DEMOGRAPHY AND HABITAT SELECTION OF NEWFOUNDLAND CARIBOU

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Abstract

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The objective of this thesis is to better understand the demography and habitat selection of Newfoundland caribou. Chapter 1 provides a general introduction of elements of population ecology and behavioural ecology discussed in the thesis. In Chapter 2, I examine the causes of long-term fluctuations among caribou herds. My findings indicate that winter severity and density-dependent degradation of summer range quality offer partial explanations for the observed patterns of population change. In Chapter 3, I investigate the influence of climate, predation and density-dependence on cause-specific neonate survival. I found that when caribou populations are in a period of increase, predation from coyotes and bears is most strongly influenced by the abiotic conditions that precede calving. However, when populations begin to decline, weather conditions during calving also influenced survival. I build on this analysis in Chapter 4 by determining the influence of climate change on the interplay between predation risk and neonate survival. I found that the relative equilibrium between bears and coyotes may not persist in the future as risk from coyotes could increase due to climate change. In Chapter 5, I investigate the relationships in niche overlap between caribou and their predators and how this may influence differential predation risk by affecting encounter rates. For coyotes, seasonal changes in niche overlap mirrored variation in caribou calf risk, but had less association with the rate of encounter with calves. In contrast, changes in niche overlap during the calving season for black bears had little association with these parameters. In Chapter 6, I examine broad-level habitat selection of caribou to study trade-offs between predator avoidance and foraging during the calving season. The results suggest that caribou movements are oriented towards increased access to foraging and the reduction of encounter risk with bears, and to a lesser extent, coyotes. Finally, I synthesize the major findings from this thesis and their relevance to caribou conservation in Chapter 7, to infer that Newfoundland caribou decline is ultimately driven by extrinsic and intrinsic elements related to density-dependence. Reduction in neonate survival emerged from nutritionally-stressed caribou females producing calves with lower survival.

Keywords

Woodland caribou (*Rangifer tarandus*), black bear (*Ursus americanus*), coyote (*Canis latrans*), population ecology, behavioural ecology, conservation biology, predator-prey interactions, habitat selection, movement, density-dependence, climate, survival, climate change, migration, niche overlap, foraging.

Preface

I have written my thesis in manuscript format, as each of my chapters has been, or will be, published in the peer-reviewed literature. Chapter 2 has been published in Canadian Journal of Zoology, Chapter 3 will be submitted to Journal of Animal Ecology, Chapter 4 will be submitted to Ecology Letters, Chapter 5 has been submitted to Behavioral Ecology, and Chapter 6 has been submitted to Ecography. Each chapter is therefore written in as stand-alone manuscript in the style of the relevant journal, and I am first author on each of these manuscripts. All of my research has been done in collaboration with other people; I have used the plural, “we”, where appropriate throughout this thesis. Each chapter also presents the list of people whose contributions have been sufficiently important to merit authorship. Permission to reprint articles from the copyright holders can be found in Appendix A.

Acknowledgements

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I spent two amazing summers conducting fieldwork in Newfoundland, flying around, camping, and observing caribou. Evan Downey and Maria-Camila Roy-Avilan were helpful field assistants, despite the sometimes harsh field conditions. These two summers were also made a lot more enjoyable by the presence of other fine individuals: Nathaniel Rayl, Matt Mumma, Chris Zieminski, and Steven Seagal. I have excellent memories of all the time spent with them at Conne River.

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Table of Contents

List of Tables

List of Figures

Prologue

> "*We have become, by the power of a glorious evolutionary accident called intelligence, the stewards of life's continuity on earth. We did not ask for this role, but we cannot abjure it. We may not be suited to it, but here we are*."
>
> - Stephen Jay Gould

> "*Mathematics without natural history is sterile, but natural history without mathematics is muddled.*"
>
> - John Maynard Smith

Ecology, the study of interactions among organisms and their environment, is a science composed of multiple levels of organization spanning the cellular to planetary levels. Studying ecological problems requires a holistic approach that necessitates using tools such as satellites, binoculars and microscopes to extract cues from noisy systems. Solving these problems presents numerous challenges, and one has to conceptualize rigorous experimental design or challenge the limit of observational study through clever and innovative use of statistical tools. In large part, this is what brought me to the study of ecology, more precisely animal ecology -- in addition to the opportunity to do fieldwork in interesting settings.

Animal ecology itself can be categorized into multiple sub-disciplines such as behavioural, population, conservation, theoretical, etc. Animal ecologists also sometimes become species-specialists by focusing on the ecology of a single species;

this has never been my goal, despite having spent a large proportion of my graduate journey working with a charismatic species: woodland caribou (*Rangifer tarandus*). Nevertheless, each sub-discipline of animal ecology overlaps with others, and I believe it is hard to become a specialist in one discipline without having a good grasp of other sub-disciplines. This thesis cannot be classified into one unique sub-discipline; rather, it looks at the population and behavioural ecology of a species in relation to its environment, notably its predators. From these observations, I tried to draw insights that improved our theoretical understanding of animal ecology, but that also served the conservation needs of the focal species. This species was caribou, specifically the populations inhabiting Newfoundland island, but before delving into the vast literature regarding caribou, I will first briefly introduce elements of population ecology, predator-prey interactions and prey behavioural responses, that are central to this thesis.

Chapter 1 - General introduction

Population ecology: Interactions between intrinsic and extrinsic drivers of animal abundance

Animal population abundance and/or density are rarely stable through time; rather they fluctuate following numerous patterns. Fluctuations in animal population density can be driven by a range of factors, including intrinsic factors that are specific to a species (Kendall *et al.* 1999; Turchin 2003a) or extrinsic factors such as inclement weather (Stenseth *et al.* 1999) or anthropogenic influences (Faille *et al.* 2010). Density-dependent processes are those that are governed by the density of the population and affect population growth rates. Intra-specific competition for resources, parasitism or predation are processes that can be affected by population density and then modulate population growth rate (Krebs 2001). Although predation is sometime considered as being density-dependent, the role of predation is not necessarily straightforward when predators can switch between multiple prey. In these instances, predation rate can become density-independent (Holt & Lawton 1994; Fryxell & Lundberg 1994) or even inversely density-dependent (Allee effect; Courchamp, Clutton-Brock & Grenfell 1999).

Climate can have a major influence on many aspects of an animal's fitness (Stenseth *et al.* 2002). Climate can directly impact foraging ability by affecting phenology and availability of vegetation (Parmesan 2006; Hansen *et al.* 2013). Climate can also have indirect effects via its influences on resource competition or predation risk (Melis *et al.* 2009). Such complexity in climate-predator interactions is highlighted by wolf-ungulate interactions, where winter and summer temperature or precipitation can influence ungulate forage availability and foraging behaviour, predator behaviour, and ultimately, predation rates (Post *et al.* 1999; Cook *et al.* 2004). Recent studies (e.g. Griffin *et al.* 2011; Brodie *et al.* 2013) have further shown that climate-predator interactions can drive population dynamics through recruitment and adult survival. Climate-predator interactions can be influential when the impact of climate on available food alters the foraging habit of a prey species, altering their exposure to predation risk (Yasué, Quinn & Cresswell 2003; Griffin *et al.* 2011). Alternatively, climate-predator interactions can occur when climate facilitates predator hunting, reduces prey ability to escape predation, or alters the interplay between multiple predators (Post *et al.* 1999; Mills *et al.* 2013). In a system with multiple predators, these complexities mean that climate can potentially direct predation risk among predators and favour a specific predator under a given set of climatic conditions, particularly when predator species differ in their hunting strategies.

The influence of climate on population dynamics can also be modulated by density-dependent processes (Coulson, Milner-Gulland & Clutton-Brock 2000; Simard *et al.* 2010). Numerous animal populations are limited by food resources, where over time individuals are exposed to favourable foraging conditions followed by nutritionally poor conditions (Sinclair 1977; Fryxell & Sinclair 1988). Periods of nutritional stress can lead to reduced adult and juvenile survival and reduced reproductive effort (Gaillard *et al.* 2000; Sinclair, Fryxell & Caughley 2006; Owen-Smith 2014). It is expected that nutritionally-stressed individuals will have more difficulty coping with stochastic variation in forage availability, for example, when induced by changes in climate (White

2008). When we consider such variability in light of climate-predator interactions, we should expect the nature of climatic influence on predation also to be modulated by density-dependence, therefore impacting population dynamics together (Messier 1991; Lima, Stenseth & Jaksic 2002; Wang *et al.* 2009).

Population ecology: Recurring fluctuations and synchrony among animal populations

Fluctuations in abundance within animal populations can take multiple forms. Some populations currently show steady, non-sustainable declining trends whereas others experience repeatable fluctuations marked by a period of high density followed by a period of low density. Prime examples of repeatable fluctuations can be found in the snowshoe hare - Canadian lynx system or in lemmings inhabiting the Arctic (Krebs 2011). Extensive field studies in these systems have greatly improved our understanding of cyclic population dynamics. Repeatable fluctuations could first be driven by large-scale and recurring changes owing to stochastic elements such as climate variability (Post & Forchhammer 2002). Repeatable fluctuations can also be induced by time-delayed changes in intrinsic stressors related to density-dependence (Kendall *et al.* 1999). Much attention has been devoted to the origin of these time-delays and whether they emerge from bottom-up maternal effects (Inchausti & Ginzburg 2009) or top-down influences (Krebs *et al.* 1995).

Cyclic fluctuations in population abundance are frequently highly synchronous among spatially-isolated populations (e.g. Sinclair *et al.* 1993; Ranta *et al.* 1997). This indicates that processes affecting population dynamics operate at scales that span beyond local environments. Thus, synchronized dynamics across broad landscapes may be directed by common extrinsic or environmental factors (Moran effect; Ranta *et al.* 1997; Ims & Andreassen 2000). Synchrony among populations can also emerge through the role of predator regulation (Korpimäki & Norrdahl 1998). Lastly, trends in population abundance also may be synchronized via dispersal, even in the absence of large-scale extrinsic or intrinsic drivers (Ranta *et al.* 1995).

Bridging population ecology and behavioural ecology: Predator-prey interactions

From classic theoretical work on predator-prey population dynamics by historical figures such as Lotka (1925) and Volterra (1931), to classic examples of predator-prey population abundance cycles (Elton & Nicholson 1942), strong interest in predator-prey relationships is indeed present in our foundations of modern ecology. Predation can have a strong impact on prey population abundance by the direct removal of individuals (known as a direct or lethal effect). Consequently, most animals try to reduce their risk in their daily activities by displaying anti-predator behaviours (Brown, Laundré & Gurung 1999; Creel & Christianson 2008). For example, in response to predation, prey can alter their patterns of space-use, vigilance, foraging, gregariousness, and movement (Lima & Bednekoff 1999; Creel *et al.* 2005; Fortin *et al.* 2005, 2009; Hebblewhite, Merrill & McDonald 2005).

Although costs of predation on prey are more intuitively associated with the lethal aspect of predation, predation can also reduce fitness through the consequences of anti-predator behavioural responses (Peacor & Werner 2001; Luttbeg & Kerby 2005).

These behaviours carry varying costs by reducing foraging efficiency or increasing physiological stress (Creel, Winnie & Christianson 2009; Sheriff, Krebs & Boonstra 2009). Recent evidence shows that in some systems, risk effects (also frequently termed as indirect, non-consumptive or sublethal effects) of predation can have a larger impact on population dynamics than the direct effect of predation (Preisser, Bolnick & Benard 2005; Creel & Christianson 2008). However, it would be presumptuous to suggest that the importance of nonlethal effects is broadly accepted, and there continues to be debate over the relative roles of lethal and nonlethal effects of predators on prey populations (White, Garrott & Hamlin 2011; Middleton *et al.* 2013b). Therefore, understanding the prevalence of anti-predator behavioural responses and the efficiency by which animals trade-off food versus safety is crucial to explaining population dynamics (Gaillard *et al.* 2010).

Behavioural ecology: Movement and space-use strategies at the core of the predator-prey game

Predator-prey interactions are generally conceptualized as complex games of fear and stealth between predators and prey (Brown *et al.* 1999; Laundré 2010). In these games, predators attempt to maximise their success during search, encounter, and attack stages through selective movement, habitat patch-use and hunting behaviour (Lima & Dill 1990; Hebblewhite *et al.* 2005). Movement is a central process in ecology (Nathan 2008) and a key element of any predator-prey game (Mitchell & Lima 2002; Laundré 2010). Animals need to move in response to a variety of competing demands such as the need to feed, avoid predators, rear offspring, and breed (Brown *et al.* 1999; Cresswell 2008). These demands give rise to trade-offs that individuals must mediate through their space use and movement patterns (Lima 1998; Hebblewhite & Merrill 2009), resulting in unique patterns of habitat selection. Habitat selection is defined as the disproportionate use of a habitat relative to its availability (Johnson & Johnson 1980; Manly *et al.* 2002), and clarifying habitat selection processes remains a central concept bridging spatial and temporal scales in ecology (Morris 2003; Mayor *et al.* 2007).

Different theoretical models predict how predator and prey might move across the landscape, such as the shell-game concept (Mitchell & Lima 2002), the behavioural response race (Sih 1984) and the landscape of fear model (Laundré, Hernandez & Altendorf 2001). Both the behavioural response race and landscape of fear model predict a negative relationship between the spatial distribution of predator and prey, leading to a leapfrog effect (Sih 1998): prey will select patches of lower quality, but with lower predation risk, while predators will select areas of high prey vulnerability but, correspondingly, low prey density. Mitchell and Lima's (2002) shell-game concept, however, predicts that prey should move randomly (or use habitat patches randomly) when hunted by a learning predator. These models are, however, lacking rigorous testing across species with variable ecological characteristics and temporal differences in resource use.

Interspecific variation in predator hunting strategies may have implications for the behavioural predator-prey game (Preisser, Orrock & Schmitz 2007; Schmitz 2008). Predators that stalk or ambush their prey from cover are usually more efficient at short distances; in contrast, pursuit predators improve their success in open habitat (Murray *et al.* 1995; Husseman *et al.* 2003). Space-use patterns of cursorial predators are therefore expected to match habitat use of their prey to increase encounter rate, whereas ambush predators tend to ambush prey as they move between habitats (Schmitz, Krivan & Ovadia 2004). Unfortunately, models such as the shell-game concept or the landscape of fear, even if they consider predator behaviour, are typically oriented towards specialist predators and their primary prey (Laundré *et al.* 2001; Mitchell & Lima 2002). Thus, predator-prey dynamics involving generalist predators, specifically as they relate to predator ability to alter hunting strategy to suit multiple prey types, are relatively unknown (but see Schmidt, Goheen & Naumann 2001; Schmidt 2004).

Generalist predators differ from specialists in that they have a broader diet rather than a few alternate prey when the primary prey type becomes rare (Holt & Lawton 1994). Generalist predators can also display broader ranges of movement and search tactics that shape the risk for targeted and untargeted prey (incidental predation; Schmidt *et al*. 2001). Predation risk for non-primary prey from a generalist predator at a given density is a function of resource overlap between predator and prey (enemy-free space; Schmidt 2004), movement strategies leading to co-encounter (Mitchell & Lima 2002; Bastille-Rousseau *et al.* 2011), and inherent vulnerability of the prey (Lima & Dill 1990). Intraspecific variability in the form of individual specialization is also common within populations of generalist predators (Bolnick *et al.* 2003; Woo *et al.* 2008). It is common to observe individual specialization that is unrelated to specific traits, but in many cases, individual specialization is related to differences in experience, dominance, or size, that is driven by age and/or sexual characteristics (Bolnick *et al.*

2003). For example, size differences between males and females or greater levels of experience due to age may cause individuals to specialize on specific prey items (Woo *et al*. 2008). If follows that a detailed understanding of predator-prey interactions in a generalist predator context requires information on population-level and individual-level patterns (Woo *et al*. 2008, Bastille-Rousseau *et al*. 2011), especially since the effect of a small number of specialized individuals can sometimes have major impacts on prey populations (Festa-Bianchet *et al.* 2006).

Caribou ecology: Newfoundland caribou as a study system

Caribou (or reindeer) are a northern ungulate that are limited to circumpolar areas. Although caribou can be classified into different sub-species in North America (Banfield 1961), they are more effectively classified as one of three ecotypes: boreal (or forest-dwelling or sedentary), migratory (or tundra), or mountain caribou ecotype (Hummel & Ray 2008; Festa-Bianchet *et al.* 2011). These ecotypes are based on caribou calving strategies, habitat use, and distance traveled (Bergerud 1988; Hummel & Ray 2008), and align rather closely with threats faced by caribou (Festa-Bianchet *et al*. 2011). Boreal caribou occur on the landscape in small groups or individually in the boreal forest across Canada. At calving, female boreal caribou will try to space-away from each other to avoid predation. Migratory caribou are normally found in the far North, where individuals exhibit long migrations prior to calving and are gregarious during calving season. Lastly, mountain caribou are found in alpine areas of Canada and calve at high elevations.

Over the last two decades, many caribou populations have undergone dramatic declines in numbers (Schaefer 2003; Vors & Boyce 2009; Festa-Bianchet *et al.* 2011), with climate and anthropogenic activities usually being invoked as the most likely ultimate factors causing these declines; the mechanism underlying these dynamics is through direct effects on plant phenology, predation risk and extreme weather events (Vors & Boyce 2009; Tyler 2010; Joly *et al.* 2011). Aside from this current broad-scale decline, historically, most caribou populations of the migratory ecotype experience repeatable fluctuations in abundance (Gunn 2003; Zalatan, Gunn & Henry 2006), with population trajectories often being synchronous across broad landscapes (Gunn 2003).

While they are sometimes considered to be the boreal ecotype (Festa-Bianchet *et al.* 2011), Newfoundland caribou do not easily fall into one ecotype distinction. While their movement extent and predator guild is more similar to boreal caribou, their gregariousness, pre-calving migration and fluctuations in abundance are similar to those of migratory caribou. During the last 50 years, caribou herds in Newfoundland have undergone marked changes in abundance, with numbers being generally low during the 1960s and 1970s, increasing rapidly during the 1980s to mid-1990s, and declining precipitously following the mid-late 1990s (Mahoney & Schaefer 2002a; Mahoney *et al.* 2011). There are about 14 major and a few smaller caribou herds on the island. Wolves have been extinct on the island since about 1922, and rather, predation from black bears, coyotes, and lynx on calves seems to be the main proximate cause of the decline (Weir *et al.* 2014). Recent declines in caribou body size and morphometrics also hint at density-dependent nutritional effects (Weir *et al*. 2014). Further indirect evidence points to the deteriorated condition of caribou calving range (e.g. reduction of time spent in summer on calving and summer range; Mahoney & Schaefer 2002a; Schaefer & Mahoney 2013), but the origin of the density-dependent effects is still unclear. A potential result of the nutritional stress induced by habitat deterioration is that females with calves may search for richer habitats where encounter risk with predators can also be higher.

Thesis structure

Newfoundland caribou represent an excellent species to study how extrinsic and intrinsic processes interact and influence population dynamics and behavioural ecology, notably space-use. The overall objective of this thesis is to better understand the demography and habitat selection of Newfoundland caribou, principally in the context of the current numerical decline. Specifically, in Chapter 2, I look at the causes behind long-term fluctuations among Newfoundland caribou herds. In Chapter 3, taking a more proximate view, I investigate the influence of climate, predators and density-dependence on cause-specific neonate survival. I further this analysis, in Chapter 4, by looking at the influence of climate change on the interplay between predators and neonate survival. Chapter 5 marks the transition to a more behavioural ecology viewpoint, where I look at the relationships among niche overlap between caribou and their predators in the context of their co-encounter and mortality risk. In Chapter 6, I look at broad level habitat selection of caribou to study trade-offs between predation and foraging during the calving and post-calving season. Finally, I synthesize the major findings of the previous chapters in Chapter 7.

Chapter 2 - Population decline in semi-migratory caribou: Intrinsic or extrinsic drivers?

Guillaume Bastille-Rousseau, James A. Schaefer, Shane Mahoney and Dennis L. Murray

A version of this chapter is published in Canadian Journal of Zoology.

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Abstract

Many caribou populations (*Rangifer tarandus* L., 1758) across North America, including Newfoundland, are in a state of decline. This phenomenon may reflect continental-scale changes in either the extrinsic or intrinsic factors affecting caribou abundance. We hypothesized that caribou decline reflected marked resource limitation and predicted that fluctuations should correspond to time-delayed density-dependence associated with a decline in range quality and decadal trends in winter severity. By conducting time-series analysis using 12 populations and evaluating correlations between caribou abundance and trends in: (i) vegetation available at calving (NDVI); (ii) winter weather severity (NAO); and (iii) caribou morphometrics, we observed strong evidence of density-dependence in population dynamics (i.e., a negative relationship between caribou population size and caribou morphometrics). Caribou population trajectories were time-delayed relative to winter severity, but not relative to calving ground greenness. These island-wide correlations could not be traced to dispersal between herds, which appears rare at least for adult females. Our results suggest that trends in winter severity may synchronize broad-scale changes in caribou abundance that are driven by time-delayed density-dependence, although it remains possible that calving ground deterioration also may contribute to population limitation in Newfoundland. Our findings provide the basis for additional research into density-dependence and caribou population decline.

Key words

Density-dependence, climate influence, synchrony, predation, caribou, *Rangifer tarandus*

Résumé

Plusieurs populations de caribou (*Rangifer tarandus* L., 1758) en Amérique du Nord, dont celles de Terre-Neuve, sont en déclin. Ce phénomène peut refléter des changements continentaux dans les facteurs extrinsèques ou intrinsèques affectant leur abondance. Nous supposons que le déclin observé reflète un cycle naturel, et prédisons que les fluctuations devraient correspondre à des effets densité-dépendants différés dans le temps, associés à la qualité de l'habitat et à la sévérité des hivers. Afin de mieux comprendre les raisons expliquant les tendances observées à Terre-Neuve, nous avons conduit des analyses temporelles en utilisant 12 populations et nous avons évalué les corrélations entre l'abondance des caribous et : (i) la végétation disponible durant la mise-bas (NDVI); (ii) la sévérité de l'hiver (NAO); et (iii) les mesures morphométriques. Nous avons observé une forte corrélation entre la taille des populations et les effets densité-dépendants. La trajectoire des populations de caribou était aussi corrélée, mais différée avec la sévérité des hivers, mais pas avec la qualité des aires de mise-bas. Ces corrélations n'étaient pas liées à la dispersion des individus entre les troupeaux, qui semblait rare, du moins chez les femelles. Nos résultats suggèrent que les tendances dans la sévérité des hivers pourraient synchroniser à grande échelle les changements d'abondance chez le caribou, bien qu'il semble possible que la dégradation de l'habitat puisse contribuer à la limitation des populations.

Mots-clés

Densité-dépendence, influence du climat, synchronie, prédation, caribou, *Rangifer tarandus*

Introduction

Fluctuations in animal population density can be driven by a range of factors, including endogenous (i.e. density-dependent) factors linked to predation, competition, and parasitism (Kendall *et al.* 1999; Turchin 2003a), or exogenous factors such as inclement weather patterns (Stenseth *et al.* 1999). Fluctuations among many spatially-isolated populations frequently are highly synchronous (Sinclair *et al.* 1993; Ranta *et al.* 1997), implying that processes governing population dynamics may operate at scales that span beyond local environments. In light of the variability in environmental and ecological conditions facing caribou across Newfoundland, it is notable that population trajectories remain so closely aligned. It follows that such similarity speaks to the stabilizing influence of exogenous and/or endogenous factors influencing large-scale caribou population dynamics (Ranta *et al*. 1997; Ims & Andreassen 2000).

