson 2002). The model with the lowest AIC_c was considered the top model and best at approximating the

data within the set of candidate models. Differences in AIC_c values (ΔAIC_c) were calculated by subtracting the smallest AIC_c value from each of the candidate models' AIC_c . Any model with ΔAIC_c within two to four units of the top model was considered equally efficient at approximating the data (Burnham and Anderson 2002). If there was more than one top model, the most parsimonious model (i.e., fewest variables) was selected as the 'best' model (Burnham and Anderson 2002). Akaike weights were also calculated to provide evidence for the best model within the set of candidate models (Burnham and Anderson 2002). We evaluated the predictive ability of the best models for each caribou for each season using k -fold cross validation and Spearman's rank correlation (r_s) (Boyce et al. 2002). We then determined p -values for r_s following Siegel (1956).

3.4.4 Model averaging

We created a resident caribou population-level RSF model using the best model for each resident caribou within each season and averaging the β_i coefficients among caribou following the two-step modelling approach from Fieberg et al. (2010). In cases where a variable, x_j , was not in a particular model, β_j was set to zero which served to shrink the conditional parameter back towards zero; this shrinkage helped improve model selection bias of the mean parameter (Burnham and Anderson 2002). Population-level RSF models calculated this way are unaffected by potential autocorrelation because spatial and temporal autocorrelation concerning habitat units and concerning animal locations do not bias model coefficients for individual radio-collared caribou models (McCullagh and Nelder 1989, Sawyer et al. 2006). Sexes were pooled in the population

level model because the small number of males would have resulted in low statistical power for male population models.

Once released, translocated caribou moved widely throughout the landscape and encountered different available habitats which prevented us from applying the two-step model averaging approach. However, average β_i coefficients were calculated using the two-step modelling approach, but we excluded variables from the averaging process when they were not included in the candidate model set. Direct comparisons using these averages are unreliable (Fieberg et al. 2010), but rather used to garner a general understanding of habitat selection by translocated caribou. The two-step modelling approach requires that animals encounter the same habitat features to ensure reliable estimations of averaged coefficients and to avoid deriving information about a particular habitat type from a subset of the sample population. Therefore we examined individual translocated caribou models to obtain the most reliable results. We determined the autocorrelation structure of model residuals using partial autocorrelation functions (Nielsen et al. 2002). This autocorrelation was accounted for by estimating standard errors for each translocated caribou model using Newey-West Estimators (Newey and West 1987). Statistical analyses, model evaluation, and model validation was performed using R statistical software (R Core Team 2014)

3.4.5 Model inputs

Topography

A Terrain Resource Information Management (TRIM) digital elevation model (DEM) with a spatial resolution of 25 m was used to determine elevation (m), slope ($^{\circ}$),

and aspect (categorical) attributes. We included a squared term for continuous covariates (e.g., elevation + elevation²) when they were detected to be used nonlinearly (Walker et al. 2007). Graphical representations of selection functions for squared terms were constructed by holding all other variables in a model constant while multiplying the β_i of the squared terms by actual locations used by the animals within a designated season (Boyce et al. 2003). The RSFs were then rescaled between zero and one to show seasonal differences in the selection of the squared variable. Aspect was categorized into north (315-45°), east (45-135°), south (135-225°), and west (225-315°). However, preliminary data analysis indicated that caribou predominantly used north and south aspects, therefore only these categories were analysed. Road density (km/km²) was estimated using a weighted system, giving a weight of one for low volume logging roads and two for high volume paved roads (Chruszcz et al. 2003).

Vegetation

Vegetation classes were defined by biogeoclimatic (BEC) zones, as delineated by the BC Ministry of Forests, Lands and Natural Resource Operations (MFLNRO 2013). BEC zones were grouped according to vegetation structure in the PS study area (Table 3.2). Using RESULTS (Reporting Silviculture Updates and Land status Tracking System) silviculture data, we reclassified cut blocks into two age classes (0-5 years and 5-20 years old) given that after approximately five years sightability from both a cougar's and caribou's visual perspective becomes more difficult due to increased shrub and tree height. Vegetation classes were rasterized in ArcGIS 10.0 (ESRI, Redlands, CA) at a 25 m resolution grid.

Cougar Predation Risk

To quantify potential cougar predation risk we used logistic regression to develop RSFs (Johnson et al. 2006, Manly et al. 2010) that identified habitats selected by cougars. We assumed predation risk was directly related to habitat selection by cougars as defined by RSFs and this predation risk could be assessed by caribou.

A set of eight *a priori* candidate models for cougars were created (Table 3.3). To ensure temporal and spatial consistency with the scale of caribou RSFs, we defined cougar availability by resident caribou seasons within 95% KDEs (Seaman and Powell 1996). Because KDEs of the radio-collared cougars did not provide full coverage of the study area in any season, we pooled cougar RSFs within each season to extrapolate selection values for areas without data. Cougar population-level RSFs were developed similarly to resident caribou population-level RSFs using the two-step modelling approach from Fieberg et al. (2010). Variables used in the cougar RSFs included elevation (m), slope ($^{\circ}$), south aspects, road density (km/km²), and vegetation classes defined by BEC zones (Table 3.2). Southerly aspects were chosen because they are commonly used by ungulate prey species and therefore are more likely selected by cougars (Stewart et al. 2010, Elbroch et al. 2013). Both elevation and road density were included as squared terms because they were detected to be nonlinear.

We developed five seasonal cougar predation-risk landscapes by applying the coefficients (β_i) in each seasonal population-level cougar model to each pixel in the PS study area. We then created a mask for large bodies of water in the study area where cougars are unlikely to traverse and assigned those areas a value of zero (Gustine et al. 2006). RSF values were range standardized to scale predation risk surfaces from zero to

one. These scaled values were assumed to represent estimates of ‘actual’ predation risk to caribou.

The estimated probability of use for each grid cell was assigned a value of one to four based on the quartiles of predation risk distribution for each seasonal map. Grid cells in the 76 to 100 percentiles were classified as high risk, grid cells in the 51 to 75 percentiles were classified as medium-high risk, grid cells in the 26 to 50 percentiles were classified as medium-low risk, and grid cells in the 0 to 25 percentiles were classified as low risk (Sawyer et al. 2006). High, medium-high, and medium-low categories of risk were not available in all caribou KDEs and therefore it was not possible to estimate the associated coefficients across caribou. The low risk category was available within all caribou KDEs, consequently it was the variable used to assess cougar risk in the caribou RSF models.

3.5 Results

3.5.1 Evaluation of cougar predation risk model

All of the top RSF cougar models had high k -fold cross-validation scores, which indicated strong predictability for each season (all $r > 0.74$, $n=46$, p -value < 0.05 , Appendix A: Table A1). Cougars selected for cut blocks 5-20 years old and ICH zones in all seasons (Figure 3.3). Other ESSF zones were selected in calving, summer and early winter seasons and IDF zones were selected in summer, early winter and late winter seasons (Figure 3.3). ESSF Parkland and ESSF Woodland zones were not incorporated into the models because of their low proportion of availability. They selected south facing aspects in all seasons, except in late winter where no selection was apparent (Figure 3.3). Cougars selected moderate slopes in spring, calving, and late winter

seasons, and selected against steep slopes in summer (Figure 3.3). Cougars tended to select low to mid elevations (500 - 1,500 m) in all seasons (Figure 3.4). They selected highest elevations during calving and summer seasons ($1,290 \pm 326$ and $1,360 \pm 350$ m, respectively) and lowest elevations during late winter ($1,046 \pm 194$ m). Throughout all seasons, cougars selected against low and high road densities, selecting areas with moderate road densities (1.5 - 2.5 km/km²) (Figure 3.4).

3.5.2 Cougar risk - predicted probability of use

Predictive maps (Figure 3.5) of the relative probabilities of cougar habitat use show a high preference for ICH zones at low elevations in each season. Cougars strongly selected slopes ranging between $14.67 \pm 0.53^\circ$ in early winter and $20.38 \pm 11.90^\circ$ in late winter. Low risk areas were associated with high elevations (> 2,000 m) and steep slopes (between $25.69 \pm 13.88^\circ$ to $29.48 \pm 12.06^\circ$). Average road density in high risk areas ranged between 1.16 ± 1.37 km² in spring and 2.14 ± 0.79 km² in calving season. Low risk areas contained high road densities in early winter, calving, and summer seasons (3.68 ± 0.47 km², 3.78 ± 0.44 km², and 3.58 ± 0.45 km², respectively), while late winter and spring low risk areas had low road densities (0.43 ± 0.44 km² and 1.01 ± 0.51 km², respectively). Aspects with the highest probability of cougar use were south and east, and aspects with the lowest probability of use were north and west.

3.5.3 Seasonal selection by resident caribou

All top RSF models for resident caribou had k-fold cross-validation scores which indicated good predictability for caribou within each season (all $r > 0.818$, $n=25$, p-value <0.01, Appendix A: Table A2). The global model was selected as the top model for 17 of 25 top models (Appendix A: Table A2). Resident caribou selected low risk areas in

calving season but displayed no preference for low risk areas in spring, summer, and early winter (Figure 3.6). Resident caribou selected ESSF Woodland, ESSF Parkland, and Other ESSF zones in all seasons with the exception of ESSF Parkland zones in early winter when they did not select or avoid this habitat (Figure 3.6). Throughout all seasons, resident caribou avoided steep slopes (Figure 3.6). High road density areas were avoided in spring, calving, and summer seasons, and not selected for or against during early and late winter. They selected north facing aspects in calving and summer seasons (Figure 3.6). Throughout all seasons, resident caribou selected upper elevations, with relatively lower elevations selected in summer ($1,966 \pm 133$ m) and higher elevations in late winter ($2,138 \pm 104$ m) (Figure 3.7).

3.5.4 Seasonal selection by translocated caribou

All top RSF models for translocated caribou had k-fold cross-validation scores that indicated good predictability for caribou within each season (all $r > 0.74$, $n=54$, p -value < 0.05 , Appendix A: Table A3). Following release, translocated caribou travelled broadly throughout the landscape in a wide range of habitat types (Figure 3.5), rendering resource selection generalization problematic. There was considerable variation in habitat selection patterns among individual translocated caribou. Averaged models indicated that selection and avoidance for low risk habitats was variable among seasons. Translocated caribou had the greatest preference for low risk cougar areas in the first late winter season and the greatest avoidance of low risk areas during spring. In general, no selection was apparent for ICH zones or cut blocks (Figure 3.8 and Appendix B). ESSF Woodland zones were selected in the first late winter and calving seasons, avoided in summer, and were not selected or avoided in spring and early winter (Figure 3.8 and

Appendix B). ESSF Parkland zones were avoided by one individual in the first late winter season, three individuals in calving season, and two individuals in summer season (Appendix B). One translocated caribou selected ESSF Parkland zones in early winter. In general, Other ESSF zones were selected by most individuals throughout all seasons (Figure 3.8 and Appendix B). IDF zones were only available in the seasonal home ranges of five translocated caribou: three in the first late winter, one in early winter, and one in summer (Appendix B). IDF zones were positively selected, except in the early winter season (Appendix B: Table B5).

Topographic variables were more consistent than BEC zones in explaining translocated caribou habitat selection. Steep slopes were avoided by all translocated caribou in all seasons except for three individuals in the first late winter season, three in spring, and one in calving season (Figure 3.9 and Appendix B). There were inconsistencies in the selection of roads, where 16 models showed positive selection, 17 models showed avoidance, and 21 models showed no preference across all seasons (Appendix B). North aspects were avoided or not selected in 47 of 54 models (Figure 3.9 and Appendix B). Selection for south aspects was variable among translocated caribou throughout all seasons (Figure 3.9 and Appendix B).

Translocated caribou tended to select upper elevations in the spring, calving, and summer seasons, while selecting lower elevations in both late winter and early winter seasons (Figure 3.10 and Appendix B). Lowest elevations were selected in late winter during 2012 and 2013 ($1,031 \pm 332$ m) and highest elevations were selected in calving season ($1,897 \pm 316$ m).

3.6 Discussion

Translocated animals are exposed to unfamiliar habitats associated with potentially novel risks, one being the risk of predation. However, even though translocations have been documented in association with predation risk, few have explored predation risk of translocated animals with a novel predator (but see Frair et al. 2007). Understanding this is particularly important for caribou because evidence suggests they are now a conservation reliant species (Schaefer 2003, DeCesare et al. 2011) and translocations are likely to be used more in the future as a management tool to mitigate declines in small caribou populations. When translocating northern caribou to a mountain caribou herd with cougars as a novel predator, we found evidence that mountain caribou and northern caribou respond differently to the landscape of fear shaped by cougars. Resident mountain caribou remained at low risk, high elevations throughout the year, while translocated northern caribou traversed the landscape through high risk areas. Our study highlights that translocated caribou may be inadvertently exposed to high predation risk due to their lack of knowledge of the landscape of fear shaped by a novel predator.

Resident caribou selected low risk areas during calving season, the most vulnerable time for female caribou and their offspring (Bergerud and Page 1987, Rettie and Messier 1998). During calving, female mountain caribou space-out by moving to higher elevations and show site fidelity for calving areas where they previously avoided predators (Bergerud and Page 1987). During the remaining seasons, resident caribou showed no preference for low cougar risk areas at Johnson's (1980) third-order habitat selection, i.e. within their home range. However, since only low and medium-low risk

areas were available in the resident caribou home ranges during each season, it is likely that resident caribou were avoiding medium-high and high risk areas at a scale larger than within their home range. This pattern of selection suggests resident caribou are selecting low risk areas at Johnson's (1980) second-order habitat selection, i.e. the location of their home range on the landscape. Logistic regression is unable to estimate explanatory variables with missing data which limits the scope of inference regarding the selection of habitat attributes excluded from modeling (Menard 2002), which in this study was avoidance of high risk areas by resident caribou. Nonetheless, because only low and medium-low risk areas at high elevations were available within resident caribou home ranges we believe resident caribou avoided lower elevation habitats associated with high cougar predation risk and a high abundance of alternative prey (e.g. deer and elk). This is in agreement with the spatial separation hypothesis found in other populations of caribou, other ungulates, and wolves (Bergerud et al. 1984, Seip 1992, Latham et al. 2011).

Translocated caribou displayed risky behaviour in all seasons by travelling between mid and low elevations, and traversing habitats highly selected by cougars (i.e. ICH zones). Low cougar risk areas were selected during late winter, post-release; however, this could be an artefact of releasing translocated caribou in low risk habitats. During the remaining seasons low risk habitats were not selected and, in fact were avoided in spring.

Translocated caribou utilized elevation in a similar way to the northern caribou donor herd (Leech and Jelinski unpublished data). Translocated caribou used lower elevations during the early winter and late winter, and higher elevations in the spring, calving, and summer seasons. By comparison, northern caribou occupy valley bottoms

during the winter months and move to higher elevations during calving periods (Bergerud et al. 1984, Bergerud and Page 1987). This pattern is different from mountain caribou, which move down to mid elevations in summer to benefit from increased forage quality and quantity, and to high elevations during winter when the snowpack consolidates and deepens providing access to arboreal lichen, their main food source (Stevenson et al. 2001). The selection of high altitudes by mountain caribou enables the PS resident caribou herd to spatially separate from predators. Since translocated caribou failed to join resident caribou they were unable to learn the resident caribou's patterns of habitat use, especially remaining at elevations above 1400 m year-round and therefore were subject to greater predation risk and mortality rates.

