Influence of disturbances on the movements of female woodland caribou (*Rangifer tarandus caribou*) across multiple spatiotemporal scales

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A thesis

in

The Department

of

Geography, Planning and Environment

Presented in partial fulfillment of the requirements

for the degree Masters of Science (Geography, Urban and Environmental Studies) at

Concordia University

Montreal, Quebec, Canada

April 2012

CONCORDIA UNIVERSITY

School of Graduate Studies

This is to certify that the thesis prepared

By: David Beauchesne

Entitled: Influence of disturbances on the movements of female woodland caribou (*Rangifer tarandus caribou*) across multiple spatiotemporal scales

and submitted in partial fulfillment of the requirements for the degree of

Masters of Science (Geography, Urban & Environmental Studies)

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Abstract

Influence of anthropogenic disturbances on the movements of woodland caribou (*Rangifer tarandus caribou*) across multiple spatiotemporal scales in the boreal forest

David Beauchesne

As human encroachment in natural habitats increases ubiquitously, understanding its impacts on wildlife is crucial. We investigated the impacts of anthropogenic disturbances (i.e. clearcuts and roads) on the movements of the woodland caribou, a threatened species inhabiting the highly managed southern fringe of the boreal forest. We used GPS telemetry data from 49 females followed between 2004 and 2010 in the Saguenay-Lac-Saint-Jean region (Québec, Canada). Space use was evaluated at a coarser scale using individual home-range size as a function of observed disturbance levels within home ranges. Individuals first expanded their home ranges alongside increases in disturbance levels, yet subsequently shifted their behaviour when certain disturbance thresholds were exceeded by contracting home ranges and potentially trapping individuals in sub-optimal habitats. Fine-scale movements were investigated using a use-availability design contrasting observed and random steps (i.e. straight-line segment between successive locations). Individuals, although mostly avoiding disturbances, nonetheless regularly came in close contact with them. As a consequence, females modulated their movements daily and annually, avoiding disturbances predominantly during periods of higher vulnerability (i.e. calving, early and winter) during the day, while using them in periods of higher energy requirements (i.e. spring, summer and rut) during dusk/dawn and at night. Additionally, individuals altered their behaviour depending on the context in which they were moving, either relocating or remaining in altered habitats as disturbance levels increased. Our results suggest that current disturbance levels observed in the boreal forest cause behavioural shifts that may compel females to use suboptimal habitats, likely threatening the persistence of woodland caribou populations in North-American forests.

Acknowledgements/Dedication

This thesis, much more than a mere document, represents a period of my life filled with both passions and struggles, but also – hopefully at least – with a deepened sense of myself as an individual and a scientist. This whole project has undeniably been an adventure, from which I firmly believe I was able to improve my understanding of what being a scientist truly represents. I also feel that it allowed me to gather inestimable tools for which I will be greatly thankful in any future project I may be part of. Yet behind any achievements there lie hidden numerous influential colleagues, friends and family members who provided much needed support and this project is no exception. I therefore wish to write this section in order to extend my warmest gratitude to all the people who helped me along the way.

First and foremost, I wish to thank both my supervisors, Jochen and Martin-Hugues, without whom this project would not have been possible. I learned a lot through our countless exchanges and I am immensely grateful for your support and the opportunity you gave me. I would also wish to extend a particular thank to Martin-Hugues, who believed in me and sought me out for this master's project. Without you, I would not be writing these acknowledgments today.

I am also greatly thankful to the members of my examining committee, Dr. Chris Johnson and Dr. Robert Weladji. They provided valuable helpful comments and suggestions, both at the onset and the end of my project.

I also wish to thank Alain Caron and Marc Mazerolle for their help in all the spatial and statistical analyses I had to perform throughout this project. It still amazes me to this day how I could spend a week trying to solve a technical problem, yet all I had to do was expose the problem to them and within one short e-mail they were able to provide a solution.

Countless valuable moments with colleagues and friends also shaped my degree: Solène, Limoilou, Fred, Mathieu, Rémi, William, Martin, Rob, Magdalena, Francisco and Paul. Thank you for your presence and all the exchanges we had, whether serious or hilarious! I also wish to thank my friends from Ultimate Frisbee. I continued practicing sports intensively throughout my master`s and I believe that the sport as much as the people I played it were partly responsible of my focus on my research by providing an outlet every time I entered the field or the gym. My family also played a role throughout my degree, by encouraging me in whatever project I decide to begin, whether they fully agree or not. Thank you Chantal, André and Gilles for your support!

Lastly, I wish to thank my girlfriend Arran, who has followed me through the better part of my degree. I want you to know how grateful I am for your patience, comprehension, support, presence, sense of humor and simply for being who you are! I can fully appreciate how intense the last 2 years and a half of my life have been and it amazes me how you were able to cope with all the periods when I was not fully present (both physically and mentally!). This project would have been much harder if it had not been for you. Thank you!

To all, whether I have named you here or if you were involved in my master's, this thesis is a testament to the help each of you gave me in your very own manner and I deeply appreciate it in ways I cannot properly express into words!

– David

Table of Contents

List of Figures

List of Tables

List of Equations

Chapter 1. Introduction

The current worldwide rate of biodiversity loss can be mainly attributed to over-exploitation of wildlife populations, introduction of invasive species, diseases, climate change and anthropogenic disturbances, mainly through habitat alteration, resource exploitation, and human settlement (White *et al.* 2009). Public concern is now focused on human impacts on wildlife, of which habitat loss and fragmentation are predominant factors affecting biodiversity loss (Fahrig 1997, 2003). Conservation strategies are therefore needed in order to offset such impacts on animal populations. Threatened species however often inhabit environments of economic interest (e.g. forest harvesting and mining; Seip 1998) and conservation strategies in such areas should ideally be economically viable while still benefiting the overall ecology of the system. The North American boreal forest is currently faced with this issue due to forest-harvesting targeting undisturbed forest, with which many species are strongly associated (e.g. Burton *et al.* 1999; McRae *et al.* 2001; Courtois *et al.* 2007a).

A sustainable forest management approach has recently been proposed for species found in the boreal forest in an effort to combine forest harvesting alongside conservation strategies for multiple wildlife species (Seip 1998; Courtois *et al.* 2003a). This ecosystem approach aims at managing the ecosystem using silvicultural techniques emulating an ecosystem's dominant natural disturbance regimes (e.g. forest fires and insect outbreaks; McRae *et al.* 2001; Hebert *et al.* 2003; Fenton *et al.* 2009). The approach acts at a coarse-filter level through strategies aiming to retain the overall landscape structure and vegetation diversity within forest stands. It also further aims at preserving diversity of forest stands at the landscape level, in the same manner as would be expected under a natural disturbance regime. These actions could thus potentially enable the conservation of species associated with undisturbed forest (Noss 1987; Hebert *et al.* 2003). A fine-filter level also exists, with the focus centered on the requirements of indicator species (e.g. species characteristic of environmental conditions found in a given system) that are threatened or of some cultural importance (Noss 1983, 1987). Additionally, species with extensive habitat ranges are interesting targets for such a management strategy, since protecting their habitat could potentially protect the habitat of other species (i.e. umbrella species; Simberloff 1998) and many are being targeted for fine-filter conservation strategies, e.g. trumpeter swan (*Cygnus buccinator*) and woodland caribou (*Rangifer tarandus caribou)* in Alberta (Dyer 2004).

Conservation strategies focusing on a particular species require a thorough understanding of the species' population dynamics (Hebert *et al.* 2003). Since anthropogenic disturbances vary spatiotemporally and induce responses that are scale-specific, knowledge on the species must also cover different spatiotemporal scales. The Biological Scales of Impacts (Figure 1.1; Johnson and St-Laurent 2011) is a useful framework for understanding the impacts of anthropogenic development on wildlife through spatiotemporal and biological scales. Impacts on animal populations should be primarily perceived at the individual level through modifications in behaviour (e.g. avoidance of disturbed areas) and be followed by increases in energy expenditure as organisms modify their movement patterns (Johnson *et al.* 2002). Forage intake could then be reduced due to these behavioural changes and decreases in body condition might follow (Chan-McLeod *et al.* 1999), potentially leading to community-level alterations by decreasing survival and reproduction rates of organisms (Johnson and St-Laurent 2011).

Large-scale population dynamics could thus be affected by variations in individual interactions with their environment at finer spatiotemporal scale. Understanding the Biological Scales of Impacts is crucial when studying how individuals and populations are affected by modifications of their environment.

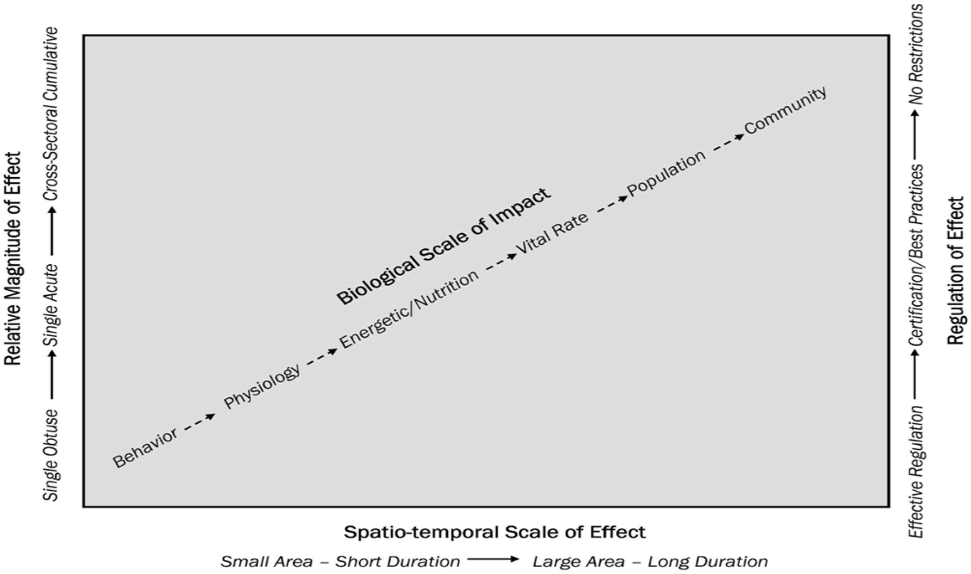

Figure 1.1 – Biological Scales of Impacts (from Johnson and St-Laurent 2011)

The threatened populations of woodland caribou in North-America offer a good opportunity to study multi-scale impacts of a highly managed boreal forest (mainly through forest harvesting activities) on wildlife behaviour. Traditionally evolving in the boreal forest under a natural disturbance regime dominated by fires, windthrows and insect outbreaks (Hins *et al.* 2009), caribou range suffered severe constrictions as a result of clearing for forest products and agriculture. Many remnant populations are now inhabiting areas with intensive forest harvesting while declining throughout the majority of the sub-species' range (Vors and Boyce 2009). Defining specific management strategies is therefore an important challenge in order to ensure the future persistence of woodland caribou in the boreal forest (Courtois *et al.* 2003a). A lot of research has been conducted on the broad-scale effects of anthropogenic disturbances on woodland caribou population dynamics (e.g. Sorensen *et al.* 2008; Vors and Boyce 2009), although knowledge is still lacking in order to accurately predict the impacts of harvesting practices on populations (Sleep and Loehle 2010). There is also an increasing amount of literature available on fine-scale behavioural responses to habitat alteration and disturbance (e.g. Dyer *et al.* 2002; Gustine 2005; Faille *et al.* 2010).

Although past studies are informative, our understanding of ungulate behaviour (in general) and caribou response (in particular) to heterogeneous landscapes is still incomplete. Many habitat selection studies have been conducted using Resource Selection Function (RSF) analyses (e.g. Fortin *et al.* 2008; Courbin *et al.* 2009), defining habitat availability as the amount of resource accessible to the organisms while building on the assumption that the whole landscape under study is accessible to individuals (Manly *et al.* 2002). Nevertheless, disturbances can modify habitat accessibility and connectivity, both related to the movements of individual animals (Jaeger 2007; Eigenbrod *et al.* 2008); often, these parameters are not taken into account in RSF analyses (but see Johnson et al. 2002).

While providing useful information on individual landscape and habitat use, the study of habitat selection provides little insights on the underlying processes, (but see Dyer *et al.* 2002; Laurian *et al.* 2008 for examples). The distributional patterns observed in habitat selection studies are a result of individual movements (Dyer *et al.* 2002, Fauchald and Tverra 2003) and it is therefore important to improve our understanding of how organisms move through their habitat in order to fully understand their behaviour and guide our management and conservation strategies. St-Laurent *et al.* (2009) demonstrated that landscape features such as roads and watercourses can be important variables when analyzing wildlife response to habitat alteration. Accordingly, studies conducted on wildlife habitat use in heterogeneous landscapes have found that static features (e.g. roads) can affect movement behaviour such as the speed of travel, tortuosity and clustering of movement by acting as barriers (e.g. Turchin 1998; Dyer *et al.* 2002; Coulon *et al.* 2008). Furthermore, the presence of linear features can facilitate movements for alternative prey species, predators, and humans, thus augmenting caribou vulnerability via increased encounter probabilities with predators (Bergerud et al. 1984; Bergerud 1985; Dyer *et al.* 2002). Conversely, certain natural barriers such as water bodies and high elevations can be used by caribou to decrease encounter probabilities with predators as they are often avoided by those species (Bergerud *et al.* 1984; Bergerud 1985).

How woodland caribou move in the landscape in relation to different disturbance types will ultimately dictate how they use their habitat. Studying animal movements should provide a more thorough understanding of their responses to habitat alterations and are expected to provide additional guidelines for management strategies. Furthermore, potential thresholds to the amount and configuration of different barrier types tolerable by woodland caribou could provide key values to implement in those strategies.

Chapter 2. Literature review

2.1 Woodland caribou

The woodland caribou found in North-America is one of the eight sub-species of the circumpolar European reindeer and the North-American caribou (*Rangifer tarandus*), which was traditionally divided into distinct ecotypes defined as a population or group of populations that evolved different mechanisms to deal with different environments and limiting factors (Courtois *et al.* 2003b; COSEWIC 2011), albeit being part of the same species. The woodland caribou (hereafter caribou) evolving in the boreal forest is distributed discontinuously principally south of the 52nd parallel; in Québec, it can be found between the 49th and 55th parallel. This ecotype lives at low densities (1 to 3 individuals / 100 km^2) and only undertakes short migrations (< 50 km) (Courtois *et al.* 2003b). It is also closely associated with old-growth forest (Schaefer 2003; Hins *et al.* 2009). The caribou has received much attention in contemporary literature due to its vulnerability, with most of the monitored populations declining over the last few decades (Rettie and Messier 1998; Vors and Boyce 2009; Festa-Bianchet *et al.* 2011). It is also confronted with a high number of limiting factors in its environment (e.g., predation and anthropogenic disturbance; Mallory and Hillis 1998). The woodland caribou has thus been attributed the status of threatened species in Canada in 2002 (COSEWIC 2011) and vulnerable species in Québec in 2005 (MRNF 2010). Furthermore, the boreal caribou, which comprises the woodland caribou described above, has recently been added as 1 of the 12 Designatable Unit of significance in North-America (COSEWIC 2011)

Multiple hypotheses have been suggested since the middle of the 20th century to explain observed caribou population declines: over-harvesting and poaching (Bergerud

1974), increased predation (Bergerud 1974; Seip 1991, 1992), transmission of diseases (Bergerud 1985) and anthropogenic disturbances, essentially human settlement and forestry activities (McLoughlin *et al.* 2003; Schaefer 2003). The traditional range occupied by woodland caribou has gone through major alterations (Schaefer 2003; Vors *et al.* 2007; Vors and Boyce 2009; Festa-Bianchet *et al.* 2011). For instance, the range of woodland caribou in Ontario has been halved over the last century with an approximate regression rate of 34 km per decade since 1880, which is closely related to human settlement and forest harvesting (Bergerud 1974; Schaefer 2003; Vors *et al.* 2007). Those activities have led to the loss and fragmentation of old-growth forest inhabited by woodland caribou, and an important proportion of their range in North America is still located in actively harvested ecosystems (Shaefer 2003; Vors *et al.* 2007; Hins *et al.* 2009). Although other species' range regressions can be attributed to global climate change (e.g. birds and butterflies; Schaefer 2003), the rate of caribou population extirpation is much faster than what climate change has induced in other species. Climate change is thus unlikely to represent a major factor contributing to observed caribou range regression (Vors *et al.* 2007; Vors and Boyce 2009; Festa-Bianchet *et al.* 2011).

Predation is acknowledged as the most important limiting factor affecting caribou populations, especially from wolves (*Canis lupus*) and bears (*Ursus spp*.; Bergerud and Page 1987; Seip 1991; Serrouya and Wittmer 2010). Because caribou are especially vulnerable to predation and have low reproductive productivity compared to other ungulates (Bergerud 1974), they use an anti-predation strategy that consists of using habitats that are less frequented by predators, alternative prey species, and conspecifics (spacing out strategy; Bergerud and Page 1987; Seip 1991, 1992). This strategy renders them more inconspicuous to predators, which lowers predation rates and enables caribou to survive at low densities throughout the boreal forest (Bergerud and Page 1987; Seip, 1992; Ferguson and Elkie 2004). This anti-predation strategy is however rendered less effective in areas where predators are sustained by alternative prey species (e.g. moose *Alces alces* and deer *Odocoileus spp.*; Seip 1992). Species like moose and deer, historically absent from caribou range, are more productive and can sustain wolf populations at higher densities. This naturally places caribou in apparent competition with these alternative prey species (Seip 1991, 1992). Human-made disturbances have however exacerbated this natural process by increasing the spatiotemporal overlap between caribou and those species by increasing the amount of young forest stands in the boreal forest so that an increasing part of caribou range is now located in multi-prey environments (Harrington *et al.* 1999; Vors and Boyce 2009). Accordingly, clearcuts have been found to be a good predictor of woodland caribou extirpation. For example, Vors *et al.* (2007) showed that caribou in Ontario are avoiding cutovers and that extirpation usually occurs ~20 years following forest harvesting, a time lag associated with the necessary amount of time for moose densities to increase. Furthermore, bears are also attracted by recently harvested sites because of the abundance of berries found in regenerating habitats, increasing the encounter probabilities with caribou and opportunistic predation, especially on calves (Gustine *et al.* 2006; Bastille-Rousseau *et al.* 2011). Depensatory predation thus arises, with predators unaffected by decreases in caribou density due to alternate food sources (Bergerud 1985; Seip 1991, 1992; Rettie and Messier 2000), closely linking anthropogenic disturbances to modifications in predator-prey dynamics (Hebblewhite 2008).