Caribou populations (*Rangifer tarandus* L., 1758) offer one remarkable example of largely synchronous fluctuations spanning broad geographical expanses. During the last 20 years, many caribou populations across the circumpolar North have undergone dramatic declines in numbers (Schaefer 2003; Vors & Boyce 2009; Festa-Bianchet *et al*. 2011), with climate and anthropogenic activity usually being invoked as the most likely ultimate factors causing these declines; the mechanism underlying these dynamics is through direct effects on plant phenology, predation risk and extreme weather events (Vors & Boyce 2009; Tyler 2010; Joly *et al*. 2011). Notwithstanding this current broad-scale decline, historically, most caribou populations of the migratory ecotype experienced repeatable fluctuations in abundance (Gunn 2003; Zalatan *et al*. 2006), with population trajectories often synchronous across broad landscapes (Gunn 2003). Repeatable fluctuations could be driven by large-scale changes owing to climate variability or time-delayed changes in stressors like predation. It follows that synchronized dynamics across broad landscapes may be related to common ecological and environmental factors driving caribou population abundance and change (Ranta *et al*. 1997; Ims and Andreassen 2000). However, populations also may be synchronized via dispersal, even in the absence of large-scale extrinsic or intrinsic drivers (Ranta *et al.* 1995). To date, few studies have tackled questions relating to factors driving synchronous and sometimes recurring large-scale caribou population declines (but see Solberg *et al.* 2001; Tyler *et al.* 2008 for example).

We investigated population trajectory of caribou herds on Newfoundland, and sought to disentangle the influence of factors implicated in the decline. Specifically, we developed four hypotheses and attendant predictions to compare between potential causes of caribou population change (Table 2-1). The winter severity hypothesis (Hypothesis 1; WS) implicates exogenous factors such as decadal trends in winter climate (Gunn 2003) as the driving force behind caribou population decline. Specifically, nutritional status and body condition may be markedly compromised by periodic winter severity and lead to decline in numbers due to lower survival and/or productivity. Logically, since the effects of a harsh winter may be transferred to newly born calves (maternal-effects; Inchausti & Ginzburg 2009), the WS hypothesis predicts that change in adult caribou body condition will relate to population size change in a time-delayed manner (>1 year). Second, trends in caribou numbers should be lag-correlated with trends in winter severity but not with vegetation available at calving (spring). It follows that the WS hypothesis predicts a strong between-herd synchrony related to a phase-locking mechanism (sensu Sinclair *et al*. 1993), rather than due to inter-herd dispersal (Hypothesis 1, Table 2-1).

Alternatively, the spring forage hypothesis (Hypothesis 2; SF) invokes time-delayed density-dependence that is driven by fluctuations in spring range quality caused by caribou population size (Couturier *et al.* 2009b). The SF hypothesis should be supported by delayed density-dependence in addition to a delayed correlation between population size and trend in range quality that is not associated with annual weather impact. It follows that the SF hypothesis is less likely to involve between-herd synchrony if the catalyst for herd decline is related to local forage deterioration (Table 2-1). However, it is possible that winter severity and forage deterioration act in tandem, such that winter weather affects not only winter foraging but also spring foraging.

Next, according to the “interaction” hypothesis (Hypothesis 3; INT), caribou should exhibit delayed density-dependence in body condition indices, and population trends should be lag-correlated with both winter severity and spring vegetation indices. Under this hypothesis, it is notable that caribou herds should fluctuate synchronously (Table 2-1).

Finally, the last hypothesis (Hypothesis 4; PR) invokes the direct effect of predation on caribou decline, which is supported by the lack of density-dependence in caribou body indices and no correlation between population abundance and winter severity or spring forage. Predators, mainly through predation sensitive foraging, can also induce reduction in body condition indices similar to those induced by density-dependence (Sinclair & Arcese 1995). Such an effect on adult caribou body indices would, however, be minimal since wolves (*Canis lupus* L, 1758) have been extinct in Newfoundland since 1922 and no other predators efficiently hunt adult caribou. If predation drives fluctuations, it should induce some degree of between-herd synchrony, mainly due to the mobility and dispersal of predators (Hypothesis 4, Table 2-1).

*Table 2-1. Four hypotheses and their predictions proposed to explain fluctuations of Newfoundland caribou (*Rangifer tarandus*).*

Hypotheses		Predictions			
		1. Delayed density-dependence	2. Correlation between SF and population estimate	3. Correlation between WS and population estimate	4. Between herd-synchrony
1	Winter severity (WS)[1]	Yes	No	Delayed	Strong, despite modest dispersal
2	Spring forage (SF) [2,3]	Yes	Delayed	No	Absent, unless dispersal is important
3	Interaction SF decline and WS (INT)	Yes	Delayed	Delayed	Strong, despite modest dispersal
4	Predation (PR)	No	No	No	Strong

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[1] Gunn, A. 2003. Voles, lemmings and caribou - population cycles revisited? Rangifer, Spec. Issue **14**: 105-111.

[2] Messier, F., Huot, J., Lehenaff, D., and Luttich, S. 1988. Demography of the George river herd - Evidence of populations regulation by forage exploitation and range expansion. Arctic, **41**(4): 279-287.

[3] Mahoney, S.P., and Schaefer, J.A. 2002. Long-term changes in demography and migration of Newfoundland caribou. J. Mammal. **83**(4): 957-963.

Methods

Study area

Newfoundland is a 108,860-km² island in eastern Canada (47º44'N, 59º28'W - 51º44'N, 52º38'W), with humid-continental climate and ample year-round precipitation (Environment Canada 2013). Natural habitat consists of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*) as well as bogs, lakes, and barren rock. During the last 50 years, caribou herds on Newfoundland have undergone marked numerical changes in abundance, with numbers being generally low during the 1960s and 1970s, increasing rapidly during the 1980s to mid-1990s, and declining precipitously following the mid-late 1990s (Mahoney & Schaefer 2002a; Mahoney *et al*. 2011). There are about 14 major and a few smaller caribou herds on Newfoundland, their population ranges varying from <100km² to 11,000 km^2; most herds exhibit semi-migratory characteristics involving philopatric movements similar to those of other caribou populations (Schaefer, Bergman & Luttich 2000; Schaefer & Mahoney 2013). Philopatry is apparent among females that move to traditional calving grounds during spring and summer (Mahoney & Weir 2009; Schaefer & Mahoney 2013). Caribou herds are largely distinct and spatially independent in Newfoundland. Despite some spatial overlap between a minority of herds, we show that interchange of females between herds is uncommon (see below and Supplementary Information 1, Appendix B). Thus, it is appropriate to consider each herd as a distinct unit. Newfoundland caribou overlap with moose (*Alces alces* L. 1758), and potential predators on the island include coyote (*Canis latrans* Say, 1823), black bear (*Ursus americanus* L., 1758) and Canada lynx (*Lynx canadensis* Kerr, 1792).

Caribou population data

During 1960-2008, 12 caribou herds were intermittently surveyed in spring or fall using traditional aerial counting methods in a systematic strip, random block, stratified–random block, or mark-resight design (Mahoney *et al.* 1998; Mahoney & Schaefer 2002a). Herds were monitored opportunistically and with variable regularity and intensity; for most populations, surveys occurred regularly during the 1960s, sporadically during the 1970s, and somewhat less frequently during the remaining period (Figure 2-1). On average, population sizes were estimated 12.2 ± 1.3 (SE) (n=12) times for each herd during the 48-year study period. Our analysis presumed changes in population size were indicative of changes in density, an assumption that appears valid for Newfoundland caribou since the area of herd's range tends to change in tandem with population size (Schaefer & Mahoney 2003). We estimated annual population size by fitting orthogonal polynomial regression equations to each time series and, through a stepwise process, evaluating any increase in fit following addition of higher-order terms (Venables & Ripley 2002). Orthogonal polynomial regression allows for estimation of the appropriate process order since each new order is independent; this reduces problems of collinearity and standard error estimation (Crawley 2007). Although the number of missing annual counts varied from 46% to 79% in the original time series (Figure 2-1 and Table 2-2), we consider that broad-scale patterns in abundance were captured reasonably well by the fitted models, including periods of low and high population density at various times during the study (Figure 2-1); patterns that were also reflected in survival and recruitment trends. To confirm the robustness of polynomial fits, we evaluated average absolute values of the residuals for every herd.

However, it remains noteworthy that smoothed time-series underestimate both process variance and observer error, compared to raw population estimates.

To determine spatial overlap between caribou and whether each herd could be considered as an independent unit, we examined movement patterns of radio-collared caribou in each of 12 populations. Since 1980, >900 female caribou have been captured and immobilized from a helicopter (Mahoney & Schaefer 2002a). From 1980 to 1999, roughly 550 captured females were fitted with VHF collars and monitored on average 1-2 times per month. Since 2005, >130 females have been fitted with GPS collars and an additional >230 received ARGOS collars. GPS collars had a fixed schedule ranging from 2-5 h whereas ARGOS collars obtained locations every 2 days. We defined core area of occupation for each herd by developing a kernel density estimator (Worton 1989) from observations collected during calving (15 May –1 July). We progressively increased the smoothing parameter value (*h*) from 500 m to 3500 m by 500 m increments, and used a kernel probability isopleth with a value of 50% to obtain a contour surface (see Supplementary information 1, Appendix B). We selected the smoothing parameter that offered the best compromise between over- vs. under-smoothing the data, as per previously-described methods (Wand & Jones 1995; Kie *et al.* 2010); this constituted a smoothing parameter value with 2500 m and isopleth value with 50%.

Since 1966, caribou morphometric measurements [jawbone length (*n*=11,923), diastema (*n*=17,888), molar row length (*n*=15,249), number of antler points (*n*=7,628)] were collected on a voluntary basis from hunter-harvested male and female caribou (Mahoney et al. 2011). This extensive dataset from across the island provided an index of animal size and status through time and such data have been used previously to assess how density-dependent competition for resources affects animal condition (Stewart *et al.* 2005; Couturier *et al.* 2009a; Mahoney *et al.* 2011). Samples from adult caribou were obtained yearly and pooled among herds, and therefore were restricted to providing an island-wide assessment of caribou body condition.

Vegetation availability and winter climate

We used the Normalized difference Vegetation Index (NDVI) to assess forage availability during calving. This remote-sensing index normally characterizes vegetation greenness and has been used to describe vegetation availability (Boelman *et al.* 2005). We evaluated annual average NDVI for each herd in June, using 20 random pixels located inside each core area of the calving ground. NDVI images were acquired from the Canadian Long term satellite Data Record (LTDR). Data were collected by the AVHRR instruments of the National Oceanic and Atmospheric Administration (NOAA) and were used to generate Canada-wide, 1-km resolution, 10-day imageries spanning 1985 to 2011. The maximum value between mid-May to 1 July for each pixel was used in calculating average population range level annual values.

Winter weather patterns were determined by the December-March NAO index (http://www.cgd.ucar.edu/cas/jhurrell/naointro.html; Hurrell 1995). High NAO values are usually related to cold and dry winters in northeastern North America (Couturier *et al.* 2009b) , although owing to a number of unique climatic influences this pattern may differ to some degree in Newfoundland. We also collected spring and early summer weather data from the Meteorological Service of Canada (Environment Canada 2013), 1980 to 2011, for 6 stations in Newfoundland. These data served to determine the yearly average daily maximum temperature and total amount of precipitation during spring (May and June). In order to remove the potential influence of current spring weather on NDVI, we first performed a linear model between three predictor variables (spring average temperature and precipitation of the closest weather station, and winter NAO) and NDVI for each herd, as the response variable. We considered the influence of previous NAO since a warmer winter can lead to faster melting of the snow (Tyler 2010). We then extracted residuals for each herd to evaluate their correlation with caribou population size; after accounting for winter and spring weather influence, these data should better reflect vegetation patterns resulting from the influence of grazing.

Statistical analysis

Evidence of cyclic fluctuations and delayed density-dependence (Prediction 1)

We used spectral analysis to estimate the duration of any time-delayed density-dependent response in caribou numbers, by determining whether each caribou population time series underwent a numerical cycle with regular period and amplitude (May 1976; Turchin 2003b; Inchausti & Ginzburg 2009). We used detrended N_t time-series for each herd and fit Lomb-Scargle periodograms to generate Fourier spectra (Lomb 1976). Populations were considered cyclic if $P < 0.05$, where $P = 1- (1 - e^{-z})^{n}$, and z is the corresponding spectral peak and n is the sample size (Horne & Baliunas 1986; Kendall, Prendergast & Bjornstad 1998). Cycle period was calculated as the reciprocal of the spectral frequency (Murray, Steury & Roth 2008). Note that, as a rule of thumb, for populations experiencing cyclicity due to time-delayed density-dependence, the time-delay in density-dependence should approximate the period length divided by 4 (May 1976).

We further assessed the nature of density-dependence in the population time series by conducting nonlinear time-series modeling using the program NLTSM (Turchin 2003b). Time-series were analyzed from response surface methodology using polynomial regression with Box-Cox transformation to approximate the general function of lagged population densities and random noise (Box & Draper 1987). Structural parameters were selected iteratively through sequential-blocks cross-validation (Turchin 2003b). The process order (PO), polynomial fit (PF) and dominant Lyapunov exponent (LE) for the cross-validated model were calculated to provide an index of higher-order interactions, nonlinearities between population growth and lagged densities, and propensity for system instability, respectively. It follows that PO reflects the feedback structure of population dynamics and PO >1 indicates when time-delayed density-dependence is present (Turchin 2003b); PF measures the degree of nonlinearity in the density-dependent relationship and PF >1 indicates that the observed dynamics are influenced by non-linearity; LE is an indicator of trajectory stability with LF >0 indicating propensity for population instability and nonlinearity (Turchin 2003b). Following our predictions, we expected PO >1, PF >1 and LE >0 for all caribou herds.

We assumed that density-dependent competition for resources would be manifest in poorer body condition of caribou and therefore evaluated lagged correlations between caribou morphometrics and population numbers. We produced a multi-herd population estimate by pooling estimates for every herd (Figure 2-2). The multi-herd caribou population estimate served as basis for a comparison with caribou morphometric features. We developed age-specific time-series for caribou morphometrics (1978-2005) by averaging annual measurements across each age category (0, 1, 2 … 9, $\geq$10 years). For this analysis, jaw length, diastema length and antler point counts were segregated by gender, whereas for molar row characteristics the time-series was pooled across gender due to lower sample size and comparable values between males and females (Bastille-Rousseau, unpublished). To assess the correlation between caribou morphometrics and population size, we correlated each morphometric measurement to a population size estimate both in current (N_t) and delayed (N_{t-1}, N_{t-2}, … N_{t-5}) time. This approach allowed us to evaluate: (i) if a negative relationship existed between a given morphometric measurement and population size, as predicted if density-dependence is important; and (ii) whether the measurement was most correlated to the current or time-delayed population density, as would be appropriate if caribou populations are cyclic and regulated by time-delayed density-dependence.

To rigorously evaluate if each correlation coefficient for a given morphometric measure and a given time-lag was significantly different from zero, we performed a permutation exercise involving a unidirectional *t*-test. For each time lag, we generated a set of normally distributed values having a mean of zero and a standard deviation equal to that of the observed set of correlation coefficients from all the different age categories for a specific morphometric. We then evaluated whether the distribution of observed correlation coefficients from the different age groups for a specific morphometric and time-lag combination was significantly different from the generated set of random values. We performed this test 10 000 times for each combination of morphometric and time-lag, and reported the average *t*-value and average significance level across every permutation.

Correlation between population and environmental factors (Predictions 2 and 3)

We consider cumulative effects of winter severity on population dynamics, by applying a moving average on the NAO time series using the four previous NAO values with the current value for a given year. A 5-year window was chosen based on previous work evaluating time lags associated with NAO (Hurrell 1995; Hurrell, Loon & Van Loon 1997) while also seeking to avoid excessive smoothing. The average NAO value for a given year was correlated with population estimates for each herd and island-wide estimates. Since each herd was independent and acted as a replicate, we used a Bonferroni correction ($\alpha = 0.05 / 12$ herds $= 0.0041$) to assess whether herd sizes were significantly correlated with NAO and to obtain an average correlation coefficient with confidence interval. We intended to fit each NDVI series for each herd in a similar fashion as NAO, especially since Newton *et al*. (2014) found a 5-year lag between population size and NDVI, but none of our NDVI series based on actual NDVI values or residuals exhibited significant trends (all $P > 0.25$). Therefore, we did not assess further the correlations between NDVI and individual population estimates.

Between-herd synchrony (Prediction 4)

We tested between-herd synchrony in population size by comparing pairwise correlations between each herd. We also assessed the effect of herd proximity on synchrony by first calculating the inter-herd distance as the distance from the centre of one calving ground to another, for all herd pairs. We then used a linear model to evaluate if inter-herd distance influenced the observed correlation (synchrony) between population size estimates. Considering that the Avalon herd was isolated in the southeastern portion of the island and appeared to decline earlier than other herds due to an epizootic disease (Ball, Lankester & Mahoney 2001), we also conducted the analysis excluding this herd to confirm that results were consistent without the outlier. Statistical analyses were conducted using R 2.12.2, and we report averages ± 1 standard error (SE) and Pearson's R as a measure of correlation fit, except for polynomial fit where R^2 values are presented.

Results

Multi-herd population estimate

All polynomial models fit population trajectories significantly and provided acceptable explanatory power (mean residual = 404.542 ± 92.857, mean R^2 = 0.960 ± 0.014, Table 2-2). Model selection revealed that most herds were structured as 3rd or 4th order polynomials although one population having the lowest abundance estimate (Hampton Downs) had a 2nd order fit (Table 2-2). Even among the herds with sparse population estimates or shortened time-series, models seemed to capture the broad-scale temporal variability in numbers, including the ubiquitous population peaks during 1990-2000 and the lows before and after this period (Figure 2-1). Models fit to Avalon and Buchans populations fell short of their highest numerical estimates, but otherwise models reasonably approximated the amplitude and timing of peak abundance for each herd (Figure 2-1).

Prediction 1: Delayed density-dependence

Spectral analysis revealed significant evidence of phases of increase and decrease for all herds (Table 2-3). All time-series had a single significant spectral peak (Sine component 1 only), and the mean estimated period for the fluctuation (1/frequency) was 47.7 ± 2.4 years (n=12); it was significantly higher, 51.7 ± 1.7 years, (n=9; paired-t=6.989, P<0.001) when we excluded time-series <40 years (Cape Shore, Hampden Downs, St. Anthony herds). Such a period should theoretically correspond to a time-delay in density-dependent regulation of roughly 10-14 years if caribou population fluctuations actually reflect periodic fluctuations. Spectral power also was significant among all caribou herds and averaged 18.1 ± 0.9 (n=12) units (Table 2-3).

Nonlinear time-series analysis suggested that caribou herds had complex structuring. Specifically, all populations had process order (PO) ranging between 2-3 units (Table 2-4), implying that their dynamics were governed by long-term time-delays in density-dependence. The analysis also revealed that all populations had higher-order polynomial fit (PF) indicating nonlinearities between population growth and lagged densities, as well as non-negative Lyapunov exponents indicating propensity for population instability and nonlinearity (Table 2-4). Collectively, these findings further supported the importance of delayed density-dependence in caribou.

Correlation of caribou morphometrics with current and delayed population size estimates revealed evidence of density-dependent constraints on growth patterns. For female and male antler points, between-age average correlation coefficients were negative and significant (different from zero) both with current population estimates and when delayed up to 5 years (Table 2-5). Female diastema length also showed significant or marginally significant average correlation coefficients with population density for delays from 1-5 years. Molar row characteristics also were negatively related to current and 1-year delayed population estimates (Table 2-5). Correlation coefficients across age groups and morphometric attributes are provided as supplementary material (See Supplementary Information 2, Table S1, Appendix B).

*Table 2-2. Summary of population estimates for 12 caribou (*Rangifer tarandus*) herds in Newfoundland (1955-2008). Equations from the polynomial fit of population time series, as well as mean values of absolute residuals ± SE and associated R are given.*

Herds	Year range		Count	Proportion of year with a count	Population range Min	Population range Max	Mean	Mean absolute value of residuals ± SE	R
Avalon	1960	2005	20	0.44	189	7104	1637.55	701.7 ± 170.5	0.826
Buchans	1960	2007	17	0.36	450	9834	3229.88	661.1 ± 138.3	0.942
Cape Shore	1976	2000	13	0.54	28	1410	416.23	28.00 ± 6.25	0.997
Gaff Topsails	1969	2007	9	0.23	720	5980	2207.33	494.5 ± 91.6	0.964
Grey River	1960	2007	16	0.34	1200	11225	5526.69	319.9 ± 86.0	0.984
Hampden Downs	1978	2008	6	0.20	69	877	520.83	61.5 ± 15.5	0.971
Lapoile	1960	2007	16	0.34	500	11210	5145.25	1035.8 ± 220.5	0.942
Middle Ridge	1960	2006	13	0.28	257	19765	5349.31	896.4 ± 185.1	0.983
Mount Peyton	1962	2007	10	0.22	95	1762	550.10	155.3 ± 39.0	0.932
Northern Peninsula	1966	2008	9	0.21	400	8246	2456.33	192.8 ± 51.3	0.994
Pot Hill	1966	2007	11	0.27	250	5250	1649.64	193.3 ± 51.4	0.987
St. Anthony	1976	2008	10	0.31	21	8405	1131.40	114.2 ± 45.9	0.995

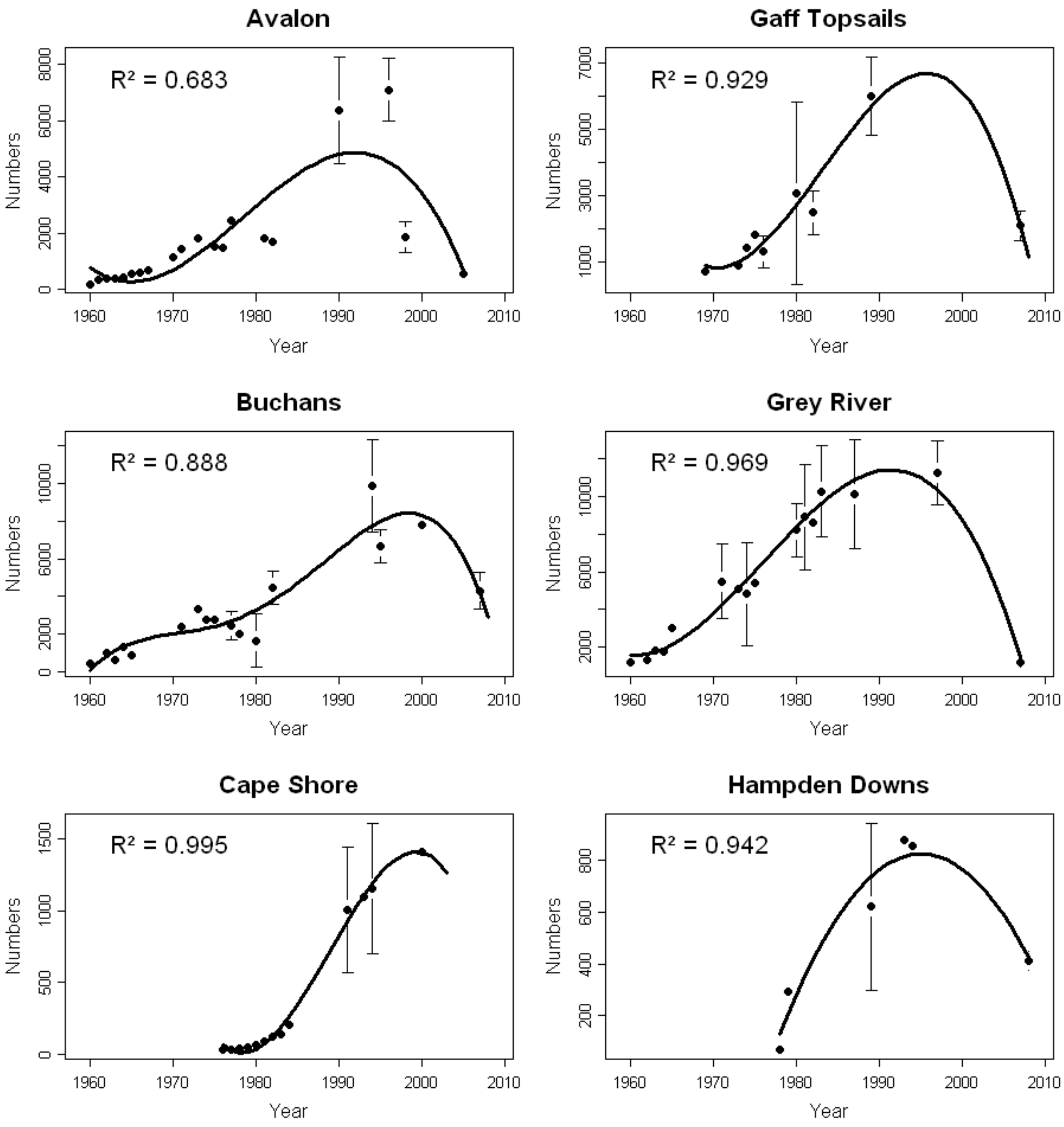
Avalon
R² = 0.683
Numbers
0
2000
4000
6000
8000
1960
1970
1980
1990
2000
2010
Year
Gaff Topsails
R² = 0.929
Numbers
1000
3000
5000
7000
1960
1970
1980
1990
2000
2010
Year
Buchans
R² = 0.888
Numbers
0
2000
6000
10000
1960
1970
1980
1990
2000
2010
Year
Grey River
R² = 0.969
Numbers
2000
6000
10000
1960
1970
1980
1990
2000
2010
Year
Cape Shore
R² = 0.995
Numbers
0
500
1000
1500
1960
1970
1980
1990
2000
2010
Year
Hampden Downs
R² = 0.942
Numbers
200
400
600
800
1960
1970
1980
1990
2000
2010
Year