Variability in translocated caribou habitat selection patterns demonstrates they lack knowledge of the spatial distribution of resources in the PS landscape. This may have resulted in possible exploratory movements and high predation rates, as movement attracts the attention of predators (Yoder et al. 2004). The natal habitat preference induction concept of Stamps and Swaisgood (2007) proposes translocated animals often reject release site habitats and rapidly travel long distances in search of stimuli comparable to their natal habitat, such as certain landscape features, sights, sounds, or odors. Warren et al. (1996) found when both northern and mountain caribou were translocated into mountain caribou habitat their patterns of habitat use, movement, and dispersal appeared to be related to traditional habitat use and movement patterns learned prior to relocation. Additionally, Scillitani et al. (2012) found translocated Alpine ibexes (*Capra ibex ibex*) exhibited wandering movements for one to two years post-release until they gained enough experience with their new landscape to settle into spatial patterns

similar to residents. Movement patterns and habitat selection differences among translocated individuals generally suggests an inability to acclimate to unfamiliar habitats resulting in increased movements (Stamps and Swaisgood 2007).

Caribou are naturally gregarious animals and thus frequently benefit from a lower individual encounter rate with predators due to the dilution effect (Fryxell et al. 2007). However, translocated caribou did not aggregate with resident caribou despite the attempt to release them near the resident herd. Moreover, individual translocated caribou travelled in small groups of two or three for up to four months before separating and travelling as individuals, which precluded them from the benefit of predation risk dilution. Furthermore, gregarious species develop appropriate responses to predators through social learning (Griffin 2004). However, the effects of social learning about one type of predator do not usually generalize to other types of predators (Griffin 2004). An animal raised and living in a habitat with one type of predator might be at a disadvantage if moved to a habitat containing a different type of predator (Stamps and Swaisgood 2007). So, prey with little to no experience with a predator and that do not have the opportunity to learn from others will likely fail to display appropriate avoidance behaviours resulting in elevated predation risk (Berger et al. 2001, Atwood et al. 2007). In this case, translocated caribou were unfamiliar with cougars and unable to learn appropriate cougar avoidance strategies from experienced resident caribou since they did not band together.

Predation is an important cause of evolutionary change (Dawkins and Krebs 1979), however on shorter timescales an individual animal may not be able to learn or adapt antipredator strategies for a novel predator. Natural selection in favor of

antipredatory traits can only occur when some members of a prey population survive to reproduce after encountering a predator (Vermeij 1982). If a predator is 100% efficient at killing their prey then there will be no opportunity for prey to learn or adapt to the predator. However, predator efficiency (% success per kill attempts) for a variety of predators is approximately 8-26% (Nellis and Keith 1968, Mech 1966, Temple 1987, Longland and Price 1991, Mech et al. 2001) allowing prey to evolve defensive adaptations (Vermeij 1982). Yet, increased predation is a widely cited cause of mortality of translocated individuals (Matson et al. 2004, McKinstry and Anderson 2003, Moorhouse et al. 2009, Moreno et al. 2004, Rosatte et al. 2002, Rouco et al. 2008, Van Zant and Wooten 2003, Watland et al., 2007). Thus, it is possible cougars were highly efficient when encountering translocated caribou, preventing any type of learned antipredator strategy.

At the conclusion of this study, eight of 17 translocated caribou mortalities were attributable to predation – six by cougars and two by wolves (Figure 3.2). LK northern caribou are familiar with wolves, but when translocated to the PS Mountains they encountered cougars, a novel predator. The hunting strategies of wolves and cougars differ and therefore these predators differ in the extent to which they contribute to and shape the overall landscape of fear (Cresswell and Quinn 2013). Predation risk from cougars, an efficient stalk and ambush predator, is expected to be higher in structurally complex habitats (Murphy 1998, Kunkel et al. 1999, Husseman et al. 2003), while predation risk from wolves, a coursing predator, is expected to be higher in open areas where wolves can effectively test prey for their vulnerability (Mech 1970). Therefore, the non-lethal effect of shifting habitats to avoid one predator may lead to increased exposure

to another predator (Sih et al. 1998). Atwood et al. (2009) found elk avoided direct predation from wolves by moving to dense cover, but this increased the risk of direct predation from cougars. Likewise, translocated caribou may have increased their predation risk from cougars by avoiding wolves, a familiar predator, and occupying cougar preferred habitats.

At the time of translocation, cougar harvest data (Forests, Lands and Natural Resource Operations (FLNRO) unpublished) indicates cougar abundance was high in the Kootenay Region. So, it is possible that high predation rates on translocated caribou were also related to cougar density. Similarly, Kinley and Apps (2001) found the PS caribou herd declined from 78 to 18 between 1995 and 2000, which corresponds to a peak in cougar population. The correlation between cougar abundance and caribou declines has not been explicitly studied, but evidence suggests cougars are a limiting factor to caribou in the PS Mountains (Kinley and Apps 2000, 2001). It is possible the inexperience of translocated caribou with cougars led to their selection of risky habitats, corresponding to a higher rate of mortality than experienced by resident caribou (32% versus 0%).

3.7 Conclusions

Understanding the link between predation risk, habitat selection, and survival of translocated animals will increase the chances of translocation success. The probability of survival post release, settling in the released area, and ultimately breeding (Letty et al. 2007) is dependent upon the ability of the translocated individuals to adequately construct a landscape of fear and select safer habitats. In this study, almost half (i.e. 47%) of 17 confirmed translocated caribou deaths were due to predation (six by cougars and two by

wolves). Improving the probability of translocated caribou's survival may depend upon using a suitable source population that is experienced with similar landscapes, the release site's mortality risks, and non-lethal effects from local predators (Bright and Morris 1994, Letty et al. 2007, Frair et al. 2007). In this case, translocated caribou were native to a northern landscape with different topography and a different suite of predators, which we found reduced their chances of survival. But by identifying and removing limiting factors at the release site such as high predator densities, disease, and habitat degradation, translocated individuals will have a better chance at surviving in a foreign environment (Pérez et al. 2012).

Also, ensuring translocated caribou have the best opportunity to learn from resident caribou will aid in survival of translocated caribou. To encourage herd amalgamation a soft release is recommended. Soft releases are associated with lower mortality rates and individuals that stay closer to their release point (Jefferies et al. 1986, Bright and Morris 1994). Additionally, a soft release can be used to decrease the novelty of the release site by penning animals in a large corral with some resident caribou prior to release. This conditioning period would allow translocated caribou to recover from the stress of the move and ideally develop social bonds with resident caribou.

Until limiting factors are addressed future translocations should not be attempted. We recommend that prior to translocation there is a thorough understanding of predator habitat use and predator density at the release site to determine if predator removal is necessary. Additionally, ensuring the behaviour and habitat use of donor and resident animals are similar prior to translocation will likely increase translocated animals' persistence. This research will aid in informed decision-making on whether the donor

population is appropriate, where and when to translocate animals, as well as potential mitigation strategies to increase translocation success.

References

- Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *Journal of Wildlife Management* 65:65–77.
- Apps, C. D., B. N. McLellan, T. A. Kinley, R. Serrouya, D. R. Seip, and H. U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *Journal of Wildlife Management* 77:1409–1419.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2007. Comparative Patterns of Predation by Cougars and Recolonizing Wolves in Montana's Madison Range. *Journal of Wildlife Management* 71:1098–1106.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. *Journal of Wildlife Management* 73:876–884.
- Baasch, D. M., J. W. Fischer, S. E. Hygnstrom, K. C. VerCauteren, A. J. Tyre, J. J. Millsbaugh, J. W. Merchant, and J. D. Volesky. 2010. Resource selection by elk in an agro-forested landscape of northwestern Nebraska. *Environmental Management* 46:725–37.
- Barshaw, D.E., K.L. Lavalli, and E. Spanier. 2003. Offense versus defense: responses of three morphological types of lobsters to predation. *Marine Ecology Progress Series* 256:171-182.
- BC Ministry of Environment. 2010. Caribou Distribution in British Columbia by Ecotype. http://www.env.gov.bc.ca/wld/speciesconservation/caribou_by_ecotype.html#_.
- BC Ministry of Environment. 2013. Mountain Caribou Recovery. <http://www.env.gov.bc.ca/wld/speciesconservation/mc/index.html>.
- Berger, J., J. E. Swenson, and I. Persson. 2001. Recolonizing Carnivores and Naive Prey: Conservation Lessons from Pleistocene Extinctions. *Science* 291:1036–1039.
- Bergerud, A.T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515–1529.
- Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566–1575.
- Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology* 65:1597–1606.

- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. M. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421–431.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Bright, P. W., and P. A. Morris. 1994. Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. *Journal of Applied Ecology* 31:699–708.
- Brodie E.D., Jr., D.R. Formanowicz, Jr., and E.D. Brodie III. 1991. Predator avoidance and antipredator mechanisms: distinct pathways to survival. *Ethology Ecology & Evolution* 3:73–77.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- Burnham, K., and D. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edi. Springer, New York, New York, USA.
- Chruszcz, B., A. P. Clevenger, K. E. Gunson, and M. L. Gibeau. 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81:1378–1391.
- Cresswell, W. 2008. Non-lethal effects of predation in birds. *Ibis* 150:3–17.
- Cresswell, W., and J. L. Quinn. 2013. Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behavioral Ecology* 24:871–876.
- Dawkins, R., and J.R. Krebs. 1979. Arms races between and within species. *Proceedings of the Royal Society of London B* 205:489-511.
- DeCesare, N. J. 2012. Separating spatial search and efficiency rates as components of predation risk. *Proceedings. Biological Sciences / The Royal Society* 279:4626–33.
- DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. 2014. Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology* 83:343–352.
- DeCesare, N. J., J. Whittington, M. Hebblewhite, H. Robinson, M. Bradley, L. Neufeld, and M. Musiani. 2011. The role of translocation in recovery of woodland caribou populations. *Conservation Biology* 25:365–73.

- Elbroch, L. M., P. E. Lendrum, J. Newby, H. Quigley, and D. Craighead. 2013. Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLOS ONE* 8:e83375.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580–586.
- Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 365:2233–44.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management* 71:541–554.
- Fryxell, J. M., A. Mosser, A. R. E. Sinclair, and C. Packer. 2007. Group formation stabilizes predator-prey dynamics. *Nature* 449:1041–1043.
- Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. *American Zoology* 14:205–220.
- Griffin, A. S. 2004. Social learning about predators: a review and prospectus. *Learning & Behavior* 32:131–140.
- Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* 165:1–32.
- Hatter, I. 2006. Mountain Caribou 2006 Survey Results, Subpopulation Trends and Extinction Risks. Proceedings, Multidisciplinary Approaches to Recovering Mountain Caribou in Mountain Ecosystems, May 29–31, 2006, Revelstoke, BC, May 29–31, 2006, Columbia Mountains Institute of Applied Ecology. Pp. 22.
- Hernández, L., and J. W. Laundré. 2005. Foraging in the “landscape of fear” and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* 11:215–220.
- Holt, R. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.

- Hosmer, D. W., and S. Lemeshow. 2002. Applied logistic regression, second edition. Wiley & Sons, New York.
- Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101:591–601.
- James, A., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- Jefferies, D. J., P. Wavre, and R. M. Jessop. 1986. Reinforcing the native otter *Lutra lutra* population in East Anglia: an analysis of the behaviour and range development of the first release group. *Mammal Review* 16:81–88.
- Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61:65–71.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347–357.
- Jones, E. S., M. P. Gillingham, D. R. Seip, and D. C. Heard. 2007. Comparison of seasonal habitat selection between threatened woodland caribou ecotypes in central British Columbia. *Rangifer* 27:111–128.
- Kinley, T. A. 2010. Augmentation plan for the Purcells-South mountain caribou population. BC Ministry of Environment (Ecosystems Branch), Prepared for BC Ministry of Environment (Ecosystems Branch), Victoria, BC.
- Kinley, T. A., and C. D. Apps. 2000. Population Status and Mortality of Mountain Caribou in the Southern Purcell Mountains, British Columbia. Pages 655–661 in L. M. Darling, editor. Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, British Columbia, 15-19 Fe. 1999. Volume 2. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College .
- Kinley, T., and C. Apps. 2001. Mortality Patterns in a Subpopulation of Endangered Mountain Caribou. *Wildlife Society Bulletin* 29:158–164.
- Kinley, T. A., J. Bergenske, J. A. Davies, and D. Quinn. 2003. Characteristics of early-winter caribou, *Rangifer tarandus caribou*, feeding sites in the southern Purcell Mountains, British Columbia. *Canadian Field Naturalist* 117:352–359.

- Knopff, A. A. 2011. Conserving Cougars in a Rural Landscape: Habitat Requirements and Local Tolerance in West-Central Alberta. M.Sc. thesis, University of Alberta, Edmonton, Alberta.
- Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78:150–157.
- Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management* 63:901–9010.
- Latham, A., M. Latham, N. Mccutchen, and S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *Journal of Wildlife Management* 75:204–212.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2010. The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal* 3:1–7.
- Letty, J., S. Marchandea, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. *Ecoscience* 14:420–431.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Longland, W.S., and M.V. Price. 1991. Direct observations of owls and heteromyid rodents, can predation risk explain microhabitat use? *Ecology* 72:2261–2273.
- Manly, B., L. McDonald, D. Thomas, T. McDonlad, and W. Erickson. 2010. *Resource Selection by Animals*. Second Edi. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Matson, T.K., A.W. Goldizen, and P.J. Jarman. 2004. Factors affecting the success of translocations of the black-faced impala in Namibia. *Biological Conservation* 116:359–365.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Second Edition. (U. Chapman and Hall, Boca Raton, Florida, Ed.).

- McKinstry, M.C., and S.H. Anderson. 2003. Survival, fates, and success of transplanted beavers (*Castor canadensis*) in Wyoming. *Journal of Wildlife Rehabilitation* 26:17–23.
- Mech, L.D. 1966. The wolves of Isle Royale. *Fauna of the National Parks of the United States* Fauna series 7.
- Mech, L.D. 1970. The wolf: ecology and behavior of an endangered species. Natural History Press, Doubleday, N.Y.
- Mech, L.D., D.W. Smith, K.M. Murphy, and D.R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* 65:998-1003.
- Menard, S. 2002. *Applied Logistic Regression Analysis*. Sage Publications, Inc., Thousand Oaks, California, USA.
- Ministry of Forest Lands and Natural Resource Operations (MFLNRO). 2013. Biogeoclimatic Ecosystem Classification Program. <http://www.for.gov.bc.ca/hre/becweb/>.
- Moorhouse, T.P., M. Gelling, and D.W. Macdonald. 2009. Effects of habitat quality upon reintroduction success in water voles: evidence from a replicated experiment. *Biological Conservation* 142:53–60.
- Moreno, S., R. Villafuerte, S. Cabezas, and L. Lombardi. 2004. Wild rabbit restocking for predator conservation in Spain. *Biological Conservation* 118:183–193.
- Murphy, K. M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone Ecosystem: interactions with prey, bears, and humans. University of Idaho, Moscow, USA.
- Newey, W. K., and K. D. West. 1987. A simple, positive semi-definite, heteroskedasticity and autocorrelation consistent covariance matrix. *Econometrica* 55:703–708.
- Nielsen, S. E., M. S. Boyce, B. Stenhouse, Gordon, and R. Munro. 2002. Modeling Grizzly Bear Habitats in the Yellowhead Ecosystem of Alberta: Taking Autocorrelation Seriously. *Ursus* 13:45–56.
- Nellis, C.H., and L.B. Keith. 1968. Hunting activities and success of lynxes in Alberta. *Journal of Wildlife Management* 32:718-722.
- Pérez, I., J. D. Anadón, M. Díaz, G. G. Nicola, J. L. Tella, and A. Giménez. 2012. What is wrong with current translocations? A review and a decision-making proposal. *Frontiers in Ecology and the Environment* 10:494–501.

- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rettie, W., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology* 76:251–259.
- Rosatte, R., J. Hamr, B. Ranta, J. Young, and N. Cool. 2002. Elk restoration in Ontario, Canada: infectious disease management strategy, 1998–2001. In: *Annals of the New York Academy of Sciences*. pp. 358–363.
- Rouco, C., P. Ferreras, F. Castro, and R. Villafuerte. 2008. The effect of exclusion of terrestrial predators on short-term survival of translocated European wild rabbits. *Wildlife Research* 35:625–632.
- Ruckstuhl, K. and P. Neuhaus. 2000. Sexual segregation in ungulates: A new approach. *Behaviour* 137: 361-377.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- Schaefer, J. 2003. Long-Term Range Recession and the Persistence of Caribou in the Taiga. *Conservation Biology* 17:1435–1439.
- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Scillitani, L., E. Sturaro, A. Menzano, L. Rossi, C. Viale, and M. Ramanzin. 2012. Post-release spatial and social behaviour of translocated male Alpine ibexes (*Capra ibex ibex*) in the eastern Italian Alps. *European Journal of Wildlife Research* 58:461–472.
- Seaman, D. E., and R. A. Powell. 1996. An Evaluation of the Accuracy of Kernel Density Estimators for Home Range Analysis. *Ecology* 77:2075–2085.
- Seip, D. R. 1991. Predation and caribou populations. *Rangifer* 7:46–52.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494–1503.
- Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. *Journal of Wildlife Management* 71:1539–1544.

- Siegel, S. 1956. *Non-Parametric Statistics*. McGraw-Hill, New York, New York.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 in W.C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, NH.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution* 13:350–355.
- Stamps, J., and R. Swaisgood. 2007. Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392–409.
- Stevenson, S. K., H.M. Armleder, M.J. Jull, D.G. King, B.N. McLellan, D.S. Coxson. 2001. *Mountain Caribou in Managed Forests: Recommendations for Managers*. Second Edition. 58pp.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, and M. A. Hurley. 2010. Spatial Distributions of Mule Deer and North American Elk: Resource Partitioning in a Sage-Steppe Environment. *American Midland Naturalist* 163:400–412.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology* 68:669-674.
- Thaker, M., A.T. Vanak, C.R. Owen, M.B. Ogden, S.M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92:398-407.
- Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology* 87:1129–1137.
- Van Zant, J.L., and M.C. Wooten. 2003. Translocation of choctawhatchee beach mice (*Peromyscus polionotus allophrys*): hard lessons learned. *Biological Conservation* 112:405–413.
- Vermeij, G.J. 1982. Unsuccessful Predation and Evolution. *American Naturalist* 120:701-720.
- Vermeij, G.J. 2002. Evolution and the consumer age: predators and the history of life. *Paleontol. Soc. Pap.* 8:375-393.
- Walker, A. B. D., K. L. Parker, M. P. Gillingham, D. D. Gustine, and R. J. Lay. 2007. Habitat selection by female Stone's sheep in relation to vegetation, topography, and risk of predation. *Ecoscience* 14:55–70.

- Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. *Conservation Biology* 10:547–553.
- Watland, A.M., E.M. Schauber, and A. Woolf. 2007. Translocation of swamp rabbits in southern Illinois. *Southeastern Naturalist* 6:259–270.
- Wittmer, H., B. McLellan, D. Seip, and J. Young. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wittmer, H., A. Sinclair, B. McLellan, and R. Sinclair. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Wittmer, H., B. McLellan, R. Serrouya, and C. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* 76:568–79.
- Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* 15:469–476.

Table 3.1 *A priori* candidate models used to explain resident and translocated caribou habitat selection in the Purcell South Mountains, southeastern British Columbia.

Model No.	Covariates ^a
1	L + E + E ² + V + SL + SO + NO + R
2	L
3	L + E + E ²
4	L + V
5	L + E + E ² + V
6	L + E + E ² + V + SL
7	L + V + SL + SO + NO
8	L + V + SL + SO + NO + R
9	L + E + E ² + V + R
10	L + E + E ² + V + SL + R
11	L + E + E ² + V + SL + NO + R
12	L + E + E ² + V + SL + SO + R

^a L = low cougar risk, V = vegetation type, E = elevation, SL = slope, SO = south, NO = north, R = road density

Table 3.2 Description of vegetation types in the Purcell South Mountains ecosystem, southeastern British Columbia.

Vegetation Type	Description
ESSF Parkland Zones	<p>Subalpine parkland at upper elevations. Clumps of trees occur together in areas of heath, meadow, and grasslands. Includes krummholz.</p> <p>Typical species include Sitka valerian (<i>Valeriana sitchensis</i>), Indian hellebore (<i>Veratrum viride</i>), arrow leaved groundsel (<i>Senecio triangularis</i>), western meadowrue (<i>Thalictrum occidentale</i>), bracted lousewort (<i>Pedicularis bracteosa</i>), common red paintbrush (<i>Castilleja miniata</i>), and various heather species (<i>Cassiope sp.</i> and <i>Phyllodoce sp.</i>)</p> <p>Elevation range: 1850 to 3500</p>
ESSF Woodland Zones	<p>Open and continuous, upper elevation forest dominated by Engelmann spruce (<i>Picea englemannii</i>) and subalpine fir (<i>Abies lasiocarpa</i>)</p> <p>Elevation range: 1650 to 2650m</p>
Other ESSF Zones	<p>Engelmann spruce and subalpine fir dominate wetter areas, with lodgepole pine (<i>Pinus contorta</i>) as a pioneer after disturbance and mountain hemlock (<i>Tsuga mertensiana</i>) in higher snowfall areas. Whitebark pine (<i>Pinus albicaulis</i>) and limber pine (<i>P. flexilis</i>) occur on drier sites. White rhododendron (<i>Rhododendron albiflorum</i>) and false azalea (<i>Menziesia ferruginea</i>) are common understory plants.</p> <p>Elevation range: 720 to 2600</p>
ICH Zones	<p>Upland coniferous forests with high diversity of tree species. Western red cedar (<i>Thuja plicata</i>) and western hemlock (<i>Tsuga heterophylla</i>) dominate mature climax forests. Grand fir (<i>Abies grandis</i>) is common. Steeply sloping, mountainous terrain.</p> <p>Elevation range: 300 to 1980</p>
IDF Zones	<p>Open to closed, mature forests containing Douglas-fir (<i>Pseudotsuga menziesii</i>) and lodgepole pine. Ponderosa pine (<i>Pinus ponderosa</i>) occurs at lower elevations.</p> <p>Elevation range: 440 to 1500</p>
0-5 year cut blocks	<p>High proportion of woody shrubs and herbaceous species (Pypker and Fredeen 2003).</p> <p>Elevation range: 440 to 2200 m</p>
5-20 year cut blocks	<p>Woody shrubs with many conifer seedlings (Pypker and Fredeen 2003).</p> <p>Elevation range: 436 to 2400 m</p>

Table 3.3 *A priori* candidate models used to explain cougar habitat selection in the Purcell South Mountains, southeastern British Columbia.

Model No.	Covariates ^a
1	$V + E + E^2 + SL + SO + R + R^2$
2	$V + E + E^2 + SL$
3	$V + E + E^2 + SL + SO$
4	$V + E + E^2 + R + R^2$
5	$V + E + E^2 + SL + R + R^2$
6	$V + E + E^2 + SO + R + R^2$
7	$V + E + E^2 + SO$
8	$V + E + E^2$

^a V = vegetation type, E = elevation, SL = slope, SO = south, R = road density



Figure 3.1 Location of translocated caribou donor herd and Purcell South study area located in British Columbia, Canada.

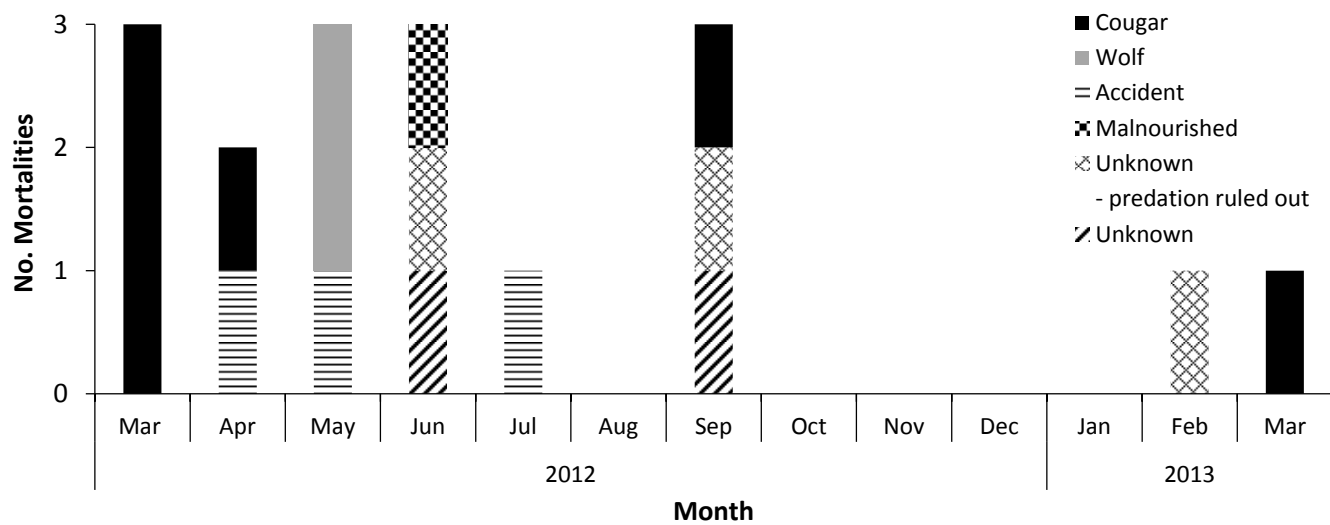


Figure 3.2 Number and cause of mortalities for translocated caribou post-release in the Purcell South Mountains, southeastern British Columbia.

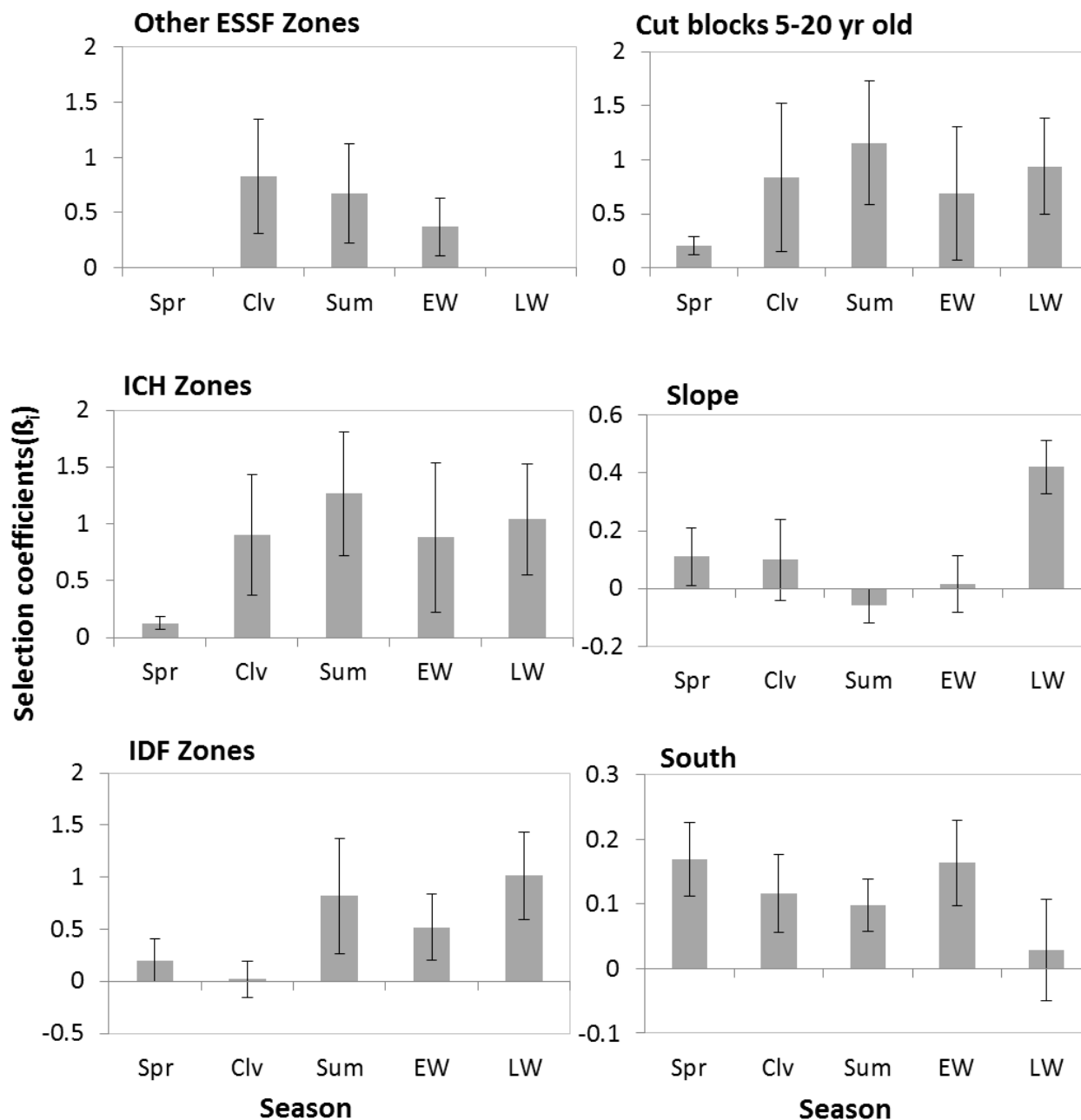


Figure 3.3 Vegetation and topographic attributes from seasonal global resource selection models for cougars in the Purcell South Mountains, southeastern BC. Selection coefficients ($\beta \pm SE$) for Other ESSF Zones, ICH Zones, IDF Zones, cut blocks 5-20 years old, slope, and south aspects. Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, as defined in text. Habitat attributes which could not be incorporated into the model are not shown.