In order to get as much nutrient intake as possible in critical periods, population dynamics of caribou is also strongly cued to plant phenology (Vors and Boyce 2009). This is especially important for parturient females during spring and early summer when they are at their lowest body condition of the year and lactation requires a lot of energy (Chan-McLeod *et al.* 1999; Barten *et al.* 2001). By spacing out, woodland caribou are able to decrease predation risk, albeit at the price of lowered forage quality and increased uncertainty associated with open habitats (Sih 1992; Barten *et al.* 2001). Since both forage and protection from predation are important for caribou, a trade-off decision is expected between predator avoidance and use of habitats with higher forage quality in an effort to optimize both factors simultaneously (Barten *et al.* 2001; Gustine 2005).

2.2 Landscape fragmentation and habitat fragmentation

Landscape fragmentation has been a subject of growing interest for a few decades and there are now multiple definitions and methods used to describe it (see Fahrig 2003 for a review). Landscape fragmentation can be defined as the presence of obstacles against the movement of organisms (functional) and as a disruption of ecological interrelations between different locations (structural; Chetkiewicz *et al.* 2006). These definitions highlight the fact that landscape structure is composed of different land cover types (determining landscape composition) along with a certain spatial arrangement of those types (landscape configuration). Landscape fragmentation can be anthropogenic (e.g. roads and urban areas), but it can also be natural, or geogenic (e.g. rivers and fires; Jaeger 2000). Landscape fragmentation and habitat fragmentation are two closely linked but separate notions that need to be discerned. Since habitat is species-specific (Hall *et al.*

1997), organisms' responses to disturbances will be species-specific as well, so that loss and fragmentation of habitat for a particular species can on the contrary imply an increase in habitat connectivity for another species (Fischer and Lindenmayer 2007). Landscape fragmentation, on the other hand, is concerned with the cumulative amount of disturbances impacting a particular geographic area, regardless of any particular living organism (Chetkiewicz *et al.* 2006).

Habitat loss and fragmentation are also closely linked. Their respective influence on wildlife can vary both in direction and intensity, and managing them independently is possible to some extent (Smith *et al.* 2009). The fact that they are closely linked however renders their distinction challenging when conducting spatial analyses. Habitat loss results in an overall decrease in a particular habitat's original representation in the landscape, combined with the increase of another habitat type (i.e. change in landscape composition; St-Laurent *et al.* 2009). Habitat fragmentation *per se* is defined as "the breaking apart of habitat after controlling for habitat loss" (i.e. landscape configuration; Fahrig 2003). There have been attempts to partition the effects of loss and fragmentation using different statistical tools such as classical variance partitioning (Barbaro *et al.* 2007), hierarchical variance partitioning (Radford and Bennett 2007), residual regression (Debuse *et al.* 2007), multimodel inference using summed AIC weights and averaged coefficients (Yates and Muzika 2006), and traditional variable selection (Reunanen *et al.* 2002). However, these approaches have so far been found to include biases associated with the methods used, which makes it difficult to compare results (see Smith *et al.* 2009 for a review of methods). For example, certain types of analysis frequently cause an underestimation of suppressor variables (i.e. variables with conflicting or inverse effects;

Smith *et al.* 2009). The distinction between habitat loss and fragmentation can become quite important, because of their respective influence on wildlife, and their distinction can also be essential for landscape planners, especially when considering the management of threatened species (Smith *et al.* 2009; St-Laurent *et al.* 2009). Nonetheless, there is no acknowledged method to solve this problem, but the subject is an ongoing discussion in the literature.

For the purpose of this study, habitat fragmentation will be defined as the reduction of connectivity within a landscape (With *et al.* 1997; Jaeger 2007). Landscape connectivity refers to "the degree to which landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1997). Since the concept of connectivity is scale- and species-specific (Tischendorf and Fahrig 2000; Jaeger 2007), landscape connectivity will be referred to as habitat connectivity in order to avoid any confusion, because of the distinction made between landscape and habitat fragmentation. Connectivity also highlights that barriers can exhibit a certain degree of permeability that ranges from no barrier effect to complete impermeability.

2.3 Impacts of landscape fragmentation

Anthropogenic disturbances such as forest harvesting and human settlement act cumulatively to impact wildlife (St-Laurent *et al.* 2009). The resulting habitat loss is acknowledged as having more severe impacts on population dynamics than habitat fragmentation *per se*. The influence of fragmentation seems less acute, even if significant, and its impacts have been reported to be both negative and positive in some cases (Fahrig 2003; Fischer and Lindenmayer 2007; St-Laurent *et al.* 2009). At the population level, alteration of habitat can lead to an isolation and fragmentation of populations into smaller and more vulnerable subpopulations, which in turn are more susceptible to stochasticity and natural stress factors, increasing the probability of local extinction (Fahrig 2003). Landscape fragmentation can also lead to the permanent extirpation of populations, e.g., when recolonization of habitats is not possible (Fahrig 1997, 2003; Jaeger and Fahrig 2004). On a finer spatiotemporal scale, physiology and behaviour can also be affected by landscape fragmentation. Loss of accessibility to high-quality habitats can force organisms to use less suitable habitat or make more extensive movements in order to access suitable habitat (Eigenbrod *et al.* 2008), resulting in increases in energy expenditure and decreases in individual body condition (Chan-McLeod *et al.* 1999). Furthermore, the evaluation of the impacts of habitat loss and fragmentation on wildlife can potentially be biased when habitat connectivity is not considered in the analyses (Eigenbrod *et al.* 2008). Landscape configuration and the organisms' movement capacities are therefore paramount when studying the influence of landscape alterations on individual habitat use.

2.4 Impacts of disturbances

The presence and configuration of many static features in the landscape affect wildlife and may act as barriers to their movement, drastically reducing connectivity of habitat patches (Jaeger 2007; St-Laurent *et al.* 2009). This section discusses the impacts of natural (e.g. water bodies, topography lines, snow accumulation, fires, windthrows and insect outbreaks) and anthropogenic (e.g., roads, clearcuts and human settlements) barrier types on wildlife, focusing mainly on caribou populations and secondarily on ungulate species in general where information on caribou response is not available.

2.4.1 Natural disturbances

Woodland caribou have evolved in a dynamic ecosystem shaped by natural disturbances. Individuals have naturally adapted to such disturbances by mostly avoiding those resulting in deforestation (i.e. fires, windthrows and insect outbreaks; Gustine and Parker 2008; Faille *et al.* 2010), while taking advantage of other natural features (e.g. water bodies and elevation; Bergerud *et al.* 1984; Rettie and Messier 2000). Natural disturbances resulting in deforestation may impact caribou in the same manner as clearcuts do (Fischer and Wilkinson 2005; Brodeur *et al.* 2008), yet mostly in areas where anthropogenic disturbance levels are quite low (Faille *et al.* 2010). Individuals have been known to abandon parts of their range for up to 55 years following large wildfires (Schaefer and Pruitt 1991), which is roughly similar to the 60-year period of abandonment associated with logged areas (Courtois *et al.* 2007a). Even though such disturbances seem to redistribute caribou within their range, they do not appear to have population level consequences (Dalerum *et al.* 2007). This seems to be mainly due to large home ranges that allow individuals to naturally avoid those areas (Fisher and Wilkinson 2005).

Some natural features of the landscape, although not considered as disturbances, have been found to affect wildlife movements (e.g. topography and water bodies), yet seem to be used by caribou. For instance, some females typically calve on islands, using water bodies as barriers to the movements of predators, alternative prey species, and conspecifics, as part of their spacing out strategy (Bergerud 1985; Rettie and Messier 2000). Females using high elevation calving sites in mountainous terrain also have been found to use topography as a way to enhance their anti-predation strategy (Bergerud *et al.* 1984; Poole *et al.* 2000; Gustine 2005). As predators such as wolves typically move at low elevation valley bottoms, the use how higher elevations could enable females decrease risks of encounters while increasing their efficiency to detect predators (Bergerud *et al.* 1984; Coulon *et al.* 2008; Skarin *et al.* 2010). Furthermore, movement paths of wildlife species were found to follow the topography of the landscape (roe deer; Coulon *et al.* 2008; cougar; Dickson *et al.* 2005; elk; Kie *et al.* 2005). An individual moving up- or down-slope will expend more energy and following topography could be a more efficient movement strategy (Leblond *et al.* 2010). Moose preferentially use valley bottoms (Dussault *et al.* 2007; Laurian *et al.* 2008), making it unlikely for caribou to exhibit the same kind of selection due to their spacing out strategy (Gustine 2005). Winter snow accumulation could also affect movements as snow accumulates throughout the winter, eventually causing a decrease in winter home range size and a decrease in movement rates (Bradshaw *et al.* 1997; Stuart-Smith *et al.* 1997; Smith *et al.* 2000).

2.4.2 Anthropogenic disturbances

Considering the ubiquitous increase of anthropogenic disturbances in the boreal forest (Cyr *et al.* 2009), this study primarily focused its attention on the impact of anthropogenic disturbances. They represent a broad category of features that may drastically impact wildlife populations across all biological scales, including permanent and temporary features as well as human activities, whether economical or recreational.

For this study, we decided to focus our review on the impact of permanent and temporary anthropogenic features found in our study area, i.e. roads and clearcuts.

2.4.2.1 Roads

The transportation infrastructure is one of the most prominent anthropogenic features acting as a barrier to wildlife movements (Jaeger 2007; Fahrig and Rytwinski 2009). Primary impacts of roads on wildlife include increases in mortality through wildlife-vehicle collisions, reduced permeability, increases in landscape fragmentation, and decreases in the amount and quality of neighbouring habitats (Forman and Alexander 1998; Spellerberg 1998; Fahrig and Rytwinski 2009). Wildlife species can also be impacted at the individual level through an increased avoidance of roads due to noise, smell, road surface and traffic (Jaeger *et al.* 2005; Fahrig and Rytwinski 2009). When individuals cannot cross roads (e.g., due to complete avoidance, road mortality or physical impermeability of the road), habitat on the other side of the road can be inaccessible and effectively lost, and populations subdivided into sub-populations with higher extinction probabilities (Dyer *et al.* 2001).

Depending on the species, the type of road and its context, impacts of roads on wildlife can vary (Hebblewhite 2008). Species like caribou with a low productivity and extensive home ranges are more likely to be affected by the presence of roads than other species (Alexander and Waters 2000; Fahrig and Rytwinski 2009). Furthermore, it has also been discussed that the woodland caribou may be particularly vulnerable to the presence of roads due to their sedentary behaviour (Dyer *et al.* 2002). This would make it more difficult for individuals to avoid roads located within their home ranges (Dyer *et al.*

2002). Roads and other linear features (e.g. seismic lines) can also induce an increase in the interactions between humans and predators with caribou by increasing accessibility to different parts of the landscape. This can render the presence of caribou more predictable due to range constriction, effectively compromising their spacing out strategy (Dyer *et al.* 2002; Hebblewhite 2008). For example, wolves have been found to use roads during certain periods of the year (Gurarie *et al.* 2011; Whittington *et al.* 2005, 2011; Tremblay-Gendron 2012)

Studies conducted so far on the impact of roads on ungulates have mainly been focused on road avoidance behaviour. Ungulate species typically tend to avoid areas that are in close proximity to roads, as the influence of roads extends beyond their immediate location for certain species (Dyer *et al.* 2002; Coulon *et al.* 2008; Laurian *et al.* 2008). Conversely, road crossings are observed much less often than expected by chance (Alexander and Waters 2000; Dyer *et al.* 2002; Laurian *et al.* 2008). For instance, woodland caribou were found to cross roads six times less often than expected (Dyer *et al.* 2002) and moose were found to cross highways and forestry roads respectively sixteen and ten times less often than expected by chance (Laurian *et al.* 2008). Furthermore, crossing rates can also differ daily and seasonally in response to certain limiting factors (e.g. road traffic or resource requirements; Dyer *et al.* 2002; Dussault *et al.* 2007; Laurian *et al.* 2008). It is however interesting to note that certain ungulate populations have been found to stay closer to roads and other anthropogenic features potentially as a way to avoid predation pressure (e.g. moose in Yellowstone Ecosystem, Berger 2007; elk in Banff National Park, Hebblewhite and Merrill 2008; elk in Yoho National Parks; Rogala *et al.* 2011).

2.4.2.2 Clearcuts

Forest harvesting creates early-seral forest stands that can lead to habitat loss for certain species, while conversely creating preferential habitat for others. Some species do not respond in any particular way to harvested areas (white-tailed deer; Campbell *et al.* 2004), while others, such as caribou, are more severely impacted (Chubbs *et al.* 1993; Smith *et al.* 2000; Schaefer and Mahoney 2007). For woodland caribou, logging results in habitat loss that can last up to 60 years (Courtois *et al.* 2007a) and creates a hostile matrix through the increase in densities of predators and their alternative prey (Dussault *et al.* 2005; Brodeur *et al.* 2008; Houle *et al.* 2010). Caribou have been found to move away from logged areas during and after timber removal (Chubbs *et al.* 1993; Smith *et al.* 2000; Shaefer and Mahoney 2007). In general, however, the impact of anthropogenic disturbances is much more pronounced while logging activities are occurring (Hebblewhite 2008). Such displacements can ultimately lead to an increase in movement rates and home range sizes over a short time period (Chubbs *et al.* 1993; Smith *et al.* 2000; Courtois *et al.* 2007b) as individuals move away from disturbances. As harvesting becomes more intensive and it becomes harder for individuals to avoid logged sites, however, movement rates may decrease and ultimately jeopardize the spacing out strategy used by caribou, thus linking avoidance behaviour with observed population declines (Smith *et al.* 2000; Hebblewhite 2008).

Shifts in habitat selection may also be observed as a result of forest harvesting (Chubbs *et al.* 1993; Schaefer and Mahoney 2007). Those shifts could potentially be of great consequences for caribou since their preferential habitat, the old-growth forest, is the same forest type that is harvested (Courtois *et al.* 2008). For instance, females in Alberta were found to select more softwood forests when logging occurred, whereas that habitat type was previously used in proportion to availability (Smith et al. 2000). Furthermore, as clearcuts are spatially associated with mature forest remnants (such as linear strips or blocks), caribou may consequently be compelled to spend more time in unsuitable habitat as they need to cross clearcuts in order to reach their preferential habitat (Hins *et al.* 2009). Home range fidelity also decreases as disturbances grow in importance in the landscape, although individuals nonetheless still have a tendency to remain in altered habitats as disturbance levels increase (Courtois *et al.* 2007b; Faille *et al.* 2010). These kinds of factors can result in a decrease in the productivity and survival of wildlife populations (Fahrig 1997, 2003; St-Laurent *et al.* 2009).

2.4.2.3 Synergistic impacts of anthropogenic disturbances

Anthropogenic disturbances have been found to combine synergistically when impacting wildlife populations (Dyer *et al.* 2002; Coulon *et al.* 2008). For example, Coulon *et al.* (2008) found that roe deer's avoidance of roads and human settlements was higher when both features were located in proximity. Dyer *et al.* (2002) also found that pipelines, when present as a single barrier, do not hinder movements of caribou, but when parallel to roads induce heightened avoidance behaviour. However, most studies have focused primarily on a single particular feature in the landscape without incorporating additional barriers found in the area (see Fortin *et al.* 2005 for examples). Some landscape features might also be associated with a higher degree of avoidance or decreased crossing rates (Coulon *et al.* 2008) and the identification of those features might lead to a better understanding of what drives caribou movements and where mitigation measures should be implemented. Furthermore, impacts of barriers discussed in the literature focus mainly on the avoidance behaviour of individuals (e.g. Dyer et al 2002; Laurian et al. 2008). Very few studies have looked at the actual influence of landscape structure on movement parameters of ungulates such as movement rates, speed, tortuosity of movement and step selection (but see Bradshaw *et al.* 1997; Smith *et al.* 2000; Johnson et al. 2002).

2.5 Movement analysis

Population densities at a particular location at one point in time result from births, deaths and movement or dispersal of organisms (Hanski 1998). As discussed by Turchin (1998), the first two are quite easily analyzed. The study of movement, however, is much more complex, since it varies spatially and temporally. Landscape use can vary with both spatial and temporal scales with respect to varying behavioural state of organisms and changing environmental conditions (e.g. Hebblewhite and Merrill 2008; Godvik *et al.* 2009; Hins *et al.* 2009). For example, numerous species modify their behaviour annually (e.g. Hebblewhite and Merrill 2008; Hins *et al.* 2009), but also over the span of a single day (e.g. Godvik *et al.* 2009; Skarin *et al.* 2010; Bjørneraas *et al.* 2011), reflecting different behaviours in response to different factors. Relevant scales in the study of species habitat selection were classically considered under a framework developed by Johnson (1980), considering habitat selection through a series of hierarchical scales. Accordingly, species are expected to respond to their habitat in a hierarchical spatiotemporal manner, responding to different limiting factors at different scales (Rettie and Messier 2000). Studying only a single scale could thus leave out habitat associations at other scales (Mayor *et al.* 2009).

The challenge of conducting movement studies is also much more complex when dealing with far-ranging species inhabiting in heterogeneous environments, which is why early studies on movement mainly focused on insects (Johnson *et al.* 1992; Turchin 1998). However, the study of movement in heterogeneous landscapes can give relevant information on the distribution of individuals in space and time and can be used complementarily with classic habitat selection in order to better understand the patterns observed (Leblond *et al.* 2010). With the arrival of GPS telemetry and similar technologies, it has become possible to study movements of far-ranging animals much more accurately and efficiently than what could be achieved in the past (Bascompte and Vilà 1997; Chetkiewicz 2006).