Figure 2-1 (continued)

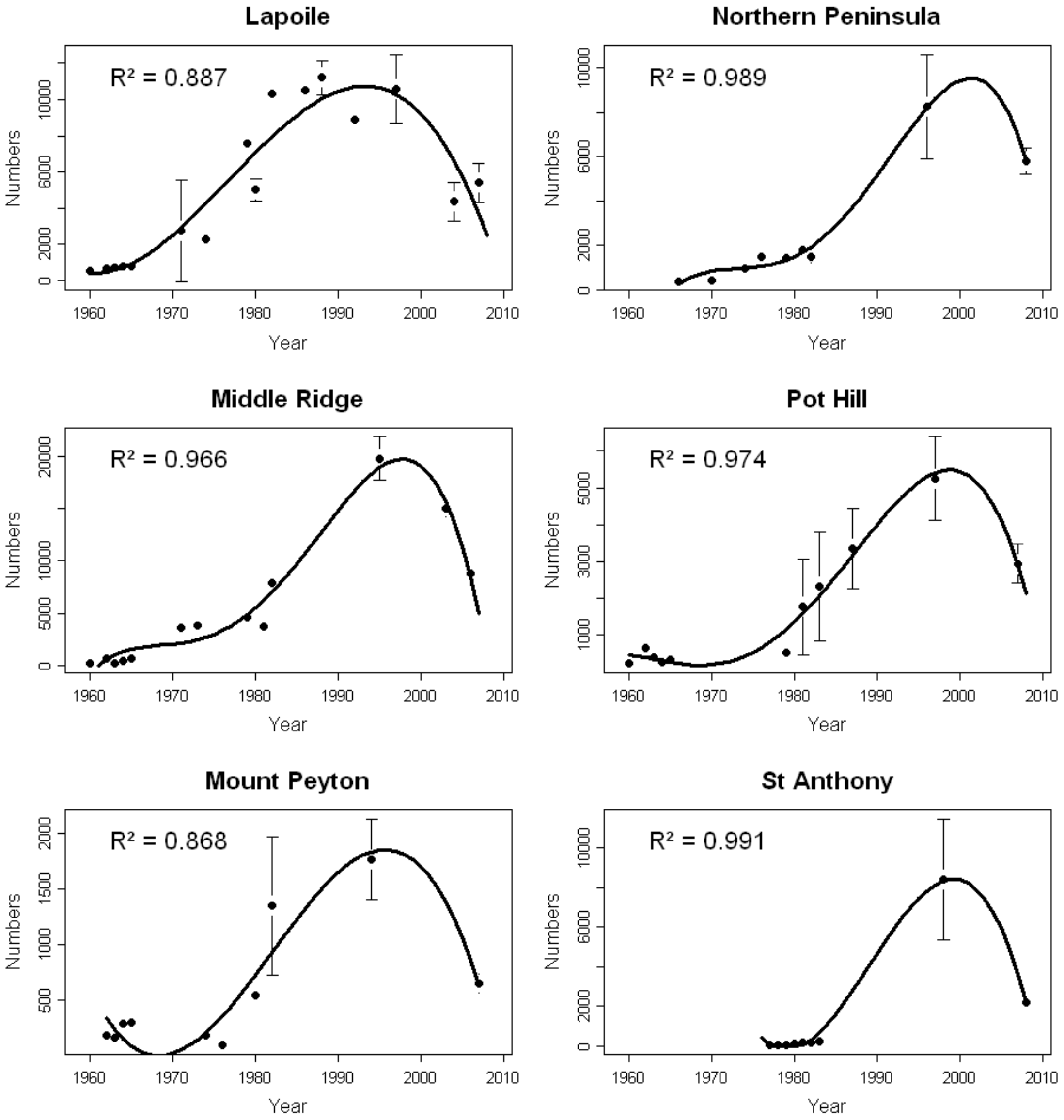

*Figure 2-1. Population trajectories for 12 caribou (*Rangifer tarandus*) herds on Newfoundland. Points represent actual population estimates with confidence limits and lines represent estimated population size using the best-fit polynomial equation.*

*Table 2-3. Spectral analysis results for 12 caribou (*Rangifer tarandus*) herds in Newfoundland (1960-2008). Analysis was conducted on detrended untransformed values and includes estimated spectral frequency, and spectral power for Sine component 1 only. P-values are in parentheses.*

Herd	Years	Frequency	Spectral Power
Avalon	1960-2005	0.0210 (<0.001)	20.153 (<0.001)
Buchans	1960-2008	0.0171 (<0.001)	19.014 (<0.001)
Cape Shore	1976-2007	0.0261 (<0.001)	13.415 (<0.001)
Gaff Topsails	1969-2008	0.0390 (0.040)	17.681 (0.040)
Grey River	1960-2007	0.0200 (0.028)	21.413 (0.028)
Hampden Downs	1978-2008	0.0288 (0.073)	13.129 (0.073)
Lapoile	1960-2008	0.0185 (<0.001)	21.366 (<0.001)
Middle Ridge	1961-2008	0.0190 (<0.001)	19.065 (<0.001)
Mount Peyton	1962-2008	0.0205 (0.002)	20.375 (0.002)
Northern Peninsula	1966-2008	0.0176 (<0.001)	17.292 (<0.001)
Pot Hill	1960-2008	0.0180 (<0.001)	20.106 (<0.001)
St. Anthony	1976-2008	0.0278 (<0.001)	14.209 (<0.001)

*Table 2-4. Nonlinear time series analysis results for 12 caribou (*Rangifer tarandus*) herds in Newfoundland (1960-2008). Process order (PO: number of time delays best explaining density-dependence), polynomial fit (PF: degree of nonlinearity in the density-dependent relationship) and Lyapunov exponent (LE: index of population stability/ instability) are provided.*

Herd	Years	*n*	Variance	PO	PF	LE
Avalon	1960-2005	46	0.414	3	2	0.178
Buchans	1960-2008	49	0.356	3	2	0.056
Cape Shore	1976-2007	32	0.644	3	2	0.073
Gaff Topsails	1969-2008	40	0.304	3	2	0.309
Grey River	1960-2007	48*	0.288	3	2	0.672
Hampden Downs	1978-2008	41	0.188	2	2	0.210
Lapoile	1960-2008	39	0.427	2	2	0.055
Middle Ridge	1961-2008	48*	0.535	2	2	0.142
Mount Peyton	1962-2008	47	0.743	3	2	0.483
Northern Peninsula	1966-2008	43	0.443	3	2	0.892
Pot Hill	1960-2008	49	0.520	3	2	0.148
St. Anthony	1976-2008	28*	0.572	2	2	0.709

* Excludes portions of the population time series due to fitted population estimates having negative values

*Table 2-5. Correlation coefficients (R) between seven body condition indices and island-wide caribou (*Rangifer tarandus*) population size in Newfoundland (1978-2005). Averages of age-specific correlation coefficients (±SE) are given for a lag of up to 5 years (R_t - R_{t-5}). Probability values refer to t-values from permutation tests (see Methods) and significant values (P<0.05) are in bold. See Supplementary Information 2, Appendix B for complete results.*

Morphometrics	Rt	T	Rt-1	Tt-1	Rt-2	Tt-2	Rt-3	Tt-3	Rt-4	Tt-4	Rt-5	Tt-5
Antler points, females	-0.72 ± 0.13	**4,15**	-0.734 ± 0.129	**4,12**	-0.735 ± 0.13	**4,08**	-0.734 ± 0.13	**4,07**	-0.732 ± 0.13	**4,06**	-0.73 ± 0.13	**4,06**
Antler points, males	-0.48 ± 0.10	**3,37**	-0.472 ± 0.105	**3,25**	-0.445 ± 0.105	**3,03**	-0.42 ± 0.106	**2,86**	-0.401 ± 0.105	**2,75**	-0.386 ± 0.105	**2,64**
Diastema, females	-0.24 ± 0.09	2,02	-0.296 ± 0.066	**3,24**	-0.351 ± 0.041	**6,12**	-0.436 ± 0.05	**6,24**	-0.483 ± 0.053	**6,56**	-0.485 ± 0.05	**7,00**
Diastema, males	0.17 ± 0.08	-1,59	0.168 ± 0.084	**-1,44**	0.162 ± 0.09	-1,29	0.099 ± 0.096	-0,75	0.015 ± 0.1	-0,11	0.013 ± 0.095	-0,10
Jawbone length, females	-0.214 ± 0.143	1,09	-0.263 ± 0.144	1,31	-0.291 ± 0.142	1,47	-0.403 ± 0.153	1,89	-0.438 ± 0.157	2,00	-0.445 ± 0.159	2,01
Jawbone length, males	-0.100± 0.05	1,33	-0.077 ± 0.05	1,11	-0.076 ± 0.049	1,13	-0.038 ± 0.059	0,45	0.021 ± 0.072	-0,21	0.051 ± 0.07	-0,52
Molar tooth row (both sexes)	-0.435 ± 0.097	**3,22**	-0.376 ± 0.093	**2,90**	-0.304 ± 0.093	2,36	-0.241 ± 0.095	1,83	-0.189 ± 0.097	1,41	-0.148 ± 0.098	1,09

Predictions 2 and 3: Correlations of NDVI and NAO with population size

No temporal trends were observed in the residuals of NDVI values after accounting for the influence of spring and winter weather, thereby negating the ability to test for further correlations with caribou population time-series. Correlations between population size and the 5-year average NAO values were strictly positive and significant for each herd (mean *R* = 0.697 ± 0.026, *n*= 12; Table 2-6) as well as for the island-wide population estimate (*R* = 0.792 ± 0.068).

Prediction 4: Between-herd synchrony

Correlations in population size among herds were high (mean *R* = 0.792 ± 0.029, *n*=66), consistently positive, and almost always statistically significant (Supplementary Information 2, Appendix B, Figure S1). Moreover, correlation between herds decreased slightly with linear distance between their calving grounds (*R*= -0.263, *t*= -2.184, *P*= 0.032). However, this correlation was strongly influenced by the Avalon herd (the south-easternmost herd), which when removed from the analysis, reduced the statistical significance of distance on herd synchrony (*R*= -0.209, *t*= -1.555, *P*= 0.126).

*Table 2-6. Mean +/- SE correlation coefficients for population size of 12 caribou (*Rangifer tarandus*) herds on Newfoundland (1960-2008) and average index of the North Atlantic Oscillation (NAO) representing winter severity during the preceding 5 years. All correlation coefficients are significant (bold) when adjusted using Bonferroni correction. Newfoundland represents island-wide estimate of caribou.*

Herd	R ± S.E.
Avalon	**0.747 ± 3.1e-04**
Buchans	**0.753 ± 2.3e-05**
Cape Shore	**0.519 ± 0.0001**
Gaff Topsails	**0.685 ± 3.3e-05**
Grey River	**0.701 ± 1.9e-05**
Hampdon Downs	**0.694 ± 0.0003**
Lapoile	**0.753 ± 1.6e-05**
Middle Ridge	**0.762 ± 8.9e-06**
Mount Peyton	**0.782 ± 8.8e-05**
Northern Peninsula	**0.604 ± 2.3e-05**
Pot Hill	**0.746 ± 3.0e-05**
St. Anthony	**0.526 ± 2.4e-05**
Newfoundland	0.792 ± 1.8e-06
Mean	0.689

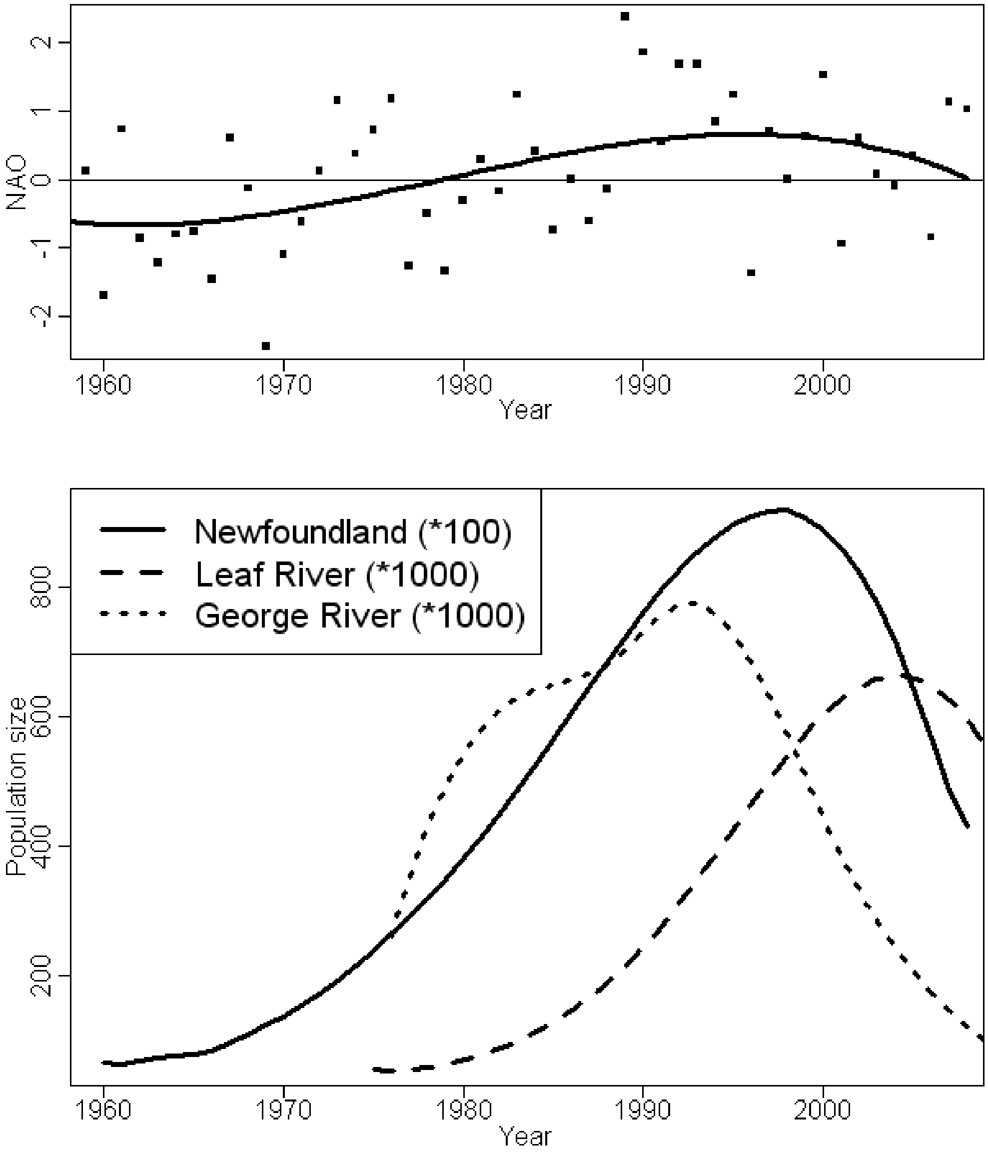

Figure 2-2. Trends in (a) the North Atlantic oscillation (NAO) showing phase of positive and negative values and (b) and smoothed population estimate of the George River herd, Leaf herd and Newfoundland herds, 1960 - 2008.

Discussion

Different hypotheses have been proposed to explain fluctuations in migratory caribou abundance, the prevalent ones being decadal trends in winter severity (Gunn 2003) and density-dependent degradation in range (Crête & Huot 1993; Bergerud 1996; Mahoney & Schaefer 2002a). We showed that all herds in Newfoundland fluctuated dramatically over the last 40 years, and that these were synchronized as would be the case if driven by an extrinsic factor (Moran effect; Ranta *et al*. 1995; Ranta *et al.* 1997). Herd trajectories correlated in a time-delayed manner with NAO values representing winter severity. Because we also found a signature of delayed density-dependence between caribou morphometrics, our findings collectively point to winter severity as offering at least a partial explanation for the observed patterns of population change (Table 2-1). We consider that our results offer new insight into the relative roles of extrinsic and intrinsic drivers affecting population dynamics, and thereby provide a basis for further tests of the natural processes affecting caribou numbers.

All caribou populations on Newfoundland underwent a dramatic increase and decline during the last 40 years, a pattern that was highly synchronous island-wide. Currently, fluctuations among migratory caribou in eastern North America focus on the idea that time-delayed density-dependence drives the decline in populations. This process may arise from forage deterioration on calving grounds (Hypothesis 2, Table 2-1), which could be driven by overgrazing and trampling of vegetation (Messier *et al.* 1988; Bergerud 1996; Mahoney & Schaefer 2002a). Our analyses revealed support for density-dependence in the absence of evidence of either direct or interactive effects of calving range decline, whereas the strongest support for density-dependence was the negative correlation between caribou body condition indices (but mostly antler point counts) and population size. Although time-series analysis should be more sensitive to higher-order complexity and structuring in caribou populations, the predicted 2-3 year time-lags were considerably shorter than the approximately 10-14 year time-lags necessary to produce a 50 year numerical cycle, should they exist in caribou. Many ecologists have found difficulty in conceiving of intrinsic factors that could drive such a prolonged time-delay in density-dependence, and population fluctuations exceeding 10 years should normally be driven by density-independent forces associated with climate (Sinclair *et al.* 1993). Yet, it is conceivable that the slow rate of growth of lichen, a critical component in caribou diet, could provide such a time delay. Indeed, lichens grow at a rate of 3-5mm/yr and available biomass almost invariably represents an accumulation that spans multiple decades (Pegau 1968). Accordingly, recovery of this resource following its over-exploitation by high-density caribou populations could prolong the normal timeline for population recovery and explain the difference in the time lag observed and required for ~50 year cycles. Historical accounts from travel writing and early game management suggest a previous population peak in Newfoundland caribou in the 1890s, followed by a swift decline and long period of stasis which included another, smaller peak in the 1930s (Newfoundland Department of Environment and Conservation, unpublished). This may suggest an even longer cycle period than that revealed by our data.

Large-scale climatic indices such as the North Atlantic Oscillation (NAO), North Pacific Oscillation (NPO) or the Arctic Oscillation (AO) are correlated with weather severity in different areas and follow decadal trends (Hurrell 1995); variation in these indices also are associated with variation in caribou population demography (Solberg *et al*. 2001; Couturier *et al*. 2009a; Joly *et al*. 2011). Associated with the high level of between-herd synchrony, we found that individual herd size correlation with delayed NAO values were relatively high, supporting the contention that winter severity may cause fluctuations in Newfoundland caribou population trajectories and thereby drive synchrony through a Moran effect. Hegel *et al*. (2012) similarly found partial support for the synchronizing role of winter severity on mountain-dwelling caribou dynamics.

Two others factors may contribute toward synchrony in population dynamics: dispersal and caribou removal by predators or human hunting. Inter-herd dispersal was uncommon (see Appendix B) and likely had little influence on population dynamics, which is consistent with the observation that female caribou tend to be highly philopatric (Schaefer *et al.* 2000; Faille *et al.* 2010). Similarly, predation seems to be playing a major role in non-migratory caribou fluctuations (Seip 1991; Wittmer, Sinclair & McLellan 2005), but most migratory populations can escape predator limitation (Seip 1991) and fluctuations in those herds likely involve multiple causes. Although we did not explicitly test for the role of predation and hunting on population synchrony, we do note that coyotes arrived on Newfoundland in the 1980s and contributed to caribou mortality. Considering the high rate of mortality in neonate caribou mortality owing to predation from other predators like black bears (Mahoney & Weir 2009), the current role of such a force on caribou populations in Newfoundland remains unclear. More importantly, it is notable that caribou population synchrony was quite strong in the increase phases from the 1970s (Figure 2-1) and is therefore apparent before the arrival and spread of coyotes across the entire island, leaving coyote predation as an unlikely causative agent in the observed long-term fluctuations in caribou numbers. Hunting has been implicated in the decline of caribou populations under specific circumstances (Payette *et al.* 2004; Bergerud, Luttich & Lodewijk 2008), but many migratory herds have declined and recovered despite sustained hunting pressure (Zalatan *et al*. 2006), and over the long term, harvesting of Newfoundland caribou has been regulated through license quotas. Although we cannot entirely discount a lag in management response, which can amplify numerical swings of harvested populations (Fryxell *et al.* 2010), over-hunting was not a causative factor in the decline, despite gaps in population monitoring resulting in higher than intended harvest rates likely exacerbated the rate of decline (Luther, unpublished).

Even though we argue that polynomial fits were appropriate for capturing broad-scale patterns in caribou population trends, our approach notably did involve interpolation and did compromise to an unknown degree annual variability in numbers. Yet, such variability is an important characteristic of density-dependence when evaluating population time-series (Clark & Bjørnstad 2004) and should reflect constraints imposed by extrinsic and intrinsic factors acting on the population. However, we believe that complementing analyses of density-dependence with time-series analysis of morphometrics clearly illustrate time-delayed density-dependent forces acting on Newfoundland caribou populations. Although our sample of harvested caribou may be biased toward larger individuals, we consider this unlikely. Resident hunters in Newfoundland tend to be less selective and represent a much larger proportion of the harvest than non-residents (Mahoney *et al*. 2011). While other measures of density-dependence may be more accurate in documenting density-dependent constraints on growth, trends observed in morphometric sizes should nonetheless be representative of the entire population as any size-related bias would have been consistent. Further, to characterize population density-dependence and cyclicity would require more observations and ideally multiple oscillations; the markedly long period of caribou fluctuations (Figure 2-1 and Figure 2-2b) currently restricts our analysis to a single oscillation.

The absence of patterns in NDVI time-series may reflect low data reliability when assessing yearly variability, particularly since lichens are such a critical resource for caribou (Bergerud 1972) but variation in biomass lead to smaller variation in NDVI than vascular plants (Olthof *et al.* 2008). Despite our effort in accounting for the influence of winter and spring weather on vegetation growth, NDVI values were still highly variable between consecutive years. However, it is unlikely that Newfoundland caribou have no influence on their range quality. For example, at least one herd, the Buchans herd, spent progressively less time on their historical summer range as population density increased over a period of 40 years (Mahoney & Schaefer 2002a). Notably, this pattern has since reversed, which is coincident with the population decline in the Buchans herd and, presumably, a concomitant relaxation of food competition

(Schaefer & Mahoney 2013). The correlation observed between antler point counts and population size for both sexes further corroborates the likely role of range decline in caribou fluctuations. Indeed, because antlers grow mainly during spring and summer, reduction in habitat quality should be reflected more-or-less instantaneously than through the observed time-delay. We therefore consider both Hypothesis 1 and Hypothesis 3 as being non-refutable given our data.