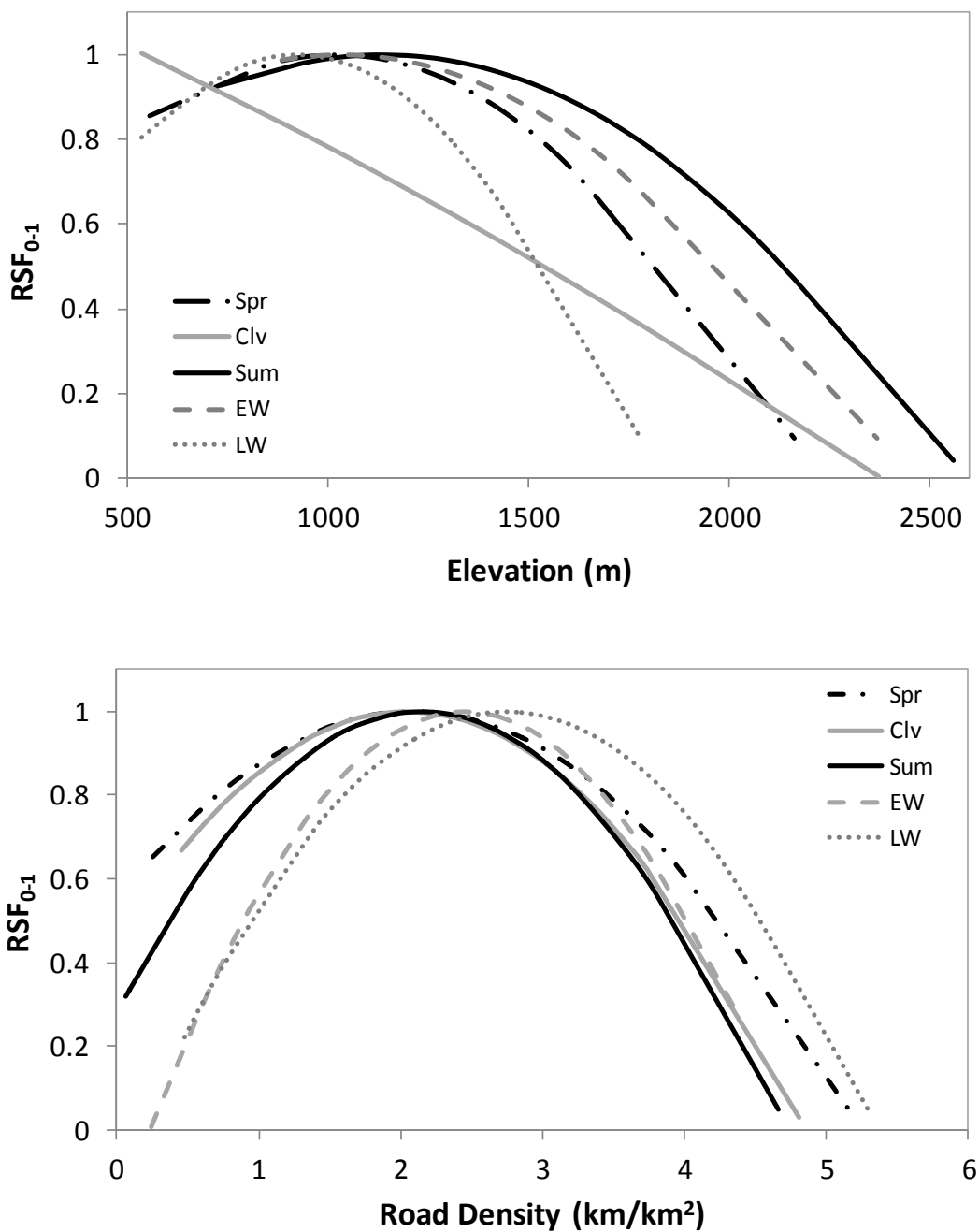


Figure 3.4 Relative selection by cougar for elevation (top) and road density (bottom) assuming other habitat variables are constant in the global resource selection models, by season in the Purcell South Mountains, southeastern British Columbia. Resource selection functions were scaled 0-1 (RSF_{0-1}). Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, as defined in text.

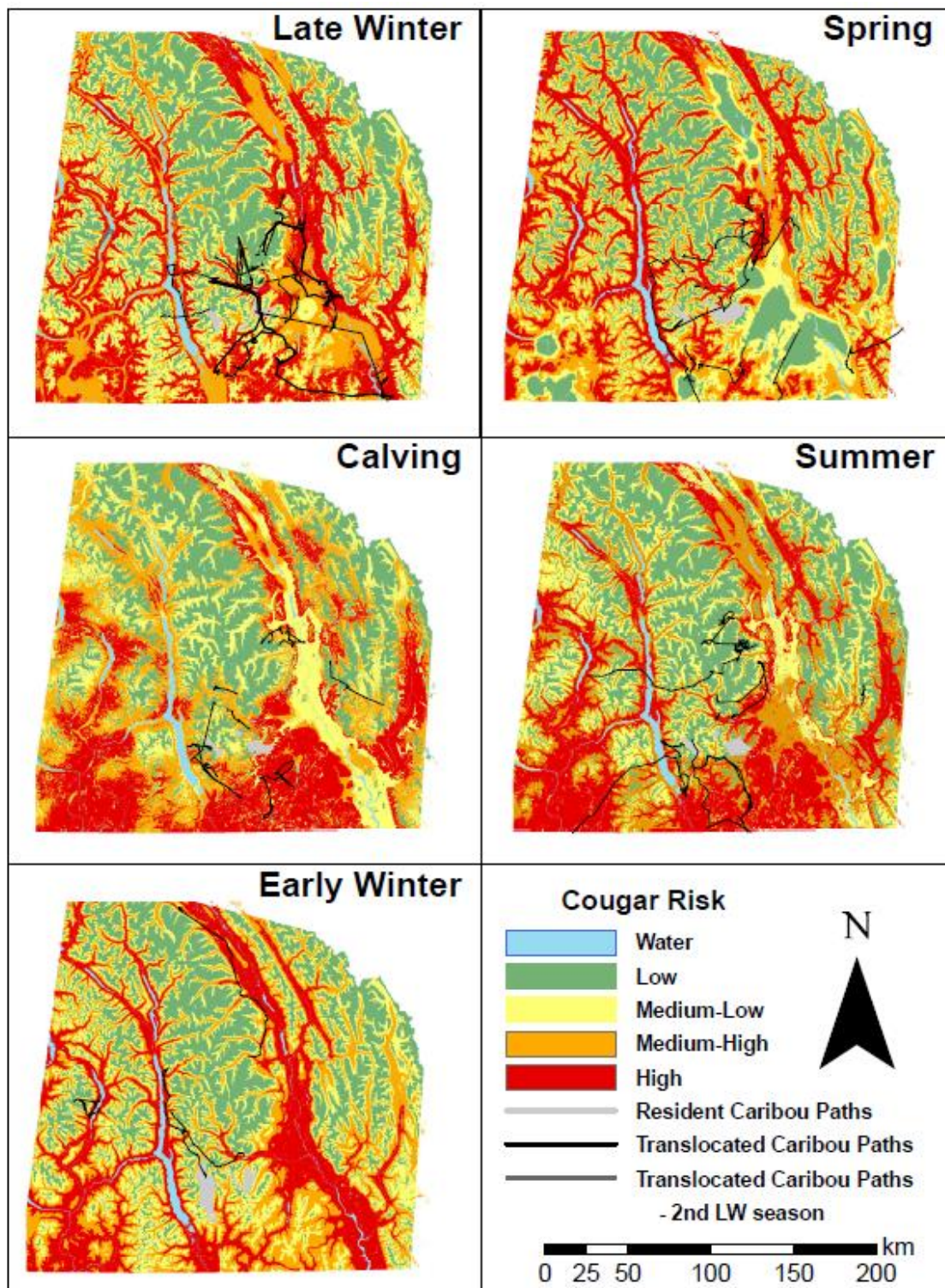


Figure 3.5 Predicted probability of cougar occurrence in terms of low, medium-low, medium-high and high predation risk; and travel paths of translocated (black lines) and resident (grey lines) caribou in the Purcell South Mountains, southeastern British Columbia.

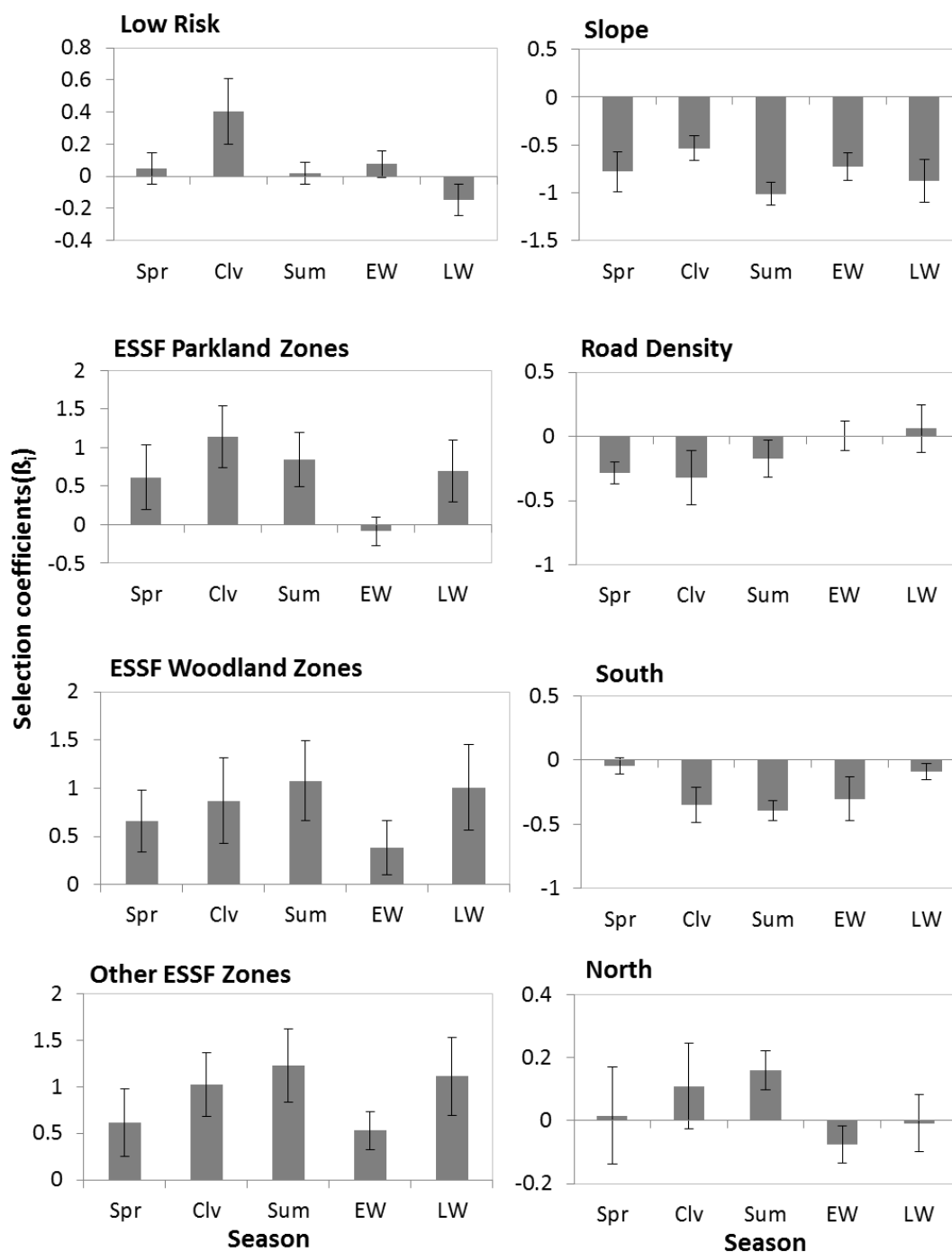


Figure 3.6 Vegetation and topographic attributes from seasonal global resource selection models for resident caribou in the Purcell South Mountains, southeastern BC. Selection coefficients ($\beta \pm SE$) for low cougar risk, ESSF Parkland Zones, ESSF Woodland Zones, Other ESSF Zones, slope, road density, and north and south aspects. Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, as defined in text. Habitats attributes which could not be incorporated into the model are not shown.

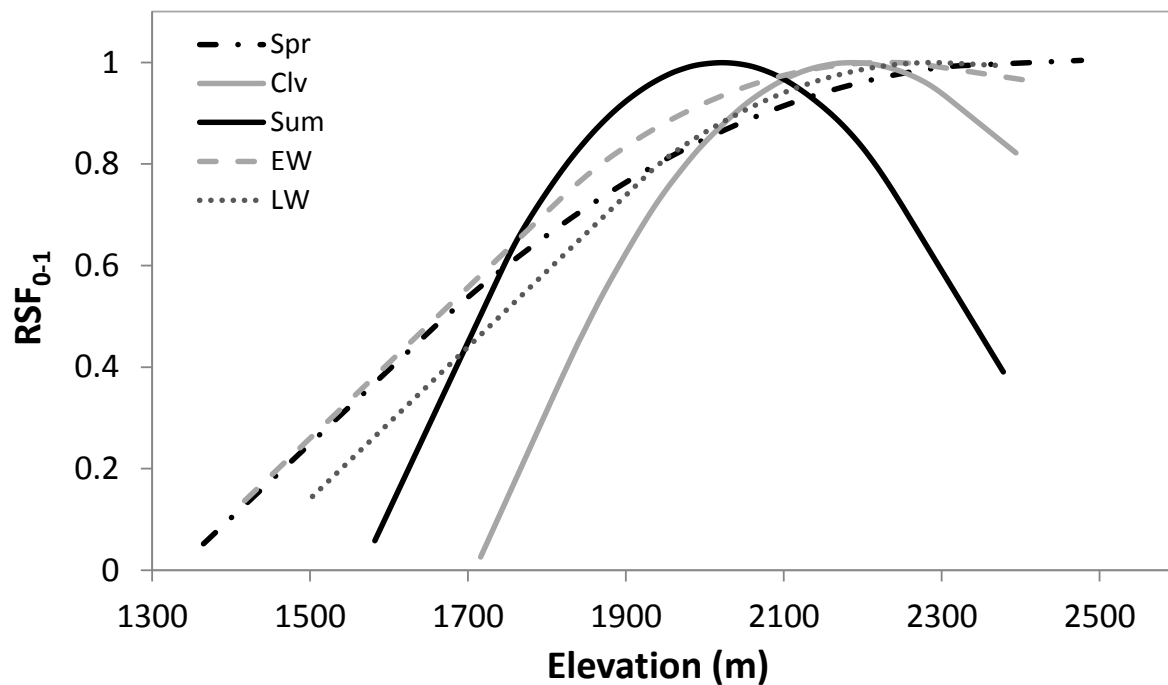


Figure 3.7 Relative selection by resident caribou for elevation assuming other habitat variables are constant in the global resource selection models, by season in the Purcell South Mountains, southeastern British Columbia. Resource selection functions were scale scaled 0-1 (RSF_{0-1}). Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, as defined in text.