Animal movement has typically been simulated and analyzed using random walks (Benhamou 2007). Even though the use of random walks has provided important insights on the movements of individuals in homogeneous environments (Turchin 1998), its use may be insufficient when trying to emulate movement patterns in complex environments where animals modify their movements in response to landscape heterogeneity (Viswanathan *et al.* 1999; Fauchald and Tveraa 2003; Benhamou 2007).

Therefore, a series of methods have been proposed in order to study fine-scale movement including fractal analysis (Bascompte and Vilà 1997; Webb *et al.* 2009), first passage time (Fauchald and Tveraa 2003), hidden Markov models (Franke *et al.* 2004), identification of different movement types (e.g. intra-patch and inter-patch; Johnson *et al.* 2002; Benhamou 2007), and mixtures of random walks (Morales *et al.* 2004) and correlated random walks (Mårell *et al.* 2002). Analyses can now be performed based on the observation of complete pathways and their comparison with environmental cues (Turchin 1998). Animal behaviour could also be seen as a coarse-scale representation of wildlife movement and can be described using parameters such as home range size, movement rates, and overlap among conspecifics (Ims *et al.* 1993; Andreassen and Ims 1998).

2.6 Research context

The data used for the analyses was obtained from 49 female caribou that were captured between 2004 and 2010 (see Table 2.1 for more details on number of individuals per year per area) using net-gunning from a helicopter (Potvin and Breton 1988) and monitored using GPS (Global Positioning System) collar receiver (Lotek® models 2200L and 3300L and Telonics TGW-4680). The area where captures were performed is located in the boreal forest in the Saguenay Lac St-Jean and Côte-Nord regions in Québec, Canada, and consists of two sections (Figure 2.1). The southern section is located in the lake Portneuf zone (49°30'N, 70°30'W) and covers approximately 10 496 km^2. The second section is located in the lake Piraube zone (50°50'N, 71°50'W) and covers approximately 20 564 km^2. Caribou were captured every spring since 2004 in the Portneuf area and since 2005 in the Piraube area and were recaptured every one or two years depending on the programming and the battery pack in order to download locations. Collars were also recovered following the death of an individual or the failure of the collar. Depending on study area and collar models, receivers were programmed to obtain a location every 1, 2, 3, 4 or 6 hours. Only locations with a dilution of precision lower than 10 were kept in order to assure a location precision less than 20 meters (Dussault *et al.* 2001). Landscape attributes that were used in the analyses were obtained from digitized ecoforest maps provided by the Ministère des Ressources naturelles et de la Faune du Québec dating from 2004 to 2009.

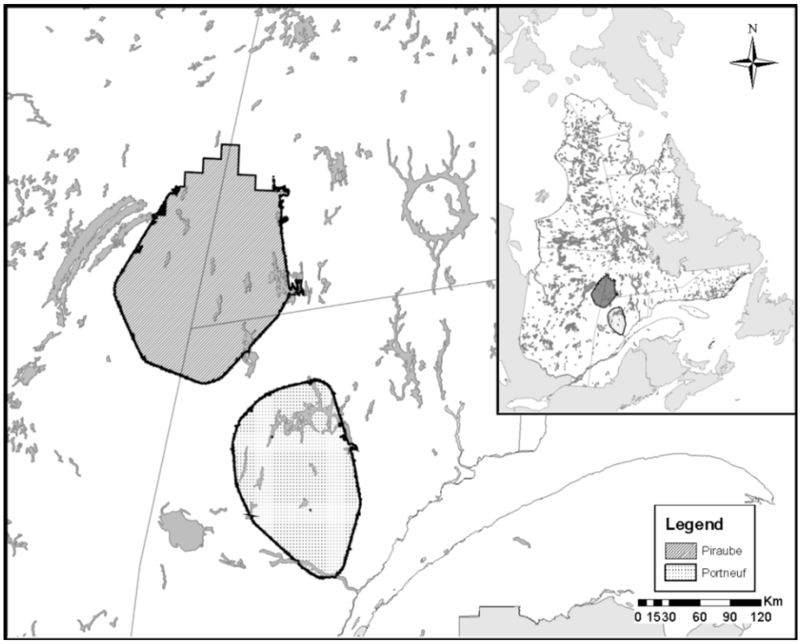

Figure 2.1 – Figure of the study area with the two zones delimited using 100% minimum convex polygons based on all telemetry locations collected between 2004 and 2010 and an extra buffer zone of 10km.

Table 2.1 – Details on the number of individuals captured, recaptured and removed (death, removed or not spotted) from both study areas with the total number of individuals (***n***) monitored each year. All individuals are females unless otherwise mentioned.

	Portneuf area				Piraube area			
Capture period	Capt.	Recapt.	Individuals removed	***n***	Capt.	Recapt.	Individuals removed	***n***
2004-03-17	18			24				
2004-04-01	6[a]							
2005-03-04	3	10	8	19				
2005-03-16	3[b]	3	3[c]					
2005-04-06					6			6
2006-03-05	1	4	2	18				
2006-03-10	1	12	2					
2006-03-13					3	3	3	6
2007-03-31	3	4	2	20				
2007-04-01	4	8	1					
2007-07-11		1						
2007-xx-xx						4	2	4
2008-03-11	6	8	2	20				
2008-03-06	2	4	3					
2008-03-17					7	3	1	10
2009-03-12		13		20				
2009-03-10		7						
2009-xx-xx						10		10
Total number of animal-years				121				36

[a] 3 females and 3 males
[b] 3 females
[c] 3 males

2.7 Research objectives

The main objective of this study was to investigate the impact of anthropogenic (i.e. mainly roads and clearcuts) and natural (i.e. fires, windthrows and insect outbreaks) disturbances on the movements of species inhabiting highly managed habitats across multiple spatiotemporal scales, using the woodland caribou as a biological model. Caribou habitat selection is known to be a hierarchical process (Rettie and Messier 2000) and we believed that individual habitat use would follow a similar pattern. A minimum of two spatial scales were thus needed in order to verify this. The global purpose of this study was thus sub-divided in two research objectives:

1. to analyze the influence of anthropogenic and natural disturbances on the coarse-scale space use behaviour of caribou using variations in home-range size as a function of the amount of different types of disturbances included in them.

2. to study the fine-scale movements of caribou when individuals are moving through or close to anthropogenic disturbances using a use-availability design contrasting observed movements with immediate habitat availability. Natural disturbances were left out of the fine-scale analysis in order to primarily focus on the influence of anthropogenic features.

We used measured variation in home-range size in relation to changing disturbance levels in order to characterize coarse-scale space use. Home-range size can be used as a proxy of space use (Andreassen *et al.* 1998) and has also been used by other studies done in our system (e.g. Hins *et al.* 2009; Faille *et al.* 2010).

We used Step Selection Functions (SSF; Fortin *et al.* 2005) to investigate the influence of anthropogenic disturbances on the movements of woodland caribou. This method, closely related to Resource Selection Functions (RSF; Manly *et al.* 2002), represents a valuable descriptor of fine-scale movements by contrasting landscape characteristics along a straight line connecting two consecutive locations (hereafter called “step”; Turchin 1998) with local habitat availability. Unlike traditional RSFs, which characterize habitat availability as any location within individual home ranges (Arthur *et al.* 1996), the SSFs use random steps originating from the same beginning point as the observed step. Availability thus changes with each observed step, representing habitats readily available to individuals during their movement. Another interesting feature of an SSF is that it partially controls for serial autocorrelation, as it analyzes the independence of two successive points forming a step and considers the other steps as independent (Martin *et al.* 2009).

Chapter 3

Evidence of thresholds in the capacity of female caribou to cope with cumulative disturbances.

I wrote this article with my supervisor, Dr. Jochen A.G. Jaeger, and my co-supervisor, Dr. Martin-Hugues St-Laurent. This manuscript was submitted to the journal *Landscape Ecology* on October 25th, 2011 and is currently under review. It has been presented orally at the *13th International Arctic Ungulate Conference* in Yellowknife, Canada in August 2011, and at the *36th Annual meeting of the Société Québécoise pour l'Étude Biologique du Comportement* in November 2011. As first author, I was responsible for the development of the research objectives and predictions, the data extraction, the spatial and statistical analyses, and the writing of the manuscript. Dr. Jochen A.G. Jaeger helped in the elaboration of the research objectives and the manuscript revisions. Dr. Martin-Hugues St-Laurent was involved in the elaboration of the research objectives, the spatial and statistical analyses, the manuscript revisions and the financial support necessary for all the steps required for the completion of the project (i.e. capture, telemetry, stipend, etc).

Abstract

Woodland caribou (*Rangifer tarandus caribou*) are closely associated with the boreal forest, an ecosystem that has been significantly modified by anthropogenic activities over the last century. A lot of interest has been given to the species' response to disturbances in order to implement management plans successful in ensuring the species' conservation. We investigated how caribou cope with disturbances using GPS telemetry data collected on 51 females in a highly managed landscape in Québec, Canada, between 2004 and 2010, using home-range size as a proxy of caribou space use behaviour. Individuals were found to expand their home ranges as the amount of disturbances in their habitat increased, up to a point where further increase caused home range contraction. The density of major roads and the proportion of clearcuts had an important impact on space use throughout the whole year, but the impact of roads was particularly important during calving, summer and rut, while the impact of clearcuts prevailed in spring, early and late winter. Furthermore, we found that a more convoluted shape of cutblocks amplified the effect of clearcuts on caribou space use. These non-linear responses suggest that there is a limit to the adaptability of individuals in coping with anthropogenic disturbances. While home range expansion could affect survival through the use of unknown habitats, individuals confined in smaller home ranges could be forced into an ecological trap and easily be detected by predators, making current disturbance levels observed in the boreal forest and their cumulative amount in the landscape a major issue for the conservation of these woodland caribou populations.

Keywords: Canadian boreal forest; woodland caribou; forest loss and fragmentation; space use; movement; home-range size; disturbance threshold; roads; forest harvesting; non-linear responses.

3.1 Introduction

Human-induced disturbances play a major role in modifying many ecosystems worldwide and the resulting habitat loss (or alteration) and fragmentation are widely acknowledged as the most important factors impacting wildlife (Venter *et al.* 2006; Fisher and Lindenmayer 2007). For instance, in the North-American boreal forest, anthropogenic disturbances have superseded natural disturbances over the last century (Cyr *et al.* 2009). Forest harvesting, the main anthropogenic activity in the boreal forest, is known to modify the natural age structure of forest stands, greatly alter the quality of natural habitats and decrease overall landscape connectivity for numerous species (Burton *et al.* 1999). Harvesting also implants an increasingly dense road network (Forman *et al.* 2003), further fragmenting the landscape and impeding many species' movements (Dyer *et al.* 2002).

Habitat loss (i.e. an overall decrease in a particular habitat's representation in the landscape associated with the increase of other land-cover types; St-Laurent *et al.* 2009) and habitat fragmentation (i.e. breaking apart of habitats, implying a decrease in habitat connectivity; With *et al.* 1997 and Fahrig 2003) are both species-specific and their impacts can differ in direction and intensity depending on a species' habitat requirements (Fischer and Lindenmayer 2007; Smith *et al.* 2009). At the population level, habitat alterations can lead to the fragmentation and isolation of populations into smaller and more susceptible subpopulations more likely affected by stochasticity and natural stress factors (Fahrig 2003). At the individual scale, disturbances can modify physiology and behaviour of organisms through a permanent or temporary loss of access to suitable habitats (Eigenbrod *et al.* 2008). Moreover, a loss of potentially suitable habitats may arise as the impacts of disturbances extend beyond the source of the disturbance (Dyer *et al.* 2001). Impacts of anthropogenic disturbances can be severe (e.g. Vistnes and Nellemann 2008), especially for far-ranging species whose movements encompass areas larger than the patches the forest mosaic is generally composed of (Ims *et al.* 1993). For such species, changes in habitat use patterns in response to disturbances may result in important repercussions at multiple biological scales and ultimately affect population viability (Ims *et al.* 1993; Seip et al. 2007; Johnson and St-Laurent 2011).

Individuals exhibit different space use patterns in response to varying degrees of disturbance (e.g. Redpath 1995; Andreassen and Ims 1998) depending on the amount of suitable habitat left after alteration, landscape connectivity and the propensity of individuals to display site fidelity behaviour (Frair *et al.* 2008; Faille *et al.* 2010). For far-ranging species, it is likely that individuals will make more extensive movements and thus expand their home range as disturbance levels increase in order to access enough suitable resources and compensate for functional habitat loss, relative to the hostility of the matrix, inter-fragment distances and the presence of habitat corridors (Andreassen *et al.* 1998; Selonen *et al.* 2001). When movements are hindered by disturbances, however, individuals may become constrained to smaller areas and consequently constrict their home ranges, potentially increasing spatiotemporal overlap with conspecifics and predators (Ims *et al.* 1993). Numerous wildlife species have been reported to be impacted by disturbances across multiple facets of their ecology and respond in a non-linear manner with respect to the relative intensity of disturbances they are confronted with (e.g. Forman *et al.* 2003; Frair *et al.* 2008). Therefore, it seems reasonable to expect a non-linear response from individuals from the same population yet occupying different landscape contexts. Primary home-range expansion followed by home-range contraction as the amount of disturbance passes some threshold compromising naturally occurring space use patterns could thus be expected. We hereafter define a threshold as the disturbance level over which a sudden or gradual shift in wildlife behavioural response is observed (Johnson *submitted*).

The objective of our study was to analyze the influence of anthropogenic and natural disturbances on space use behaviour. We used the threatened woodland caribou (*Rangifer tarandus caribou*, hereafter referred to as caribou), declining throughout its range and closely associated with the boreal forest (Vors and Boyce 2009), as a biological model. Traditionally evolving under a natural disturbance regime, the distribution of caribou contracted over the last century and remnant populations now inhabit areas under intensive forest harvesting activities (Schaefer 2003; St-Laurent and Dussault 2012). Logging increases the conversion rate of old-growth coniferous forests, the preferential habitat of caribou, into early-seral stages, which can lead to functional habitat loss that can last up to 60 years (Courtois *et al.* 2007a). Conversely, the resulting early successional forests favour an increase in the distribution and abundance of moose (*Alces alces*), gray wolf (*Canis lupus*) and black bear (*Ursus americanus*; Dussault *et al.* 2005; Brodeur *et al.* 2008; Houle *et al.* 2010). Particularly vulnerable to predation, this change likely jeopardizes caribou's anti-predator strategy (i.e. spacing out; see Bergerud and

Page 1987) by increasing their encounter rates with predators (i.e. apparent competition with moose; Bergerud and Elliot 1986; Seip 1992). The caribou thus appears like an ideal candidate to study the impacts of disturbances on wildlife space use at a large scale due to its close association with undisturbed boreal forest (Hins *et al.* 2009), its known sensitivity to human development (Fortin *et al.* 2008) and its historical adaptability to natural disturbances (Gustine and Parker 2008).

We used home-range size as a proxy of caribou space use behaviour (i.e. a synthesis of movements; Andreassen *et al.* 1998). We predicted that (1) caribou would first expand their home ranges with increased levels of disturbances in their habitat (i.e. clearcuts, roads and natural disturbances), followed by home-range contraction as certain disturbance thresholds are exceeded. We also expected that (2) clearcuts associated with a higher degree of fragmentation (measured as edge-to-surface ratio) would have a higher impact than those resulting in less overall fragmentation and that (3) the impact of anthropogenic features would be greater than that of natural disturbances. Finally, we predicted that (4) due to annual variations in biological states and environmental conditions, the relative importance of disturbances would differ depending on the period of the year.

3.2 Methods

3.2.1 Study area

The study area is located north of Lac Saint-Jean and the Saguenay River in Québec, Canada, and covers approximately 31 000 km². The area overlaps two regions centered on Piraube Lake in the north (49°42’– 51°00’N, 71°10’– 72°09’W) and Portneuf

Lake in the south (48°21'– 49°45'N, 69°51'– 71°12'W) that are distinguished by their dominant forest cover. The southern region of the study area is dominated by black spruce (*Picea mariana*) with balsam fir (*Abies balsamea*), white birch (*Betula paperifera*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and jackpine (*Pinus banksiana*). The northern region is dominated by old-growth coniferous forest and open forest with black spruce, balsam fir and jackpine stands (see Lesmerises *et al.* 2011). Weather conditions throughout the study area are comparable, with mean annual temperatures between -2.5 and 0.0 ^{o}C (extremes ranging from -38 to 33 ^{o}C) and mean annual precipitation between 1,000 and 1,300 mm, of which 30-35% falls as snow (Robitaille and Saucier 1998). Moose, gray wolf and black bear compose the main other large mammal species found in the study area. Forest harvesting is the main anthropogenic disturbance in the area, with a logging history of ~40 years for the southern and ~15 years for the northern region. Prior to data collection, the southern and northern regions were disturbed by anthropogenic features on ~35% and ~4% of their surface, respectively. Being significantly less impacted by harvesting, the disturbance dynamic in the northern area is mainly driven by natural disturbances (i.e. major fires, windthrows and insect outbreaks).

3.2.2 Data collection

We monitored 48 adult female caribou from 2004 to 2010 (18 to 25 per year) using global positioning system (GPS) collars (Lotek models 2200L and 3300L, and Telonics TGW-4680). Individuals were captured using net-gunning and recaptured periodically in order to retrieve data, change batteries or remove collars. Collars were also recovered following failure or death of an individual. They were programmed to attempt recording a location every 1, 2, 3, 4 or 6 hours. We based our telemetry survey on females only due to their strong association to calves, which constitutes the most vulnerable portion of the population, makes them strongly linked to population dynamics (Barten *et al.* 2001). Captures and manipulations were approved by Animal Welfare Committees for the Université du Québec à Rimouski (certificate #CPA-36-08-67).