Considering that decadal trends in winter severity are unlikely to give rise to such long periods in caribou fluctuations, calving ground or summer range decline also may be implicated in the observed numerical trends. For instance, if NAO was the only factor contributing to caribou population fluctuations, it would be surprising to observe such an early and sharp decline in population size (Figure 2-2). This may suggest that trends in winter severity can act as the *zeitgeber* (sensu Sinclair *et al*. 1993) that would promote synchronized increase in caribou population, whereas spring vegetation ultimately would limit herd abundance. Similar patterns of increase and decrease with respect to the NAO also are observed for other migratory woodland caribou in eastern North America (Figure 2-2), where deterioration of forage also has been reported (Bergerud 1996; Couturier *et al*. 2009b). However, it is worth reiterating that our current analyses involve correlations meant to test the main factors driving fluctuations in caribou but that other factors (e.g. parasites, disease, insect harassment or hunting) also may influence population dynamics. It follows that our observations provide a basis for further study of caribou populations, specifically focusing on long-term trends in forage availability relative to broad-scale climate patterns.

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Chapter 3 - Shifting interactions between climate, predators and density-dependence explain three decades of variation in neonatal caribou survival

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Abstract

1. Climate can have direct effects on population dynamics and indirect effects via changes in resource competition or predation risk, but this influence can be modulated by density-dependent processes. We hypothesize that for many large mammals climatic conditions during parturition are more important for predator-driven neonate mortality when individuals are already under nutritional stress triggered by food limitation.
2. We examined interactive effects among climate, predation and density-dependence on neonate survival by comparing spatial and temporal fluctuations in climatic conditions, predation, and density-dependence. We determined cause-specific fates of 1384 caribou (*Rangifer tarandus*) from 10 herds spanning more than 30 years during periods of numerical increase and decline. We tested the prediction that post-partum climatic events have little influence on predator-induced mortalities during population increase, but that these forces have a stronger influence during population decline when adults are nutritionally-stressed.
3. We conducted Cox proportional hazards analysis for competing risks, fit as a function of weather metrics to assess pre- and post-partum climatic influences on survival. We did this analysis on herds separately during periods of population increase and decline. Cumulative incidence functions were used to compare temporal changes in risk from predators.
4. Our results support our main hypothesis: when caribou populations increased, weather conditions preceding calving were the main determinants of cause-

specific survival, but when populations declined due to nutritional stress, weather conditions during calving also influenced predator-driven mortality. Cause-specific analysis showed that weather can differentially affect the risk of multiple predators.

5. For caribou, the effect of nutritional-stress on body condition increases predation risk which is further exacerbated by susceptibility to climatic events. This framework provides clear predictions of how abiotic and biotic elements can interact, as well as serving as a powerful approach to deal with demographic interactions.

Key-words

Black bear (*Ursus americanus*), cause-specific survival analysis, climate-predator interactions, conservation biology, coyote (*Canis latrans*), Newfoundland caribou (*Rangifer tarandus*), population dynamics.

Introduction

Animal population dynamics are driven by a variety of factors, including abiotic conditions, density-dependent food limitation, and predation, as well as interactions from two or more factors. For example, climate can have direct effects on population dynamics through its influence on plant productivity or inclement weather (Coulson *et al.* 2000; Pettorelli *et al.* 2007), as well as indirect effects via changes in resource competition or predation risk consequent to direct effects (Melis *et al.* 2009). Since climate occurs in tandem with other risk factors, its effects may be highly variable (Brook, Sodhi & Bradshaw 2008; Griffin *et al.* 2011). A prime example of such complexity is highlighted by wolf-ungulate interactions, where winter and summer temperature or precipitation can influence forage availability for ungulates but also predator behaviour, and ultimately, predation rates (Post *et al.* 1999; Cook *et al.* 2004). Recent studies (e.g. Griffin *et al.* 2011; Brodie *et al.* 2013) have further shown that climate-predator interactions can drive population dynamics through variable recruitment and adult survival, yet the mechanisms linking climate to predator impacts on prey populations are poorly elucidated for most systems (Lima *et al.* 2002). It nevertheless remains that small fluctuations in temperature and precipitation can affect predator-driven mortality (Yasué *et al.* 2003; Griffin *et al.* 2011; Brodie *et al.* 2013).

The influence of climate on population dynamics can also be modulated by density-dependent processes (Coulson *et al.* 2000; Simard *et al.* 2010). Many animal populations are limited by food resources, where individuals are exposed to a food-favourable period followed by a period of nutritional restriction (Sinclair 1977; Fryxell &

Sinclair 1988). Periods of nutritional stress can lead to density-dependent regulation through reduced adult and juvenile survival and reduced reproductive output (Gaillard *et al.* 2000; Sinclair *et al.* 2006), which can be exacerbated by climate variability. For example, many ungulate species face increased starvation following harsher weather conditions (Coulson *et al.* 2000; Patterson & Power 2002). Nonetheless, it is expected that nutritionally-stressed individuals will have more difficulty coping with stochastic variation in forage availability, for example, when induced by climate (White 2008). When considered in light of climate-predator interactions, we might expect the nature of climatic influence on predation also to be modulated by density-dependence in a complex set of interactions (Messier 1991; Lima *et al.* 2002; Wang *et al.* 2009).

The influence of these complex interactions is likely to be realized first in juvenile mortality rates. In general, ungulate population dynamics are driven by the interplay between relatively high and stable adult survival and more variable juvenile survival, which ultimately leads to juvenile mortality rates having a strong influence on population trajectories (Gaillard *et al.* 2000; Raithel, Kauffman & Pletscher 2007). Griffin *et al*. (2011) formalised two mechanisms underlying climate-predation interactions in neonate ungulates (although these mechanisms have been examined before; e.g. Bergerud 1996). The first is a 'maternal condition' mechanism − that pre-partum climatic conditions affect the physical condition of parturient females, for example, by influencing fat reserves and thus neonate survival during the subsequent calving season. Females in poorer condition are expected to give birth to calves in poorer condition that may be more vulnerable to predation, or these females may have to forage in habitats conferring higher risk to sustain the cost of lactation (Clutton-Brock *et al.* 1987; Patterson & Power 2002; Pettorelli *et al.* 2005b; Couturier *et al.* 2009b). The second is a 'current condition' mechanism − that negative and stochastic post-partum climatic conditions negatively influence neonate survival. Females and newborn calves may alter their foraging behaviour or nutrient intake due to exposure to variable weather events, leading to increased or decreased risk from predators (Pettorelli *et al.* 2005b, 2007; Gustine *et al.* 2006). Therefore, the maternal condition hypothesis reflects previous weather, whereas the current condition hypothesis is associated with current weather.

The maternal condition and current condition interactions have rarely been examined in detail (Wang *et al.* 2009), especially in the context of neonate survival and when considering multiple causes of death. Contrary to the view that the maternal condition and current condition hypothesis are independent, we suggest that density-dependence may be especially important in influencing the strength and interrelations between these mechanisms in resource-limited populations. Nutritionally stressed individuals should have more difficulty compensating for the stochastic variation in climatic conditions than those in better body condition, leading to increase predator-driven mortality. We surmise, therefore, that climatic influences on juvenile survival during calving will be more pronounced under nutritional stress than under resource abundance periods. This would give rise to what we call density-dependent-climate-predator (DDCP) interactions (Stenseth *et al.* 2004; Wang *et al.* 2009).

We tested for DDCP interactions affecting neonate survival by comparing spatial and temporal fluctuations in weather conditions, predation, and indirect evidence of resource limitation across 10 caribou (*Rangifer tarandus*) herds in Newfoundland, Canada. These populations represent a good system for such a test. Unlike most ungulates, migratory caribou − including those in Newfoundland (Bastille-Rousseau *et al.* 2013) − display long-term, periodic oscillations in population size originating from resource limitation and climatic events (Festa-Bianchet *et al.* 2011). Studies of nearby populations have shown strong correlation between female body condition and body condition of calves at birth and weaning (Taillon *et al.* 2012); temperature, precipitation and their impact on vegetation prior to and during gestation also influence weight at birth (Bergerud *et al.* 2008; Couturier *et al.* 2009b). Likewise, females in poorer body condition due to nutritional-stress produce calves having lower mass at birth (Taillon *et al.* 2012). These findings underscore the importance of female adult condition, calf condition, and the influence of adult condition on neonate survival (Clutton-Brock *et al.* 1987).

We amassed information on these herds spanning 30 years. We focussed on the main prediction that current climatic events have little influence on predator-induced mortalities during a period of population increase and adequate resources, but that such forces have a stronger influence during a population decline when adult individuals are likely nutritionally-stressed. We confirm that adult body condition decreased during the decline period over all populations in Newfoundland, leading to compromised calf condition. Next, we evaluated how DDCP interactions shape patterns of neonate predation risk. We predicted divergent weather influences on cause-specific predation risk during the increase and decline periods − notably that temperature, precipitation and primary production, putatively associated with maternal body condition, play a stronger role during the increase period, whereas influence of climatic conditions during the calving period are limited to the period of population decline. Lastly, we predicted that calves born during the increase period (in better condition) experience lower mortality and achieve a lower level of mortality throughout the season than during the decrease period.

Material and methods

Study area

Newfoundland is a 108,860 km^2 island in eastern Canada (47°44'N, 59°28'W to 51°44'N, 52°38'W) dominated by a mixture of coniferous and mixed forest, bogs, lakes and barren rock. It has a humid-continental climate, with ample year-round precipitation and generally mild winters (Environment Canada 2013). Over the last 50 years, caribou herds on Newfoundland have undergone drastic changes in abundance; a population low occurred prior to 1950s and persisted until the 1970s, at which time there was a period of rapid growth with a peak occurring in the late 1990s (hereafter, “period of increase”), followed by a precipitous decline (hereafter, “period of decline”; Mahoney & Schaefer 2002a; Mahoney *et al.* 2011). These fluctuations appear synchronized among herds and are partly a consequence of cyclic pattern in winter severity (Bastille-Rousseau *et al*. 2013). During the period of decline, reduced recruitment, parturition rate, and body size of adults were strong indicators that density-dependence played an important role in determining demographic trends (Mahoney & Schaefer 2002a; Mahoney & Weir 2009; Bastille-Rousseau *et al.* 2013). Most importantly, neonate survival decreased drastically during the decline, with average survival during the first year of <35% (Lewis & Mahoney 2014). Black bears (*Ursus americanus*) have been a common predator of neonates throughout the increase and decline periods, whereas coyotes (*Canis latrans*) became an important predator only in the 2000s, after colonizing the island in the previous decade. Similar to caribou populations elsewhere, most herds exhibit semi-migratory characteristics involving philopatric movements (Schaefer & Mahoney 2013). Other, less frequent predators of calves are lynx (*Lynx canadensis*), bald eagles (*Haliaeetus leucocephalus*), and red foxes (*Vulpes vulpes*).

Caribou data

We estimated survival time of neonate caribou calves based on VHF telemetry, 1979-2013, for 10 herds (Figure 2-1). During late May and early June of each year, we located calves from helicopters and captured them on foot, generally $\leq$5 days after birth. We sexed and marked captured calves with ear-tags, although information on weight and sex were missing for calves in the 1980s. We verified re-bonding with the mother by helicopter <24 hours of capture. Aerial monitoring varied slightly among years. In general, calf survival was monitored every 2-4 days from live-capture to early July, every 5-10 days until August, and fortnightly to monthly thereafter.

When a mortality signal was detected, we conducted field investigations to find calf remains and determine cause of mortality. Starting in 2003, when sufficient remains were available, we sent carcasses to a veterinarian for independent necropsy; from

2010 to 2013, we used cotton swabs to sample wounds for residual predator DNA from saliva (Mumma *et al.* 2014). When contradictory assessments were obtained from field, necropsy, and genetic evidence, we chose the most likely outcome based on the weight of evidence. Because our focus was on the two main predators of neonates, we considered three categories of cause of mortality: black bear, coyote, and other causes. We censored animals when radio transmitters detached prematurely or were lost. All individuals were censored after 200 days as monitoring became less frequent (less than twice per month) and the cause of mortality was more ambiguous.

Since 1980, morphometric measurements of jawbones were collected from voluntarily submissions of hunter-harvested caribou (Mahoney *et al*. 2011). This extensive data set from across the island provided an index of animal size and status through time; such data have commonly been used to assess how density-dependent and nutritional stress affects animal condition (Stewart *et al.* 2005; Couturier *et al.* 2009a; Mahoney *et al.* 2011). These samples from adult (≥4-yr-old) males and females provided an annual, island-wide assessment of body condition.

Weather and vegetation data

We identified three periods: spring (April-June) which reflected the pre-calving and calving period, summer (May-October) which reflected the growing season, and winter (December-March), the period of continuous snow cover. We collected mean daily temperature, mean precipitation (rain or snow) and mean number of growing degree-days (base temperature = 10 ^{o}C, GDD_{10}) for each season each year, 1974-2013 (Environment Canada 2013). We also used the December–March North Atlantic

Oscillation (NAO) index (http://www.cgd.ucar.edu/cas/jhurrell/naointro.html; Hurrell 1995). Since population dynamics of caribou are frequently a function of a multiple-year lags and additive effects through time (Bastille-Rousseau *et al.* 2013; Newton *et al.* 2014), we took the average of each variable over the preceding 5 years to reflect winter and summer weather (hereafter, "$\text{Variable}_{(t-5)}$").

To estimate variables related to vegetation cover, we used the Normalized Difference Vegetation Index (NDVI). NDVI is based on the absorption of visible (or red) light by plant pigments such as chlorophyll and the reflectance of near-infrared light related to leaf cellular structure. Specifically, it is the ratio of the difference of near-infra red and visible light and the sum of near-infra red and visible light. NDVI can be used to measure plant growth, vegetation cover, or biomass production as well as other metrics (Pettorelli *et al.* 2005a; b).

NDVI 10-day composites from the Advanced High Resolution Radiometer (AVHRR), 1985-2013, at 1-km resolution were processed by the Canadian Centre for Remote Sensing following Latifovic & Trishchenko (2005). A correction for systematic bias between AVHRR sensors was applied as described in Latifovic et al. (2012) to improve radiometric consistency over the period. The average cloud- and shadow-free NDVI value for each 10-day composite was extracted for each herd's core area of occupation. The time series of average NDVI values was temporally smoothed to remove outliers using a robust Lowess filter where in each iteration data falling below the fit line was removed for the next iteration (Fernandes, Latifovic & Chilar 2005). Several time series metrics were extracted for each year and included: (1) the maximum difference between 10- day composites from May to July as a measure of the rate of spring green-up, (2) the beginning of the growing season taken as the point where 50% of the maximum NDVI was observed, and (3) the average seasonal NDVI for each year as a measure of annual productivity. The annual NDVI based productivity for the birth year and the preceding year were used in the modeling analysis to account for previous year conditions.

The core area of occupation for each caribou herd was defined using a kernel density estimator from mortalities and final locations of censored individuals. The smoothing parameter was estimated using the ad hoc method of Worton (1989). We used a kernel probability isopleth of 90% for all herds, except when herds with few locations resulted in illogically large delineations, in which case we used a 50% isopleth (i.e. Pot Hill and Mount Peyton herds).

Statistical analyses

Presence of density-dependence

We used jawbone size of harvested female caribou across Newfoundland (see Mahoney *et al*. 2011 for analysis of two herds, see also Chapter 2) as an index of nutritional stress and density-dependence (e.g. Høye & Forchhammer 2006). Skeletal measurements are useful for examining long-term trends in body-size and are strongly correlated with body mass (Veeroja *et al.* 2008). Jawbones were measured for total mandible length, molar row length, and diastema width. Caribou age was determined by cementum analysis. Annual jawbone size was corrected for age by using the residuals from a Gompertz growth curve model fitted to the data (Weir *et al.* 2014). Further evidence of density-dependence with other morphological indicators can be found in Weir *et al*. (2014).

Interactions between weather, predation and density-dependence

Our objective was to contrast periods of caribou population increase and decline, to infer differences that could be attributed to weather and density-dependence based on cause of mortality. We classified mortality causes for neonates into three categories: black bear, coyote, and other (other predators, natural and unknown causes). We measured the relative influence of these mortality risk categories on neonate caribou survival using cause-specific mortality analyses. We used cumulative incidence functions to estimate mortality rates from each category under a competing risk framework (Fine & Gray 1999; Heisey & Patterson 2006). This allowed us to test for our prediction of whether a calf born during a resource-favourable period experienced lower mortality.

We then used data augmentation in the competing risk framework to assess cause-specific hazards to investigate the mechanisms between weather and predation (Lunn & McNeil 1995). Cause-specific risk analyses are analogous to standard hazard-based regression approaches except that the survival function in cause-specific risk analyses considers both the cause of mortality and survival time. Since direct causes of mortality are mutually exclusive in our study, cause-specific mortality probabilities sum to the total mortality probability (Murray *et al.* 2010). The data augmentation approach takes advantage of the additive relationships of hazard functions; the dataset is duplicated for each cause of mortality and a dummy variable assigns a risk to each cause. Within each risk set, death is identified only for the appropriate cause, while other entries are censored (Murray & Bastille-Rousseau, in review). We used a flexible semi-parametric Cox Proportional Hazards (CPH) model with herd as a random factor. We used a right-censored design with time-at-risk based on the time (days) since the animal was live-captured (Fieberg & Delgiudice 2009). Because we captured most calves at <5-days-old, we are confident that survival timelines are strongly associated with age.

To test for DDCP interactions on survival, we performed analyses separately on periods of increase and decline. For each herd, we used the estimated year of the population peak to distinguish the two periods (Bastille-Rousseau *et al.* 2013, see Table 3-1). Even though the strength of density-dependence effects may vary prior to reaching carrying capacity (Sinclair *et al.* 2006; Figure 2-2), our population size estimates were, to some degree, interpolated (Bastille-Rousseau *et al.* 2013); therefore, the precise year of peak population density was uncertain for some herds. Furthermore, owing to low number of collared caribou during the late 1990s when most herds peaked, our distinction between increasing vs. decreasing phases for each herd were not unduly influenced by slight inexactness in estimating change in direction of growth. For three herds (Corner Brook Lakes, Gros Morne and Sandy Lake), we did not have herd-specific estimates; we relied on island-wide population estimates to approximate their peaks. We also ran our analyses using a common, fixed year (1998), representing island wide-trends, to denote the year of peak abundance; we observed no qualitative difference in results (Bastille-Rousseau, unpublished).

To test our general prediction about the specific mechanisms for DDCP interactions, we used model selection based on AIC_c (Burnham & Anderson 2002). Our global model had a suite of variables representing current weather (post-partum) and vegetation and two suites of variables representing previous winter weather, and previous summer weather and vegetation (maternal condition; Table 3-2). To unravel the influence of weather on survival in a hierarchical manner, we also considered subsets of the global model containing different combinations of each suite − i.e., one model involving only the current variables, one model including all previous variables and two models involving only previous summer or previous winter variables (Table 3-2).

To select which variables to include in each suite of variables in the final models (Table 3-2), we first assessed if the proportional hazard assumption was met with model diagnostics based on Schoenfeld residuals (Fox 2002). We also assessed collinearity through Pearson correlation coefficients between each pair of predictor variables and kept only those predictors that had the strongest influence when two predictors were highly correlated ($|r| > 0.70$; Dormann *et al.* 2012). Since NDVI variables were not available prior to 1985, we first performed the model selection exercise with the dataset restricted to post-1985. As none of the NDVI-related variables were statistically significant in the top models (Bastille-Rousseau, unpublished), we conducted the analysis using all years of data, but without these variables, to maximize its duration.

Coyotes were confirmed on Newfoundland in the mid-1980s (McGrath 2004), but did not appear as a major cause of mortality for neonate caribou until the early 2000s. Hence we considered only two categories of mortality during the period of increase: black bear and other. During the period of decline, we considered all three categories, including coyote. We consider that including “other causes” − which represents multiple predators, much less frequent mortalities and therefore less biological interest − makes our approach more robust and our inferences regarding coyote and black bear predation more conservative. We used black bear as our reference category in models and reconstructed cause-specific hazard ratios for coyotes and other causes by adding the single effect of a given variable for black bear with the interaction between another predator and the variable. Standard errors were then easily calculable using the covariance matrix. Since cause of mortality did not conform to the proportional hazards assumptions based on Schoenfeld residuals, we stratified each model by cause of mortality; each had its own baseline hazard (Kleinbaum & Klein 2012). We reported pseudo R^2 based on Cox & Snell (1989) log-likelihood derivation but corrected for number of censored observation (O’Quigley, Xu & Stare 2005). All analyses were conducted using the statistical software R v3.0.2 with packages “survival”, “cmprsk”, “coxme” and “adehabitatHR” (Calenge 2006). Scripts similar to our approach can be found in Murray & Bastille-Rousseau (in review).

Table 3-1. Summary of survival monitoring of caribou neonates, Newfoundland, 1979-2013. The number of collared neonates is represented by n. *The causes of mortality is expressed as a proportion of all radio-collared neonates in a given herd.*

			Cause of mortality (%)			
Herd	Years monitored	Year of population peak	Black bear	Coyote	Other	*n*
Corner Brook Lakes	1994-1997	1998	10.87	0.00	4.35	46
Gaff Topsails	2003-2004	1996	2.08	18.75	43.75	48
Grey River	1979-1992	1991	7.31	0.00	9.59	219
Gros Morne	1993-1996	1998	19.12	0.00	13.25	68
Lapoile	1985-2012	1988	10.69	11.72	17.93	290
Middle Ridge	1983-2013	1995	23.35	16.15	16.54	514
Mount Peyton	1993-2003	1996	15.79	0.00	21.05	19
Northern Peninsula	2008-2012	1996	13.79	11.03	17.24	145
Pot Hill	1980-1982	1998	0.00	0.00	28.57	14
Sandy Lake	1982-1984	1998	4.76	0.00	14.29	21

Table 3-2.Variables included (bold) and excluded (italic) in each suite of candidate models of caribou neonate survival. Candidate models including each suite are also given.