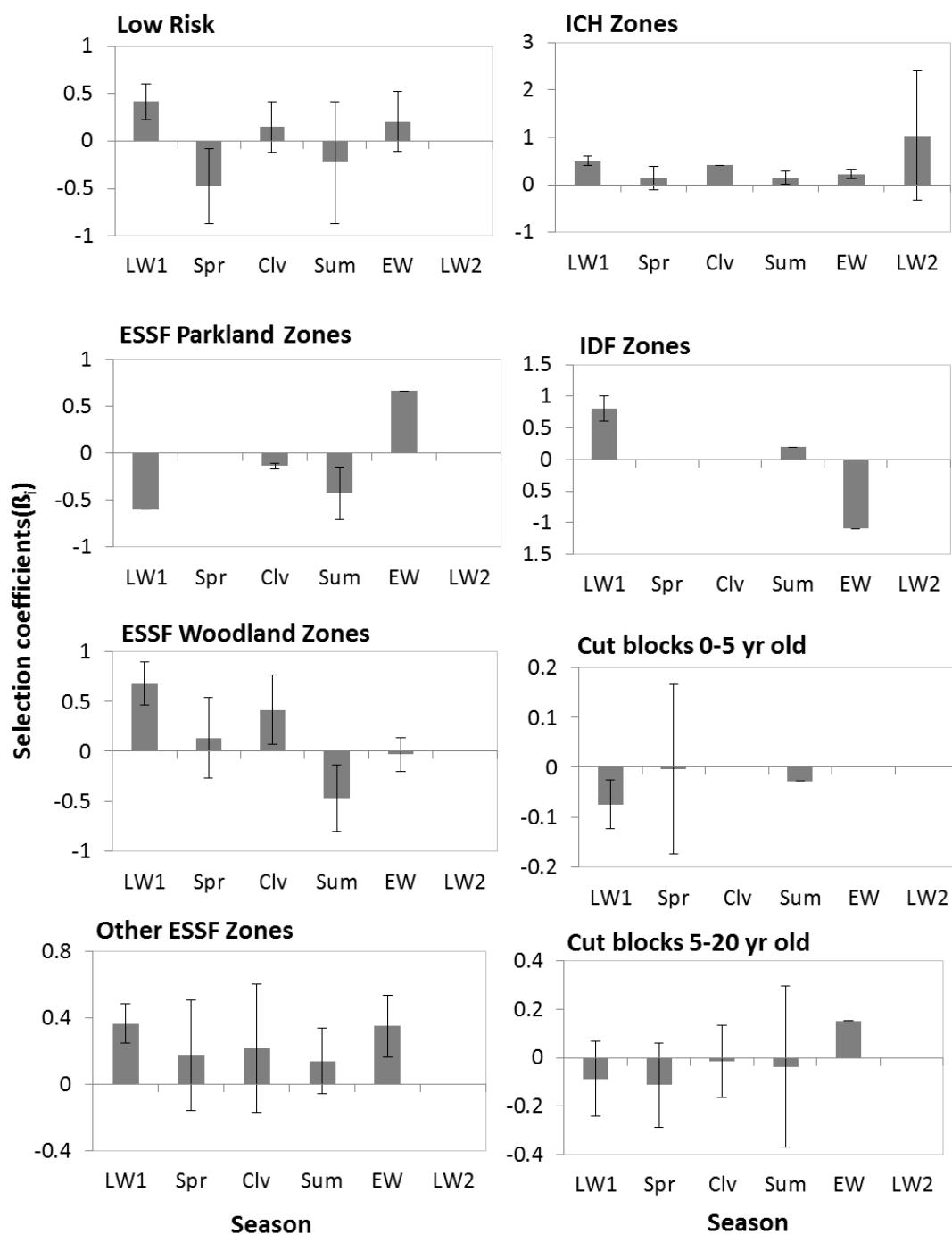


Figure 3.8 Vegetation attributes from seasonal global resource selection models for translocated caribou in the Purcell South Mountains, southeastern BC. Selection coefficients ($\beta \pm SE$) for low cougar risk, ESSF Parkland Zones, ESSF Woodland Zones, Other ESSF Zones, ICH Zones, IDF Zones, cut blocks 0-5 and cut blocks 5-20 years. LW1 = late winter 2012 (immediately following translocation), Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW2 = late winter 2012/2013, as defined in text. Habitats attributes which could not be incorporated into the model are not shown.

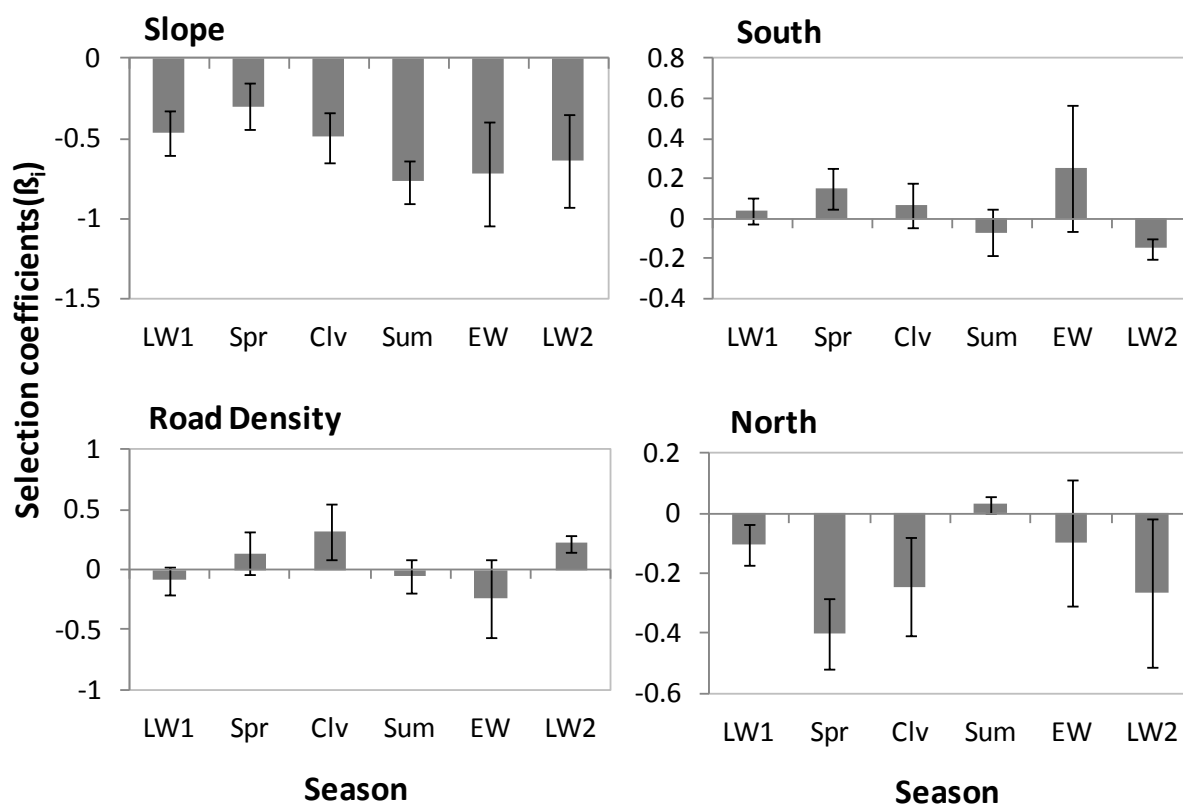


Figure 3.9 Topographic attributes from seasonal global resource selection models for translocated caribou in the Purcell South Mountains, southeastern BC. Selection coefficients ($\beta \pm SE$) for slope, road density, and north and south aspects. LW1 = late winter 2012 (immediately following translocation), Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW2 = late winter 2012/2013, as defined in text.

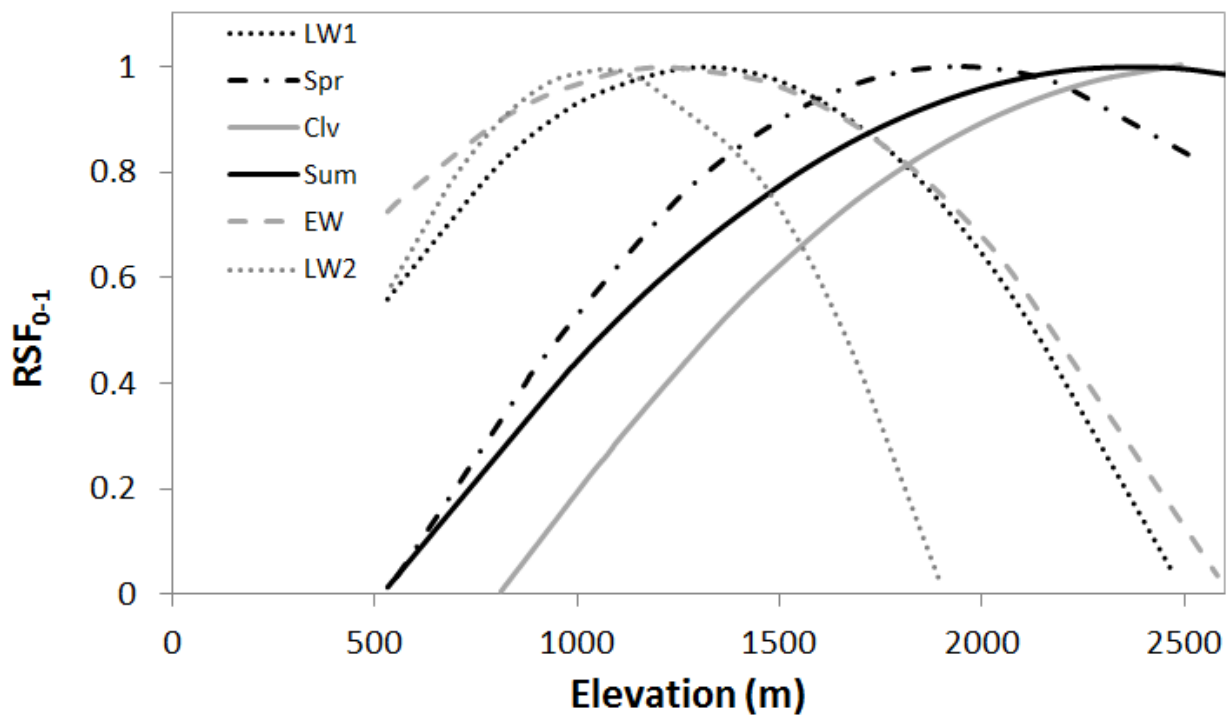


Figure 3.10 Relative selection by translocated caribou for elevation assuming other habitat variables are constant in the averaged resource selection models, by season in the Purcell South Mountains, southeastern British Columbia. Resource selection functions were scaled 0-1 (RSF_{0-1}). Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, LW1 = late winter 2012 (immediately following translocation), LW2 = late winter 2012/2013, as defined in text.

4.0 Conclusions

4.1 Discussion and conclusions

Within an animal's lifetime, the risk of being preyed upon may vary greatly depending on location, season, day or even minute (Lima and Dill 1990). Optimal foraging theory states that animals will adjust the amount of time spent foraging to coincide with the predation risk they experience at a given place and time (Sih 1984, Laundré et al. 2001). In the absence of predation risk, space-use of an animal is likely determined by availability of resources (Lima and Dill 1990). However, high predation risk can cause a prey animal to select their space-use patterns based on spatiotemporal variations in risk, rather than environmental or resource factors (Tolon et al. 2009).

Prey typically alter behaviour in response to changing levels of predation risk (Lima and Dill 1990, Laundré et al. 2001) which may be depicted through a landscape of fear model (Laundré et al. 2001). The landscape of fear model assumes that predation risk varies in a measureable manner over time and space (Laundré *et al.*, 2010). Prey use the knowledge of this 'landscape of fear' to minimize their predation risk by relocating to safer areas (Laundré et al. 2001, Tolon et al. 2009). For example, the reintroduction of wolves (*Canis lupus*) into Yellowstone National Park (YNP) changed the landscape of fear for elk (*Cervus canadensis*). Specifically, elk shifted their habitat from high risk open sagebrush meadows to safer forested areas (Hernández and Laundré 2005). Hence, animals adaptively switch their spatiotemporal habitat use with changing levels of predation risk.

Furthermore, seasonality can have a dramatic effect on the temporal aspects of predator-prey dynamics within a system. Seasonal variation in predation risk may vary depending on predator numbers, prey preferences, and overlap in predator-prey distributions (Lima and Dill 1990, Gervasi et al. 2013). Yet, many studies define seasons based on climate or expert opinion, which do not necessarily match the biological reality of the species' life history (Vander Wal and Rodgers 2009, Basille et al. 2012). This can lead to inconclusive or inaccurate results when performing data analysis based on seasonality. By defining seasons biologically, based on temporal variation in animal behaviours (Fryxell et al. 2008), one can better understand many aspects of animal ecology, including habitat selection and species interactions (Basille et al. 2012).

Caribou are in global decline and mountain caribou have been decreasing in numbers and range for many decades (Spalding 2000). Currently, mountain caribou are listed by the Canadian government as Endangered (COSEWIC 2014) and are red-listed by the BC government (BC Conservation Data Centre 2014). Habitat loss and fragmentation, direct human disturbance, and predation have all contributed to this decline (Bergerud 1974, Kinley and Apps 2001, Wittmer et al. 2005b, Seip et al. 2007). Predation is the main proximate cause of caribou mortality, ultimately due to shifts in the predator-prey community (Bergerud and Elliot 1986, Seip 1992, Wittmer et al. 2005b). That is, increased amounts of anthropogenic land use change produces early seral habitats preferred by moose (*Alces alces*), deer (*Odocoileus spp.*), and elk (*Cervus canadensis*) triggering a numerical response of predators which incidentally kill an unsustainable number of caribou (Kinley and Apps 2001, Wittmer et al. 2005a). This process is

deemed apparent competition, defined as the indirect interaction between species sharing a common predator (Holt 1977, Apps et al. 2013).

Mountain caribou reduce predation risk by spatial separation; a hypothesis that maintains prey move to spatial refuges to isolate themselves from predators, thereby avoiding an encounter (Bergerud and Page 1987, James et al. 2004). As habitat changes seasonally, caribou move across the landscape to obtain available food and to reduce predation risk by selecting for safer spatial refuges (Bergerud and Page 1987, James et al. 2004). In mountainous regions of British Columbia (BC) high levels of spatial separation have been noted between caribou and wolves in winter (Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1992). At this time caribou ascend to higher elevations, while wolves descend to valley bottoms, which experience lower snow accumulations and higher densities of other prey, such as deer and moose (Bergerud and Page 1987, Seip 1992). Wolves select for shallower snow depths in valley bottoms and for roads or linear features for the purposes of increasing their efficiency of movement (Nelson and Mech 1991, Whittington et al. 2011). The selection of different habitats by caribou and wolves decreases the predator-prey range overlap making caribou a less profitable prey choice. In southern BC, cougars (*Puma concolor*) are a main predator of caribou (Kinley and Apps 2000, 2001), yet most research involving predation risk to caribou involves wolves.

One management action used to mitigate the decline or extirpation of small mountain caribou populations is translocation (Integrated Land Management Bureau 2007). The Purcells-South (PS) mountain caribou herd is at high risk of extirpation, and thus identified for translocation in the Mountain Caribou Recovery Implementation Plan

(Integrated Land Management Bureau 2007). Approximately 15 caribou form the PS herd, which is further divided into two sub-herds. In March 2012, 19 northern caribou from the Level Kawdy (LK) herd were experimentally translocated to the PS herd in an attempt to augment the small population.

The goals of this research were to (1) provide a greater understanding of how cougar predation risk affected resident and translocated caribou seasonally; and (2) examine if translocated caribou could adopt the predator avoidance and habitat selection strategies of the resident caribou. To meet these research goals, two objectives were addressed: (1) biologically relevant caribou and cougar seasons were delineated to assess seasonal variation in cougar risk to resident, translocated, and donor caribou (non-translocated LK caribou) by comparing spatial patterns of movement and habitat use; and (2) a cougar landscape of fear was estimated and used to compare seasonal predation risk and habitat selection between resident and translocated caribou using resource selection functions (RSFs).

The major objective of Chapter Two was to determine biologically based seasons for resident PS mountain caribou, donor LK northern caribou, translocated caribou and cougars and use these seasons to determine how seasonality impacts cougar predation risk to resident and translocated caribou. More specifically, I predicted (1) cougar predation risk would be greatest when seasonal similarity in habitat use is high between caribou and cougars; and (2) resident and translocated caribou would spatially separate from cougars to minimize their risk of predation. I defined five resident caribou seasons, two donor caribou seasons, and two cougar seasons using a cluster analysis framework. I also identified translocated caribou seasons; however, the data clustered into two groups

consistent with the date of translocation and was likely a statistical artefact. The delineated seasons were then used to investigate seasonal habitat selection of resident, translocated and donor caribou, and cougars.