We used the home ranges of individual caribou, defined as the 100% minimum convex polygon (MCP; Mohr 1947), as a proxy of space use. This method was preferred over the kernel method as it yields more precise area estimates when dealing with a large number of GPS telemetry locations (Downs and Horner 2008). Furthermore, kernel estimates have been found to be biased when used on animals exhibiting site fidelity behaviour (Hemson *et al.* 2005), as observed for females in our study area (Faille *et al.* 2010). We only used home ranges based on a minimum of 100 locations to obtain unbiased estimations (Girard *et al.* 2002). According to behavioural changes throughout the year related to biological phases of the caribou life cycle (see Hins *et al.* 2009, companion project in the same study area), home ranges were assessed for six relevant periods of the year for caribou: spring (15 April – 14 May), calving (15 May – 14 June), summer (15 June – 14 September), rut (15 September – 14 November), early winter (15 November – 21 February) and late winter (22 February – 14 April). The winter period was divided in two parts in an effort to account for potential alterations in space use behaviour due to changing climatic and snow conditions (Smith *et al.* 2000).

As our primary focus was the impact of disturbances on caribou home-range size, only habitat categories that were suspected or recognized to have a detrimental influence on caribou behaviour (e.g. avoidance, see Courtois *et al.* 2007a; Vistnes and Nellemann 2008; Hins *et al.* 2009) were included in our analyses (Table 3.1). We also considered natural disturbances and water bodies as landscape features potentially influencing home-range size. Habitat features were obtained from digitized ecoforest maps provided by the *Ministère des Ressources naturelles et de la Faune du Québec* which were updated each year with new natural and anthropogenic disturbance polygons (e.g. forest fires, cutblocks). Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies, bogs). Anthropogenic features consisted of different types of roads and clearcuts of varying age. Roads were distinguished according to their width and then grouped as major roads (i.e. principal and secondary roads of width equal to 35 and 30 m, respectively) and minor roads (i.e. tertiary and quaternary roads of width equal to 25 and 20 m, respectively). No paved roads were found in our study area. Clearcuts were divided according to the time elapsed since logging activities: recent clearcuts (0-5 years old), old clearcuts (6-20 years old) and established regenerating stands (21-40 years old). However, strong correlations between minor road density and the proportions of 0-5 and 6-20 year-old clearcuts prevented us from using them in the same models. As minor roads are used to access clearcuts, they are inherently co-dependent; we therefore decided to include only the proportions of clearcuts in the candidate models.

The proportion of the different clearcut categories and natural features as well as the density of major roads and clearcut edges (km/km^2) were measured within each home range using ArcView 3.2 and ArcGIS 9.3 (ESRI Inc., Redlands, CA). The proportion of clearcuts and its associated edge density were highly correlated and therefore could not be included in the same analysis. We thus calculated an edge-to-surface ratio (used here as a proxy of mature forest fragmentation) by dividing the density of each type of clearcut edge by the proportion of the same clearcut type within individual home ranges. This significantly reduced the correlation between the variables and allowed us to investigate how a variation in edge-to-surface ratio would modify the impact of the surface lost through clearcutting. We also expected to observe a spatial structure in our study area due to a gradient of forest stand composition, habitat disturbance and forest management practices (Lesmerises *et al.* 2011). Consequently, we included the latitude of each home range centroid as a covariate in our candidate statistical models (Dale and Fortin 2002; Legendre *et al.* 2002). Initial expectations and *a priori* visual inspection of our data also suggested that a non-linear relationship might exist between the amount of certain disturbances and home-range size; quadratic terms were thus included in our analysis for the density of major roads and the proportions of 0-5 year-old clearcuts, 6-20 year-old clearcuts and 21-40 year-old regenerating stands.

Table 3.1 – Description of variables considered in the linear mixed candidate models relating caribou home-range size to disturbance variables and latitude for 51 female caribou in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2010. Latitude was measured in km while proportions were in % (or km^2/km^2) and densities in km/km^2. Roa34 (and associated quadratic term) were not included in candidate models because of collinearity problem (see text).

Group	Variable	Description	Representation in home ranges	
			Average	SD
Latitude	Lat	Latitude of home range centroid	4504.962	2053.202
Roads	Roa12	Major road density (classes 1 and 2)	0.044	0.054
	Roa12^2	Quadratic term for Roa12		
	Roa34	Minor road density (classes 3 and 4)	1.104	0.837
	Roa34^2	Quadratic term for Roa34		
Clearcuts	Cut05	Proportion of 0-5 year-old clearcuts	0.036	0.052
	Cut05^2	Quadratic term for Cut05		
	Cut620	Proportion of 6-20 year-old clearcuts	0.202	0.188
	Cut620^2	Quadratic term for Cut620		
	Regen	Proportion of regenerating stands (21-40 years old)	0.056	0.064

	Regen^2	Quadratic term for Regen		
ESR	ESR_{05}	Density of 0-5 year-old clearcut edge divided by Cut05	12.328	14.606
	ESR_{620}	Density of 6-20 year-old clearcut edge divided by Cut620	13.408	8.372
	ESR_{rgn}	Density of regenerating stand clearcut edge divided by Regen	22.127	13.259
Natural	Water	Proportion of water bodies	0.1260	0.080
	Natpt	Proportion of natural disturbances	0.048	0.092

3.2.3 Statistical analysis

Generalized linear mixed models were used with home-range size as response variable, proportion or density of each disturbance category (Table 3.1) as independent variables and individuals as random factor. We used a logarithmic transformation on home-range sizes in order to respect the test assumptions. Candidate models (see Table 3.2) referring to competing hypotheses were ranked using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). The random factor, the intercept, the residual variance and the model covariates were included in the number of parameters (k) for the AICc ranking. Model averaging was conducted when competing models ranked within a ΔAIC_c value ≤ 2 of the most parsimonious model (Burnham and Anderson 2002). Informative variables in explaining variations in home-range size were identified using a confidence interval of 0.95 (95%CI), i.e. when their 95%CI did not encompass zero. This enabled us to identify variables that could have been included in best ranking models without adding significant strength to the model (see Arnold 2010). We hereafter use the term "significant" to refer to the informative variables and this term is not based on null-hypothesis testing using *p*-values. We identified the thresholds associated with the significant quadratic terms by measuring the maxima of the relationship using the coefficients obtained in the statistical analysis. We then performed Monte Carlo simulations (i.e. parametric bootstrap using the mean values and their associated standard errors from the models) to generate theoretic distributions of threshold values on which we measured the standard deviation as a measure of uncertainty. Figures of predicted home-range size values were obtained on the range of the observed values of the variable of interest on the x-axis (i.e. for major roads and the different types of clearcuts) while all other variables were set to their mean value for that period.

3.3 Results

We obtained home range estimations for 48 individuals (i.e. 37 in the south of the study area and 11 in the north) followed between 1 and 6 consecutive years. The mean number of locations per individual home range was 507.82 ± 427.84 (SD), but differed between periods of the year. The final analysis included a total of 633 home ranges, with a mean annual size of 160.22 ± 224.83 km^2. Average home-range size differed greatly between periods (mean ± SD: Spring: 182.49 ± 280.18 km^2; Calving: 118.75 ± 154.50 km^2; Summer: 208.38 ± 280.85 km^2; Rut: 168.66 ± 134.18 km^2; Early winter: 229.28 ± 259.51 km^2; Late winter: 78.17 ± 155.52 km^2).

The global model was the most parsimonious for all periods in explaining variation in home-range size. The model including only anthropogenic features was found to be important (i.e. $\Delta AIC_c \leq 2$) for the summer period and model averaging was employed. For the best ranking models, the model fit (adj-R^2) varied between periods, from 0.59 in Late winter to 0.82 in Early winter (Table 3.2). Considering that preferential habitats were not included in the analysis and that they could account for an important part of home-range size variation, we believe that explaining between 59 and 82% of the variance means that our models performed well in explaining variations in caribou home-range size.

Table 3.2 – Candidate model ranking based on the AIC_c for each period. Latitude of each home range centroid was included in all candidate models. Most parsimonious models (i.e., with $\Delta AIC_c \leq 2$) are shown in bold, model number of parameter (K), log-likelihood (LL), difference in AIC_c values (ΔAIC_c) and weight (ω_i) are given. Model performance was assessed using the adjusted R^2. See Table 3.1 for description of variables and models. (Roads only included major roads).

Period	Model structure	K	LL	ΔAIC_c	ω_i	adj-R^2
Spring (*n*=113)	**Roads + Clearcuts + ESR + Natural**	**17**	**-123.31**	**0.00**	**0.86**	**0.67**
	Roads + Clearcuts + ESR	15	-127.87	3.62	0.14	0.64
	Clearcuts + ESR	13	-140.36	23.34	0.00	0.55
	Clearcuts	10	-145.56	26.22	0.00	0.51
	ESR	7	-159.88	47.76	0.00	0.37
	Roads	6	-166.59	58.92	0.00	0.29
	Natural	6	-175.36	76.44	0.00	0.17
Calving (*n*=112)	**Roads + Clearcuts + ESR + Natural**	**17**	**-131.13**	**0.00**	**0.99**	**0.58**
	Roads + Clearcuts + ESR	15	-138.43	9.09	0.01	0.54
	Clearcuts + ESR	13	-149.54	26.04	0.00	0.42
	Roads	6	-159.20	28.43	0.00	0.36
	Clearcuts	10	-161.42	42.24	0.00	0.31
	ESR	7	-168.30	48.91	0.00	0.24
	Natural	6	-180.88	71.79	0.00	0.06
Summer (*n*=109)	**Roads + Clearcuts + ESR + Natural**	**17**	**-105.80**	**0.00**	**0.56**	**0.59**
	Roads + Clearcuts + ESR	**15**	**-108.85**	**0.53**	**0.43**	**0.62**
	Clearcuts + ESR	13	-117.93	13.37	0.00	0.56

	Clearcuts	10	-131.97	33.86	0.00	0.48
	Roads	6	-137.04	34.57	0.00	0.41
	ESR	7	-136.72	36.21	0.00	0.38
	Natural	6	-157.11	74.72	0.00	0.12
Rut (*n*=93)	**Roads + Clearcuts + ESR + Natural**	**17**	**-56.47**	**0.00**	**0.87**	**0.72**
	Roads + Clearcuts + ESR	15	-61.33	3.80	0.13	0.69
	Roads	6	-84.97	27.81	0.00	0.43
	Clearcuts + ESR	13	-81.01	37.53	0.00	0.52
	Clearcuts	10	-85.08	37.71	0.00	0.47
	Natural	6	-107.23	72.33	0.00	0.06
	ESR	7	-106.78	73.77	0.00	0.09
Early winter (*n*=86)	**Roads + Clearcuts + ESR + Natural**	**17**	**-57.84**	**0.00**	**1.00**	**0.82**
	Roads + Clearcuts + ESR	15	-75.03	28.23	0.00	0.74
	Clearcuts + ESR	13	-80.61	33.59	0.00	0.70
	Clearcuts	10	-88.43	41.10	0.00	0.64
	ESR	7	-118.73	94.22	0.00	0.27
	Natural	6	-120.43	95.23	0.00	0.25
	Roads	6	-128.50	111.38	0.00	0.07
Late winter (*n*=120)	**Roads + Clearcuts + ESR + Natural**	**17**	**-179.12**	**0.00**	**0.72**	**0.59**
	Roads + Clearcuts + ESR	15	-183.16	2.70	0.19	0.56
	Clearcuts	10	-187.07	5.34	0.05	0.53
	Clearcuts + ESR	13	-190.94	5.66	0.04	0.50
	Roads	6	-219.37	53.26	0.00	0.20
	ESR	7	-224.11	64.98	0.00	0.13
	Natural	6	-229.10	72.72	0.00	0.06

Disturbances found to be important initially caused an increase in home-range size (except the edge-to-surface ratio for 21-40 year-old regenerating stands in early winter), indicating that an increase in the amount of any type of disturbance within caribou habitat induced an expansion of home ranges (Figure 3.1, Table 3.3). Major roads were significant in explaining home-range size variation for all periods and had a particularly strong impact during calving, summer and rut (Table 3.3). The influence of clearcuts was strongest during spring, early and late winter, although 21-40 year-old regenerating stands also had a strong effect throughout most of the year besides the calving period. The extent of the impact on home-range size variation of 0-5 year-old clearcuts and 21-40 year-old regenerating stands was higher than that of 6-20 year-old clearcuts throughout the whole year (Table 3.3). Edge-to-surface ratios were also important in explaining home-range size variation, especially for 0-5 year-old clearcuts during all periods and for 6-20 year-old clearcuts for spring and calving. Natural disturbances had significant influence on home-range size for all periods (except during calving), while water bodies were important during calving and early winter. Even though they were always included in the most parsimonious models and seemed to have a significant influence on home-range size year-round, natural disturbances alone were less important in explaining individual responses than anthropogenic disturbances for all periods.

Table 3.3 – Coefficient estimates (β) and 95% confidence intervals (95% CI) of the independent variables of the most parsimonious models ($\Delta AIC_c \leq 2$) explaining female caribou home-range size. Coefficients for which the 95% CI were not overlapping zero are shown in bold. Model averaging was conducted for Summer, Rut and Late winter periods.

	Lat	Roa12	$Roa12^2$	Cut05	$Cut05^2$	Cut620	$Cut620^2$	Regen	$Regen^2$	ESR_{05}	ESR_{620}	ESR_{rgn}	Water	Natpt
Spring														
β	**0.02**	**19.30**	**-102.39**	**23.95**	**-237.83**	**6.86**	**-9.13**	**13.73**	-11.73	**0.02**	**0.03**	0.01	1.20	**2.19**
*±95%CI**	*<0.01*	*6.92*	*36.80*	*19.87*	*185.86*	*3.68*	*6.17*	*9.29*	*37.69*	*0.02*	*0.02*	*0.02*	*2.59*	*1.39*
Calving														
β	**0.01**	**25.27**	**-141.30**	2.00	-13.50	3.49	-5.41	8.52	-8.84	**0.03**	**0.02**	0.01	**5.36**	1.10
*±95%CI**	*<0.01*	*11.64*	*88.29*	*5.82*	*14.92*	*3.62*	*8.07*	*8.84*	*30.93*	*0.02*	*0.02*	*0.01*	*2.74*	*2.35*
Summer														
β	**0.01**	**23.94**	**-144.02**	-0.19	-11.89	**4.12**	-7.36	**22.57**	**-71.23**	**0.05**	0.01	0.01	1.27	**6.23**
±95%CI	*<0.01*	*10.16*	*73.82*	*7.52*	*26.00*	*4.09*	*8.87*	*9.73*	*32.68*	*0.02*	*0.02*	*0.02*	*2.29*	*4.70*

Rut														
β	**0.01**	**24.60**	**-141.69**	**9.04**	-42.11	**3.22**	-5.20	**16.77**	**-57.01**	**0.03**	-0.01	0.01	0.39	**3.48**
*±95%CI**	*<0.01*	*7.42*	*57.36*	*7.85*	*47.09*	*2.97*	*6.63*	*6.69*	*22.76*	*0.02*	*0.02*	*0.02*	*1.24*	*2.14*
Early winter														
β	**0.02**	**13.53**	**-55.36**	12.92	-40.59	**8.72**	**-9.38**	**25.10**	**-70.08**	**0.01**	0.01	**-0.02**	**5.61**	**3.10**
*±95%CI**	*0.01*	*7.73*	*39.86*	*14.23*	*153.80*	*3.87*	*6.44*	*6.77*	*24.67*	*0.01*	*0.03*	*0.01*	*1.98*	*1.42*
Late winter														
β	**0.01**	**9.90**	**-24.02**	**34.50**	**-101.66**	**7.55**	-5.96	**23.03**	-69.302	**0.01**	-0.01	0.01	1.44	**3.36**
*±95%CI**	*<0.01*	*7.24*	*22.92*	*12.68*	*40.04*	*4.90*	*7.77*	*15.91*	*82.70*	*0.01*	*0.04*	*0.01*	*1.95*	*2.35*

*Confidence intervals can be obtained by adding and subtracting the ±95%CI value to its associated β value.

Significant non-linear relationships were found in several periods for major roads, 0-5 year-old clearcuts, 6-20 year-old clearcuts and 21-40 year-old regenerating stands (Figure 3.1). Threshold values were relatively constant between periods for roads and clearcuts, except for 0-5 year-old clearcuts in late winter and regenerating stands in early winter. However, these estimates are uncertain due to a lack of observed data points spanning the range of disturbance levels predicted. Lower threshold values seemed to be associated with periods of the year when the impact of the different disturbance types was at its highest (Tables 3.3-3.4).

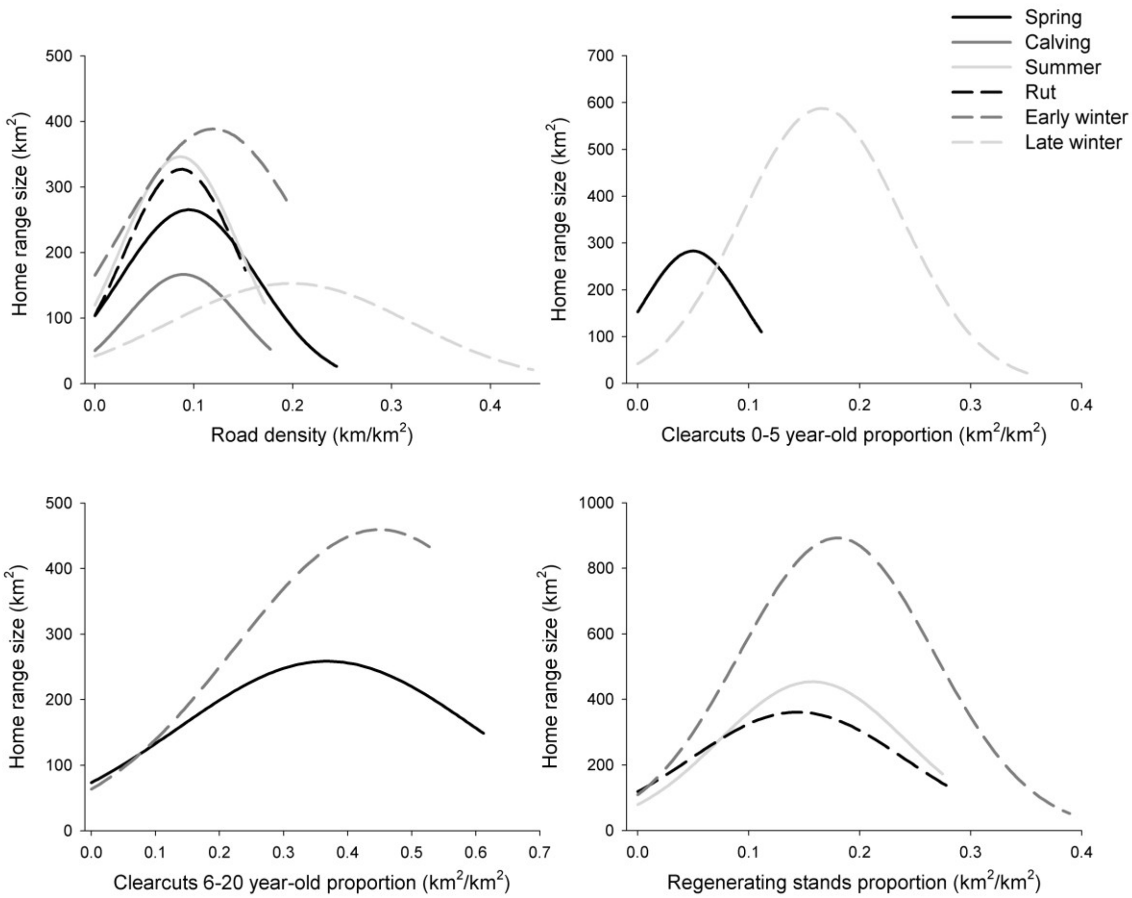

Figure 3.1 – Predicted home-range sizes based on a log-transformation of home-range sizes for all significant quadratic relationships. Predicted values were obtained on the range of the observed values of the variable of interest on the x-axis while all other variables were set to their mean value for that period. Home-range sizes were back-transformed into km^2 for the graphical representation.