Variable Suite	Variables	Models with variable suite included
Spring	**Spring growing degree days (GDD)**	Global
	Spring rain	Current weather
	Rate of spring*	
	Winter snow	
	Spring temperature	
	Beginning of growing season	
$\text{Summer}_{(t-5)}$	**$\text{Summer}_{(t-5)}$ growing degree days (GDD)**	Global
	$\text{Summer}_{(t-5)}$ rain	Previous weather
	Average $\text{NDVI}_{(t-5)}$*	Previous summer
	$\text{Summer}_{(t-5)}$ temperature	
	Duration of growing season	
$\text{Winter}_{(t-5)}$	**$\text{Winter}_{(t-5)}$ temperature**	Global
	$\text{Winter}_{(t-5)}$ snow	Previous weather
	North Atlantic Oscillation (NAO)	Previous winter

* Not included in model for the increase period

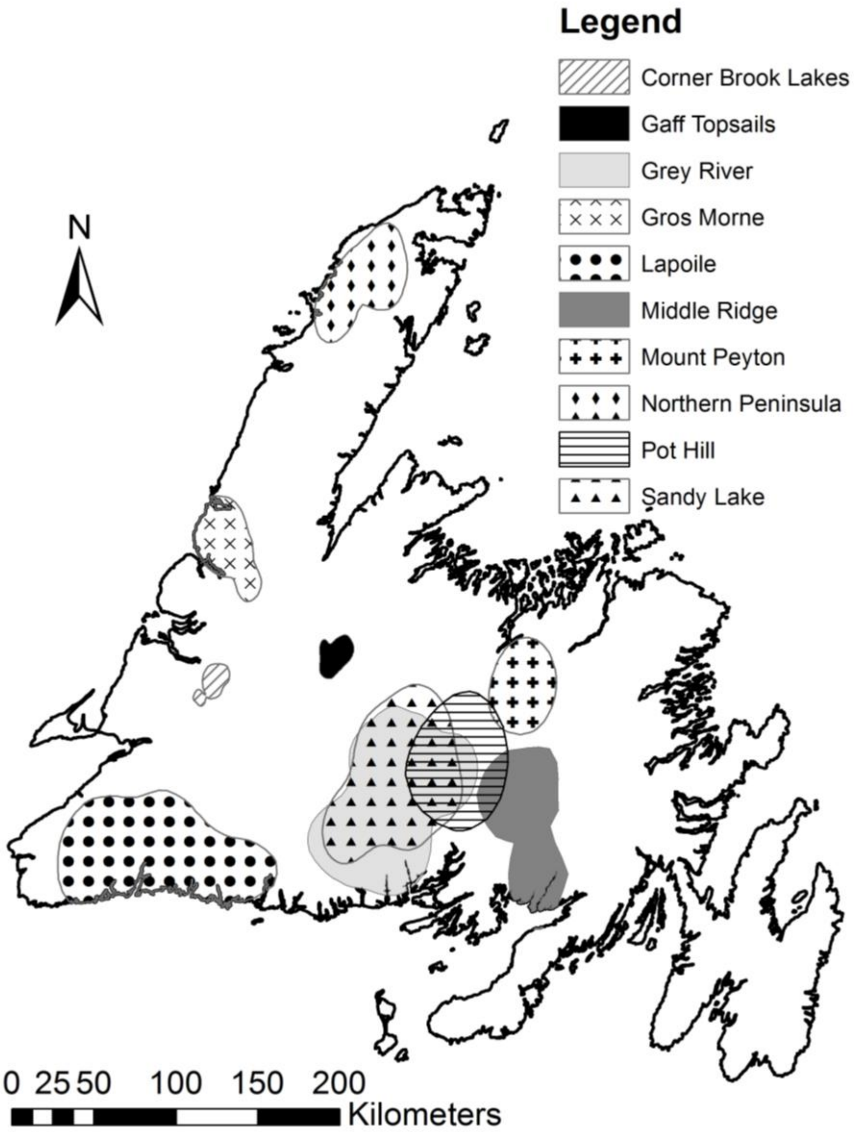

Figure 3-1. Location of caribou herds monitored for neonate survival, Newfoundland, 1979-2013.

Results

During 1979-2013, we monitored cause-specific fates of 1384 neonates (Table 3-1). The period of increase comprised 537 individuals and 110 mortalities. Cause of death was roughly comparable between black bears (*n*=51) and other causes (*n*= 59); many in the latter category, we suspect, also were due to bear predation. During the period of decline, we monitored 847 individuals and recorded 468 mortalities, of which 159 were attributed to black bear, 142 to coyote, and 167 to other causes.

There was clear evidence of strong density-dependence during the study, with jawbone size of adult females varying substantially from 1980 to 2009 (Figure 3-2). Jawbone size increased in the late 1980s before declining into the 1990s and finally increasing again in the early 2000s. Therefore, density-dependence weakened during 1979-1984, strengthened during 1985-1994, was consistently strong during 1995-1998, and diminished thereafter.

The rate of neonate mortality from either black bear predation or other causes of death roughly doubled from the population increase to decline period (Figure 3-3). Risk quickly leveled off roughly 10 days since birth during the increase period; this pattern was not evident during the decline period. This notable rise in risk during the decline period implies that the recent and pronounced reduction in recruitment is not simply due to the recent arrival of a new predator (coyote) in Newfoundland, but also due to increased risk from historic predators, primarily bear. During the period of population decline, risk from black bears was slightly higher than risk from coyotes, but overall the probability of succumbing to any of the 3 causes increased similarly (Figure

3-3). Thus, we infer that calves were subject to dramatic differences in risk, depending on the phase of the population fluctuation during which they were born.

DDCP interactions

We predicted that influences of weather during spring calving would play a stronger role during the period of decline, when adult females and their calves were presumably under nutritional stress. During the period of population increase, the most parsimonious model for neonatal survival included a set of variables strictly related to previous weather conditions (AIC_c w = 0.90; pseudo $R^2 = 0.26$; random effect variance < 0.01), whereas the top model during the period of decline was the global model, which included variables related to both previous and current weather (AIC_c w = 0.95; pseudo $R^2 = 0.28$; random effect variance =1.02; Table 3-3). This relationship is in direct support of our hypothesis, since variables related to weather during calving represented only part of the top model during the period of population decline.

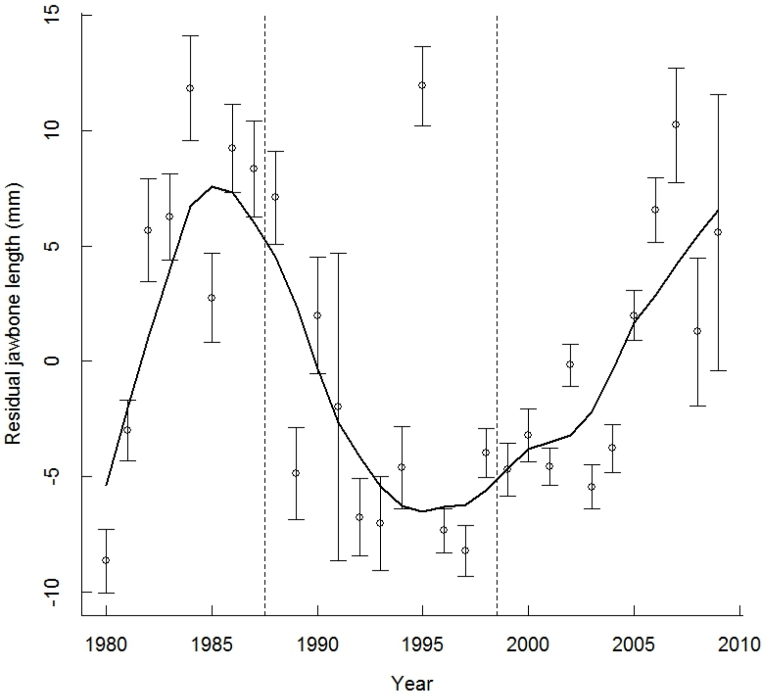

Figure 3-2. Jawbone size (mean ± SE) of adult female caribou, Newfoundland, 1980-2007, based on residuals from Gompertz growth equations. Loess smoothing curve is provided to indicate trend. Vertical dashed lines indicate the variation among herds in the year of peak population size.

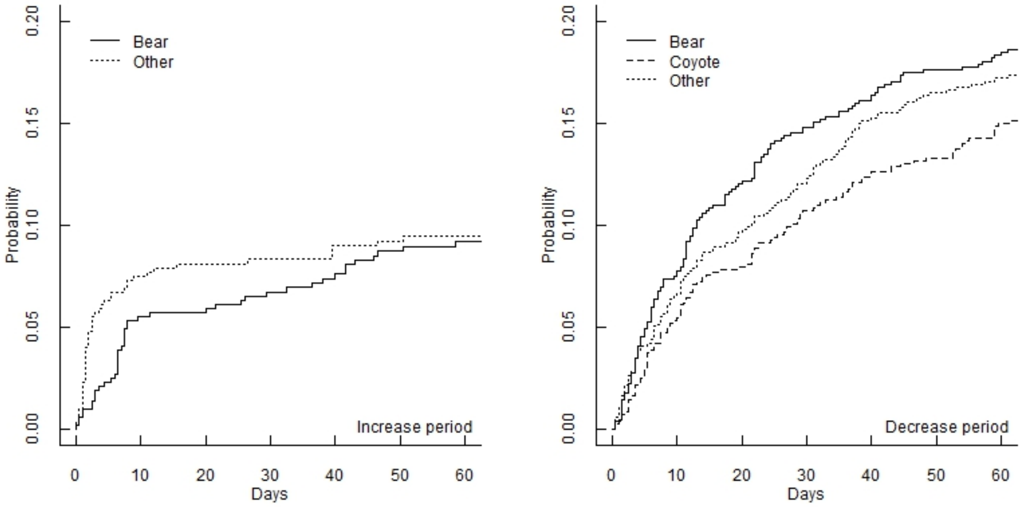

Figure 3-3. Cumulative incidence function to 60 days for 1384 neonate caribou, Newfoundland, 1979-2013, during the periods of population increase and decline.

Table 3-3. Selection results of five cause-specific Cox proportional hazards models of neonatal caribou survival, Newfoundland, 1979-2013, during periods of population increase and decline. The number of parameters (K), AIC_c, change in AIC_c compared to the best-ranked model (Δ AIC_c), and Akaike model weights (w) are indicated. Variables in each model appear in Tables 3-2 and 3-4.

	Model	*K*	AIC_c	Δ AIC_c	*w*
Period of increase					
1	Previous weather	8	1324.1		0.900
2	Global	14	1329.1	5.026	0.073
3	Previous winter	4	1331.9	7.834	0.018
4	Previous summer	4	1333.4	9.270	0.009
5	Current weather	6	1338.3	14.178	0.001
Period of decline					
1	Global	27	5777.2		0.950
2	Previous weather	15	5783.1	5.876	0.050
3	Previous summer	9	5804.9	27.688	0.000
4	Current weather	12	5820.2	43.057	0.000
5	Previous winter	6	5835.6	58.398	0.000

Roles of weather variables on cause-specific survival

Weather conditions had variable influences on the categories of mortality risk (Table 3-4). Temperature during the previous winter was the only variable influencing black bear risk during both the population increase and decline periods. Black bear risk decreased by 45% per Celsius degree during the period of increase, but rose by 230% per Celsius degree during the decline (Table 3-4). None of the previous summer variables seemed to play a strong role during the period of population decline; their effects were marginal during the period of increase (Table 3-4). During the period of decline, current weather played a strong role. Increase in rain of one millimetre and increase of temperature by 1 GDD decreased risk by 41% and 61% from bear, respectively. Higher amounts of snow in the previous winter also decreased risk by 47% for every centimetre of snowfall (Table 3-4).

Although we could assess coyote risk only during the period of population decline, we found that risk was influenced by different weather conditions compared to black bears (Table 3-4). The number of degree days in previous summers increased risk increased risk by 474% from coyotes (Table 3-4). Other causes of mortality also were influenced by weather conditions. During the period of population increase, a 1-cm increase in snowfall in the previous five winters increased risk by 505% while a 1-mm increase in the amount of rainfall in the previous five summers decreased risk by 86%. However, during the period of population decline, only the number of degree-days in the previous five summers increased risk of mortality due to other causes, increasing risk by 219%.

Table 3-4. Cause-specific hazard ratios for bear, coyotes, and other causes (95% CI) for variables in the top causes-specific Cox Proportional Hazard models for caribou neonate survival, Newfoundland, 1979-2013, during the population increase and decline periods. Hazards ratios >1 indicate increase in risk while hazard ratios <1 indicate reduction in risk. Statistically significant hazards ratios (α=0.05) are indicated in bold while marginal differences (α=0.10) are in italic. For coyote and other causes, significant differences (i.e. interaction, α=0.05) between estimated responses and black bears are underlined.

Variable	Black bear	Coyote	Other causes
Period of increase			
Winter$_{(t-5)}$ temperature	**0.553 (0.383, 0.800)**		1.054 (0.791, 1.404)
Winter$_{(t-5)}$ snow	1.493 (0.263, 8.466)		**6.053 (1.222, 29.984)**
Summer$_{(t-5)}$ GDD$_{10}$	*0.223 (0.042, 1.186)*		1.277 (0.496, 3.283)
Summer$_{(t-5)}$ rain	*3.361 (0.862, 13.111)*		**0.141 (0.034, 0.586)**
Period of decline			
Spring GDD$_{10}$	**0.391 (0.176, 0.867)**	1.182 (0.593, 2.359)	1.189 (0.617, 2.293)
Spring rain	**0.591 (0.44, 0.795)**	*1.289 (0.954, 1.740)*	0.989 (0.775, 1.262)
Spring rate	>100 (<0.000, > 100)	5.424 (0, >100)	0.013 (0.000, >100)
Winter snow	**0.528 (0.364, 0.767)**	1.053 (0.739, 1.502)	1.180 (0.848, 1.641)
Winter$_{(t-5)}$ temperature	**3.297 (1.735, 6.267)**	1.173 (0.665, 2.068)	0.989 (0.586, 1.668)
Winter$_{(t-5)}$ snow	0.690 (0.213, 2.242)	1.852 (0.602, 5.695)	0.471 (0.158, 1.405)
Summer$_{(t-5)}$ GDD$_{10}$	0.541 (0.173, 1.688)	**5.744 (1.966, 16.78)**	**3.188 (1.103, 9.212)**
Summer$_{(t-5)}$ rain	1.055 (0.359, 3.099)	2.626 (0.916, 7.529)	1.710 (0.610, 4.793)
Average NDVI$_{(t-5)}$	0.000 (0.000, 1.001)	25.537 (0.003, >100)	0.000 (0.000, 0.015)

Discussion

In this paper, we investigated how an intrinsic process (density-dependence) can interact with biotic (predation) and abiotic (climate) processes to influence the demography of an ungulate population. We tested the hypothesis that climatic conditions during the calving period are more important for predator-driven neonate mortality when individuals are already under nutritional stress triggered by food limitation, in contrast to when individuals are not nutritionally stressed. Our results support this hypothesis. When caribou populations were in their increase period (and food was presumably abundant), predation was most strongly influenced by conditions during the summer and winter preceding calving (maternal condition mechanism); when populations began to decline from nutritional stress, weather conditions during calving (current condition mechanism) influenced survival as well. Our cause-specific survival analysis also showed that weather can provide differential and compensatory changes in risk according to predator species.

Weather often influences juvenile survival for ungulates (Patterson & Power 2002; Pettorelli *et al.* 2007; Couturier *et al.* 2009b), but the importance of seasons varies across species and their geographical locations (Gaillard *et al.* 2000; Coulson *et al.* 2000). In general, favourable weather during summer and winter prior to calving helps the female sustain neonates by increasing access to forage and reducing the energetic cost of movement and thermoregulation (Pettorelli *et al.* 2005b; Couturier *et al.* 2009a). Likewise, suitable spring conditions may also enhance survival by facilitating foraging

(Gustine *et al.* 2006; Pettorelli *et al.* 2007), but little is known on how these climatic influences affect risk from specific predators.

For Newfoundland caribou, the effect of climate was not consistent among predators. For example, during the period of population decline, there were few weather-related features that affected risk to neonates similarly from both black bears and coyotes; spring rain even marginally increased risk from coyotes while it decreased risk from bear (Table 3-3). This is a clear illustration of how multiple predators can act in a compensatory way in regards to climate (Griffin *et al*. 2011; see also Chapter 4). Indeed, some of our findings run counter to the general understanding of how climate affects survival (Pettorelli *et al.* 2005b, 2007; Gustine *et al.* 2006; Couturier *et al.* 2009b), possibly indicating that predator-mediated indirect effect of climate can counteract positive, direct effects. Notably, for juvenile Newfoundland caribou, warmer winters increased risk from bears during the population period of decline. This conceivably reflects the effect of warmer winters on denning behaviour and food foraging habits of bears in spring.

Another sharp contrast between our results and general predictions in term of climate on neonate survival is in regard to the number of growing degree days in summers prior to calving. These previous summers should improve the body condition of parturient females and the increase weight (Taillon *et al.* 2012) and survival of calves (Bergerud *et al.* 2008). Our results, however, showed an increase in predation risk from coyotes. We speculate that another simple mechanism − unrelated to the maternal condition or conditions during calving − is involved. Previous summers, spanning 5 years in our analysis, potentially have a positive impact on coyotes; they could increase numerically, thereby increasing predation risk. This leads us to propose a third mechanism for climate-predator interactions, whereby climate favours predators either by improving hunting success or by increasing predator density (Post *et al.* 1999; Yasué *et al.* 2003). Further research is needed regarding how these small changes in weather translate mechanistically into difference in predation risk, but our results unarguably show the important influence of climate on cause-specific mortality.

Although the role of climate differed among the causes of death, variation in risk through time was surprisingly consistent among these causes (Figure 3-3) − largely invariant in its effect on young caribou during periods of both population increase and decline. Indeed, we were surprised to see similar shapes in cumulative hazard functions between coyotes and bears; black bears are regarded as effective predators only during the first 4-6 weeks of life (Zager & Beecham 2006).

The striking difference was in the shape of the cumulative risk curves between the periods of population increase and decline. During both periods, cumulative risk during the first 10 days of life was similar; the distinction emerged in the ensuing post-calving interval. Caribou neonates are considered highly mobile 2 weeks following birth (Gustine *et al*. 2006). Jenkins and Barten (2005) found that mortality risks within the first 2 weeks were independent of birth mass and suggested that these young animals are essentially defenseless against predators. This corresponds well with the cumulative risk during the increase period (Figure 3-3).

The period of population decline was remarkably different (Figure 3-3). This contrast in cumulative hazards might be attributable to different, non-exclusive causes. One possibility is that calves born to nutritionally stressed dams are smaller and there is a corresponding delay in improved calf mobility − i.e., an increase in the period of defencelessness and therefore a delay in the reduction of predation risk, but this should be limited to the first month of life (Taillon *et al.* 2012). Second, nutritionally-stressed females may need to forage in riskier habitats to sustain lactation (Brown 1999). Third, predators may interact in a synergistic ways. In Newfoundland, following the colonization and establishment of coyotes in the 1990s, calving caribou may have a reduction in predator-free refuges, leading to increased predation of all types (Holt & Lawton 1994; Schmidt 2004). This would explain the higher mortality rates from all causes in the most recent period.

There is support for all three possibilities in the decline of neonate survival in Newfoundland. The evidence presented here and elsewhere (Mahoney & Schaefer 2002a; Mahoney *et al.* 2011; Bastille-Rousseau *et al.* 2013) more strongly supports the first two that invoke the effect of nutrition on calf risk. Nevertheless, habitat selection analysis of black bears and coyotes during calving reveals a difference between these predators in their space-use (see Chapter 6), which supports the hypothesis that coyotes now occupy otherwise predator-free space for caribou. Whether the decrease in recruitment is driven by coyote colonization or food limitation, it is evident that coyotes are responsible for calf mortality that is at least partly additive to other risks. Regardless, this reduction in recruitment is the main proximate cause of decline of

Newfoundland caribou (Lewis & Mahoney 2014, Weir *et al*. 2014). Differentiating between these mechanisms is critical from a conservation standpoint, and further analysis of fine-scale space-use patterns of parturient females and their predators is a logical next step toward a better understanding of caribou regulation.

Similar to other broad-scale survival studies involving broad temporal and spatial scales (e.g. Griffin *et al*. 2011, Brodie *et al.* 2013, Murray *et al*. 2010), ours, too, is constrained by its observational nature. Notably, we did not consider predator density as a covariate in our survival models; such information was not available for our system over the whole study period and is notoriously difficult to obtain for large carnivores. This is an important point, as predator density may have varied with caribou population density as has been observed elsewhere (Holling 1959; Dale, Adams & Bowyer 1994). However, it is unlikely that our results are driven substantially by variability in predator density because black bear and coyote densities are not homogenous across Newfoundland (Fifield & Lewis 2013), enabling us to consider variation in predator density within herds experiencing similar levels of nutritional stress. Our mixed-effects Cox Proportional Hazards model included herds as a random factor; it explicitly addressed among-herd variation independent of variables such as predator density. Marginal inferences from these mixed models therefore indicate trends in response to weather variables representing population average response among all 10 herds experiencing variation in predator density. Our results indicated little variation among herds.

Another key variable not included in our analysis was weight of the calf, which can be affected by maternal condition, weather, and density-dependence. Weight at birth plays an important role in survival in migratory caribou (Bergerud *et al.* 2008; Couturier *et al.* 2009b; Taillon *et al.* 2012). This variable was missing in more than 40% of our observations and we were unconvinced of the appropriateness of techniques for the recovery of missing data such as multiple imputation (Nakagawa & Freckleton 2011). Despite these shortcomings, cause-specific analysis provides a powerful, and yet underused, approach in ecology (Murray & Bastille-Rousseau, in review) which allowed us to quantify the impact of weather conditions independently on risk from each predator − and ultimately with a refined understanding of how variables associated with weather can differentially influence predator-specific mortalities.

Ecology is rife with interactions. With respect to animal survival, numerous studies have examined interactions between intrinsic and extrinsic factors and their effects. Climate can affect survival through interactions with density-dependent food resources (Coulson *et al.* 2000; Hone & Clutton-Brock 2007; Simard *et al.* 2010) or predation (Post *et al.* 1999; Cook *et al.* 2004; Mills *et al.* 2013). Likewise, predation can interact with density-dependent food limitation and hence survival (Owen-Smith & Mills 2006; Wilmers, Post & Hastings 2007). However, few studies have considered these three common elements at the same time (but see Wang *et al*. 2009; Lima *et al*. 2002). We formalized a new mechanism linking density-dependence, climate and predation for survival: density-dependence climate predator (DDCP) interactions where maternal body condition influences susceptibility to climate-related events and, subsequently, risk from predation. For large mammals, DDCP interactions may be more apparent on neonate survival than adults; the reduction in survival due to density-dependence has been observed more frequently in neonates (Festa-Bianchet, Gaillard & Côté 2003). DDCP interactions are also likely to be variable in magnitude among species (Stearns 1992) and across a species' range (Bjørnstad, Falck & Stenseth 1995; Stenseth, Bjørnstad & Saitoh 1998). It is too soon to confirm the generality of the DDCP hypothesis, but this framework is particularly useful as it provides a clear set of predictions of how density-dependence, climate and predation can interact, a framework largely absent to date (Lima *et al.* 2002; Wilmers *et al.* 2007). In a rapidly changing world, cause-specific survival analysis offers an effective tool to understand how changes in climate or predator community governs population dynamics.

Acknowledgements

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Chapter 4 – Climate-mediated variability in predator-prey dynamics: Shifting predation risk influences viability of caribou populations

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Abstract

Climate change is causing rapid declines and extinctions in many populations unable to adapt to these changes. Understanding the effect of climate change on species persistence has been the subject of considerable research, yet predicting how environmental change affects biotic interactions remains challenging, especially in the case of predator-prey relationships. We tested whether current and projected climate variability alters predator-prey interactions in a multi-species ungulate-carnivore system. We examined climate impact on the relative and cause-specific predation risk by different predators on neonate survival of woodland caribou (*Rangifer tarandus*); we then projected how these dynamics would fluctuate under predicted changes in climate. Our analyses indicated that current weather patterns have disparate effects on caribou calf vulnerability to depredation from black bears (*Ursus americanus*) and coyotes (*Canis latrans*). The influence of most of these climatic attributes was largely antagonistic between predators; climate change was predicted to favour coyote and increase overall mortality for juvenile caribou. Our findings provide an important link between predation risk and climate change, and thereby emphasize the importance of complex biotic interactions stemming from shifts in the abiotic environment.

Introduction

Climate change is altering the distribution and abundance of many species (Tylianakis *et al.* 2008; Sih, Ferrari & Harris 2011; Bellard *et al.* 2012) and causing numerical declines and extinctions in native populations unable to adapt quickly (Robertson, Rehage & Sih 2013). Understanding the effect of climate fluctuations on species persistence has been the subject of considerable research, yet predicting how climate disruption affects biotic interactions remains a challenge (Manchester & Bullock 2000; Walther *et al.* 2002; Heller & Zavaleta 2009). Attempts to forecast its impact on population dynamics, species distribution, and species interactions have only begun to reveal the complex role of biotic interactions on persistence (Van der Putten, Macel & Visser 2010; Bateman *et al.* 2012). In general, we have insufficient understanding of how biotic interactions vary with climate, and how this variation affects population dynamics.