Resident caribou reduced spatial and temporal overlap with cougars by remaining at high elevations year round, which is consistent with the spatial separation hypothesis (Bergerud and Elliot 1986, James et al. 2004, Robinson et al. 2010). On the contrary, translocated caribou displayed risky behaviour throughout the year by travelling through habitats selected by cougars. Translocated caribou failed to exhibit movement patterns and habitat use similar to resident caribou. On the contrary, donor and translocated caribou shared more similarity in elevational use than resident and translocated caribou, despite being in different locals.

In this study, an additional factor increasing the risk of predation to translocated caribou was the presence of cougars, a novel predator (Frair et al. 2007). Unfamiliarity with cougars, a main predator in the study area, may have increased predation risk to translocated caribou because they were likely unaware of the spatial avoidance strategies specific to the novel predator. These predator avoidance strategies may have been learned from resident caribou but translocated caribou failed to join the resident caribou herd and this was not possible.

In Chapter Three, I estimated the cougar-influenced landscape of fear in the PS study area in five biologically defined mountain caribou seasons (defined in Chapter Two). I then compared the seasonal habitat selection and risk to cougar predation between resident and translocated caribou. Cougars generally selected low to mid elevations (500 – 1500 m). They consistently selected for Interior Cedar – Hemlock

(ICH) Zones and cut blocks 5-20 years old across all seasons which was likely linked to increased hunting success due to a greater abundance of alternate prey in these habitats (Seip 1998, Kinley and Apps 2000, Smith 2004). Resident caribou avoided high risk areas at the landscape scale year-round and selected low risk habitats during calving season, which is consistent with the spatial separation hypothesis. Translocated caribou showed variability in habitat selection patterns and displayed risky behaviour by traveling to mid to low elevations and traversing habitats highly selected for by cougars. This suggests naivety to cougars their new environment. The elevational movements of translocated caribou were similar to those of the donor herd in the Level Kawdy. Translocated caribou used lower elevations during early winter and late winter, and higher elevations in the spring, calving, and summer seasons. In general, northern caribou occupy valley bottoms during the winter months and move to higher elevations during calving periods as an anti-predator tactic (Bergerud et al. 1984, Bergerud and Page 1987). This elevational pattern is opposite to mountain caribou and my findings suggest translocated caribou did not learn resident caribou predator avoidance and habitat selection strategies subsequent to translocation. Six of 17 known translocated caribou mortalities were attributed to cougar predation. At the time of translocation cougar abundance was high in the Kootenay Region (FLNRO, unpublished data). The additive effect of translocated caribou being inexperienced with cougars, in addition to high cougar abundance at the time of translocation, may have contributed to increasing cougar predation risk to translocated caribou during the study.

Mountain caribou are a conservation-reliant species and recovery strategies are needed to maintain declining populations. If translocation is chosen as a management

tool, I would recommend removing or reducing limiting factors at the release site such as high predator densities, disease, and habitat degradation (Pérez et al. 2012). In addition, a suitable source population that is experienced with the release site's mortality risks would promote the survival of translocated animals (Warren et al. 1996, Frair et al. 2007). Moreover, translocated northern caribou likely experienced increased predation risk because they were unaware of how to mitigate predation risk from cougars (a novel predator), which are absent in their natal range. Therefore, conservation managers should consider translocating animals familiar with the same suite of predators existing at the release site to avoid unnecessary predation events due to naivety of a particular predator.

A soft release may be employed to encourage herd amalgamation and decrease the novelty of the release site by penning animals in a large corral with some residents prior to release (Letty et al. 2007, Stamps and Swaisgood 2007). This conditioning period would allow translocated caribou to develop social bonds with resident caribou. However, given that caribou are an endangered species, conservation managers must be cautious when selecting the source of translocated caribou, as to not negatively impact other populations. Perhaps maternal penning or captive rearing programs can be the solution to this problem. This involves placing wild pregnant caribou inside a maternity pen to give birth, and raise their calves until they are strong enough to be released. During this time they are protected from predators and given adequate food (RCRW 2014). These captive-reared caribou can then be soft released into a wild population.

4.2 Research contributions

The first major contribution of this research was the delineation of biologically relevant seasons for PS mountain caribou and cougars, and for LK northern caribou.

Failure to accurately define seasons may lead to inconclusive results about ecological phenomena related to seasonality. The seasons defined here can be used in near-term analysis (as seasonal timing may change in the future due to climate change) of PS mountain caribou and cougars, and LK caribou to achieve a better understanding of seasonal habitat selection processes, predator-prey dynamics, and other seasonally governed ecological processes within the mountain caribou-cougar or northern caribou systems.

The caribou recovery team, the International Mountain Caribou Steering Committee, and the International Mountain Caribou Technical Committee drafted an action plan outlining efforts needed to maintain existing populations of caribou. One identified task was to study cougar predation on mountain caribou (United States General Accounting Office 1999). The second main contribution of this research addressed this task by developing seasonal cougar predation risk layers in the PS Mountains. These cougar predation risk layers, divided into five mountain caribou seasons, can be used in future management decisions pertaining to PS mountain caribou. For example, Engelmann Spruce – Subalpine Fir (ESSF) Zones were selected by both resident caribou and cougars and therefore a zone of potential risk. Conservation managers could use this information when considering management options to lower cougar predation risk to resident caribou. With regards to translocated caribou, conservation managers may be able to increase the survival of translocated caribou by implementing a soft release of caribou into core low risk cougar habitat, decreasing the chance of caribou-cougar encounters.

The third main contribution of this research extends the knowledge in the first and second contributions by examining the seasonal variation in cougar predation risk to resident and translocated caribou in the PS Mountains. My research demonstrates resident PS caribou selected habitats and avoided predation by residing at high elevations year-round in ESSF Woodlands and Parkland zones. It also reveals movement and habitat selection patterns of translocated caribou are not necessarily plastic, resulting in risky behaviour, such as traversing high cougar risk areas. Additionally, the inexperience of translocated caribou with a novel predator likely compounded predation risk. Using translocated animals familiar with predators and habitats similar to the release area would likely increase the chances of survival post-release.

4.3 Research opportunities

Future research should investigate soft releases to determine whether they increase the success rates of caribou translocations. To my knowledge a soft release has yet to be implemented when translocating caribou. Soft releases may increase behavioural plasticity by increasing fidelity to the release site and therefore the potential for translocated caribou to join the resident herd. Additionally, soft releases of many mammals have been found to reduce movement rates and increase survival rates (Bright and Morris 1994, Letty et al. 2000, 2007). However, wildlife managers should be cautious when selecting donor animals in future caribou translocations. Although it would be beneficial to translocate caribou from a mountain caribou ecotype to a mountain caribou ecotype because habitat and predator similarities, mountain caribou are in limited supply – only four of 15 herds are greater than 100 individuals. Therefore, experimenting with donor caribou from maternal penning and captive rearing programs

would be valuable as not to take caribou from presently endangered and declining populations. Translocations are likely necessary to maintain small mountain caribou populations in the near future. Therefore, finding suitable donor caribou and implementing strategies that improve the success of translocation is necessary to achieve mountain caribou conservation.

References

- Apps, C. D., B. N. McLellan, T. A. Kinley, R. Serrouya, D. R. Seip, and H. U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *Journal of Wildlife Management* 77:1409–1419.
- Basille, M., D. Fortin, C. Dussault, J.P. Ouellet, and R. Courtois. 2012. Ecologically based definition of seasons clarifies predator-prey interactions. *Ecography* 35:1–10.
- BC Conservation Data Centre. 2014. Conservation Status Report: *Rangifer tarandus* pop. 1 Caribou (Southern Mountain Population). <http://a100.gov.bc.ca/pub/eswp/>.
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38:757–770.
- Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566–1575.
- Bergerud, A.T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515–1529.
- Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology* 65:1597–1606.
- Bright, P. W., and P. A. Morris. 1994. Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. *Journal of Applied Ecology* 31:699–708.
- COSEWIC. 2014. COSEWIC assessment and status report on the Caribou *Rangifer tarandus*, Northern Mountain population, Central Mountain population and Southern Mountain population in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxii + 113 pp.
- Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management* 71:541–554.
- Fryxell, J. M., M. Hazell, L. Börger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America* 105:19114–19119.
- Gervasi, V., H. Sand, B. Zimmermann, J. Mattisson, P. Wabakken, and J. D. C. Linnell. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications* 23:1722–34.

- Hernández, L., and J. W. Laundré. 2005. Foraging in the “landscape of fear” and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* 11:215–220.
- Holt, R. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Integrated Land Management Bureau. 2007. Mountain Caribou Recovery Implementation Plan. Species at Risk Coordination Office, Integrated Land Management Bureau, Victoria, BC.
- James, A., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- Kinley, T. A., and C. D. Apps. 2000. Population Status and Mortality of Mountain Caribou in the Southern Purcell Mountains, British Columbia. Pages 655–661 in L. M. Darling, editor. Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, British Columbia, 15-19 Fe. 1999. Volume 2. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College .
- Kinley, T., and C. Apps. 2001. Mortality Patterns in a Subpopulation of Endangered Mountain Caribou. *Wildlife Society Bulletin* 29:158–164.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Letty, J., S. Marchandean, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. *Ecoscience* 14:420–431.
- Letty, J., S. Marchandean, J. Clobert, and J. Aubineau. 2000. Improving translocation success: an experimental study of anti-stress treatment and release method for wild rabbits. *Animal Conservation* 3:211–219.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Nelson, M. E., and L. D. Mech. 1991. Wolf predation risk associated with white-tailed deer movements. *Canadian Journal of Zoology* 69:2696–2699.
- Pérez, I., J. D. Anadón, M. Díaz, G. G. Nicola, J. L. Tella, and A. Giménez. 2012. What is wrong with current translocations? A review and a decision-making proposal. *Frontiers in Ecology and the Environment* 10:494–501.

- RCRW. 2014. Revelstoke Caribou Rearing in the Wild. <http://rcrw.ca/>.
- Robinson, H. S., M. Hebblewhite, N. J. DeCesare, J. Whittington, L. Neufeld, M. Bradley, and M. Musiani. 2010. The effect of fire on spatial separation between wolves and caribou. *Rangifer* 20:277–294.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494–1503.
- Seip, D. R. 1998. Ecosystem management and the conservation of caribou habitat. *Rangifer Special Issue No. 10*:203-211
- Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. *Journal of Wildlife Management* 71:1539–1544.
- Sih, A. 1984. The behavioral response race between predator and prey. *American Naturalist* 123:143–150.
- Smith, K. G. 2004. Woodland Caribou Demography and Persistence Relative to Landscape Change in West-central Alberta. M.Sc. thesis, University of Alberta, Edmonton, Alberta.
- Spalding, D. J. 2000. The early history of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. Ministry of the Environment. Victoria, BC. Wildlife Bulletin No. B-100. BC.
- Stamps, J., and R. Swaisgood. 2007. Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392–409.
- Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology* 87:1129–1137.
- United States General Accounting Office. 1999. Endangered Species: Caribou Recovery Program Has Achieved Modest Gains. Resources, Community, and Economic Development Division. Washington, D.C., USA.
- Vander Wal, E., and A. R. Rodgers. 2009. Designating seasonality using rate of movement. *Journal of Wildlife Management* 73:1189–1196.
- Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. *Conservation Biology* 10:547–553.

- 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.
- Wittmer, H., B. McLellan, D. Seip, and J. Young. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wittmer, H., A. Sinclair, B. McLellan, and R. Sinclair. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.

Appendix A
**Top RSF model statistics for cougars, resident caribou, and
translocated caribou**

Table A1 The best resource selection models for individual cougars in the Purcell South Mountains by season. Statistics include number of parameters (K), sample size (n, used, and available), log likelihood (LL), Akaike's Information Criterion with correction (AIC_c), Akaike weights (w_i), Spearman's rank correlation (r_s), and its associated P-value from k-fold cross-validation procedure indicating the model's ability to predict habitat attributes selected by cougars.

Season ^a	Cougar	Model No. ^b	K	n	AIC _c	LL	w _i	r _s	P-value
Spr	C2	5	8	966	744.250	-362.529	0.275	0.863	0.001
Spr	C3	5	8	924	678.985	-329.868	0.005	0.994	<0.001
Spr	C4	1	9	2364	1823.228	-901.327	0.000	0.952	<0.001
Spr	C5	1	9	1194	940.121	-459.475	0.000	0.924	<0.001
Spr	C6	2	4	966	686.789	-338.201	0.211	0.960	<0.001
Spr	C7	4	7	336	225.084	-103.010	0.253	0.844	0.002
Spr	C8	6	7	1206	962.247	-472.748	0.066	0.891	0.001
Spr	C9	6	7	1164	840.776	-411.999	0.313	0.948	<0.001
Spr	C10	5	8	1266	1001.703	-491.404	0.030	0.857	0.002
Spr	C11	3	7	1188	940.009	-461.623	0.000	0.903	<0.001
Spr	C12	1	8	122	889.995	-435.541	0.977	0.875	<0.001
Clv	C2	1	10	750	628.219	-301.941	0.094	0.948	<0.001
Clv	C4	5	9	1848	1525.760	-752.510	0.498	0.867	0.003
Clv	C5	8	6	930	764.159	-374.699	0.002	0.825	0.003
Clv	C8	2	6	1020	792.876	-389.092	0.326	0.821	0.004
Clv	C9	6	8	1014	706.006	-343.437	0.687	0.845	0.002
Clv	C10	4	7	1038	803.291	-393.206	0.001	0.967	<0.001
Clv	C11	5	9	978	785.137	-381.845	0.201	0.915	<0.001
Clv	C12	1	9	1020	796.577	-387.597	0.008	0.881	<0.001
Sum	C2	6	9	948	806.156	-392.330	0.000	0.939	<0.001
Sum	C4	4	8	3222	2701.985	-1341.822	0.000	0.842	0.004
Sum	C5	4	8	702	621.666	-300.992	0.417	0.891	0.001
Sum	C8	4	7	1818	1620.662	-802.086	0.028	0.745	0.018
Sum	C9	6	8	1758	1082.828	-532.096	0.271	0.912	<0.001
Sum	C10	6	9	1794	1552.858	-766.047	0.062	0.855	0.004
Sum	C11	1	10	1728	1275.979	-626.511	0.000	0.927	<0.001
Sum	C12	4	7	798	635.404	-309.121	0.031	0.875	<0.001
EW	C2	7	7	438	370.986	-176.368	0.135	0.912	<0.001
EW	C4	5	9	1710	1374.558	-676.878	0.004	0.924	<0.001
EW	C5	4	8	696	526.342	-253.322	0.243	0.964	0.001
EW	C8	5	8	1758	1530.843	-756.103	0.000	0.927	<0.001
EW	C9	6	9	1884	1300.564	-639.919	0.601	0.912	<0.001
EW	C10	1	10	2046	1600.146	-788.672	0.047	0.903	<0.001
EW	C11	1	9	1824	1476.008	-727.629	0.000	0.927	<0.001
LW	C1	5	7	1860	1021.098	-502.310	0.425	0.963	<0.001
LW	C2	5	8	2970	2481.354	-1231.491	0.000	0.915	<0.001
LW	C3	1	9	1950	1549.130	-764.215	1.000	0.952	<0.001
LW	C4	1	9	4926	4146.687	-2063.208	0.076	0.939	<0.001
LW	C5	4	7	1512	1165.202	-574.305	0.001	0.927	<0.001
LW	C6	5	8	2778	2254.244	-1117.924	0.014	0.821	0.004
LW	C7	5	8	1608	1263.748	-622.525	0.000	0.902	<0.001
LW	C8	1	8	1878	1367.530	-674.468	0.990	0.976	<0.001
LW	C9	1	9	810	582.127	-281.177	0.051	0.860	0.001
LW	C10	1	9	3324	2572.425	-1276.010	0.987	0.927	<0.001
LW	C11	1	9	3168	2669.937	-1324.756	0.081	0.842	0.004
LW	C12	5	7	3222	2507.192	-1245.460	0.528	0.782	0.012

^a Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, as defined in text. ^b *A priori* candidate models used to explain cougar habitat selection found in Table 3.3.