Table 3.4 – Threshold values for variables exhibiting significant quadratic relationships (when available; if not, noted as '*n/a*'). Disturbance threshold values are independent from the values of the other predicted variables. Uncertainty on threshold values was obtained using Monte Carlo simulations.

Periods	Disturbance thresholds							
	Roa12		Cut05		Cut620		Regen	
	(km/km^2)	sd	(%)	sd	(%)	sd	(%)	sd
Spring	0.094	0.009	0.050	0.019	0.376	0.189	*n/a*	*n/a*
Calving	0.089	0.014	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*
Summer	0.083	0.007	*n/a*	*n/a*	*n/a*	*n/a*	0.158	0.009
Rut	0.087	0.009	*n/a*	*n/a*	*n/a*	*n/a*	0.147	0.014
Early winter	0.122	0.037	*n/a*	*n/a*	0.465	0.172	0.179	0.015
Late winter	0.206	0.271	0.170	0.017	*n/a*	*n/a*	*n/a*	*n/a*

3.4 Discussion

We found that caribou respond to an increase in the amount of disturbances primarily by expanding and subsequently by contracting their home ranges as disturbance levels in their habitat increase above given thresholds. Other studies that investigated the influence of disturbances on a variety of species space use behaviour found that individuals expanded (e.g. Redpath 1995; McLoughlin and Ferguson 2000) or contracted (e.g. Wolff *et al.* 1997; Andreassen *et al.* 1998) their home ranges in response to habitat alterations and/or decreased habitat quality. Those studies suggested that different populations of the same species exhibit different behavioural responses to disturbances (see Selonen *et al.* 2001). In addition to these findings, our results further suggest that different behavioural responses may be observed from individuals of the same population depending on the immediate landscape context each individual is confronted with.

The home-range expansion response exhibited by individuals is likely due to a reduction of the amount of suitable habitats. In this context, a loss of suitable habitats includes all potential sources of disruption of biological activities that may lead caribou to displace themselves away from a certain part of the landscape (e.g. risk of predation associated with certain habitat types, human presence and traffic levels). For example, Seip *et al.* (2007) found that mountain caribou were locally displaced away from parts of their habitat due to the presence of snowmobiles in winter. Furthermore, disturbances (i.e. mainly clearcuts and roads in this study) can also drastically decrease connectivity in the landscape (Fahrig and Rytwinski 2009) and significantly reduce the amount and quality of accessible habitat available to individuals (Eigenbrod *et al.* 2008). In their effort to access alternative suitable habitats, individuals are compelled to make more extensive movements and increase their home-range size (Chubbs *et al.* 1993; Smith *et al.* 2000) which can lead to an increase in energy expenditure and decrease in foraging efficiency and may result in lower individual body condition (Chan-McLeod *et al.* 1999). Additionally for caribou in our study area, as mature forest remnants such as linear strips or blocks are spatially associated with clearcuts, individuals are forced to cross clearcuts in order to reach their preferential habitat and spend more time in hostile habitats (Hins *et al.* 2009), leading to an increase in encounter probabilities with predators (Ims *et al.* 1993; Rettie and Messier 2000; Vors *et al.* 2007). Furthermore, linear features such as roads open the territory for human, predators and alternative prey species and facilitate access to caribou habitat, increasing their vulnerability (Hebblewhite 2008; Whittington *et al.* 2011). Caribou have also been found to displace themselves away from logged areas during and after operations (Chubbs *et al.* 1993; Smith *et al.* 2000; Shaefer and Mahoney 2007) and were also found to significantly avoid roads and adjacent areas (Dyer *et al.* 2002; Leblond *et al.* 2011). Ultimately, such behavioural shifts could have population level consequences by decreasing survival, reproductive output and population growth (Johnson and St-Laurent 2011).

Other studies have confirmed the synergistic impact of the clearcut area and their associated fragmentation effect on wildlife (Fahrig 1997; St-Laurent *et al.* 2009), a phenomenon that we also observed. This advocates the postulate that clearcut patches should have a resulting edge length as low as possible (i.e. round-shaped clearcuts) in order to dampen their influence on caribou space use behaviour in managed boreal forest. The fragmentation levels of a disturbance seem to play an important role and minimizing their influence on caribou could be valuable in trying to lessen the overall impact of disturbances in the landscape.

Although water bodies and natural disturbances clearly impacted home-range size to a lesser degree than anthropogenic disturbances, they nonetheless have a biological significance as they are naturally occurring in the landscape and are often outside our control. We then argue that natural disturbances induce an initial degree of mature forest loss and fragmentation that is cumulative to anthropogenic disturbances and consequently should be considered when planning logging and road building in a given landscape (see Sorensen et al. 2008 for similar conclusions).

The behavioural transition from home-range expansion to contraction suggests that there exist disturbance thresholds where the cost-benefit balance of continued expansion shifts and individuals begin using smaller areas as disturbance levels further increase. It is likely that over those thresholds individuals cannot avoid using unsuitable habitats anymore and will decrease their movement rates and access suboptimal habitats as movement in a hostile matrix becomes too risky (Smith *et al.* 2000; Hebblewhite 2008). Considering the natural propensity of caribou to exhibit site fidelity behaviour regardless of alteration levels in their habitat and combined with the limited movement capacities noted at high disturbance levels, we believe that female caribou could exhibit a maladaptive habitat selection behaviour that constrains them to such suboptimal habitats (i.e. an ecological trap; Faille *et al.* 2010). This could in turn induce changes in spatial organization, movement patterns and reproductive activities, as well as increase predator encounter rates either through the use of predator-frequented habitats or by rendering females more conspicuous in the landscape (Andreassen *et al.* 1998). This could ultimately jeopardize their anti-predator strategy. Most importantly, the observed home-range contractions suggest that current disturbance levels occurring in our study area have already reached intensities that effectively constrain individuals to smaller areas and potentially lead them into such ecological traps. Such traps could be particularly important for calves, whose mortality by predation is the most limiting factor influencing caribou populations (Barten *et al.* 2001). A decrease in successful recruitment due to the inability of females to avoid risky habitats could therefore have important repercussions for populations.

Our results also suggest that individuals do not respond consistently to disturbances throughout the year. Caribou space use behaviour changes throughout the year (Hins *et al.* 2009) as well as environmental conditions within their habitat (e.g. Smith *et al.* 2000; Dyer *et al.* 2001). Those variations visibly have an influence on the extent to which individuals are affected by modifications in their habitat, which is reflected in the different predicted home-range sizes at thresholds. Road crossing rates for ungulates have been found to differ daily and seasonally in response to factors such as road traffic and resource requirements (Dyer *et al.* 2002; Dussault *et al.* 2007). Accordingly, our results show that major roads in our study area had an important influence throughout the year, but they had the strongest impact during calving, summer and rut. Although we did not include traffic level data in our analysis, traffic levels are higher during these three periods mostly because of the absence of a snow cover. Moreover, the observed road density thresholds suggest that individuals can tolerate higher densities of roads before a behavioural shift in the winter period, especially during late winter, when traffic level is at its lowest and individuals' movement capacities are impeded by snow accumulation (Smith *et al.* 2000). Clearcuts were also important throughout the year, but especially during winter and spring, when the impact of roads was lower. Individual behaviour also shifted at lower disturbances thresholds for 0-5 year-old clearcuts and regenerating stands, which could be related to human activities in and close to young clearcuts (Burton *et al.* 1999) and to higher densities of predators in regenerating stands (Brodeur *et al.* 2008; Houle *et al.* 2010). The higher thresholds observed for 6-20 year-old clearcuts could also be related to their high availability in the landscape and their close association with preferential habitats (Hins *et al.* 2009).

Interestingly, our results showed that despite a large variability in home-range sizes depending on the period of the year (e.g. due to higher vulnerability in the calving and post-calving period), shifts between expanding and contracting phases were nonetheless relatively synchronized around given disturbance thresholds.

3.5 Conclusion

The non-linear responses exposed by our analysis suggest that there exists a limit to the adaptability of individuals in coping with anthropogenic disturbances. Even if caribou are negatively impacted by disturbances occurring in their habitat, the initial response (i.e., home-range expansion) still reflects a natural tendency to compensate for lost habitat while their movement capacities are not completely hindered and they are still able to adapt to their changing environment. Above certain disturbance thresholds, however, individuals may be confined within suboptimal habitats that can become ecological traps. Initiated by a level of disturbance that is too important, this response has a higher potential to threaten not only space use patterns, but also reproductive success and ultimately population viability. Measured within caribou home ranges, those thresholds may however not be representative of the entire landscape due to the hierarchical habitat selection exhibited by individuals (Rettie and Messier 2000) and may also be group or population specific (Pardini *et al.* 2010).

We are confident that thresholds identified in this study could potentially support conservation and forest management plans. However, they primarily underline that disturbance levels currently observed in the southern fringe of the boreal forest already constrain individuals to decrease their home-range size; consequently, any further increase of anthropogenic disturbances in caribou habitat will only accelerate this behavioural shift toward home-range contraction. Then, thresholds should not represent targets for human development but rather critical ecological levels over which individuals exhibit potentially highly detrimental behavioural changes that could result into detrimental consequences at the population level (Johnson *submitted*). Nonetheless, we believe that identifying such thresholds offered us a better understanding of the mechanisms linking space use behaviour and disturbance levels. Integrating behavioural shifts could help us act proactively to slow down the ongoing alteration rate of natural landscapes under levels individuals could sustain and ultimately ensure the persistence of caribou populations in managed landscapes.

Acknowledgements

This project was funded by the following partners: AbitibiBowater Inc., Canada Economic Development, Conseil de l’industrie forestière du Québec, Fondation de la faune du Québec, Fonds québécois de la recherche sur la nature et les technologies, Fonds de recherche forestière du Saguenay–Lac-St-Jean, Ministère des Ressources naturelles et de la Faune, Natural Sciences and Engineering Research Council of Canada (Discovery Grant to M.-H. St-Laurent), Université du Québec à Rimouski and World Wildlife Fund for Nature. We also thank the Essipit First Nation and A. Chabot for providing access to their caribou telemetry data, via the Aboriginal Funds for Species at Risk (Environment Canada). Many thanks to J.-P. Ouellet and C. Dussault for their scientific and logistical support coordinating the project, É. D’Astous, R. Moriarity, R. Weladji and C. Johnson for providing useful comments on an earlier version of this

manuscript, and to A. Caron, L.F. Madriñán and M.J. Mazerolle for their assistance with statistical and GIS analyses.

Chapter 4

Disentangling female woodland caribou movements in response to clearcuts and roads across temporal scales

I wrote this article with my supervisor, Dr. Jochen A.G. Jaeger, and my co-supervisor, Dr. Martin-Hugues St-Laurent. This manuscript has not yet been submitted for publication, but we plan on submitting to *The Journal of Applied Ecology*. As first author, I was responsible for the development of the research objectives and predictions, the data extraction, the spatial and statistical analyses, and the writing of the manuscript. Dr. Jochen A.G. Jaeger helped in the elaboration of the research objectives and the manuscript revisions. Dr. Martin-Hugues St-Laurent was involved in the elaboration of the research objectives, the spatial and statistical analyses, the manuscript revisions and the financial support necessary for all the steps required for the completion of the project (i.e. capture, telemetry, stipend, etc).

Abstract

Although prey species typically respond to the most limiting factors at coarse spatiotemporal scales while addressing biological needs at finer scales, such behaviour may become challenging for species inhabiting human altered landscapes. We investigated how woodland caribou, a threatened species inhabiting North-American boreal forests, modified their fine-scale movements when confronted to the presence of forest management features (i.e. clearcuts and roads) across multiple facets of their ecology. We used GPS telemetry data collected between 2004 and 2010 on 49 female caribou in a heavily managed area in Québec, Canada. Movements were studied using a use-availability design contrasting observed steps (i.e. line connecting two consecutive locations) with random steps (i.e. proxy of immediate habitat availability). Although caribou mostly avoided disturbances, individuals nonetheless modulated their fine-scale response to disturbances on a daily and annual basis, potentially compromising between risk avoidance in periods of higher vulnerability (i.e. calving, early and late winter) during the day and foraging activities in periods of higher energy requirements (i.e. spring, summer and rut) during dusk/dawn and at night. Additionally, although females typically avoided crossing clearcut edges and roads at low densities, crossing rates were found to rapidly increase in greater disturbance densities. In some instance, however, females were less likely to cross edges and roads as densities increased. This may trap females or increase the use of habitats associated with higher vulnerability. It appears that caribou found in our system may need to address limiting factors even at finer scales and thus disrupt their biological activities in response to increases in perceived risk. Further increases in anthropogenic disturbances would then exacerbate such behavioural responses and likely endanger the future persistence of caribou in the boreal forest.

Keywords: Anthropogenic disturbances, Canadian boreal forest, daily response, clearcuts, forest harvesting, forest roads, movements, step selection function, woodland caribou.

4.1 Introduction

Most species inhabit environments where biological requirements (e.g. foraging, reproductive activities and parental care) with local threats to survival (Frid and Dill 2002). Organisms thus adapt how they use their habitat as a result of their perception of habitat uncertainty (e.g. risk of predator encounters; Sih 1992), often doing so across multiple spatial scales (Johnson *et al.* 2001). Typically, species orient habitat use hierarchically, following the hierarchy of factors likely to affect individual fitness (Rettie and Messier 2000). Likewise, individuals may address limiting factors differentially on a temporal basis with respect to changes in biological states of both prey and predators alongside variation in environmental conditions (e.g. Hebblewhite and Merrill 2008; Godvik *et al.* 2009; Hins *et al.* 2009). Accordingly, numerous species are strongly cued to plant phenology in periods of high energy requirements (Post *et al.* 2003), yet particularly vigilant when moving through their habitat in periods of higher vulnerability (Zollner and Lima 2005).

Complete avoidance of limiting factors is however a daunting task for individuals inhabiting heterogeneous environments and they may consequently need to be addressed at gradually finer spatiotemporal scales (Sih 1992; Rettie and Messier 2000). Such responses may be particularly apparent in species with extensive movement patterns through the inclusion of a greater diversity of habitats in their range (Ims *et al.* 1993). Individuals may thus be compelled to compromise between biological requirements and risk avoidance on a daily basis, potentially at the expense of other biological activities.

While risk assessment is typically associated with predation, it nonetheless involves multiple factors that combine to affect levels of uncertainty associated with a given habitat. Some ecologists have proposed that anthropogenic disturbances (hereafter called disturbances) could trigger behavioural responses that are similar to those elicited by predators (see Frid and Dill 2002), thereby increasing habitat uncertainty and combining with natural stressors to impact prey species. In the context of this study, habitat uncertainty thus encompasses factors that induce disturbance stimuli (e.g. predation risk, forage availability and traffic levels) and influence the risk perceived by organisms, which may trigger behavioural responses. Environments affected by expanding human activities impose significant pressures on prey species (e.g. Renaud 2012), increasing the likelihood that wildlife found in such habitats would modify their fine-scale behaviour. North-American wildlife inhabiting the boreal forests is currently faced with such a scenario and many species suffer from intensified human activities (Burton *et al.* 1999). Of greatest concern, timber harvesting creates early-seral forests and a dense road network that significantly alters the natural structure of the landscape (Forman *et al.* 2003). As a result, the historical natural disturbance regime has been superseded by forestry-related features over the last century (Cyr *et al.* 2009).

The objective of this study was to evaluate the impacts of disturbances on individual movements of woodland caribou (*Rangifer tarandus caribou*, hereafter referred to as caribou), a threatened species throughout North-America (COSEWIC 2011). This species offered a unique opportunity to study the fine-scale movements of species typically associated with mature forests yet inhabiting heavily managed environments (Environment Canada 2011). Naturally adapted to cope with natural disturbances across their range (Gustine and Parker, 2008), remnant caribou populations have nonetheless suffered severe constrictions of their range that are strongly correlated with forestry activities (Schaefer 2003; St-Laurent and Dussault 2012). The early successional forests created by harvesting jeopardizes the anti-predation strategy used by caribou (i.e. spacing out; Bergerud and Page, 1987) by favouring local increases in moose (*Alces alces*), gray wolf (*Canis lupus*) and black bear (*Ursus americanus*) densities (Dussault *et al.* 2005; Brodeur *et al.* 2008; Houle *et al.* 2010). As a consequence, encounter rates with alternative prey species and predators increase, exacerbating caribou vulnerability.