Climate can have a major influence on many factors that affect an animal's fitness (Stenseth *et al.* 2002). For primary consumers, for example, climate could impact foraging ability by affecting the quality and availability of vegetation (Parmesan 2006; Post & Forchhammer 2008; Hansen *et al.* 2013). Interactions with other species, such as predators, also can vary with climate if, for example, inclement weather influences mortality risk (Stenseth *et al.* 2002; Griffin *et al.* 2011; Brodie *et al.* 2013). Proximally, these climate-predation interactions may be driven, in part, by weather-dependent variability in feeding or nutritional status of prey; it follows that such changes may be influential to predation risk (Yasué *et al.* 2003; Griffin *et al.* 2011). Alternatively, climate-predation interactions can occur when climate facilitates predator hunting or reduces the ability of prey to escape predation (Post *et al.* 1999; Mills *et al.* 2013). In systems with multiple predators, climate might even alter the relative importance of different predators on vulnerability to predation, as one predator might be increasingly favoured in response to climate-related changes. However, such ecosystem-level complexity remains largely unexplored, notwithstanding the numerous examples of binary predator-prey interactions driven by climate (Post *et al.* 1999; Yasué *et al.* 2003). Detecting climate influences on cause-specific risk requires environmental and demographic data on climate, causes of mortality, and their interactions. Such observations are still rare.

Current ecological theory provides divergent predictions regarding climate change. Community stability theory suggests that the impact of climate change on community processes (such as predator-prey interactions) should be controlled by community structure (i.e. the environmental or biotic resistance hypothesis; Chapman 1931; Wilmers & Getz 2005). A general prediction is that communities with lower biodiversity or those lacking keystone species will be more vulnerable to the disruption of predator-prey interactions (review in Levine, Adler & Yelenik 2004). However, the invasive species literature offers mixed support for the biotic resistance hypothesis, often revealing facilitating interactions between multiple stressors, independent of species richness (i.e. the invasional meltdown hypothesis; Simberloff & Holle 1999; Simberloff 2006).

Caribou (*Rangifer tarandus*) represent a useful test case for unravelling these complex interactions. This species is declining throughout its circumpolar distribution

(Vors & Boyce 2009; Festa-Bianchet *et al.* 2011) -- a decline that may be driven by a changing climate, as well as anthropogenic habitat loss, by shifting plant phenology and predation risk (Vors & Boyce 2009; Tyler 2010; Joly *et al.* 2011). In Newfoundland, black bears (*Ursus americanus*) are common predators of neonatal caribou (Mahoney *et al.* 1990; Pinard *et al.* 2012). The recent colonization of the island by coyotes (*Canis latrans*) represents a notable, additional predator of caribou. How these two carnivores interact is unclear, as they differ in their hunting strategies and habitat selection (see Chapter 5). Black bears are opportunistic, relying on short chases, whereas coyotes are more cursorial (Young & McCabe 1997; Thibault & Ouellet 2005; Bastille-Rousseau *et al.* 2011).

We assembled observations, spanning more than a decade, on cause-specific mortality of 847 neonate Newfoundland caribou to examine the influence of climate on relative and cause-specific predation risk and to test the effect of current and projected climate on predator-prey interactions. First, we quantified the impact of weather on the relative importance of predation risk by different carnivores; we then explored whether this risk would respond to projected changes in future climate. Owing to the disparate hunting behaviours, we predicted differences in climate-related predation risk between black bears and coyotes and that, for most climatic variables, variable-specific antagonistic[4] interactions. Second, because the resulting impact of these interactions on future caribou populations is uncertain, we explored if future predation risk is

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[4] We are using antagonistic throughout to refer to the possibility of specific climatic variables that increase the risk from one predator and decrease the risk from another predator, therefore cancelling or reducing the direct effect of this climatic variable on survival.

associated with a changing climate and whether caribou population viabilities are affected. We predicted that, unless impacts of climate on risk are perfectly antagonistic between these two predators, climate change will favour one predator, potentially leading to an increase in overall risk for caribou.

Material and methods

Study area

The study was conducted on the island of Newfoundland, Canada (47°44'N, 59°28'W to 51°44'N, 52°38'W), in areas composed of coniferous and mixed forests, bogs and barren habitats. Humid-continental climate, with ample year-round precipitation and mild winter temperatures are predominant (Environment Canada 2013). During the last 50 years, caribou in Newfoundland have undergone drastic numerical change, with low abundance prior to 1980, a rapid increase during the 1970s to mid-1990s, then a precipitous decline, beginning in the late 1990s, of more than 65% by 2011 (Mahoney & Schaefer 2002a; Mahoney *et al.* 2011). Neonate survival dropped substantially -- frequently lower than 30% during this decline period (Lewis & Mahoney 2014) -- while adult survival remained relatively constant (Weir *et al.* 2014). Apart from coyotes and black bears, the main predators of calves, the other documented, but much less frequent, predators are Canada lynx (*Lynx canadensis*), red foxes (*Vulpes vulpes*), and bald eagles (*Haliaeetus leucocephalus* (Mumma *et al.* 2014).

Caribou mortality

We monitored calves from five herds, 1990-2013 (Table 1), during a period when predation from coyotes was also likely. Survival of neonates was estimated using VHF telemetry. Calves were located from helicopter and captured on foot, generally 1-3 days following birth. Re-bonding with the mother was verified by helicopter within 24 hours of capture. Aerial monitoring schedules varied across years, ranging from every 2-4 days in June and early July, 5-10 days until August and then fortnightly to monthly after August. Field investigation of caribou remains were conducted when a VHF collar indicated a mortality signal. Remains were examined for causal indicators of mortality; when sufficient, carcasses were sent to a veterinarian for necropsy. Beginning in 2010, predator salivary DNA was used to help in diagnosis (Mumma *et al.* 2014). We identified the most likely cause of death using the weight of evidence for each carcass. Animals were censored when radio transmitters detached prematurely or were lost.

Current and future climate

We collected spring (April-June), summer (May-October), and winter (December-March) weather data (Environment Canada 2014), 1974–2013, from four meteorological stations, each herd paired with its closest station. We defined the duration of summer to reflect the general growing season, whereas spring reflected the growing season during pre-calving and calving. We quantified mean daily temperature, mean precipitation (rain or snow), and mean growing degrees days (base temperature = 10 ^{o}C, GDD_{10}) for each season.

We considered different climatic mechanisms that might favour different hunting strategies − i.e. previous environmental conditions affecting maternal condition and hence neonate condition and survival; and current conditions affecting spring foraging. Current climate was defined by averages of rainfall, temperature, GDD_{10}, and snowfall during the previous winter. Since caribou population dynamics are frequently considered as a function of multiple-year lags that are additive through time (Bastille-Rousseau *et al.* 2013; Newton *et al.* 2014), we took the average climatic conditions over the previous 5 years for winter and summer conditions. Summer climate data consisted of mean daily temperature, GDD_{10} and precipitation, while mean temperature was used for winter instead of GDD_{10}.

To infer future conditions, we focussed on three periods (2011-2040, 2041-2070, 2071-2100) using four climate models (McKenney *et al.* 2011): (1) Canadian Centre for Climate Modelling and Analysis Coupled Global Climate Model (CGCM3); (2) Commonwealth Scientific and Industrial Research Organisation (CSIRO); (3) Center for Climate System Research (CCSR), University of Tokyo; National Institute for Environmental Studies (NIES) and Frontier Research Center for Global Change (FRCGC), Model for Interdisciplinary Research on Climate (MIROC); and (4) National Center for Atmospheric Research (NCAR), Community Climate System Model (CCSM). For each model, we calculated the average monthly predictions for the island of Newfoundland using the A2 and B1 scenarios, which represent the most and least severe atmospheric carbon content, respectively. Variation in predicted climatic variables in relation to current climatic variation can be found in Figure S1, Supplementary material, Appendix C.

Current climate-predator interactions

Effect of climate on mortality

We assessed the influence of climatic conditions on survival using a semi-parametric Cox Proportional Hazards (CPH) model (hereafter, the single-cause model), which grouped different causes of death into one category and stratified subjects into herds (similar to the approach used in Chapter 3). We adopted this approach initially because comparing single-cause versus cause-specific mortality allowed us to characterize predation risk according to types. For example, if particular climate variables did not affect risk in the single-cause analysis but did in the cause-specific analysis, with opposite trends in hazard ratios in the latter, we could interpret the risk incurred by these climate factors as antagonistic (Murray *et al.* 2010). We used a right-censored design with time-at-risk (days) based on time-since-capture (Fieberg & Delgiudice 2009). We selected the most parsimonious cause-specific CPH model based on AIC_c (Burnham & Anderson 2002).

Our global model included a block of variables representing environmental conditions during calving, and two other blocks representing previous winter and previous summer conditions, which can affect calf survival via maternal body condition (Griffin *et al.* 2011). Additionally, we built simpler models, two involving only current or previous conditions, and two involving only the previous summer or previous winter, given our expectation that different climatic variables can drive different patterns in cause-specific predation risk between predators with different hunting strategies. To select variables to include for each season-block, we first assessed proportionality of hazards using model diagnostics based on Schoenfeld residuals (Fox 2002). We then assessed correlations between each pair of variables, selecting only the variable having the stronger influence in unimodal regression when highly correlated ($|r|$>0.70). Number of growing degree days and temperature for both spring and summer were correlated; we used only growing degree days in our candidate set.

Climate-predator interactions

As the second step, we determined how climatic conditions interact with different proximate causes of death. We grouped causes into three categories: black bear, coyote and other (Table 4-1), which included mortalities owing to predation by lynx, eagles, or natural and unknown causes. We used a competing risk framework to assess cause-specific hazards based on data augmentation (Lunn & McNeil 1995). Cause-specific risk analysis is analogous to standard survival analysis except that the survival function considers cause of death in addition to survival time. Data augmentation takes advantage of the additivity of hazard functions; the dataset is duplicated for each cause of death and a dummy variable assigns each risk to a specific cause (Murray *et al.* 2010). Within each risk set, death is identified only for the appropriate cause, with all other entries censored. Interaction terms between the covariates and causes of death are included in the model so that the effects of covariates are not constrained to be proportional. In our case, black bear was the reference type and interactions regarding other causes of death were relative to this category. The corresponding cause-specific CPH model is:

$$h(t) = h_0(t)\exp(\beta_1 x_1 + \cdots + \beta_{co\,1} x_1{:}\,c_2 + \cdots + \beta_{ot\,1} x_1{:}\,c_3 + \cdots + \beta_{ot\,p} x_p{:}\,c_3)$$

where $h_0(t)$ is the baseline hazard (constant-only model) for which covariate x_i is one of the climatic variables; c_i indicates the causes of death and β represents coefficients for a given climatic variables and cause of death. $B_{co\ 1}$ or $B_{ot\ 1}$ is the coefficient of the interaction with covariate x_1 for mortalities by coyote or other causes, bear induced mortalities being the reference category. To respect the proportional hazard assumption, we stratified among herds and causes of death. This limited our comparison among causes of death to a largely qualitative assessment. We built the same list of candidate models as the single-cause CPH model and followed the same model selection strategy. We reported pseudo R^2 based on Cox & Snell (1989) log-likelihood derivation but corrected for number of censored observation (O'Quigley *et al.* 2005). Comparing results of the competing-risk and single-cause models provided us with strong understanding of present-day climate-predator interactions.

Predicted changes in climate-predator interactions

To assess how interactions between climate and predators are likely to be modified under climate change, we first estimated hazard ratios based on the top model coefficients using average climate conditions in Newfoundland over the last 30 years (which corresponds to the time interval between the different climate projections). We compared the estimated hazard ratio for coyote and black bear with the predicted average hazard ratio based on climate models for the two predators, reporting the mean and confidence intervals for each period and climate scenario (A2 and B1). Confidence intervals for present-day hazard ratios were calculated using bootstrapping. We generated eight values for each climatic variable based on their distribution, 1983-

2013 (mean and standard deviation), and calculated standard error of the hazard ratios. We repeated the last step 1000 times and used average standard errors in the confidence interval calculation. This bootstrap approach allowed a rigorous comparison of confidence intervals, independent of sample size.

Because our preliminary analysis indicated predation risk from coyotes would likely increase in the future, especially 2055-2085, we conducted a range of population projections to illustrate how change in risk translated into population-level consequences. Caribou population dynamics are marked by dramatic, long-term fluctuations in abundance (Bastille-Rousseau *et al.* 2013) and future uncertainty. To account for this, we retrieved vital rates (parturition rates, adult survival, calf survival) from Newfoundland spanning the three periods (Weir *et al.* 2014) to project how population size might change when initiated in phases of increase, stability or decline. For each of these abundance scenarios, we considered the impact of increased risk from coyote as fully compensatory (non-independent) with other causes, or fully additive, in which case calf survival decreased over time under a specified function based on change in the hazard risk (Heisey & Patterson 2006; Griffin *et al.* 2011). We assumed that other vital rates were not directly affected by climate variability. We performed a population viability analysis (PVA) analysis using a population-level model with 1000 iterations in Vortex 10.0 (Lacy & Pollak 2014). Details of the estimation of vital rates are provided in Supplementary material 1, Appendix C.

Results

Current climate-predator interactions

Of the 847 neonatal caribou monitored 1990-2013, 159 (19%) died from black bear predation, 142 (17%) from coyote predation, and 167 (20%) from other causes, including predation where the cause-of-death could not be confirmed (Table 4-1). Standard survival analysis, where cause-of-death was merged into a single category, indicated several plausible models explaining caribou mortalities (Table 4-2). Strongest support included only previous climatic conditions, and the global model including previous and current climate (w = 0.44 and 0.34, pseudo R^2 = 0.06 and 0.08, respectively). Model-averaged hazard ratios from these top models, however, indicated little influence of most climatic variables. The notable exception was average number of growing degree-days during previous five summers, which was positively related to subsequent risk (Table 4-3). This finding confirms the modest role of climate on neonatal survival.

When we expanded the analysis to include cause-specific risks, there was strong support for the global model ($w > 0.99$; R^2 = 0.16, Table 4-2). The increased relevance of climatic variables was evidenced by the increased hazard ratios in the cause-specific analysis (Table 4-3). Climate influenced the mortality risk by cause, with mortality by black bear reduced by more snow or rain during the winter and spring during the current year, and this risk increased with warmer previous winters. In contrast, coyote risk increased with the more rain in current spring and previous summers, as well as warmer previous winters (Table 4-3, see also previous chapter). Notably, hazards associated with spring precipitation and winter temperature differed dramatically between bear and coyote predation. Both mortality causes followed largely opposite patterns in relation to climate; this stood in contrast to only modest climate effects in the analysis on overall mortality risk. Together, these results reveal bear and coyote predation as mostly antagonistic to each other in response to climate variation. Except for snowfall, all climatic variables played opposite roles on the risk from causes of death relative to black bear (Table 4-3). Most notably, drastically increased risk could be traced to more growing degree days for current spring and previous summers, and more precipitation during these previous summers.

Predicted changes in climate-predator interactions

We assumed causal links underlying the role of climate on cause-specific risk, and that these links would remain constant in future. Hazard ratios based on projected climate models were used to forecast changes in bear predation risk; they revealed largely consistent predation risk this century (Figure 4-1). Similar calculations for coyotes, however, indicated that risk is likely to increase almost 5-fold by 2085 (Figure 4-1). This projection underscores how the current antagonism between bear and coyote predation risk may not be sustained under a changing climate. Indeed, if perfectly antagonistic, the two sources of risk would exhibit compensation. Rather, the role of coyotes appears largely additive and may become disproportionately large relative to black bears through time.

Population-level projections based on these predation risk scenarios indicated that increased risk from coyote predation caused by climate change could affect caribou demography (Figure 4-2). Under the fully compensatory scenario (calf survival constant through time), populations are predicted to decrease when simulations were initiated during a decline (*r* = -0.062, SD = 0.058) or low-density period (*r* = -0.053, SD = 0.058), respectively. Conversely, populations are predicted to increase (*r* = 0.046, SD = 0.057) when simulations were initiated during an increase phase. However, if mortality by bear and coyote predators is additive, we observed exacerbation in the decrease in population size for population initiated during a decline (*r* = -0.125, SD = 0.061) and low density (*r* = -0.115, SD = 0.061) periods, respectively. Contrary to a fully-compensatory scenario, increase in coyote risk from climate change could be sufficient to reverse trends during the increase period and cause a slow decline (*r* = -0.029, SD = 0.059). None of these scenarios indicated extinction over 30 years, but nevertheless indicated markedly lower caribou abundance for most scenarios.

Table 4-1. Summary of survival monitoring of caribou neonates (≤6 months old) in Newfoundland, 1990-2013. The number of radio-collared neonates is denoted by n.

Herd			Cause of death		
	Duration of study	*n*	Black bear	Coyote	Other
Gaff Topsails	2003-2004	48	1	9	21
Lapoile	1990-2012	192	24	34	36
Middle Ridge	1996-2013	452	112	83	81
Mount Peyton	2003	10	2	0	4
Northern Peninsula	2008-2012	145	20	16	25

Table 4-2. Top Cox proportional hazard models and cause-specific proportional hazards models of neonatal caribou survival, Newfoundland, 1990-2013, showing change in AIC_c compared to the best-ranked model (ΔAIC_c) and Akaike model weights (w). Climatic coefficients are current spring growing degree days (SpGDD), spring precipitation (SpRain), previous winter snowfall (WSnow) as well as the five years average for winter temp ($WTemp_{t5}$), summer growing degree days ($SuGDD_{t5}$) and summer precipitation ($SuRain_{t5}$).

	Model	Single cause		Cause-specific	
		ΔAIC_c	*w*	ΔAIC_c	*w*
Global	SpGDD+SpRain+WSnow+ $WTemp_{t5}$+$SuGDD_{t5}$+$SuRain_{t5}$	0.51	0.34	0.00	1.00
Previous weather	$WTemp_{t5}$+$SuGDD_{t5}$+$SuRain_{t5}$	0.00	0.44	12.82	0.00
Previous winter	$WTemp_{t5}$	23.64	0.00	43.16	0.00
Previous summer	$SuGDD_{t5}$+$SuRain_{t5}$	1.47	0.21	15.05	0.00
Current spring	SpGDD+SpRain+WSnow	23.85	0.00	32.82	0.00

Table 4-3.Model-averaged hazard ratios and cause-specific hazard ratios (95% CI) for variables in single-cause and cause-specific Cox Proportional Hazard models for caribou neonate survival in Newfoundland (1990-2013) for bear, coyotes, and other causes. Significant hazards ratios (α=0.05) are indicated in bold for the single cause model and black bear. For coyote and other causes, hazard ratios represent the reconstructed main effect of the variable on risk relative to black bear. Climatic coefficients are current spring growing degree days (SpGDD), spring precipitation (SpRain), and previous winter snow (WSnow), winter temp (WTemp$_{t5}$), summer growing degree days (SuGDD$_{t5}$) and summer precipitation as well as the five years (SuRain$_{t5}$).

Variable	Single cause	Cause-specific mortality		
		Black bear	Coyote	Other causes
SpGDD	1.209 (0.839, 1.741)	0.654 (0.344, 1.244)	0.939 (0.468, 1.883)	**2.516 (1.360, 4.657)**
SpRain	0.881 (0.758, 1.024)	**0.555 (0.420, 0.733)**	**1.191 (0.896, 1.585)**	**0.948 (0.742, 1.211)**
WSnow	0.897 (0.740, 1.087)	**0.667 (0.469, 0.948)**	1.034 (0.726, 1.472)	0.970 (0.701, 1.341)
WTemp$_{t5}$	1.186 (0.934, 1.506)	**2.432 (1.436, 4.121)**	**1.139 (0.672, 1.931)**	**0.645 (0.401, 1.038)**
SuGDD$_{t5}$	**3.032 (1.808, 5.083)**	1.444 (0.535, 3.896)	2.628 (0.848, 8.140)	**11.250 (3.769, 33.580)**
SuRain$_{t5}$	1.360 (0.735, 2.517)	0.344 (0.085, 1.399)	**3.337 (0.858, 12.970)**	**3.116 (0.789, 12.300)**

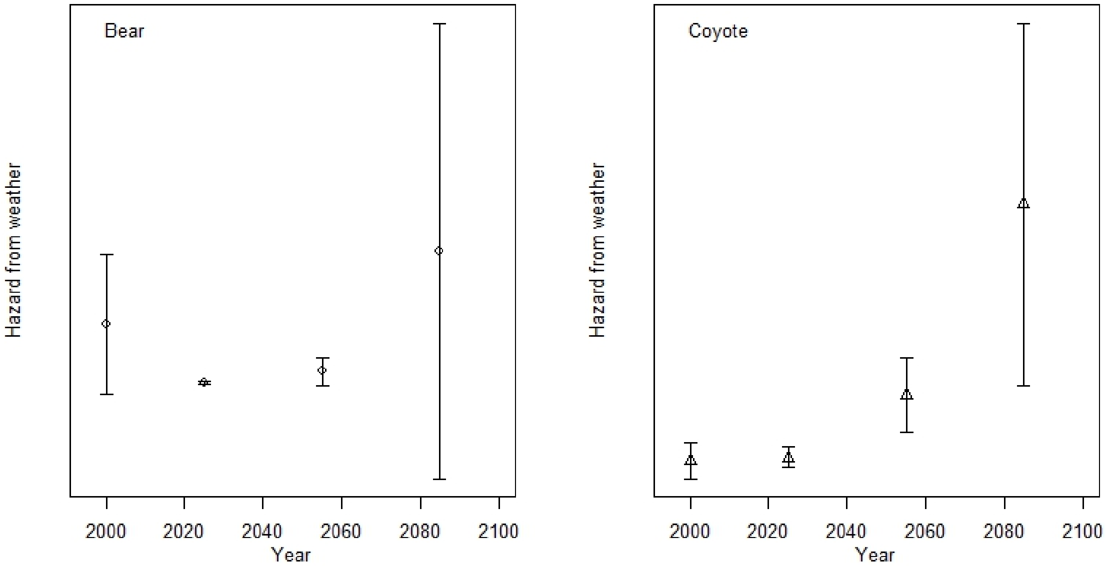

Figure 4-1.Estimated hazard ratios based on cause-specific survival analysis and projected climate models for risk from black bear and coyotes for survival of 847 caribou in Newfoundland (1990-2013).

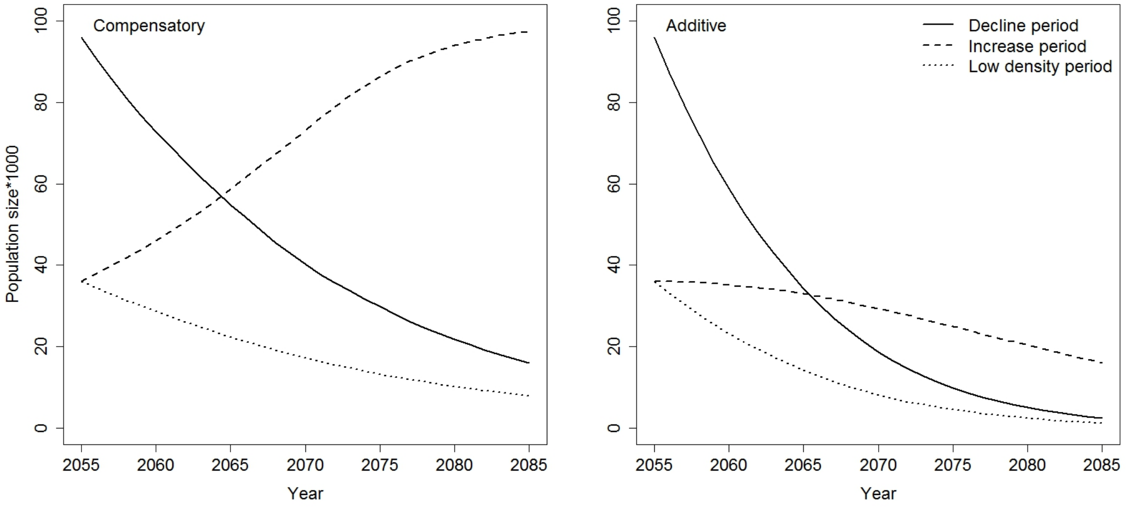

Figure 4-2.Comparison of Newfoundland caribou population trajectories, 2055-2085, under different PVA scenarios. The left panel represents no change or compensatory change in coyote risk under climate change projections while the right panel represents an additive change in calf mortality. Other population vital rates were adjusted according to whether the populations were experiencing a low density period, an increase period or a decrease period. Further details about the PVA can be found in supplementary material 1, Appendix C.