Table A2 The best resource selection models for individual resident caribou in the Purcell South Mountains by season. Statistics include number of parameters (K), sample size (n, used, and available), log likelihood (LL), Akaike's Information Criterion with correction (AIC_c), Akaike weights (w_i), Spearman's rank correlation (r_s), and its associated P-value from k-fold cross-validation procedure indicating the model's ability to predict habitat attributes selected by resident caribou.

Season ^a	Resident Cairbou	Model No. ^b	K	n	AIC _c	LL	w _i	r _s	P-value
Spr	R1	1	9	3864	2363.012	-1171.332	0.809	0.952	<0.001
Spr	R2	1	9	3780	2867.835	-1423.740	0.985	0.927	<0.001
Spr	R3	1	9	3744	2861.801	-1420.721	0.919	0.818	0.007
Spr	R4	11	8	2550	1696.933	-839.250	0.524	0.988	<0.001
Spr	R5	12	8	1104	866.874	-423.920	0.587	0.927	<0.001
Clv	R1	1	9	3294	1782.246	-880.918	0.904	0.957	<0.001
Clv	R2	1	9	3282	2059.675	-1019.632	0.999	0.932	<0.001
Clv	R3	1	9	3306	1948.143	-963.868	1.000	0.937	<0.001
Clv	R4	1	9	2046	1573.177	-776.279	0.984	0.976	<0.001
Clv	R5	10	7	798	619.394	-301.116	0.340	0.985	<0.001
Sum	R1	1	9	5538	3239.261	-1609.510	1.000	0.988	<0.001
Sum	R2	1	9	5520	4192.176	-2085.967	0.994	0.957	<0.001
Sum	R3	1	9	5430	4229.695	-2104.724	0.999	0.973	<0.001
Sum	R4	1	9	3654	2458.427	-1219.030	0.999	0.988	<0.001
Sum	R5	12	8	1374	998.745	-489.962	0.432	0.985	<0.001
EW	R1	1	9	5916	3857.202	-1918.488	0.573	0.988	<0.001
EW	R2	1	9	5868	4399.619	-2189.696	1.000	0.960	<0.001
EW	R3	1	9	3882	2863.177	-1421.416	0.913	0.985	<0.001
EW	R4	11	8	3504	2081.604	-1031.645	0.622	0.979	<0.001
EW	R5	12	7	1968	1216.795	-600.172	0.680	0.938	<0.001
LW	R1	1	9	4686	2361.625	-1170.670	0.421	0.935	<0.001
LW	R2	11	8	6198	4652.897	-2317.361	0.716	0.988	<0.001
LW	R3	11	8	3780	2947.536	-1464.623	0.735	0.951	<0.001
LW	R4	10	7	2592	1266.462	-625.061	0.275	0.957	<0.001
LW	R5	1	9	4494	2707.222	-1343.462	1.000	0.951	<0.001

^a Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW = late winter, as defined in text. ^b *A priori* candidate models used to explain resident caribou habitat selection found in Table 3.1.

Table A3 The best resource selection models for individual translocated caribou in the Purcell South Mountains by season. Statistics include number of parameters (K), sample size (n, used, and available), log likelihood (LL), Akaike's Information Criterion with correction (AIC_c), Akaike weights (w_i), Spearman's rank correlation (r_s), and its associated P-value from k-fold cross-validation procedure indicating the model's ability to predict habitat attributes selected by translocated caribou.

Season ^a	Translocated Caribou	Model No. ^b	K	n	AIC _c	LL	w _i	r _s	P-value
LW1	T1	11	7	1608	1326.120	-654.782	0.302	0.745	0.018
LW1	T2	11	8	882	582.317	-281.502	0.380	0.948	<0.001
LW1	T3	8	8	642	544.863	-262.504	0.584	0.952	<0.001
LW1	T4	10	9	1410	905.291	-442.154	0.506	0.930	<0.001
LW1	T5	1	10	1608	1316.044	-646.506	0.999	0.952	<0.001
LW1	T6	11	9	1572	1226.453	-602.788	0.589	0.988	<0.001
LW1	T7	12	8	462	280.945	-130.129	0.534	0.938	<0.001
LW1	T8	11	7	1596	971.309	-477.374	0.371	0.939	<0.001
LW1	T9	5	6	1530	1272.515	-629.031	0.157	0.755	0.012
LW1	T10	12	10	912	719.518	-347.816	0.464	0.945	<0.001
LW1	T11	11	10	1151	908.477	-442.533	0.656	0.903	<0.001
LW1	T12	6	7	98	412.866	-197.460	0.178	0.960	<0.001
LW1	T13	12	10	1602	1350.913	-663.939	0.629	0.952	<0.001
LW1	T14	10	7	1548	945.850	-464.636	0.306	0.976	<0.001
LW1	T15	10	7	1578	1192.568	-588.000	0.482	0.976	<0.001
LW1	T16	8	9	1328	1117.540	-548.326	0.238	0.976	<0.001
LW1	T17	7	6	1278	556.139	-270.797	0.179	0.942	<0.001
LW1	T18	7	6	1404	1130.051	-557.778	0.333	0.964	<0.001
LW1	T19	10	7	1542	1070.069	-526.744	0.485	0.976	<0.001
Spr	T1	1	11	1266	774.732	-374.578	0.815	0.976	<0.001
Spr	T4	11	10	1218	971.284	-473.951	0.709	0.900	<0.001
Spr	T5	12	8	1278	717.506	-349.310	0.284	0.834	0.003
Spr	T6	1	10	1248	829.821	-403.237	0.933	0.921	<0.001
Spr	T8	1	9	1284	892.435	-435.676	0.734	0.926	<0.001
Spr	T11	11	6	1290	628.917	-307.188	0.550	0.925	<0.001
Spr	T13	12	9	1230	761.370	-370.118	0.503	0.854	0.002
Spr	T15	11	8	1272	671.615	-326.362	0.386	0.816	0.004
Spr	T17	11	6	1248	1028.712	-507.076	0.648	0.988	<0.001
Spr	T18	1	10	1098	772.324	-374.390	0.998	0.884	<0.001
Spr	T19	11	10	1050	777.481	-376.931	0.742	0.811	0.004
Clv	T4	12	9	1038	668.285	-323.464	0.727	0.924	<0.001
Clv	T5	12	9	1098	701.435	-340.078	0.701	0.896	<0.001
Clv	T6	9	6	1068	733.186	-359.263	0.584	0.879	0.002
Clv	T8	6	5	1098	817.780	-402.651	0.189	0.879	0.002
Clv	T11	9	5	690	472.132	-229.677	0.231	0.936	<0.001
Clv	T13	12	9	1104	675.821	-327.275	0.495	0.862	0.001
Clv	T15	11	8	1044	690.211	-335.557	0.748	0.902	<0.001
Clv	T17	1	8	108	763.285	-372.107	1.000	0.891	0.001
Clv	T18	12	8	1050	744.695	-362.802	0.538	0.960	<0.001
Sum	T4	12	8	1600	1194.404	-587.867	0.713	0.818	0.007
Sum	T5	6	7	1872	1174.555	-579.040	0.329	0.903	<0.001
Sum	T6	10	7	1842	1442.894	-713.206	0.228	0.927	<0.001
Sum	T8	1	8	1914	1549.072	-765.245	0.978	0.948	<0.001
Sum	T13	12	9	1025	840.443	-409.652	0.293	0.988	<0.001
Sum	T15	12	8	522	417.292	-198.477	0.570	0.891	0.001
Sum	T17	12	10	1812	1364.200	-670.645	0.742	0.988	<0.001
Sum	T18	6	7	1192	956.604	-469.945	0.490	0.827	0.003
EW	T5	6	7	2046	1439.737	-712.651	0.486	0.964	<0.001
EW	T6	1	10	1668	899.332	-438.237	0.928	0.960	<0.001
EW	T17	1	9	2160	1540.243	-759.807	0.807	0.875	<0.001
EW	T18	11	10	2034	1351.668	-664.431	0.719	0.774	0.009
LW2	T5	11	7	3252	2018.889	-1002.309	0.558	0.945	<0.001
LW2	T17	11	7	1608	1353.343	-669.394	0.437	0.915	<0.001
LW2	T18	1	8	1992	1569.395	-776.418	0.740	0.939	<0.001

^a LW1 = late winter 2012 (immediately following translocation), Spr = spring, Clv = calving, Sum = summer, EW = early winter, LW2 = late winter 2012/2013, as defined in text. ^b *A priori* candidate models used to explain translocated caribou habitat selection found in Table 3.1.

Appendix B
Individual translocated caribou RSF results by season

Table B1 Estimated coefficients ($\beta \pm SE$) by translocated caribou for late winter 2012 (immediately following translocation) resource selection function models. Standard errors were determined by using Newey-West sandwich variance estimators.

Translocated Caribou	Low Risk	Elevation	Elevation ²	ESSF Parkland	ESSF Woodland	ESSF Zone	ICH Zone	IDF Zone	Cut 0-5 years	Cut 5-20 years	Slope	South	North	Road Density
T1	0.003 ± 0.284	-0.441 ± 0.300	0.036 ± 0.353	NA ^a	0.040 ± 0.163	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	0.459 ± 0.222	0 ± 0 ^b	-0.636 ± 0.209	0.514 ± 0.152
T2	0.864 ± 0.472	-1.287 ± 1.178	-2.972 ± 0.882	NA ^a	0.645 ± 0.358	NA ^a	0.818 ± 0.389	NA ^a	NA ^a	NA ^a	-0.954 ± 0.207	0 ± 0 ^b	-0.274 ± 0.147	0.406 ± 0.282
T3	-0.308 ± 0.168	NA ^a	NA ^a	NA ^a	0.350 ± 0.214	0.126 ± 0.259	NA ^a	NA ^a	NA ^a	-0.267 ± 0.202	0.186 ± 0.199	-0.623 ± 0.162	-0.476 ± 0.183	0.458 ± 0.170
T4	1.312 ± 0.578	-2.833 ± 0.735	-1.548 ± 0.315	NA ^a	0.921 ± 0.631	0.776 ± 0.392	0.219 ± 0.363	NA ^a	NA ^a	0.647 ± 0.164	-1.141 ± 0.188	0 ± 0 ^b	0 ± 0 ^b	-0.594 ± 0.251
T5	-0.057 ± 0.232	1.470 ± 0.432	-1.035 ± 0.325	NA ^a	NA ^a	-0.109 ± 0.178	0.321 ± 0.254	0.905 ± 0.326	NA ^a	NA ^a	-0.271 ± 0.180	-0.306 ± 0.186	-0.528 ± 0.112	0.141 ± 0.273
T6	0.754 ± 0.251	-1.918 ± 0.424	-0.048 ± 0.245	NA ^a	NA ^a	NA ^a	0.395 ± 0.165	NA ^a	0.061 ± 0.107	-0.130 ± 0.123	-0.252 ± 0.275	0 ± 0 ^b	0.353 ± 0.105	-1.263 ± 0.470
T7	2.221 ± 0.672	-5.049 ± 0.845	-3.802 ± 1.159	NA ^a	NA ^a	NA ^a	-0.148 ± 0.277	NA ^a	NA ^a	-0.529 ± 0.181	0.020 ± 0.235	0.634 ± 0.204	0 ± 0 ^b	0.076 ± 0.512
T8	-0.886 ± 0.307	2.480 ± 1.172	-1.184 ± 0.852	NA ^a	NA ^a	0.850 ± 0.325	NA ^a	NA ^a	NA ^a	NA ^a	-0.344 ± 0.151	0 ± 0 ^b	-0.569 ± 0.167	0.552 ± 0.179
T9	-0.663 ± 0.275	-0.487 ± 0.336	-0.051 ± 0.238	NA ^a	NA ^a	0.442 ± 0.253	0.517 ± 0.145	NA ^a	-0.171 ± 0.141	NA ^a	NA ^a	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b
T10	0.440 ± 0.596	-1.127 ± 0.471	-0.756 ± 0.764	NA ^a	NA ^a	-0.067 ± 0.333	0.524 ± 0.404	NA ^a	-0.091 ± 0.177	0.211 ± 0.308	0.269 ± 0.193	0.248 ± 0.172	0 ± 0 ^b	0.267 ± 0.327
T11	0.561 ± 0.224	1.254 ± 0.314	0.157 ± 0.238	-0.603 ± 0.142	NA ^a	0.619 ± 0.199	0.963 ± 0.238	0.426 ± 0.293	NA ^a	NA ^a	-0.712 ± 0.200	0 ± 0 ^b	0.229 ± 0.123	0.123 ± 0.233
T12	0.260 ± 0.283	0.709 ± 0.398	-0.468 ± 0.187	NA ^a	NA ^a	-0.106 ± 0.290	0.619 ± 0.352	NA ^a	NA ^a	-0.674 ± 0.380	-0.580 ± 0.163	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b
T13	-0.311 ± 0.223	0.739 ± 0.280	-0.341 ± 0.123	NA ^a	-0.017 ± 0.144	-0.343 ± 0.142	NA ^a	NA ^a	-0.099 ± 0.072	-0.516 ± 0.158	-0.363 ± 0.159	0.169 ± 0.121	0 ± 0 ^b	0.167 ± 0.183
T14	1.850 ± 0.428	-2.671 ± 0.627	-1.351 ± 0.258	NA ^a	NA ^a	0.481 ± 0.167	NA ^a	NA ^a	NA ^a	0.482 ± 0.126	-1.266 ± 0.185	0 ± 0 ^b	0 ± 0 ^b	-0.618 ± 0.237
T15	0.890 ± 0.653	-2.330 ± 0.732	-0.859 ± 0.540	NA ^a	NA ^a	-0.064 ± 0.258	NA ^a	NA ^a	NA ^a	-0.007 ± 0.114	0.617 ± 0.156	0 ± 0 ^b	0 ± 0 ^b	-1.073 ± 0.568
T16	0.284 ± 0.160	NA ^a	NA ^a	NA ^a	0.437 ± 0.166	1.051 ± 0.261	0.757 ± 0.298	1.079 ± 0.259	NA ^a	NA ^a	-0.843 ± 0.171	-0.135 ± 0.107	0.310 ± 0.099	-0.228 ± 0.222
T17	0.950 ± 0.393	NA ^a	NA ^a	NA ^a	2.202 ± 0.308	1.156 ± 0.358	NA ^a	NA ^a	NA ^a	NA ^a	-1.477 ± 0.170	0.521 ± 0.113	-0.420 ± 0.186	0 ± 0 ^b
T18	-0.328 ± 0.202	NA ^a	NA ^a	NA ^a	0.854 ± 0.201	0.517 ± 0.223	NA ^a	NA ^a	NA ^a	NA ^a	-0.798 ± 0.143	0.253 ± 0.138	-0.011 ± 0.090	0 ± 0 ^b
T19	0.089 ± 0.153	-2.036 ± 0.570	-1.441 ± 0.364	NA ^a	0.686 ± 0.326	0.150 ± 0.305	NA ^a	NA ^a	NA ^a	NA ^a	-0.871 ± 0.249	0 ± 0 ^b	0 ± 0 ^b	-0.616 ± 0.251
Average	0.417 ± 0.187	-0.902 ± 0.516	-1.044 ± 0.288	-0.603 ± NA	0.680 ± 0.220	0.365 ± 0.120	0.499 ± 0.102	0.803 ± 0.195	-0.075 ± 0.049	-0.087 ± 0.154	-0.462 ± 0.142	0.040 ± 0.062	-0.106 ± 0.067	-0.089 ± 0.119

^a Indicates variable was not included in set of variables considered for model.