Like other wildlife species, the woodland caribou has been found to respond to limiting factors across multiple spatiotemporal scales, with predation avoidance on the one hand (e.g. Bergerud and Page, 1987; Rettie and Messier, 2000) and disturbances on the other (e.g. Schaefer 2003; Hins *et al.* 2009) influencing large-scale behaviour, while biological requirements are met at finer scales (e.g. Briand *et al.* 2009). We however recently demonstrated that disturbance levels observed within our study area possess the potential to compel individuals to remain in areas increasingly altered (Beauchesne *et al. submitted*). Combined with a strong range fidelity (Faille *et al.* 2010), it seemed reasonable to expect alterations of fine-scale behaviour in response to the presence of disturbances. We therefore expected (1) that individuals would avoid moving through disturbances and crossing clearcut edges and roads. We further anticipated (2) that response to disturbances would differ both daily and annually. More specifically, we expected that (2a) individuals would avoid disturbances predominantly during periods of higher vulnerability (e.g. calving) and (2b) during the day when perceived risk in disturbances should be more important. Finally, we expected that (3) the immediate landscape contexts would impact the relative probability of individuals crossing through clearcut edges and roads.

4.2 Methods

4.2.1 Study area

The study area is located in Québec, Canada, and covers approximately 31 000 km^2 centered on two adjacent sectors north of the Saguenay-Lac Saint-Jean region: Piraube Lake in the north (49°42'– 51°00'N, 71°10'– 72°09'W) and Portneuf Lake in the south (48°21'– 49°45'N, 69°51'– 71°12'W). Mean annual temperature in both areas varies between -2.5 and 0.0 ^{o}C (extremes ranging from -38 to 33 ^{o}C) and mean annual precipitation around 1000 and 1300 mm, 30-35% of which is snow (Robitaille and Saucier, 1998). Large mammals found in the area are caribou, moose, gray wolf and black bear. The two sectors are distinguished by their dominant forest cover. Black spruce (*Picea mariana*) with balsam fir (*Abies balsamea*), white birch (*Betula paperifera*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and jackpine (*Pinus banksiana*) dominate the southern region, while old-growth coniferous forest and open forest with black spruce, balsam fir and jackpine stands dominate the northern area. The southern and northern regions have a logging history that extends over the last 40 and 15 years, respectively. Our study area thus presents an interesting latitudinal gradient of anthropogenic habitat alteration, with the southern region being altered across ~35% (Portneuf region) and the northern region by 4% of the forested landscape (Piraube region) prior to our data collection. Similarly, road densities are generally greater in the south (0.04 km/km^2 for major roads and 1.20 km/km^2 for minor roads) than in the north (0.05 km/km^2 for major roads and 0.04 km/km^2 for minor roads).

4.2.2 Data collection

We used global positioning systems (GPS) collars (Lotek models 2200L and 3300L, and Telonics TGW-4680) to monitor 49 female caribou between 2004-2010 . We programmed these collars to record a location every 1, 2, 3, 4 and 6 hours. Females were preferred for this study as their behaviour can strongly influence calf survival (Barten *et al.* 2001). Individuals were captured periodically using net-gunning to retrieve data, change batteries or remove collars. Collars were also retrieved following failure or death of an individual. Canadian Animal Welfare Committee approved captures and manipulations of study animals (certificate #36-08-67).

We used the linear segments connecting two consecutive GPS locations (i.e. steps; Fortin *et al.* 2005) to investigate the influence of anthropogenic disturbances on the sequential movements of individual caribou. In order to obtain uniform data, only time steps of 4 hours were retained for the analysis, other time fixes being subsampled or removed from the dataset. The analysis was divided between six annual periods of biological significance for caribou ecology: spring (15 April – 14 May), calving (15 May – 14 June), summer (15 June – 14 September), rut (15 September – 14 November), early winter (15 November – 21 February) and late winter (22 February – 14 April). Furthermore, as daily behaviour may also vary (e.g. Bjormeraas *et al.* 2011), each period was further divided between day, dusk/dawn and night times (CNRC 2011), resulting in a total of 18 different periods analyzed.

Steps were related to a series of features obtained from digitized ecoforest maps provided by the *Ministère des Ressources naturelles et de la Faune du Québec* and updated each year with new natural and anthropogenic disturbances. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies, bogs). For this analysis, disturbance features included clearcut and road types (Table 4.1). Clearcuts were categorized according to elapsed time since logging: 0-5 year-old clearcuts, 6-20 year-old clearcuts and established regenerating stands (21-40 years old), whereas roads were divided according to their width: major (i.e. primary and secondary roads respectively 35 and 30 m wide) and minor roads (tertiary and quaternary roads respectively 25 and 20 m wide). No paved roads are found in the study area. The proportion of steps located in each type of clearcut was measured to evaluate the relative probability of individuals moving through clearcuts and a quadratic term was included in order to test for non-linear responses. Relative probability of individuals crossing roads and clearcut edges was evaluated using the number of crossings on each step. The landscape context in which females were moving was also suspected to have an influence on caribou behaviour (e.g. higher probability of crossings when density is greater). The density of clearcut edges and roads was therefore evaluated in buffers around the beginning of each step (i.e. same density for observed and random steps). Buffer size was determined by a constant radius equal to the median of the periodical step length distributions (i.e. spring: 205 m; calving: 132 m; summer: 245 m; rut: 222 m; early winter: 125 m; late winter: 127 m). We used the median as the step length distribution was characterized by a power law distribution. Consequently, less importance was attributed to the longer and less frequent steps and thus more likely to represent distances traveled by females within the time step analyzed. Topography variables were also included (i.e. the mean elevation on the step and the difference between the elevation at the end and the beginning of the step) in the analysis as altitude and slope have been found to be important features influencing the movements of caribou and other ungulates (Leblond *et al.* 2010; Skarin *et al.* 2010).

Table 4.1 – Description of variables considered in the conditional logistic regressions explaining caribou relative movement probabilities in relation to disturbances for 49 female caribou in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2010.

Group	Variable	Description
Elevation	ElevVar	Elevation difference between beginning and end of the step
(Elev)	ElevMoy	Mean step elevation
Clearcuts (Cut)	Cut05	Proportion of 0-5 year-old clearcuts under the step
	Cut05^2	Quadratic term for Cut05
	Cut620	Proportion of 6-20 year-old clearcuts under the step
	Cut620^2	Quadratic term for Cut620
	Regen	Proportion of regenerating stands (21-40 years old) under the step
	Regen^2	Quadratic term for Regen
Cross_Edge (Cr_Ed)	Cross_{05}	Number of 0-5 year-old clearcut edge crossings
	Cross_{620}	Number of 6-20 year-old clearcut edge crossings
	$\text{Cross}_{\text{RGN}}$	Number of regenerating stand (21-40 years old) edge crossings
	Dens_{05}	Density of 0-5 year-old clearcut edge around the beginning of the step
	Dens_{620}	Density of 0-5 year-old clearcut edge around the beginning of the step
	Dens_{RGN}	Density of 0-5 year-old clearcut edge around the beginning of the step
Cross_Roads (Cr_Rd)	Roa12	Number of major road (classes 1 and 2) crossings
	Roa34	Number of minor road (classes 3 and 4) crossings
	Dens12	Density of major roads around the beginning of the step
	Dens34	Density of minor roads around the beginning of the step

Dist_Roads (Dt_Rd)	Dvar12	Difference of distance to closest major road between the beginning and end of the step
	Dvar34	Difference of distance to closest minor road between the beginning and end of the step

4.2.3 Statistical analysis

The impacts of forest management features on relative movement probabilities were evaluated using a Step Selection Function (SSF; Fortin *et al.* 2005). This method compares use-availability through a conditional logistic regression:

$$\hat{w}(x) = \exp\,(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n), \qquad (1)$$

where β_1 to β_n are coefficients estimated by the regression and x_1 to x_n are relevant predictors, with higher $\hat{w}$ values indicating greater odds of being selected by an individual. Each observed step was paired with ten random steps originating from the same location and drawn for each individual from unique distributions of step lengths and turning angles (i.e. angle between previous and subsequent location) of all other individuals in order to avoid autocorrelation. Habitat availability thus changed between each step and reflected features immediately available to individuals (Leblond *et al.* 2010). Individuals and years were included as random factors in the analysis, controlling for uneven sample sizes between years and inter-individual variability, while minimizing autocorrelation in the analysis (Duchesne *et al.* 2010). Autocorrelation between successive steps was further considered by including robust Sandwich estimates of the covariance matrix, which divides observed steps in independent clusters and performs the analysis on the clusters rather than on individual steps (see Fortin *et al.* 2005 for details).

A series of candidate models, representing competing hypotheses, was ranked from most to least parsimonious with the quasi-likelihood under independence criterion (QIC), which performs well with conditional logistic regressions (Craiu *et al.* 2008). As density measurements were the same for both observed and random steps – and therefore not applicable as fixed factors in a logistic regression – the densities were used solely as interaction terms in the analysis and we tested models with and without interactions to consider the landscape context (Leblond *et al.* 2011). Model fit was assessed for each model using a *k*-fold cross validation, which ranks each stratum using the logit values predicted by the logistic regression, with best predictions associated with higher values (see Leblond *et al.* 2010). A Spearman rank correlation (r_s) was calculated between the ranks and the sum of observed steps in each rank, with strong correlations indicating a propensity for observed steps to be ranked higher. Spearman ranks were averaged over 10 iterations in which model parameters were evaluated using a random 80% of the strata and tested against the remaining 20%. Since most models included in the analysis are nested, inference was based on models with a ΔQIC ≤ 6 (Richards *et al.* 2011). Informative variables explaining relative movement probabilities were then assessed using a confidence interval of 0.95 (i.e. when the 95%CI did not include zero).

4.3 Results

A total of 49 female caribou tracked from 1 to 6 years provided 137 867 observed steps (2657±2280 per individual) with numbers varying between each period (7824±3404 per period). Based on the QIC ranking, the best models explaining caribou step selection differed depending on the time of the year and the day (Table 4.2). The global model was the most parsimonious for 11 of the periods considered, while the global model without interaction prevailed for 4 periods. The remaining 3 periods were best explained by either the proportion of clearcuts under the step or the number of clearcut edge crossings, and partial models that ranked close to the global model (ΔQIC ≤ 6) almost always contained the clearcut variables, suggesting that clearcuts held the most weight in explaining caribou step selection within those periods (Table 4.2). Validation of best models indicated a high predictive power (r_s range from 0.74 ± 0.13 to 0.97±0.03; Table 4.2).

Table 4.2 – Candidate model ranking based on QIC for each period of the day and the year. Models were evaluated using conditional logistic regressions. Only models with ΔQIC ≤ 6 are presented. Number of parameter (K), log-likelihood (LL), difference in QIC values (ΔQIC) and weight (ω_i) are given. Model performance was assessed with a Spearman rank correlation (r_s±sd). Elevation variables were included in all models tested and models without interactions (i.e. densities of clearcuts edges and roads) are identified with a *.

		Day				
Period	Model structure	K	LL	ΔQIC	ω_i	r_s
	Cut	13	-14549.50	0.00	0.87	0.93±0.05
Spring	Cut+Cr_Ed	19	-14542.11	5.05	0.07	0.96±0.01
	Cut+Cr_Ed*	16	-14546.77	5.75	0.05	0.95±0.03
Calving	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-16094.06	0.00	1.00	0.97±0.03
Summer	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-36134.74	0.00	0.56	0.85±0.08

	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-36126.20	0.46	0.44	0.88±0.05
Rut	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-14549.51	0.00	0.73	0.74±0.13
	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-14543.53	2.04	0.27	0.84±0.06
Early winter	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-15931.48	0.00	1.00	0.79±0.15
Late winter	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-15459.15	0.00	1.00	0.92±0.06
			Dusk / dawn			
Spring	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-12116.71	0.00	0.65	0.95±0.03
	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-12113.68	2.47	0.19	0.93±0.02
	Cut+Cr_Ed*	16	-12124.81	5.03	0.05	0.94±0.03
	Cut	13	-12128.91	5.26	0.05	0.93±0.06
	Cut+Cr_Ed	19	-12122.66	5.74	0.04	0.92±0.03
Calving	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-11280.86	0.00	0.60	0.88±0.10
	Cr_Ed	13	-11303.92	1.31	0.31	0.88±0.07
	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-11288.89	4.26	0.07	0.91±0.04
Summer	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-27962.37	0.00	1.00	0.93±0.05
Rut	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-16811.61	0.00	0.99	0.91±0.03
Early winter	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-24922.37	0.00	0.55	0.82±0.06
	Cr_Rd+Dt_Rd	13	-24936.03	0.58	0.41	0.85±0.09
	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-24936.74	5.77	0.03	0.85±0.08
Late winter	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-15355.73	0.00	1.00	0.92±0.04
			Night			
Spring	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-9679.09	0.00	0.68	0.85±0.07

	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-9675.25	1.72	0.29	0.85±0.10
Calving	Cr_Ed	13	-6202.93	0.00	0.97	0.75±0.13
Summer	Cut+Cr_Ed	19	-20418.01	0.00	0.64	0.93±0.03
	Cut+Cr_Ed*	16	-20422.24	1.38	0.32	0.93±0.04
Rut	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-19502.55	0.00	0.61	0.84±0.14
	Cr_Rd+Dt_Rd+Cut+Cr_Ed*	20	-19508.29	1.15	0.34	0.83±0.07
Early winter	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-34463.18	0.00	1.00	0.93±0.05
Late winter	Cr_Rd+Dt_Rd+Cut+Cr_Ed	25	-15891.95	0.00	1.00	0.91±0.06

4.3.1 Impacts of clearcuts and roads on step selection

Caribou mostly avoided clearcuts, using 0-5 year-old clearcuts only in combination with other habitat types and distinctly increasing avoidance as stands aged (Figure 4.1; Tables 4.3-4.4-4.5). Our models predict an increase in the relative probability of caribou occurrence when steps are entirely located in regenerating stands. Yet the frequency distributions highlight that such steps have a low probability of being observed within our system (Figure 1). We thus attributed more weight to the left side of the curves when interpreting our results. Response to clearcuts also differed between annual periods. The relative probability of caribou using disturbances gradually increased in late winter and spring until summer and rut, to subsequently decrease markedly in the winter periods (Figure 4.1). Caribou avoided disturbances prominently during the day throughout all annual periods. Certain types of disturbances (e.g. regenerating stands) and annual periods (e.g. calving and winter periods) were nonetheless marked with increased avoidance during dusk/dawn and at night, although to a lesser extent (Figure 4.1; Tables 4.3-4.4-

4.5). Typically, however, female avoidance of disturbances decreased during dusk/dawn and at night, with females sometimes increasing their use instead (e.g. 6-20 year-old clearcuts during summer and rut). Females generally avoided crossing major roads, except during the rut at night. Furthermore, individuals were likely to move toward major roads only during the winter periods and spring at night and dusk/dawn. Conversely, caribou preferentially crossed minor roads for all periods except for the rut and early winter, while individuals nonetheless tended to move away from minor roads throughout all periods.

4.3.2. Impacts of landscape context on step selection

The local context in which females moved influenced their decision to cross clearcut edges and roads for most of the periods considered. Females typically avoided crossing clearcut edges and roads at low densities, yet subsequently increased their crossing rates over what would be randomly expected as densities around the beginning of the step increased (Figure 4.2a, c, d). In certain instances, however, females rather elected to avoid crossing clearcut edges and roads regardless of the density in which they were located (Figure 4.2b) Context was almost always important for major and minor roads, while it seemed to be important mostly during spring, calving and the winter periods for clearcut edges (Tables 4.3-4.4-4.5).

Table 4.3 – Coefficient estimates (β) and 95% confidence intervals (95%CI) of the independent variables of the most parsimonious models explaining caribou movements for 49 females in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2010 during **daytime**. Informative variables were identified with the 95%CI (i.e. not overlapping zero) when available (if not, noted as '*n/a*') and are identified in bold letters.

Variable	Day					
	Spring	Calving	Summer	Rut	Early winter	Late winter
	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*
ElevVar	**-0.0066±0.0014**	**-0.0069±0.0016**	-0.0007±0.0011	**-0.0049±0.0016**	-0.0015±0.0019	**-0.0094±0.0019**
ElevMoy	0.0024±0.0024	**0.0041±0.0027**	**0.0075±0.0019**	**0.0030±0.0028**	**0.0055±0.0033**	**0.0043±0.0032**
Cut05	**2.3675±1.0132**	**1.2350±0.7574**	**0.9892±0.4715**	0.3857±0.8385	**1.9528±1.8162**	1.1719±1.4769
Cut05^2	**-2.4745±1.0020**	**-1.4895±0.7478**	**-0.8088±0.4614**	-0.4003±0.8518	**-2.7657±1.9438**	**-1.9630±1.5867**
Cut620	0.1359±0.4462	**1.3224±0.6743**	0.1064±0.4417	**-0.6521±0.6360**	**-0.7579±0.5280**	-0.1725±0.5638
Cut620^2	-0.0391±0.3974	**-1.7738±0.6633**	-0.1536±0.4267	**0.7224±0.5881**	0.0450±0.5180	-0.4828±0.5478
Regen	**-1.4788±0.6993**	**-2.1337±0.7400**	**-0.7955±0.4649**	**-1.2733±0.8271**	-0.7271±0.7766	**-1.2693±0.8079**
Regen^2	**1.4014±0.7390**	**1.9552±0.7717**	**0.9527±0.4736**	**0.9661±0.8799**	0.5685±0.8243	**0.8866±0.8549**
Cross_{05}	*n/a*	0.0016±0.0334	**0.0444±0.0172**	0.0005±0.0301	-0.0848±0.0982	0.0115±0.0559

Cross$_{05}$*Dens$_{05}$	*n/a*	**0.0058±0.0048**	*n/a*	*n/a*	**0.0162±0.0113**	0.0030±0.0112
Cross$_{620}$	*n/a*	**-0.0525±0.0346**	-0.0001±0.0163	**0.0391±0.0203**	0.0152±0.0287	0.0084±0.0276
Cross$_{620}$*Dens$_{620}$	*n/a*	**0.0059±0.0040**	*n/a*	*n/a*	0.0003±0.0030	**-0.0042±0.0039**
Cross$_{RGN}$	*n/a*	**-0.0435±0.0406**	**-0.0286±0.0232**	**-0.0527±0.0392**	-0.0124±0.0473	**-0.0531±0.0465**
Cross$_{RGN}$*Dens$_{RGN}$	*n/a*	0.0044±0.0057	*n/a*	*n/a*	-0.0014±0.0079	-0.0005±0.0080
Roa12	*n/a*	0.1171±0.2190	-0.1763±0.1991	-0.2593±0.2701	**-0.3855±0.3170**	**-0.7106±0.3602**
Roa12*Dens12	*n/a*	0.3360±0.5787	*n/a*	*n/a*	0.1157±0.1625	**0.5426±0.5203**
Roa34	*n/a*	0.0357±0.0368	**0.0267±0.0203**	0.0177±0.0313	-0.0168±0.0409	**0.0570±0.0322**
Roa34*Dens34	*n/a*	**0.0201±0.0077**	*n/a*	*n/a*	**0.0168±0.0077**	**0.0151±0.0068**
Dvar12	*n/a*	-0.0277±0.0402	**-0.0558±0.0270**	**-0.0395±0.0367**	-0.0058±0.0462	-0.0248±0.0479
Dvar34	*n/a*	**-0.1490±0.0620**	**-0.0859±0.0409**	**-0.1300±0.0537**	**-0.1101±0.0710**	-0.0649±0.0742

*Confidence intervals can be obtained by adding and subtracting the ±95%CI value to its associated β value.