Discussion

We demonstrated that, at present, weather patterns differentially affect caribou calf vulnerability to predation from black bears and coyotes (Table 4-3, see also previous chapter). In Newfoundland, the influence of most climate variables was antagonistic between predators, such that the weather patterns promoting increased risk from coyote predation reduced the risk from bear predators and vice-versa. However, climate projections indicate that the current, largely antagonistic, cause-specific predation may not exist in the future (Figure 4-1). The implications for future caribou populations could be substantial and detrimental, largely because the relative risk from coyotes may increase (Figure 4-2). Overall, our results provide an important link between predation risk and climate change, and thereby emphasize the significance of abiotic change influencing complex biotic interactions and, consequently, future population dynamics.

Predators with different hunting strategies should select different types of prey; particular circumstances should reflect risk from specific predators. In theory, cursorial predators are more likely to kill weaker prey, whereas ambush predators are expected to kill prey that frequent risky habitats (Husseman *et al.* 2003; Atwood, Gese & Kunkel 2007). Cursorial coyotes (Thibault & Ouellet 2005) should experience improved hunting success in response to weather conditions that reduce food availability or quality, and thus body condition of adult and juvenile caribou (Couturier *et al.* 2009b; Taillon *et al.* 2012). Our results are consistent with this prediction: warmer winters prior to calving and summers with high precipitation increase risk from coyotes. On the other hand, black bears are opportunistic predators reliant on short chases to capture prey (Zager & Beecham 2006). As a result, the probability of encountering prey should be driven by predator and prey movement patterns (Bastille-Rousseau *et al.* 2011). Unfavourable climatic condition during calving could result in increased caribou movement (Charnov 1976; Stephens & Krebs 1986) and subsequent increases in bear predation risk. Our results largely support this prediction, too: as spring precipitation increases, risk from black bear declines, perhaps as a result of greener forages, improved feeding, and reduced caribou and bear movement. However, positive increases in previous winter temperatures increased the risk for caribou; this is contrary to our prediction based on foraging and body condition of caribou. These results indicate that influences of climate on cause-specific risk is not only influenced by impacts of climate on caribou, but also by the impacts of climate on predators (Post *et al.* 1999; Nilsen & Linnell 2009).

Antagonistic interactions among predators in response to environmental factors are not frequently discussed in the literature, despite great attention devoted to additive and compensatory mortality (Griffin *et al.* 2011; Sandercock *et al.* 2011). Our results indicated that current interactions between coyotes and bears are mostly antagonistic in response to variation in meteorological conditions − a pattern consistent with compensatory mortality between black bears and coyotes. For example, coyotes may likely kill surplus neonates in years unsuitable to bear predation. We cannot fully reject this possibility, but timing in mortality events is highly similar among predators (see Chapter 3). Moreover, following coyote colonization of the island, risk from bear also increased, an indication that coyote-bear predation is not solely compensatory (see

Chapter 3) but that antagonism between the two is partly induced by an external factor, climate. Finer-level analysis of interactions among predators can improve our understanding of the relationship between climate and predator-prey interactions, but this is not frequently achieved (Murray & Bastille-Rousseau, in review). Our results provide a strong cautionary example of the necessity of considering biotic interactions from a multiple-species point of view (Peers *et al.* 2014).

It has been hypothesised that climate change can exacerbate the effects of other stressors (e.g., invasive species or anthropogenic activities) on population persistence (Travis 2003; Hellmann *et al.* 2008; Brook *et al.* 2008). The rapid expansion of coyotes across North America (Kays et al. 2010), owing in part to their extreme plasticity, could have impacts similar to non-indigenous species (Van der Putten *et al.* 2010). Indeed, their appearance in Newfoundland coincided with the subsequent declines in caribou populations (Bastille-Rousseau *et al.* 2013). Climate change may exacerbate these circumstances for caribou. Our projections indicate that, relative to black bears, coyotes may be favoured as the climate changes − evidence suggestive of a facilitative interaction between climate change and a non-indigenous species. Such facilitative interactions among stressors are analogous to the invasional meltdown hypothesis (Simberloff & Holle 1999; Simberloff 2006).

Numerous studies have observed the potential impact of climate change on animal population persistence and dynamics (Parmesan 2006; Van der Putten *et al.* 2010; Bellard *et al.* 2012). While impacts on population can be either positive or negative, climate change consistently seems to destabilize animal populations displaying cyclic fluctuations in abundance (Kausrud *et al.* 2008; Post *et al.* 2009; Gilg, Sittler & Hanski 2009). Indeed, this destabilization emerges regardless of differences in the mechanisms that trigger delayed-density-dependence or in the complexity of trophic interactions. Likewise, our population projection analysis suggests that climate change could dampen caribou population cycles by inhibiting future periods of population increase.

Our study shares many of the same assumptions and limitations of forecasts of climate change impacts (e.g. Bateman *et al.* 2012; Peers *et al.* 2014). Most notably, we assumed that interactions − other than those between the predators and prey − were untouched by climate change. This could include, for example, interactions between predators themselves or interactions between forage and caribou. Nevertheless, interactions between coyotes and bears are unlikely to be important because they are likely agonistic predators in Newfoundland; their space-use is different (see Chapter 6), and they overlap infrequently around neonate mortality sites (Mumma *et al.* 2014). Climate can affect foraging of caribou, for example by influencing timing of phenology (Post & Forchhammer 2008). However, projected changes in climate in Newfoundland do not deviate drastically from the past 30 years (Figure S1, Appendix C), and so it is likely that changes in phenology already been experienced by caribou are, to some extent, captured by our analysis. Although our pseudo r-squared values are in the same range as those from other neonate survival analyses, it is important to consider that our predictions represent probable scenarios.

We are just beginning to appreciate the complexity of the interactions between climate change and myriad biological processes. Indeed, forecasting impacts of climate change on species distribution and persistence is emerging as a central theme in ecology (Bellard *et al.* 2012). By focusing on the influence of climate on predator-prey interactions, we illustrate that it cannot only alter the risk of depredation from specific predators, but that it can also alter the importance of regulating forces on a population. Together, these results indicate that simpler, more traditional assessments of interactions between climate change and biotic processes reveal only the tip of the iceberg. It is a challenge to ecologists to fathom the rest of this iceberg before climate change floods our world with its negative impacts.

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Chapter 5 - Population and individual variation in niche overlap, encounter, and mortality among incidental predators and a common prey

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Abstract

Incidental predators differ from traditional specialists in their broad diets that may be constrained when one species of prey becomes disproportionately available. Yet, there is poor understanding regarding whether incidental predators exhibit stereotypic relationships with their prey. We investigated how two incidental predators, coyote (*Canis latrans*) and black bear (*Ursus americanus*), interact with neonates of a common prey species, woodland caribou (*Rangifer tarandus*), which demonstrate a critical post-natal period of vulnerability. We examined how caribou and these predators shared similar habitat (niche overlap) at the population and individual level, and how this related to interspecific spatial co-occurrence (encounter rate) and mortality risk for caribou. For coyote, changes in niche overlap spanning 7 months of the year mirrored variation in juvenile hazard risk, but had less association with actual encounter risk with caribou. In contrast, bears exhibited variable patterns of niche overlap during the 3-month calving season that did not correspond with either encounter patterns or overall risk for caribou neonates. Both predators displayed high intra-specific variation in individual niche overlap with caribou, but we did not find evidence that individual characteristics increased the probability of overlap with caribou. Our work illustrates that incidental predators sharing a prey species can have markedly different temporal patterns of niche overlap and encounter. These differences in overlap between two predators speak to a high level of variability in the influence of space-use patterns on predator-prey interactions.

Keywords:

Encounter rate, niche overlap, predation risk, specialist-generalist predators, incidental predation, omnivores, caribou (*Rangifer tarandus*), black bear (*Ursus americanus*), coyote (*Canis latrans*)

Introduction

Predation is a key force shaping most ecosystems (Getz 2011) and one of the key drivers of animal evolution (Roff 1996). Predator-prey interactions are generally conceptualized as complex games of fear and stealth between predators and prey (Brown *et al.* 1999; Laundré 2010). In these games, predators attempt to maximise their success during search, encounter, and attack stages through selective movement, patch-use, and hunting behaviour (Lima & Dill 1990; Hebblewhite *et al.* 2005). Conversely, prey attempt to minimise the impact of predators by balancing their current survival with the acquisition of resources, reproduction, and maintenance of other long-term survival requirements (Stephens & Krebs 1986; Brown 1999). Researchers attempt to predict the spatial outcome of these games in regards to risk for prey and preferred habitat for predators with theoretical models such as the predator-prey shell game (Mitchell & Lima 2002), the landscape of fear (Laundré *et al.* 2001; Laundré 2010), or the behavioural response-race (Sih 1984). Despite varying outcomes of the predator-prey game, all of these models imply a positive relationship in spatial overlap and encounter risk between predator and prey, which subsequently modulate risk. These models are useful because they consider processes such as encounter and vulnerability when generating predictions of predator and prey resource use and distribution over the landscape (Lima & Dill 1990). However, these models have not considered the variation that is often inherent in species' ecological characteristics and temporal differences in resource use. As a result, their general applicability has been somewhat limited.

Interspecific variation in predator hunting strategy can have implications for the behavioural predator-prey game (Schmitz 2005; Preisser *et al.* 2007; Cresswell & Quinn 2013). Predators that stalk or ambush their prey from cover are usually more efficient hunters at short distances; in contrast, pursuit predators improve their success in open habitat and over longer distances (Murray *et al.* 1995; Husseman *et al.* 2003). Cursorial predators are therefore expected to match habitat use of their prey to increase encounter and success rate, whereas ambush predators tend to attack as prey move between habitats (Schmitz *et al.* 2004). Models examining how predator hunting mode and habitat use determine the magnitude of consumptive and non-consumptive effects on prey have been proposed and reviewed (Schmitz 2005; Preisser *et al.* 2007). These models have established that hunting strategy is a key element of any predator-prey game. Unfortunately, models such as the shell-game or the landscape of fear, even if they consider predator behaviour, are typically oriented towards specialist predators and their primary prey (Laundré *et al.* 2001; Mitchell & Lima 2002). To date, other types of predators − such as incidental predators that do not rely on a particular prey type unless environmental conditions (i.e., usually relative density or vulnerability of a given prey type) become conducive to exploitation of that particular prey type − are poorly understood. This includes many incidental predators that exhibit stereotypic hunting strategies suited to one vs. multiple prey types (but see Schmidt *et al.* 2001; Schmidt 2004).

Incidental predators differ from more specialized feeders by expanding their diet opportunistically (Holt & Lawton 1994). Such predators can also display broader ranges of movement and search tactics that affect the risk for targeted and untargeted prey (Schmidt *et al.* 2001). Predation risk for prey consumed incidentally is a function of resource overlap between predator and prey (enemy-free space; Schmidt 2004), movement strategies leading to encounter (Mitchell & Lima 2002; Bastille-Rousseau *et al.* 2011), and inherent vulnerability of the prey (Lima & Dill 1990). Yet not all incidental predators necessarily are cut from the same cloth; in many cases variability in hunting patterns may arise from the relative mortality risk driven by individual differences between predators or prey (Bolnick *et al.* 2003). For example, sex-biased vulnerability to predation may be the outcome of differences in age or experience of individual predators (Woo *et al.* 2008). It follows that a detailed understanding of predator-prey interactions in an incidental predator context requires information on population-level and individual-level patterns (Woo *et al.* 2008; Bastille-Rousseau *et al.* 2011), especially since the effect of a small number of specialized individuals can sometimes have major impacts on prey populations (Festa-Bianchet *et al.* 2006).

Here, we investigate how two omnivorous species, coyote (*Canis latrans*) and American black bear (*Ursus americanus*, hereafter "bear"), interact with neonates of a common prey species, woodland caribou (*Rangifer tarandus*), which demonstrate a critical post-natal period of high predation risk. For both predators, caribou calves are only one of many food items consumed (Matt Mumma unpublished; Bridger 2005). We examined how predators and prey share similar habitat (niche or resource overlap, hereafter "niche overlap") at the population and individual levels, and how this relates to interspecific co-occurrence in space (encounter rate) and mortality risk for neonate caribou. We first defined ecologically relevant seasons for each species (Basille *et al.* 2013). Neonate caribou are most vulnerable to predation in the few weeks following birth and quickly become mobile; the risk from bear predation is limited predominantly to the first months of life (Mahoney *et al.* 1990; Zager & Beecham 2006). While both coyotes and bears have a broad diet (Rode & Robbins 2000; Turner *et al.* 2011), they differ in their hunting strategies of neonatal ungulates: coyotes favour pursuit (Thibault & Ouellet 2005); bears rely on short chases and opportunistic encounters (Young & McCabe 1997; Bastille-Rousseau *et al.* 2011). In a simple, specialist predator-prey system, we expect niche overlap, encounter rates, and mortality risk to be closely tied with trends in neonate intrinsic vulnerability and availability. On the other hand, since both carnivores are incidental predators where neonatal caribou may or may not constitute a principal part of their diet (Zager & Beecham 2006; Turner *et al.* 2011), we hypothesized that the match between niche overlap, encounter rates, and predation risk would be stronger during the period of high calf vulnerability. Second, as individuals of both predator species demonstrate some degree of stereotypic predator behaviour and prey selection (particularly coyotes), we predicted that individuals of both species would exhibit strong niche overlap with caribou during the period of greatest calf vulnerability. Lastly, based on evidence attributing most caribou calf mortalities in Newfoundland to male coyotes or bears (Mumma *et al.* 2014), we predicted that adult males would be more likely to specialize on neonates and have greater niche overlap with caribou. Our study is among the first to explore the spatial interactions between predators and prey at both the population- and individual-level, and illustrates differences from traditional specialist predator-prey interactions.

Material and methods

Data collection

Newfoundland (47º44'N, 59º28'W to 51º44'N, 52º38'W) is a 108,860-km² island off the east coast of Canada, with humid-continental climate and ample year-round precipitation (Environment Canada 2013). Natural habitat consists mainly of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*), and in some locations substantial areas of bogs and heath or barrens. Our analyses were based on a series of Landsat 7 scenes with a resolution of 30 m (overall accuracy was >80% based on ground truthing), which was classified into eight habitat types: wetland habitats (Wetland), mixed and deciduous stands (Mixed), coniferous stands (Conifer), coniferous scrub (Scrub), barren, rocky and other open habitats (Barren), open water (Water), lichen and heathland (Lichen) and rarer habitats such as recent (<40 years) disturbances and fire (Other).

During 2006-2013, >200 adult female caribou, 89 black bears (>2 years of age) and 61 coyotes (>1 year old) were captured and fitted with global positioning system (GPS) collars that obtained locations every 1, 2 or 4 hours. We focused our analyses on animals followed for at least 3 consecutive months per year and had >90% of their locations in areas with Landsat data, resulting in 146 adult caribou females (552 caribou-years and 1,689,519 locations), 55 black bears (22 F, 33 M, 142 bear-years and 128,174 locations) and 61 coyotes (23 F, 38 M, 94 coyote-years and 68,491 locations).

We monitored the fate and estimated the survival time of 813 calves in five herds, 2003-2013, using very high frequency (VHF) telemetry (see Chapters 3 and 4). We located calves by helicopter and captured them on foot, generally <5 days following birth. We verified that collared calves rejoined their mothers within 24 hours of capture. Aerial monitoring schedules varied across years, from every 2-4 days in June and early July, every 5-10 days until the end of August, and fortnightly to monthly thereafter. When a VHF collar indicated mortality, we conducted field investigations of calf remains. We examined remains for cause of death; when sufficient, carcasses were sent to a veterinarian for necropsy. Beginning in 2010, predator salivary DNA was used as a diagnostic tool (Mumma *et al.* 2014).

Statistical analysis

Seasons

We defined homogenous space-use patterns (season) for each species using a clustering approach (Basille *et al.* 2012). We used a 15-day moving window to characterise space-use of an individual in a given year across 11 habitat and movement variables. Within a window, we calculated mean speed, tortuosity, average elevation, and proportion of locations in our eight habitat categories. We then range-standardized each individual-year measurement between 0 and 1 and averaged them, first by individual, and second for the whole set of individuals (Basille *et al.* 2012). This ensured that a behaviour displayed prominently in a given year or individual monitored over multiple years did not contribute more than others to our classification. We used *K*-means clustering to identify homogenous periods (Basille *et al.* 2012) and determined the optimal number of clusters using the DD-weighted gap method (Yan & Ye 2007). We performed a bootstrap approach where 100 sets of individual-years were resampled with replacement from the original dataset and then ran *K*-means clustering for each set to assess robustness of the classification, calculating the probability that each day fell in a specific season (Basille *et al.* 2012). Finally, delineations based on seasons that started on a day that fell in the top 20% for caribou, 25% for coyote, and 30% for bears of the weight distribution were obtained from the bootstrap. We used marginally higher criteria for predator species to ensure that seasonal delineations were representative of their biology and that seasonal differentiation occurred (e.g. below 30% only active and denning seasons were identified for bears). Because tortuosity requires animals to move, and bears were stationary during denning, we randomly assigned tortuosity values from a uniform distribution (0-π radians) and used habitat variables associated with den sites for all days when individuals were denning. Next, we created homogenous caribou-predator seasons by taking the intersection of caribou and predator delineations (hereafter, “caribou-predator seasons”). We then evaluated niche overlap, encounter rate, and hazard risk from bear and coyote using the caribou-predator seasons to test our predictions.

Niche overlap

We examined niche overlap between caribou and each predator species at two levels, population and individual. For caribou, we used adult female GPS telemetry regardless of their reproductive status as this information was not available; parturition rate was approximately 80% during the monitoring period (Weir *et al.* 2014). Population-level overlap reflects overlap in resource use of the caribou population with a predator population, whereas individual-level overlap reflects overlap between an individual predator and the caribou population. Niche overlap should be an indication of the strength of potential trophic interactions between predator and prey species (Chesson & Kuang 2008). We evaluated niche overlap using an index of overlap derived from the Jaccard index adapted to continuous data (Basille *et al.* 2012). For each habitat type and each day, niche overlap at the population- or individual-level was measured as the size of the intersection over the size of the union of a caribou population range and either a predator population species range or individual range based on maximum and minimum values for a given day:

$$Niche\ (Caribou, Predator) = \frac{min[\max(Caribou), \max(Predator)] - max[\min(Caribou), \min(Predator)]}{\max(Caribou, Predator) - \min(Caribou, Predator)}$$

where *min* and *max* represented the minimum or maximum values for use of a specific variable (habitat) within a daily moving window used in the clustering approach. For both levels of niche overlap, the index varied between 0 and 1 (no overlap to complete overlap) for each resource and day. We then computed a measure of daily global overlap by taking the average of all resources for each day for each caribou-predator season.

To further investigate possible specialization towards caribou within predator populations, we examined whether individual-level niche overlap between predators and caribou could be linked with individual characteristics of predators. For each caribou-predator season, we assessed whether individual niche overlap was influenced by age (adult vs subadult), sex, and, for coyotes, social status (resident or transient;

Ellington, unpublished). We used linear models with each of these variables as a single effect and interactions between age and sex for each predator species and each caribou-predator season. (Results are presented in Supplementary material S2, Appendix D.) Additionally, we conducted a simpler analysis focused solely on the period of highest calf vulnerability (June and July) using linear models with the same covariates but with individual overlap as the response variable.

Encounter index

We estimated caribou-predator encounter rates using our GPS telemetry dataset. We defined a potential encounter as an instance where caribou and a predator were <1 km of each other within a 24-hour window. Detection distances of 1-2 km have frequently been used to identify short-term predation risk in different large mammal predator-prey systems and are likely within predator sensory detection range (Creel *et al.* 2005; Gude *et al.* 2006; Muhly *et al.* 2010; Whittington *et al.* 2011). Though such an encounter may not indicate that a biological encounter occurred (predator notices prey or vice-versa), they represent instances where an encounter could plausibly have occurred. Latombe *et al.* (2014) found behavioural changes in caribou selection following the presence of a predator within 4.7 km in the previous 1.5days. Our radius was therefore more conservative than those generally used in definitions of encounter using GPS telemetry (e.g. Muhly *et al.* 2010; Whittington *et al.* 2011). To account for any differences in the length of season or intensity of monitoring, we standardized the number of encounters per caribou-predator season by the length of shared days of monitoring, the intensity of monitoring, and the spatial overlap between caribou and predators. The encounter index for a season was computed as:

$$Encounter = \frac{E_s}{\sum_i^n (D_{Si} * Fc_{Si} * Fp_{Si} * O_{Si})}$$

where E_s was the total amount of encounters in a season S, D_{Si} was the number of shared days of monitoring for a specific pair of animals *i* of *n* possible caribou-predator pairs, Fc_{Si} and Fp_{Si} were the average number of fixes per day for caribou and predator, respectively, in a season, and O_{Si} was the percent overlap between caribou and predator home-ranges based on 100% minimum convex polygon. For each predator species, we range-standardized values of the index over the year.

Hazard risk

We estimated mortality risk for caribou calves from predation by coyote and black bear. We estimated the hazard function (instantaneous risk) for each calf following capture. On average, calves were born approximately 1 June in Newfoundland (Bastille-Rousseau, unpublished). We used kernel-based methods to estimate the hazard function, using local bandwidth selection algorithms (Müller & Wang 1994) and an Epanechnikov boundary function (Murray & Patterson 2006; Griffin *et al.* 2011). Hazard was also range-standardized for both species. All analyses were conducted in R 3.0.2 with packages adehabitatHR (Calenge 2006), sp, rgeos, plyr, muhaz, and functions available from Basille et al. (2012; http://ase-research.org/basille/seasonality).

Results

Caribou-predator seasons

The DDgap statistic revealed the presence of three space-use modes (clusters) over the year for caribou in Newfoundland. These three clusters corresponded to four caribou-specific seasons (Winter, Calving, Summer, and Rut [Breeding]; Figure 5-1) delimited by the respective starting dates: 24 September, 27 April, 27 June, and 10 September. For black bears, the highest DDgap statistic indicated only two seasons, which differentiated between active and denning periods. Therefore, we used the second highest DDgap statistic, which revealed five clusters that corresponded to five seasons (Denning, Spring, Summer, Fall, and Pre-denning; Figure 5-1) with the respective starting dates: 28 October, 15 April, 30 May, 1 August, and 10 October. For coyote, the DDgap revealed six clusters, which corresponded to four seasons (Early Winter, Late Winter, Summer, and Fall) with the following break points: 18 February, 14 April, 12 August, and 5 November. Based on the temporal intersections between species, we identified eight caribou-coyote seasons and nine caribou-bear seasons. For a detailed description of seasonal characteristics of movement parameters and habitat use, see Figures S1, S2, S3 in Supplementary material, Appendix D.

Population- and individual-level niche overlap

On average, annual population-level niche overlap between caribou and coyote during the entire year (mean overlap = 0.110) was higher than between caribou and bear during the non-denning period (mean = 0.086, t = -4.772, df = 555.57, p < 0.001). Population-level niche overlap between caribou and coyote was highest in the summer, most notably between late-June to mid-August, whereas it was lowest during late winter (Mid-February to late-April, Figure 5-2). Niche overlap between individual coyotes and the caribou population followed a different pattern, however, with average individual-level overlap slightly higher during early winter (November to February) and spring (late-April to late-June) and lowest during late winter and late summer (mid-August to late-September and early-November to mid-February, Figure 5-2). Variation in individual-level niche overlap was largest during the early winter and early spring periods (late April to late June, Figure 5-2).