^b Indicates variable was available to be included in model but was not selected for and given a value of zero.

Table B2 Estimated coefficients ($\beta \pm SE$) by translocated caribou for spring resource selection function models. Standard errors were determined by using Newey-West sandwich variance estimators.

Variable	Translocated Caribou											
	T1	T4	T5	T6	T8	T11	T13	T15	T17	T18	T19	Average
Low Risk	0.034 ± 0.298	-0.227 ± 0.185	-3.329 ± 0.295	-1.731 ± 0.324	0.348 ± 0.284	0.323 ± 0.294	0.328 ± 0.139	1.039 ± 1.493	-0.063 ± 0.148	0.120 ± 0.326	-2.049 ± 0.387	-0.473 ± 0.397
Elevation	1.983 ± 0.536	-0.022 ± 0.639	1.525 ± 0.753	2.137 ± 0.403	-0.060 ± 0.730	1.905 ± 0.407	1.905 ± 0.612	-2.244 ± 1.965	0.244 ± 0.263	1.314 ± 0.424	2.094 ± 0.605	0.949 ± 0.407
Elevation ²	-2.007 ± 0.439	-0.792 ± 0.256	-1.211 ± 0.724	-1.041 ± 0.164	-1.891 ± 0.415	-1.774 ± 0.124	-0.799 ± 0.470	-0.477 ± 0.519	-0.658 ± 0.150	-0.409 ± 0.338	0.688 ± 0.303	-0.943 ± 0.235
ESSF Woodland	-1.226 ± 0.211	0.861 ± 0.291	NA ^a	NA ^a	0.860 ± 0.608	NA ^a	NA ^a	NA ^a	NA ^a	0.483 ± 0.183	-0.314 ± 0.250	0.133 ± 0.402
ESSF Zone	-0.478 ± 0.306	-0.090 ± 0.252	1.007 ± 0.279	0.247 ± 0.260	-0.269 ± 0.420	NA ^a	-0.984 ± 0.213	2.398 ± 1.151	NA ^a	0.169 ± 0.288	-0.425 ± 0.198	0.175 ± 0.334
ICH Zone	-0.400 ± 0.346	NA ^a	-0.122 ± 0.327	0.106 ± 0.253	NA ^a	NA ^a	-0.149 ± 0.267	NA ^a	NA ^a	1.295 ± 0.302	0.131 ± 0.314	0.144 ± 0.244
Cut 0-5 years	NA ^a	-0.173 ± 0.125	NA ^a	0.167 ± 0.176	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	-0.003 ± 0.170
Cut 5-20 years	0.116 ± 0.190	0.182 ± 0.126	NA ^a	NA ^a	NA ^a	NA ^a	-0.636 ± 0.241	0.197 ± 0.150	NA ^a	NA ^a	-0.422 ± 0.281	-0.113 ± 0.174
Slope	-0.328 ± 0.222	-0.348 ± 0.263	-0.012 ± 0.219	-0.701 ± 0.170	0.572 ± 0.242	-1.135 ± 0.189	0.067 ± 0.168	-0.326 ± 0.283	-0.513 ± 0.103	0.210 ± 0.177	-0.767 ± 0.139	-0.298 ± 0.147
South	0.367 ± 0.148	0 ± 0 ^b	-0.396 ± 0.163	0.265 ± 0.117	0.170 ± 0.172	0 ± 0 ^b	0.902 ± 0.124	0 ± 0 ^b	0 ± 0 ^b	0.371 ± 0.142	0 ± 0 ^b	0.153 ± 0.099
North	-0.273 ± 0.155	-0.264 ± 0.150	0 ± 0 ^b	0.281 ± 0.124	-0.975 ± 0.195	-0.696 ± 0.266	0 ± 0 ^b	-0.896 ± 0.384	-0.614 ± 0.207	-0.553 ± 0.205	-0.394 ± 0.189	-0.399 ± 0.119
Road Density	0.731 ± 0.397	0.312 ± 0.257	0.532 ± 0.446	1.069 ± 0.268	0.447 ± 0.215	-0.688 ± 0.207	0.137 ± 0.293	-0.796 ± 0.343	-0.242 ± 0.059	0.344 ± 0.416	-0.362 ± 0.420	0.135 ± 0.178

^a Indicates variable was not included in set of variables considered for model.

^b Indicates variable was available to be included in model but was not selected for and given a value of zero.

Table B3 Estimated coefficients ($\beta \pm SE$) by translocated caribou for calving resource selection function models. Standard errors were determined by using Newey-West sandwich variance estimators.

Variable	Translocated Caribou									
	T4	T5	T6	T8	T11	T13	T15	T17	T18	Average
Low Risk	-0.069 ± 0.295	0.711 ± 0.387	0.187 ± 0.307	-0.231 ± 0.133	-0.963 ± 0.692	-0.200 ± 1.581	1.914 ± 0.709	0.065 ± 0.182	-0.078 ± 0.204	0.148 ± 0.265
Elevation	2.787 ± 0.994	1.646 ± 0.353	1.079 ± 0.289	0.701 ± 0.338	1.440 ± 0.632	1.566 ± 0.292	-1.703 ± 0.583	0.737 ± 0.171	1.483 ± 0.555	1.082 ± 0.404
Elevation ²	-1.104 ± 0.583	-0.575 ± 0.279	1.011 ± 0.293	-0.324 ± 0.220	0.061 ± 0.263	0.843 ± 0.157	-2.299 ± 0.823	0.356 ± 0.097	-0.200 ± 0.269	-0.248 ± 0.339
ESSF Parkland	-0.172 ± 0.155	-0.079 ± 0.211	-0.166 ± 0.119	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	-0.139 ± 0.030
ESSF Woodland	NA ^a	NA ^a	NA ^a	NA ^a	1.102 ± 0.316	-0.235 ± 0.142	-0.141 ± 0.501	0.939 ± 0.224	NA ^a	0.416 ± 0.351
ESSF Zone	-0.409 ± 0.278	0.724 ± 0.226	NA ^a	NA ^a	NA ^a	-0.390 ± 0.200	1.498 ± 0.418	NA ^a	-0.348 ± 0.217	0.215 ± 0.386
ICH Zone	NA ^a	NA ^a	NA ^a	0.405 ± 0.304	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	0.405 ± NA
Cut 5-20 years	-0.516 ± 0.142	-0.175 ± 0.202	0.234 ± 0.187	NA ^a	NA ^a	0.292 ± 0.278	NA ^a	NA ^a	0.091 ± 0.256	-0.015 ± 0.149
Slope	-0.978 ± 0.134	-0.969 ± 0.194	0 ± 0 ^b	-1.097 ± 0.164	0 ± 0 ^b	0.130 ± 0.189	-0.454 ± 0.259	-0.689 ± 0.154	-0.367 ± 0.142	-0.492 ± 0.156
South	0.406 ± 0.165	-0.428 ± 0.162	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0.331 ± 0.120	0 ± 0 ^b	0.613 ± 0.136	-0.333 ± 0.136	0.065 ± 0.112
North	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	-0.762 ± 0.327	-1.185 ± 0.213	0 ± 0 ^b	-0.243 ± 0.164
Road Density	0.581 ± 0.278	1.608 ± 0.344	1.223 ± 0.398	0 ± 0 ^b	0.243 ± 0.322	-0.323 ± 0.357	-0.287 ± 0.162	0.133 ± 0.160	-0.273 ± 0.350	0.323 ± 0.230

^a Indicates variable was not included in set of variables considered for model.

^b Indicates variable was available to be included in model but was not selected for and given a value of zero.

Table B4 Estimated coefficients ($\beta \pm SE$) by translocated caribou for summer resource selection function models. Standard errors were determined by using Newey-West sandwich variance estimators.

Variable	Translocated Caribou								
	T4	T5	T6	T8	T13	T15	T17	T18	Average
Low Risk	-0.089 ± 0.176	1.167 ± 0.514	0.478 ± 0.379	-4.506 ± 0.162	0.494 ± 0.321	-0.633 ± 0.399	0.651 ± 0.355	0.641 ± 0.230	-0.225 ± 0.641
Elevation	0.981 ± 0.281	1.483 ± 0.357	0.002 ± 0.330	0.317 ± 0.399	0.138 ± 0.340	1.853 ± 0.529	0.191 ± 0.422	0.875 ± 0.554	0.730 ± 0.241
Elevation ²	-0.407 ± 0.190	0.651 ± 0.206	0.594 ± 0.174	-0.535 ± 0.239	-0.427 ± 0.276	-0.294 ± 0.173	-1.204 ± 0.302	-0.604 ± 0.257	-0.278 ± 0.219
ESSF Parkland	-0.146 ± 0.120	-0.711 ± 0.197	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	-0.429 ± 0.283
ESSF Woodland	NA ^a	NA ^a	-0.806 ± 0.278	NA ^a	NA ^a	-0.141 ± 0.304	NA ^a	NA ^a	-0.474 ± 0.333
ESSF Zone	-0.660 ± 0.149	1.031 ± 0.440	0.330 ± 0.185	0.225 ± 0.144	-0.219 ± 0.397	NA ^a	0.018 ± 0.333	0.255 ± 0.193	0.140 ± 0.197
ICH Zone	NA ^a	NA ^a	NA ^a	NA ^a	0.366 ± 0.363	0.370 ± 0.303	-0.139 ± 0.344	-0.005 ± 0.253	0.148 ± 0.130
IDF Zone	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	0.192 ± 0.203	0.192 ± NA
Cut 0-5 years	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	NA ^a	-0.028 ± 0.170	NA ^a	-0.028 ± NA
Cut 5-20 years	NA ^a	0.577 ± 0.178	NA ^a	NA ^a	-0.125 ± 0.245	NA ^a	-0.567 ± 0.278	NA ^a	-0.038 ± 0.333
Slope	-1.052 ± 0.202	-1.402 ± 0.171	-0.337 ± 0.143	-0.696 ± 0.323	-1.064 ± 0.166	-0.456 ± 0.187	-0.628 ± 0.140	-0.513 ± 0.187	-0.769 ± 0.130
South	0.452 ± 0.101	0 ± 0 ^b	0 ± 0 ^b	-0.456 ± 0.253	0.250 ± 0.102	-0.326 ± 0.220	-0.455 ± 0.196	0 ± 0 ^b	-0.067 ± 0.116
North	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0.228 ± 0.152	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0.029 ± 0.029
Road Density	-0.232 ± 0.141	0 ± 0 ^b	-0.332 ± 0.180	0.305 ± 0.217	-0.597 ± 0.172	0.656 ± 0.194	-0.241 ± 0.285	0 ± 0 ^b	-0.055 ± 0.139

^a Indicates variable was not included in set of variables considered for model.

^b Indicates variable was available to be included in model but was not selected for and given a value of zero.

Table B5 Estimated coefficients ($\beta \pm SE$) by translocated caribou for early winter resource selection function models. Standard errors were determined by using Newey-West sandwich variance estimators.

Variable	Translocated Caribou				
	T5	T6	T17	T18	Average
Low Risk	-0.218 \pm 0.236	-0.449 \pm 0.331	0.873 \pm 0.442	0.611 \pm 0.370	0.204 \pm 0.319
Elevation	0.101 \pm 0.540	-1.838 \pm 0.770	-0.145 \pm 0.383	-2.153 \pm 1.235	-1.009 \pm 0.576
Elevation ²	-1.157 \pm 0.355	-1.482 \pm 0.864	-2.515 \pm 1.543	-0.964 \pm 0.600	-1.530 \pm 0.345
ESSF Parkland	NA ^a	NA ^a	NA ^a	0.662 \pm 0.480	0.662 \pm NA
ESSF Woodland	NA ^a	NA ^a	-0.204 \pm 0.142	0.138 \pm 0.368	-0.033 \pm 0.171
ESSF Zone	0.203 \pm 0.266	0.718 \pm 0.552	0.127 \pm 0.222	NA ^a	0.349 \pm 0.186
ICH Zone	0.096 \pm 0.467	0.410 \pm 0.449	NA ^a	0.174 \pm 0.283	0.227 \pm 0.094
IDF Zone	NA ^a	-1.093 \pm 0.371	NA ^a	NA ^a	-1.093 \pm NA
Cut 5-20 years	NA ^a	NA ^a	NA ^a	0.152 \pm 0.133	0.152 \pm NA
Slope	-1.613 \pm 0.173	-0.084 \pm 0.180	-0.437 \pm 0.160	-0.733 \pm 0.143	-0.717 \pm 0.327
South	0 \pm 0 ^b	1.189 \pm 0.193	-0.181 \pm 0.201	0 \pm 0 ^b	0.252 \pm 0.315
North	0 \pm 0 ^b	-0.349 \pm 0.159	0.457 \pm 0.095	-0.498 \pm 0.173	-0.098 \pm 0.212
Road Density	0 \pm 0 ^b	0.448 \pm 0.179	-0.306 \pm 0.152	-1.101 \pm 0.299	-0.240 \pm 0.326

^a Indicates variable was not included in set of variables considered for model.

^b Indicates variable was available to be included in model but was not selected for and given a value of zero.

Table B6 Estimated coefficients ($\beta \pm SE$) by translocated caribou for late winter 2012/2013 resource selection function models. Standard errors were determined by using Newey-West sandwich variance estimators.

Translocated Caribou				
Variable	T5	T17	T18	Average
Low Risk	0 ± 0^b	0 ± 0^b	0 ± 0^b	0 ± 0^b
Elevation	1.043 ± 0.438	-0.050 ± 0.326	0.266 ± 0.562	0.420 ± 0.325
Elevation ²	-3.214 ± 0.577	-0.691 ± 0.414	-0.946 ± 0.663	-1.617 ± 0.802
ICH Zone	-0.469 ± 0.274	-0.189 ± 0.234	3.764 ± 0.105	1.035 ± 1.367
Slope	-1.190 ± 0.203	-0.513 ± 0.146	-0.212 ± 0.117	-0.638 ± 0.289
South	0 ± 0^b	0 ± 0^b	-0.149 ± 0.114	-0.050 ± 0.050
North	-0.321 ± 0.109	0.192 ± 0.135	-0.662 ± 0.135	-0.264 ± 0.248
Road Density	0.270 ± 0.276	0.311 ± 0.210	0.076 ± 0.645	0.219 ± 0.072

^a Indicates variable was not included in set of variables considered for model.

^b Indicates variable was available to be included in model but was not selected for and given a value of zero.