Table 4.4 – Coefficient estimates (β) and 95% confidence intervals (95%CI) of the independent variables of the most parsimonious models explaining caribou movements for 49 females in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2010 during **dusk/dawn**. Informative variables were identified with the 95%CI (i.e. not overlapping zero) when available (if not, noted as '*n/a*') and are identified in bold letters.

Variable	Dusk/dawn					
	Spring	Calving	Summer	Rut	Early winter	Late winter
	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*
ElevVar	**-0.0072±0.0018**	**-0.0053±0.0025**	-0.0008±0.0012	**-0.0060±0.0018**	**-0.0034±0.0017**	**-0.0071±0.0021**
ElevMoy	0.0031±0.0032	**0.0065±0.0044**	**0.0092±0.0021**	**0.0042±0.0031**	**0.0037±0.0030**	**0.0063±0.0036**
Cut05	1.0586±1.2864	0.8482±1.0360	0.4518±0.5463	0.2154±0.8591	1.1805±1.4161	**1.9011±1.4682**
Cut05^2	-1.2631±1.2689	-1.0137±1.0176	-0.2717±0.5416	-0.0335±0.8464	**-1.8990±1.5536**	**-1.7948±1.5099**
Cut620	0.0515±0.5787	0.8371±0.8610	**0.6203±0.5324**	-0.3162±0.6419	-0.1706±0.4214	-0.2224±0.5629
Cut620^2	0.1545±0.5265	**-0.9217±0.8369**	-0.3321±0.4959	**0.8097±0.5864**	-0.1304±0.4147	-0.0537±0.5483
Regen	**-1.0068±0.9710**	**-1.0825±0.9731**	0.1601±0.5133	-0.5691±0.8290	**-1.1154±0.6555**	**-1.2405±0.8813**
Regen^2	0.8723±1.0093	0.9758±0.9913	0.0481±0.5464	0.6502±0.8763	**0.8859±0.6738**	**1.0146±0.9382**
Cross$_{05}$	0.0379±0.0451	0.0485±0.0631	0.0206±0.0320	-0.0251±0.0504	0.0168±0.0557	-0.0262±0.0517

$\text{Cross}_{05}*\text{Dens}_{05}$	*n/a*	0.0039±0.0078	**0.0096±0.0054**	0.0067±0.0072	0.0029±0.0083	0.0017±0.0133
Cross_{620}	-0.0050±0.0232	0.0060±0.0539	-0.0085±0.0379	**0.0448±0.0367**	0.0131±0.0272	-0.0194±0.0304
$\text{Cross}_{620}*\text{Dens}_{620}$	*n/a*	0.0053±0.0062	**-0.0059±0.0054**	-0.0043±0.0054	-0.0005±0.0031	0.0016±0.0041
$\text{Cross}_{\text{RGN}}$	**-0.0880±0.0652**	**-0.1742±0.0998**	**-0.0747±0.0392**	**-0.1409±0.0678**	**-0.0526±0.0513**	**-0.2021±0.0759**
$\text{Cross}_{\text{RGN}}*\text{Dens}_{\text{RGN}}$	*n/a*	**0.0169±0.0125**	0.0064±0.0069	0.0110±0.0135	0.0044±0.0064	**0.0125±0.0105**
Roa12	0.0089±0.2271	-0.0349±0.4704	-0.2255±0.2783	0.0235±0.3098	-0.0712±0.2242	-0.3492±0.3668
Roa12*Dens12	*n/a*	-0.2070±0.4483	0.1763±0.2523	-0.4128±0.5183	0.0641±0.1103	**0.4890±0.3816**
Roa34	0.0267±0.0332	**0.0818±0.0628**	0.0255±0.0356	-0.0127±0.0484	-0.0054±0.0354	**0.1249±0.0342**
Roa34*Dens34	*n/a*	**0.0160±0.0151**	0.0018±0.0109	**0.0203±0.0131**	**0.0179±0.0071**	**0.0072±0.0063**
Dvar12	**0.0914±0.0517**	-0.0670±0.0761	**-0.0732±0.0324**	-0.0409±0.0450	0.0346±0.0439	-0.0016±0.0593
Dvar34	-0.0777±0.0815	**-0.1696±0.1107**	**-0.1636±0.0478**	**-0.0925±0.0642**	**-0.1284±0.0664**	-0.0600±0.0922

*Confidence intervals can be obtained by adding and subtracting the ±95%CI value to its associated β value.

Table 4.5 – Coefficient estimates (β) and 95% confidence intervals (95%CI) of the independent variables of the most parsimonious models explaining caribou movements for 49 females in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2010 at **night.** Informative variables were identified with the 95%CI (i.e. not overlapping zero) when available (if not, noted as '*n/a*') and are identified in bold letters.

Variable	Night					
	Spring	Calving	Summer	Rut	Early winter	Late winter
	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*	ß±95%CI*
ElevVar	**-0.0102±0.0033**	**-0.0086±0.0052**	**-0.0041±0.0023**	**-0.0055±0.0029**	**-0.0050±0.0019**	**-0.0097±0.0029**
ElevMoy	0.0039±0.0059	0.0039±0.0090	**0.0095±0.0041**	**0.0060±0.0052**	0.0032±0.0034	**0.0056±0.0051**
Cut05	1.2378±1.5403	*n/a*	0.6482±0.7445	0.9528±0.9577	1.2933±1.3812	**2.6660±1.6883**
Cut05^2	-1.2213±1.4777	*n/a*	-0.2734±0.7139	-0.6522±0.9238	**-1.6411±1.4286**	**-2.8620±1.7355**
Cut620	-0.1977±0.7111	*n/a*	0.0425±0.7690	**-0.7297±0.7053**	-0.0571±0.3763	**-0.6579±0.6106**
Cut620^2	0.3239±0.6602	*n/a*	**0.7780±0.7063**	**1.0794±0.6454**	-0.3348±0.3698	0.3919±0.5894
Regen	-1.2164±1.2973	*n/a*	**-1.3725±0.7122**	**-0.9673±0.9149**	**-0.6440±0.6337**	-0.0650±0.9651
Regen^2	1.2743±1.3013	*n/a*	**1.3992±0.7031**	0.9266±0.9348	0.4053±0.6393	-0.3721±0.9928

Cross_{05}	0.0022±0.0748	-0.0524±0.1268	-0.0379±0.0662	-0.0439±0.0772	-0.0432±0.0904	-0.0350±0.0639
Cross_{05}*Dens_{05}	*n/a*	**0.0215±0.0171**	**0.0131±0.0105**	0.0056±0.0122	-0.0015±0.0144	**0.0231±0.0143**
Cross_{620}	-0.0414±0.0426	0.0065±0.0629	-0.0489±0.0745	0.0490±0.0514	0.0225±0.0274	0.0009±0.0367
Cross_{620}*Dens_{620}	*n/a*	**0.0104±0.0103**	-0.0041±0.0107	-0.0009±0.0079	-0.0010±0.0027	**0.0061±0.0043**
$\text{Cross}_{\text{RGN}}$	**-0.1524±0.1031**	**-0.2606±0.1889**	**-0.0803±0.0738**	**-0.1040±0.0967**	**-0.1960±0.0745**	**-0.3086±0.1235**
$\text{Cross}_{\text{RGN}}$*$\text{Dens}_{\text{RGN}}$	*n/a*	0.0231±0.0284	0.0075±0.0109	**0.0196±0.0160**	**0.0157±0.0067**	0.0123±0.0168
Roa12	-0.1137±0.5139	*n/a*	*n/a*	-0.2058±0.5734	-0.0141±0.2459	**-1.0641±0.6100**
Roa12*Dens12	*n/a*	*n/a*	*n/a*	0.2284±0.4220	-0.1039±0.1593	0.3172±0.3305
Roa34	**0.0981±0.0549**	*n/a*	*n/a*	**-0.0720±0.0717**	-0.0364±0.0434	**0.1152±0.0472**
Roa34*Dens34	*n/a*	*n/a*	*n/a*	**0.0138±0.0134**	**0.0220±0.0078**	0.0082±0.0095
Dvar12	0.0813±0.0989	*n/a*	*n/a*	0.0583±0.0780	**0.0900±0.0499**	**0.1064±0.0809**
Dvar34	**-0.2057±0.1557**	*n/a*	*n/a*	**-0.1775±0.1060**	**-0.1501±0.0681**	**-0.1219±0.1164**

*Confidence intervals can be obtained by adding and subtracting the ±95%CI value to its associated β value.

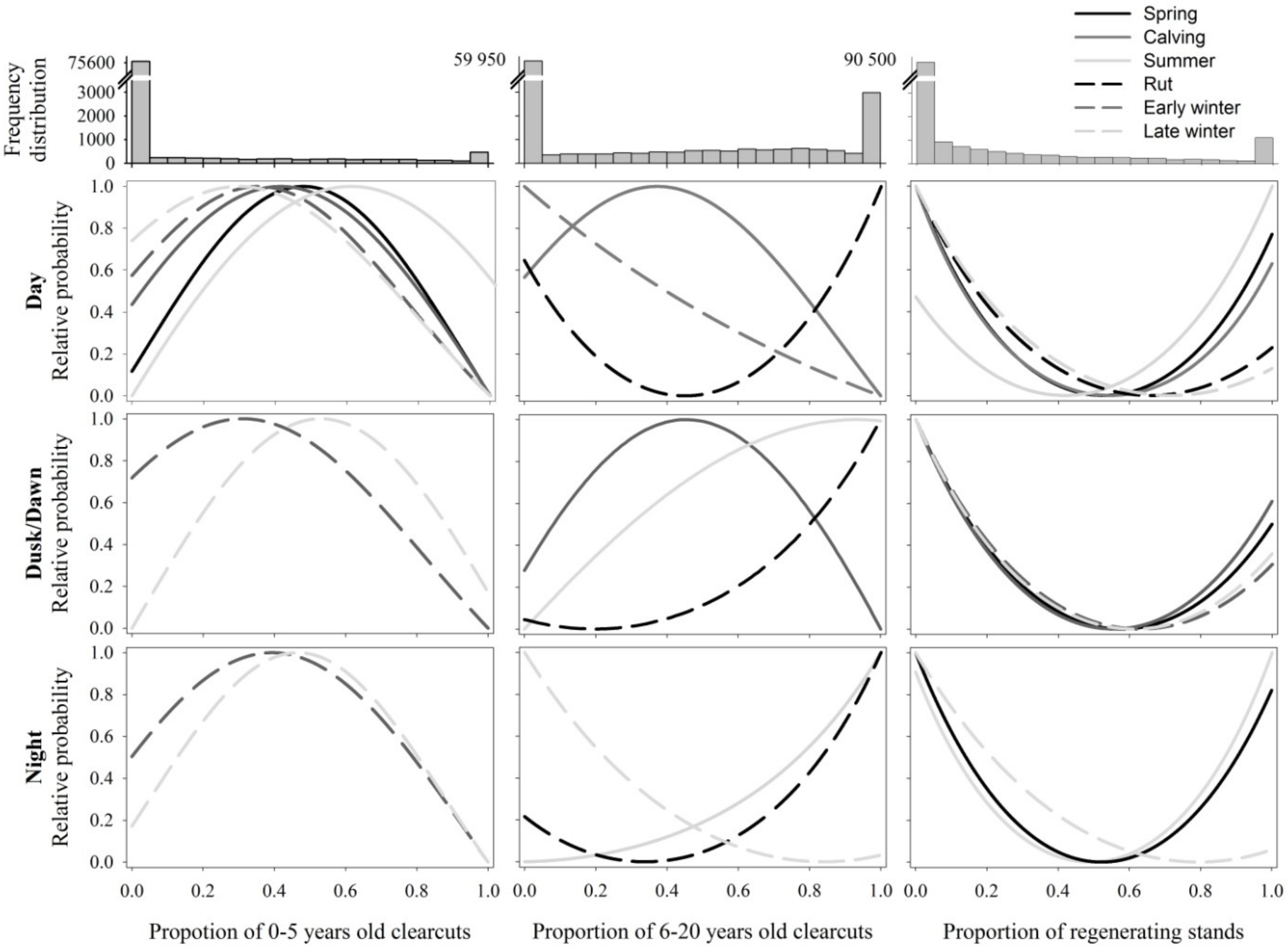

Figure 4.1 –Relative probability of caribou occurrence as a function of a) the proportion of the step in 0-5 years old clearcuts, b) the proportion of the step in 6-20 years old clearcuts and c) the proportion of the step in regenerating stands for all significant periods.

With each graph is associated the annual frequency distribution of the proportion of the step in each clearcut types. The $\hat{w}(x)$ values obtained through the logistic regression equations were standardized between 0 and 1 to obtain relative probabilities of observing caribou steps.

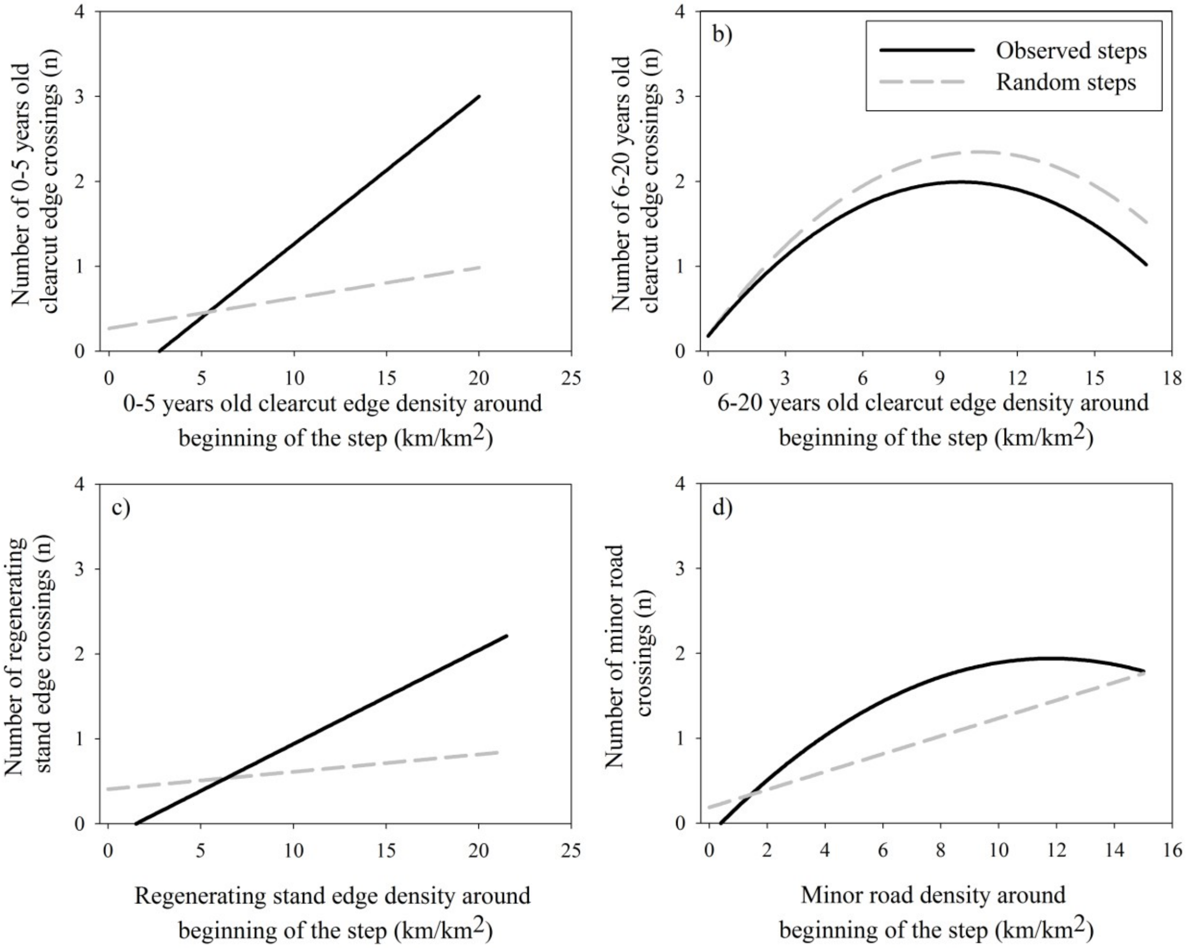

Figure 4.2 – Number of a) 0-5 years old clearcut edge crossings during calving at night, b) 6-20 years old clearcut edge crossings during summer at dusk/dawn, c) regenerating stand edge crossings during calving at dusk/dawn and d) minor road crossings during early winter at dusk/dawn as a function of their respective edge density around the beginning of the step. The figures were obtained by fitting a curve on the mean number of crossings per steps for individual caribou within intervals of 0.5 km/km^2 ranging from 0 to the maximum observed density values. We chose four representative examples of typical significant interactions obtained through our analysis (see Tables 4.3-4.4-4.5).

4.4 Discussion

Caribou are thought to orient their habitat use hierarchically to minimize the impacts of the most limiting factors (e.g. predation) at coarse spatiotemporal scales in order to attend to biological requirements at finer scales (Rettie and Messier 2000). Certain populations nevertheless inhabit heavily altered habitats where the representation of habitats associated with greater uncertainty is such that individuals are also confronted with limiting factors at finer scales (Briand *et al.* 2009). Under this scenario, we investigated the impacts of disturbances on the movements of woodland caribou in highly managed landscapes. We found that although disturbances were essentially avoided, females nonetheless regularly moved through or in close proximity to roads and clearcuts, modifying their behaviour when doing so. Our results also further demonstrate that individuals modulate their response to disturbances on a daily and annual basis. This potentially reflects an ability to adapt behavioural decisions temporally by compromising between risk avoidance and forage requirements in an attempt to optimize their respective efficiency (Godvick *et al.* 2009; Bjørneraas *et al.* 2011).

4.4.1 Daily and annual response to disturbances

Female caribou did not respond consistently to the different types of clearcuts. Females were gradually less likely to be found within clearcuts as stands aged, suggesting an evolution of perceived risk associated with those habitats. Moose – and incidentally wolf – densities increase once cutovers are regenerating (Courtois *et al.* 1998; Nielsen et al. 2005). Risks of encounter with predators may thus be lower in younger clearcuts (Houle *et al.* 2010), increasing the likelihood of caribou using those habitats (Leblond *et al.* 2011). Those habitats are nonetheless associated with increased human and predator activity (Burton *et al.* 1999), which may explain that females preferred using young clearcuts when other habitats were locally available. Furthermore, as regeneration will inevitably replace young disturbances, any gain will be temporary until those habitats are colonized by predators and their alternative preys.

Females also modified their response to disturbances annually. Avoidance of disturbances seemed to be most acute during periods of greater vulnerability for calves (i.e. calving) and adults (i.e. early and late winter).While calves are very susceptible to opportunistic black bear predation the first weeks following birth (Bastille-Rousseau *et al.* 2011; Pinard *et al.* 2012), adults seem to be more vulnerable to gray wolf predation during the winter as their diet becomes primarily ungulate-based (Peterson and Ciucci 2003). Specifically, wolves were found to seek caribou habitat during dusk/dawn and at night (Tremblay-Gendron 2012). Clearcut edges and roads also impacted caribou in periods of greater vulnerability. Edges are known to alter species interactions (Fagan *et al.* 1999) and may be particularly significant for caribou as edges are used by moose and wolves as a consequence (e.g. Bergman *et al.* 2006; Dussault *et al.* 2006; Gurarie *et al.* 2011). The boundary between natural and disturbed habitats could thus be particularly hazardous for caribou and may explain the distinct avoidance of regenerating stand edges. Likewise, roads and edges might be used by alternative prey species for wolves and bears, the predators themselves and humans potentially leading to greater predation risk or disturbance for caribou (Whittington *et al.* 2011). Wolves in particular increase their use of roads during winter, especially at dusk/dawn and at night (Tremblay-Gendron 2012), and encounter rates between caribou and wolves have been found to increase during that period (Whittington *et al.* 2011). As these linear features are associated with increased mortality risk, an increase in their density could have important impacts on the survival of female and especially of calves, ultimately leading to population level consequences.

Conversely, individual caribou increased their use of open habitats mainly during the spring, summer and rut periods, along with a slight increase in the use of 0-5 year-old clearcuts during late winter. This suggests that forage requirements may in part prevail over risk avoidance during those periods. Foraging opportunities become scarcer as winter progresses (Gaillard *et al.* 2000; Johnson *et al.* 2001), which is followed by periods of low body condition in spring and summer, especially for parturient females (Barten *et al.* 2001). Individuals must therefore adapt their foraging activities during those critical periods. The abundance in shrub cover found in clearcuts in our system has been previously discussed as providing complementary alternative forage for caribou in winter (see Briand et al. 2009). The green plants available in clearcuts during the snow-free periods could also be used in a similar fashion (Schaefer and Mahoney 2007; Godvik *et al*. 2009) Additionally, females tended to move towards major roads at night through the winter periods. This response may be expected from individuals accessing open habitats in our study area as they are close to roads, a pattern also observed for reindeer in Sweeden relative to trails (Skarin *et al.* 2010). Those habitats are nonetheless associated with higher risk and high adult mortality rates have been observed for multiple populations during those periods (Whittington *et al.* 2011).

Interestingly, female caribou predominantly avoided disturbances during the day. As discussed, although disturbances may offer advantages to caribou during certain annual periods, they are nonetheless associated with increased predator presence and thus higher mortality risks, especially during the day (Dussault *et al.* 2005). On the other hand, crepuscular and nocturnal activities of females were not as heavily affected by disturbances, with individuals increasing their use of 6-20 year-old during the summer and the rut. These daily variations in response to disturbances may then reflect a decrease in perceived risk by female caribou. Such a daily pattern of habitat use is also supported by comparable time-dependant habitat use demonstrated for other ungulate species (e.g. Godvik *et al.* 2009; Lykkja *et al.* 2009; Bjørneraas *et al.* 2011).

4.4.2 Influence of local context on movements

The landscape context was found to impact caribou movements, especially during periods of greater vulnerability. Females preferentially increasing or decreasing their crossing rates suggest a vigilance-relocation response potentially related to the risk associated with local disturbance levels. As individuals typically avoid crossing clearcut edges and roads, a local increase in the presence of such features can be expected to impose greater alertness on individuals (Zollner and Lima 2005). Increased crossing rates may thus reflect relocation movements in an effort to access more secure areas, increasing the likelihood of edge and road crossings (Ims *et al.* 1993). Conversely, the decrease could reflect a state of heightened vigilance compelling individuals to remain within risky habitats for a longer period of time (Zollner and Lima 2005). While increased use of edges and roads could lead to greater predation risk (e.g. Whittington *et al.* 2011; Gurarie *et al.* 2011), females that are decreasing their crossing rates may become trapped in sub-optimal habitats that may compel individuals to spend less time foraging in favor of a heightened anti-predation behaviour (Frid and Dill 2002). Such a response could have dire consequences for individual survival (Gill *et al.* 2001) and seems analogous to responses exhibited at coarser scales, with individuals decreasing space use as disturbance levels increase over certain thresholds (see Beauchesne *et al. submitted*). Alongside further local increases in disturbances, females trapped in sub-optimal habitats could ultimately be forced to spend more time foraging and less time assessing risk as they become energetically depleted (Zollner and Lima 2005).

4.5 Conclusions and recommendations

We demonstrated that woodland caribou modify their fine-scale movements temporally in response to disturbances, potentially balancing daily and annual forage requirements with risk avoidance. We also highlighted the importance of considering daily periods when studying behaviour. The failure to consider daily patterns of habitat use may obscure such behaviours like diurnal avoidance and nocturnal use through data aggregation, and potentially fail to detect relevant ecological processes. Additionally, we found that individuals modified their movements when locally confronted with higher disturbance levels, ultimately compelling them to use more risky habitats. Combined, these two findings seem to indicate that increasing disturbance levels in the boreal forest are compelling caribou to respond to limiting factors at gradually finer scales and potentially traps them in suboptimal habitats. We know that black bear predation on calves can be particularly problematic in areas of intensive forest management (see Pinard *et al.* 2012). Additionally, current management practices may increase local caribou densities and co-occurrence probabilities with wolves during the winter period (Courbin *et al.* 2009; Lesmerises 2011), alongside a potential adaptation of wolves to hunt caribou during those periods (Tremblay-Gendron 2012). It thus seems that predation risk and anthropogenic disturbance may combine and impact individual vulnerability, ultimately affecting populations through decreases in reproductive output and survival (Frid and Dill, 2002). Proportions of clearcuts within our study area (Portneuf: 41%; Piraube: 15%) being within range of established levels known to impose detrimental physiological stress (>36%; Renaud 2012) and decreased recruitment rates (>35%; Environment Canada 2011), further increases in disturbance levels are likely to jeopardize long-term caribou persistence for future generations.

Acknowledgements

This project was funded by the following partners: AbitibiBowater Inc., Canada Economic Development, Conseil de l’industrie forestière du Québec, Fondation de la faune du Québec, Fonds québécois de la recherche sur la nature et les technologies, Fonds de recherche forestière du Saguenay–Lac-St-Jean, Ministère des Ressources naturelles et de la Faune, Natural Sciences and Engineering Research Council of Canada (Discovery Grant to M.-H. St-Laurent), Université du Québec à Rimouski and World Wildlife Fund for Nature. We also thank the Essipit First Nation and A. Chabot for providing access to their caribou telemetry data, via the Aboriginal Funds for Species at Risk (Environment Canada). Many thanks to J.-P. Ouellet and C. Dussault for their scientific and logistical support, É. D’Astous, R. Moriarity, R. Weladji and C. Johnson for providing useful comments on earlier versions of this manuscript, and to A. Caron and M. Leblond for their assistance with statistical and GIS analyses.

Chapter 5. General conclusion

There exists a vast body of literature obtained through extensive research programs conducted over the past decades that allows for a thorough understanding of caribou behaviour across multiple spatiotemporal scales and on many facets of its ecology. Most caribou populations are now declining across much of their North-American distribution (Vors and Boyce, 2009) and there seems to be a strong correlation between observed declines and the northward advancement of forest harvesting activities (Schaefer 2003; Vors *et al.* 2007). Woodland caribou thus strives to remain elusive in a landscape gradually transformed by forest harvesting into prime habitats for alternative prey species and associated predators (Bergerud and Page; 1987; Schaefer 2003). In an effort to avoid altering the boreal forest too profoundly for caribou persistence, recent reports have discussed levels of disturbances over which populations are deemed unlikely to be self-sustaining and proposed thresholds of population tolerance that should not be exceeded in the boreal forest (Sorensen *et al.* 2008; Environment Canada 2011).

Long-term, extensive impacts on populations should however result from short-term behavioural shifts at the individual level (see Johnson and St-Laurent 2011). It is under this framework that we decided to study the behaviour of woodland caribou evolving in heavily managed habitats and our results support numerous studies demonstrating that individuals alter their behaviour when confronted with anthropogenic disturbances (e.g. Dyer *et al.* 2002; Schaefer and Mahoney 2007; Hins *et al.* 2009). Still, while most studies conducted on caribou behaviour focused on habitat selection, the goal of this study was to investigate its underlying process, movement, in the hope of filling some gaps in the understanding of behavioural response to anthropogenic disturbances.

5.1 Summary of findings

Under the premise of individual movements emulating patterns of habitat selection observed hierarchically across multiple spatiotemporal scales, this study was able expand the knowledge on how caribou – and potentially other species – modify their movements in response to the presence of disturbances in their habitat. Using home-range size as a proxy of individual space use, we demonstrated that caribou firstly responded to increased amounts of disturbances through home-range expansion, reflecting a capacity to cope with low levels of disturbances. However, individuals modified their response when confronted with high levels of disturbances, instead contracting their home-ranges, suggesting limitations to the behavioural plasticity of caribou evolving in heavily managed landscapes. Such behavioural shifts could compel individuals to use sub-optimal habitats leading to lower survival probabilities and ultimately to population level consequences. Furthermore, the results obtained through this analysis highlight that disturbance levels currently observed in the boreal forest can already effectively compel caribou to shift their behaviour, which could be highly detrimental to the long-term persistence of caribou in the boreal forest.

The shifts in behaviour at the home-range scale causing caribou to remain in highly altered habitats led us to believe that individual coarse-scale segregation from disturbances may thus be deficient in highly managed areas. Individuals could then be compelled to move in close proximity to disturbances at gradually finer scales (Rettie and Messier 2000). We thus tested whether individual caribou respond to disturbances at the fine-scale. We found that although females mostly avoided disturbances when moving through their home range, they nevertheless regularly came in contact with them. Individuals modulated their movements temporally on an annual and daily basis in response to anthropogenic disturbances. Females avoided disturbances during periods of higher vulnerability (calving, early and late winter) during the day. Conversely, they decreased avoidance behaviour or even increased their use of disturbances during periods of higher energy requirements (spring, summer and rut) during dusk/dawn and night. It therefore seems that individuals balance their biological requirements with risk avoidance by predominantly avoiding habitats associated with higher uncertainty when perceived risk is higher and conversely using them when risk is lower. Furthermore, the context in which individuals moved also affected relative probabilities of females crossing clearcut edges and roads. This suggested either relocation movemetns to other – and potentially more suitable – habitats or increased vigilance that may cause individuals to remain in locally altered habitats for a longer period of time. This latter response, which is analogous to that exhibited at coarse-scale through home-range contraction, could cause individuals to remain in risky habitats for longer periods even at finer scales. This could also disrupt the daily time budget allocated to biological activities (Zollner and Lima 2005), while increasing mortality risks. Ultimately, individuals could either increase or decrease their time spent assessing risk, resulting in less time spent on biological activities or increased vulnerability due to insufficient risk assessment (Sih 1992; Zollner and Lima 2005). Furthermore, this study also highlights the importance of considering daily processes when studying behaviour as differential responses could be obscured through data aggregation.

5.2 Management implications

Our results suggest that forest harvesting and predation risk combine to impact the survival of caribou by increasing risk perceived by females (e.g. presence of human, predators and alternative prey species) and increasing predator densities. An increase of both could easily render coarse-scale risk avoidance strategies deficient, especially when individuals are forced to occupy risky habitats through the majority of their annual distribution. Caribou may be unable to avoid predators efficiently in such habitats with respect to fortuitous predation on calves by black bears (Bastille-Rousseau *et al.* 2011; Pinard *et al.* 2011) and similarities between caribou and wolf fine-scale habitat use during winter (Chapter 4; Tremblay-Gendron 2012). Under such a scenario, remaining elusive at the landscape scale becomes much more vital to caribou survival, a strategy compromised under a heavy disturbance regime which exacerbates caribou vulnerability (e.g. Renaud 2012). The non-linear and contextual responses found in Chapters 3 and 4 are critical in understanding the limits in individual plasticity to cope with disturbances and suggest that current disturbance levels may already be well above thresholds of natural adaptability. As a result, individuals could be forced into a secondary behavioural state from which a backwards transition is highly uncertain (Johnson *submitted*). This also seems supported by levels of disturbances observed in our study area (Portneuf: 41%; Piraube: 15%) falling within a range known to impose lasting physiological stress on individuals (>36%; Renaud 2012) and decreased recruitment rates leading to a decrease in the likelihood of populations being self-sustaining in the future (>35%; Envionment Canada 2011).

While most conservation policies are concerned with threats to survival and aim at quantifying how species are impacted by human activities from a population standpoint, focusing on populations rather than behaviour could lead to reactive management initiatives. In order to observe population level alteration due to natural or anthropogenic factors, a chain of events moving through the whole biological scales of impact must first typically occur (see Johnson and St-Laurent 2001). In essence, there would be a time lag between the initiation of stressing factors and population level consequences as stressors gradually work up the scale of biological impacts to affect populations. Focusing solely on the population level thus ignores the mechanisms underlying population change and potentially overlooks crucial events leading to their demise. Proactive management plans focusing rather on behaviour could therefore be highly valuable in order to prevent the chain of events leading to population consequences, or at the very least help avoid behavioural shifts as limits of natural adaptability are reached. It has been argued that behavioural changes with respect to increasing human activities can only be meaningful from a conservation perspective when there are clear threats to population persistence (Gill and Sutherland, 2000; Gill *et al.* 2001). The same authors also argued that anthropogenic activities may not translate into population level consequences for species that possess the ability to avoid humans as they may access other suitable habitats (also see Ydenberg and Dill, 1986). Rather, species that do not relocate may in fact be much more vulnerable to anthropogenic activities since they might be constrained within suboptimal habitats caused by unsuccessful relocation to other suitable habitats, possibly due to their nonexistence. The increasing disturbance levels noted in the boreal forest have been found, through this study, to impose such constraints on individuals across multiple spatiotemporal scales. It is thus reasonable to assume that they must also impact populations.

Several suggestions for management strategies could be developed from the results obtained in this project:

- The thresholds found in Chapter 3 (table 3.4) could help in the development of proactive management plans by providing known levels of disturbances over which individuals modify their behaviour in a way that could result in population level consequences. It is however important that those thresholds be considered under the actual values reported.

As defined in Chapter 3, thresholds presented correspond to levels over which a sudden or gradual shift in behavioural response is observed, rather than a regulatory limit (Johnson *submitted*). As such, these thresholds should never be reached – which includes the lower limit of their associated uncertainty – as well as never be approached.

- The representation of disturbances known to influence female caribou movements most drastically should be used to set management goals.
    - The representation of regenerating stands in the range of woodland caribou should be limited, as females acutely avoided those disturbances across all scales considered. This suggests that management strategies should take into account the ~20 years time lag needed for cutblocks to elicit their maximum impact on caribou. This strategy would also limit predator and prey densities, thereby further support caribou survival by decreasing the impact of apparent competition.
    - The density of major roads should be limited in the boreal forest as they exert a significant impact on caribou space use in particular.
    - Reconverting minor roads to natural habitats should also be considered (see Nellemann *et al.* 2010). Although minor roads were absent from our coarse-scale analysis, female movements were shown to be impacted by the density of minor roads throughout most periods. Their density in our study area seems to be important for caribou to efficiently avoid them and increases in predator-prey encounters may occur more frequently and impact caribou survival.

- The threshold values considered should correspond to periods of higher biological vulnerability or sensitivity to disturbance stimuli. The calving and winter periods are of significant importance for calf and adult survival and were characterized by marked avoidance across spatiotemporal scales. The representation of disturbances found in the landscape should therefore not exceed levels over which females modify their behaviour.

- Considering the need for forest harvesting activities, operations should be restricted to periods of lower vulnerability and decreased avoidance behaviour. Female behaviour seemed to be less impacted during the summer period across all spatiotemporal scales considered and activities restricted to the summer period could limit the effect of disturbance stimuli generated by human presence in caribou habitat.

Such additional management strategies could certainly assist in securing woodland caribou persistence in the North-American boreal forest while keeping forest harvesting activities from exerting pressures that are not sustainable for caribou populations.

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