Population-level niche overlap between caribou and bear was highest in late summer and early fall (August to mid-October) and lowest in the periods following den emergence (up to late-May, Figure 5-2). Niche overlap between individual bears and the caribou population followed similar trends at the individual-level (Figure 5-2). Although not reaching the highest levels of overlap between caribou and coyote, some individual bears nevertheless displayed stronger overlap with caribou throughout most of the summer period (late April to early September, Figure 5-2). For both predator species, individual characteristics such as sex, age or, for coyotes, social status, did not affect the level of individual overlap with caribou either during the period of high vulnerability (Table 5-1) or throughout the year (Table S1 in Supplementary material, Appendix D).

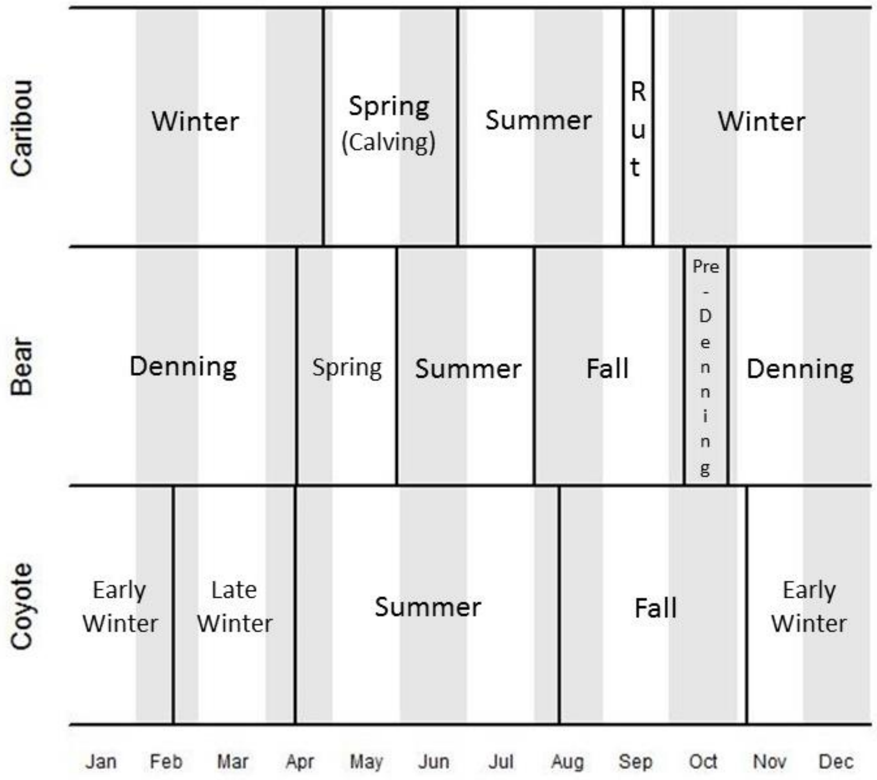

Figure 5-1. Graphical representation of the biological seasons for caribou, black bear and coyote in insular Newfoundland. Shading represents months.

Table 5-1. Linear model between predator individual niche overlap with caribou and predator characteristics for 55 black bears and 61 coyotes, Newfoundland, 1 June - 1 August, 2008-2010. Parameter estimates with standard error and model R^2 are presented. Differences between species detected at α = 0.05 are in bold.

	Bear	**Coyote**
Intercept	**0.054 (0.010)**	**0.118 (0.027)**
Adult	-0.007 (0.012)	-0.040 (0.029)
Male	0.007 (0.012)	-0.055 (0.031)
Adult x Male	0.002 (0.015)	0.053 (0.035)
Resident	-	0.000 (0.017)
R^2	0.042	0.077

Relationships between niche overlap, encounter, and hazard

Patterns of niche overlap, encounter rate, and risk should fluctuate similarly if caribou and their predators are tightly matched and caribou neonates represent a primary food source. In the case of incidental predators, however, we predicted smaller concordance in the fluctuations of niche overlap, encounter rate, and risk. We observed that hazard risk for caribou calves from coyotes decreased most abruptly from June to October, and then decreased gradually over the rest of the year (Figure 5-2). This pattern of risk generally matched population-level niche overlap between coyotes and caribou, except for the early period of calving when risk was higher and overlap was close to average. The pattern of encounter matched, to some extent, the patterns in niche overlap and risk, primarily for the periods prior to mid-August (Figure 5-2). For bears, risk also decreased through time, similarly to coyote, although there was little correspondence between patterns of overlap and risk. For bears, the pattern of encounter was even more weakly associated with the patterns of risk and overlap.

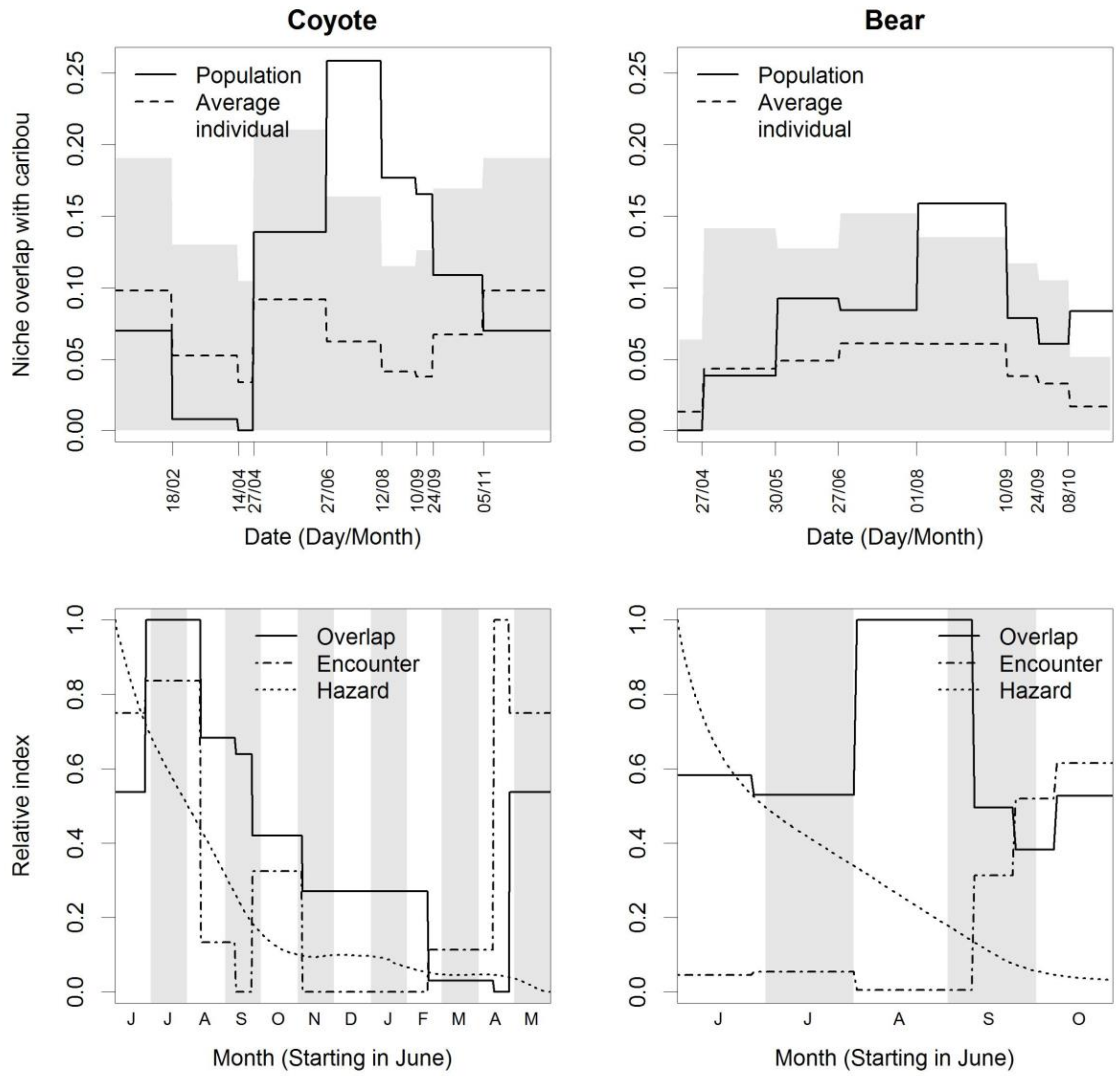

Figure 5-2. Temporal changes in niche overlap (top-panels) and in the index of niche overlap, encounter and hazard risk (lower panels) of caribou and their two main predators. For niche overlap, population level overlap (solid line) and average individual level (dashed line) niche overlap with caribou were based on habitat use; grey areas represent 90% quantiles of individual overlap. Note that the x-axis starts in June for lower-panels and extends to the non-denning period for bear.

Discussion

We explored spatial interactions between predators and prey at the population and individual level to further our understanding of incidental predator behaviour. We first explored seasonal patterns of space-use for each species (Figure 5-1) and determined that niche overlap with female caribou was slightly higher for coyote than for bear. For coyotes, seasonal changes in niche overlap mirrored variation in hazard risk to calves but had less association with encounter rate with female caribou. In contrast, changes in niche overlap during the calving season for black bears had little association with either encounter patterns or overall risk for caribou neonates (Figure 5-2). These differences in space use overlap between two predators and an identical prey species speak to a higher level of variability in the spatial interactions between incidental predators and their prey than generally expected with specialist predators.

Predator hunting behaviour is a crucial element of the predator-prey game, shaping not only the behavioural response of the prey and the magnitude of non-consumptive effects, but also potentially having broader repercussions at the ecosystem level (Preisser *et al.* 2007; Schmitz 2008). It is generally expected that ambush predators will be more efficient at short distance and more likely to attack prey moving between less risky habitats, whereas cursorial predators should favour open habitat but also match their habitat use to that of their prey to improve encounter success (Murray *et al.* 1995; Husseman *et al.* 2003; Schmitz *et al.* 2004). Where incidental predators hunt multiple types of prey in common space and time, however, expectations regarding habitat use and hunting strategies are less clear. As expected, we found that population niche overlap between coyotes (a cursorial predator) and adult female caribou decreased as calves became less vulnerable to coyote predation (Figure 5-2), indicating that coyote space-use more closely matched caribou space-use when calves were susceptible to coyote predation. The overall lower level of niche overlap observed between bears and caribou (Figure 5-2) was probably also influenced by hunting behaviour. Black bears rely on shorter chases and are known as opportunistic predators of ungulate neonates (Young & McCabe 1997; Bastille-Rousseau *et al.* 2011). Indeed, our results indicate that overlap was lower for bears than coyotes, providing support that incidental predators follow the same trend as more specialised feeders; cursorial predators have higher niche overlap with prey than do ambush predators.

Many populations of incidental predators can be considered as groups of specialized individuals (Bolnick *et al.* 2003; Woo *et al.* 2008). In our study, both predator species displayed high intra-specific variation in individual niche overlap with caribou; numerous individuals displayed little to no overlap, whereas some displayed strong parallels in resource use. Although a high degree of similarity in resource use between a predator and caribou may not be a formal indication of specialization, individuals with higher niche overlap are more likely to be preying on caribou (Basille *et al.* 2012). Contrary to our prediction, we did not find evidence that individual characteristics of either predator species increased the probability of overlap with caribou (Table 5-1). This is despite evidence that mortalities are mostly attributable to males, albeit with small sample sizes (Mumma *et al.* 2014). Such a discrepancy would be possible if males of either species are more successful than females at killing calves following encounters. Nevertheless, the minor influence of individual characteristics on niche overlap and the low level of individual overlap in comparison to more traditional specialists predators (Basille *et al.* 2012) are consistent with the notion that caribou are not primary prey for either of these carnivores.

Predators exist along a continuum regarding specialization toward resources (Bolnick *et al.* 2003; Abrams 2006). At one extreme, specialists focus on primary prey exclusively, switching to alternate prey only during periods of low primary prey density (Fryxell & Lundberg 1994). Such prey-switching behaviour is well captured by current functional response models and, therefore, the integration of specialist predators in prey population dynamics is more straightforward (Vucetich, Peterson & Schaefer 2002; Panzacchi *et al.* 2008). At the other extreme, incidental predators focus on a given prey type only in restricted space and/or time, but nevertheless orient their foraging behaviour toward a diversity of resources (Smout *et al.* 2010). This flexibility in searching behaviour increases the opportunity for incidental predation, resulting in the consumption of prey that is unintentionally encountered (Schmidt 2001, 2004). Even if ungulate neonates are an extremely profitable resource for these predators (Rode & Robbins 2000; Turner *et al.* 2011), the small overlap of both predators with caribou indicates that this particular prey type is unlikely to serve as primary prey. However, it is unclear whether these predators are actively searching for neonates or are simply incidentally encountering them. Further examination of resource selection and functional response of coyotes and black bears towards calves is needed to clarify the role of caribou in their diet.

Predation risk can be separated into two sub-components: the probability of encounter (α) and the probability of death following an encounter (Lima & Dill 1990; Hebblewhite *et al.* 2005). Space-use patterns of predator and prey comprise the main elements of the encounter component (Hebblewhite *et al.* 2005). For a neonate calf, vulnerability is highly influenced by age (Gustine *et al.* 2006). To some extent, we found that resource use matched the encounter index for coyotes, but we found little correspondence between these indices for bears. It is possible that our encounter-index does not reflect actual encounter risk, especially during shorter predator-caribou seasons. Moreover, for coyotes, the overall patterns of overlap and encounter follow the change in risk (Figure 5-2). This indicates that predation risk from coyotes was shaped by both the encounter probability and the change in neonate vulnerability. Results from bear were markedly different; overlap and encounter did not correspond with variation in risk (Figure 5-2). This indicates that risk from bear was almost uniquely driven by vulnerability of neonate caribou, and that the encounter probability had little influence on overall risk. This is corroborated by numerous studies showing a short period of vulnerability to bear predation for ungulate neonates (review by Zager & Beecham 2006). Nevertheless, it is interesting to see that these two different strategies resulted in similar levels of cause-specific predation rates (see Chapter 3).

Newfoundland caribou have been in a state of protracted decline since the mid-1990s following a numerical increase initiated in the 1970s. Just prior to this decline, coyotes colonized the island and became widespread. Factors ultimately driving caribou decline are related to a decrease in summer foraging and harsher winter conditions (Mahoney *et al.* 2011; Bastille-Rousseau *et al.* 2013), but proximately, this decline is the outcome of a drastic reduction in neonate survival (see Chapter 3 and 4). It is commonly accepted that incidental (i.e., generalist) predators can stabilize prey populations when mortality is density-dependent (Fryxell & Lundberg 1994), but local extinction may result when predators expand their diet rather than switch to alternate prey (Holt & Lawton 1994). Mortalities do not appear to be density-dependent for adult female Newfoundland caribou following the decline (see Chapter 3) but caribou are one of many food items consumed by bears and coyotes (Matt Mumma unpublished; Bridger 2005). This means that per-capita predation is unlikely to be reduced even if populations further decrease in abundance. As our analysis was limited to a period when caribou populations were at their lowest density in the last 3 decades, it is uncertain whether predators may alter their behaviour by increasing the predation rate on caribou following a positive change in abundance. This would represent a double-edged sword for Newfoundland caribou, as density-independent predation may threaten current caribou persistence whereas density-dependent predation may limit future population increase.

A great deal of literature on predator-prey interactions has focused on systems involving specialist predators. Detailed spatial models of the behavioural games for both species, or formulations of several types of functional responses, greatly improved the study of predator-prey interactions (Vucetich *et al.* 2002; Hebblewhite *et al.* 2005;

Laundré 2010). However, the behavioural strategies of more generalized consumers are not easily captured by these theoretical models, leaving ecologists ill-equipped to examine generalist predator-prey interactions. Our work addresses this knowledge gap by illustrating that generalist predators sharing a prey species can have markedly different strategies regarding patterns in niche overlap and encounter. Moreover, these strategies are highly variable within-species, but nevertheless have a similar impact on prey population dynamics. As top predators decline worldwide (Johnson, Isaac & Fisher 2007; Heithaus *et al.* 2008), it is likely that the predation impact on prey communities will be increasingly driven by highly opportunistic and incidental predators with an increased ability to respond dynamically to human development and landscape alteration. It is therefore crucial that we develop a robust theoretical foundation for predator-prey interactions involving non-specialist predators, to better predict future influences on ecosystem function.

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Chapter 6 - Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability

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Abstract

Habitat selection is a multi-level, hierarchical process that should be a key component in the balance between food acquisition and predation risk avoidance (food-predation trade-off), but, to date, studies have not fully elucidated how fine- and broad-scale habitat decisions by individual prey can help balance food versus risk. We studied broad-scale habitat selection by Newfoundland caribou (*Rangifer tarandus*), focusing on trade-offs between predation risk versus access to forage during the calving and post-calving period. We improved traditional measures of habitat availability by modeling fine-scale movement patterns of caribou and incorporated such information into standard habitat selection analysis. Remote sensing and field surveys served to create a spatio-temporal model of forage availability, whereas GPS telemetry locations from 66 black bears (*Ursus americanus*) and 47 coyotes (*Canis latrans*) provided models of predation risk. We then used GPS telemetry locations from 114 female caribou to assess food-predation trade-offs through the lens of our refined model of caribou habitat availability. We noted that migratory movements of caribou were oriented mainly towards habitats with abundant forage and lower risk of bear, and to a lesser extent coyote, encounter. These findings were generally consistent across caribou herds and would not have been evident had we used traditional methods instead of our refined model, when estimating habitat availability. We interpret these findings in the context of stereotypical migratory behaviour observed in Newfoundland caribou, which occurs despite the extirpation of wolves (*Canis lupus*) nearly a century ago. We submit that caribou are able to balance food acquisition against predation risk using a complex set of factors involving both finer and broader scale selection. Accordingly, our study provides a strong argument for refined habitat availability estimates in assessment of the food-predation trade-off.

Key-words: caribou (*Rangifer tarandus*), conservation biology, habitat selection, mechanistic modelling, step-selection function, migration.

Introduction

Understanding the drivers of anti-predator responses and the efficiency by which animals trade-off food versus safety is crucial, since anti-predator behavioural modification can have profound consequences on fitness, and ultimately, population dynamics (Gaillard *et al.* 2010). Beyond their direct lethal impact, predators can increase physiological stress in prey (Creel *et al.* 2009) and cause behavioural adjustments that contribute to the net effect of predation (Lima & Bednekoff 1999; Creel & Christianson 2008; Schmitz 2008). These anti-predator behavioural adjustments can also induce a reduction in foraging efficiency (foraging cost of predation; Brown & Kotler 2004), ultimately leading prey to compromise between food and safety. Prey are able to reduce the impact of predation through various behavioural strategies, such as vigilance, grouping, and movement (Lima & Dill 1990; Lima 1998).

One of those behavioural strategies, movement, is a central process in animal ecology, including in the study of predator-prey interactions (Mitchell & Lima 2002; Nathan 2008; Laundré 2010). Indeed, animals move in response to a variety of competing pressures such as the need to feed, avoid predators, breed, and rear offspring (Brown *et al*. 1999, Cresswell 2008). These competing demands give rise to trade-offs that individuals must mediate through their space use and movements (Lima 1998; Hebblewhite & Merrill 2009), resulting in distinctive patterns of habitat selection. Numerous studies have tried to unveil potential trade-offs for prey through the process of habitat selection (e.g. Creel *et al.* 2005; Fortin & Fortin 2009; Hebblewhite & Merrill 2009). Habitat selection is defined as the disproportionate use of a habitat relative to its availability (Johnson 1980, Manly *et al*. 2002), and elucidating habitat selection determinants remains a central and unifying concept bridging spatial and temporal scales (Morris 2003, Mayor *et al*. 2007). Indeed, studies often have compared habitat selection across multiple scales (e.g. Dussault *et al.* 2005; Hebblewhite & Merrill 2009; van Beest *et al.* 2010). Further, and especially owing to prevalent and rapid environmental change, there is increasing interest in understanding motivations associated with an animal's habitat selection, especially in the context of revealing how such selection may be mismatched with current or future environmental conditions (Sih *et al.* 2011; Middleton *et al.* 2013a). Indeed, it is reasonable to suggest that habitat selection is one of the most studied concepts in ecology.

Despite such focused attention, habitat selection studies are frequently limited in the insights they provide, due to: (1) absence of robust information (e.g. qualitative field surveys or predator data), leading to a weak or simplified definition of available forage or predation risk (Hebblewhite & Haydon 2010); (2) restrictive analysis of a single level of selection (Boyce 2006); or (3) trivial or problematic comparison of use versus availability to infer selection (Aarts *et al.* 2013). Notably, there remain substantive challenges in understanding behavioural processes underlying habitat selection and the animal motivation by which it is governed. This difficulty arises because of non-independent behavioural processes and overlapping motivations across levels of selection, as well as the conditional and statistical nature of 'selection'. This means that previous work often addressed the question of resource selection on the basis of relatively simple (and presumably imprecise) algorithms when defining habitat availability (Beyer *et al.* 2010). It follows that such an approach may mask actual patterns and drivers of habitat selection at a particular level due to artefacts of finer-scale processes also being considered in the use-availability statistical comparison. Better integration of animal decisions that are quantifiable on the basis of movement ecology should therefore be useful. Here we propose a refined approach for defining availability that considers finer scale selection patterns and thereby improves the distinction between levels of selection, while also providing insight into motivation underlying such selection.

Caribou (*Rangifer tarandus* L.) offer a unique system for studying food-predation trade-offs in habitat selection, and on the island of Newfoundland, Canada, there are 14 major herds with most exhibiting some degree of migratory behaviour involving the annual use of traditional calving grounds by females. These herds are largely distinct and spatially disjunct at calving (Bastille-Rousseau *et al*. 2013). Interestingly, during the last 50 years, Newfoundland caribou have undergone marked fluctuations in abundance, with populations increasing rapidly during the 1980s to mid-1990s, and declining during the 2000s (Mahoney & Schaefer 2002a; Mahoney *et al.* 2011). We develop a refined model of availability to study broad-scale habitat selection, with an emphasis on trade-offs between predation risk and foraging. More specifically, we use a mechanistic model based on a step-selection function that approximates fine-scale movement to create a refined sample of habitat availability. We use this model to study selection of calving grounds (referred as second-order level of selection; Johnson 1980) as well as core areas within the calving grounds (referred as third-order level of selection) in response to vegetation biomass and current predation risk (black bears [*Ursus americanus* L.] and coyotes [*Canis latrans* Say.]). Coyotes are non-native predators that became widespread in Newfoundland in the 1990s. Considering the high caribou calf mortality during calving periods (Trindade *et al.* 2011) and recent evidence of density-dependent population fluctuations (Mahoney & Schaefer 2002a; Mahoney *et al.* 2011), we first predicted that predation has a stronger effect on habitat use and that selection of calving grounds would be driven mostly by predation risk avoidance. Second, we predicted that access to rich foraging sites would be the main factor driving habitat selection at the third order − i.e., the selection of core areas within the calving ground. As a side contribution emanating from our analysis, we compared insights obtained from our mechanistic definition of availability to the traditional approach, and predicted that our refined model would provide insights into the processes underlying caribou decisions vis-à-vis food-predation trade-offs, otherwise not evident. We believe that our approach could provide a major shift in how ecologists approach questions related to animal behavioural adjustments in response to the subtle interplay between risks and rewards in their environment.

Material and methods

Study area

Newfoundland is a 108,860-km² island at the eastern extremity of Canada (47º44'N, 59º28'W to 51º44'N, 52º38'W), with humid-continental climate and ample year-round precipitation (Environment Canada 2013). Natural habitat consists mainly of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*), and in some locations substantial areas of bogs and heath or barren habitats. Most of our analyses were based on a Landsat TM satellite imagery (overall accuracy >70%), with a resolution of 25 m, classified into 5 different habitat types: wetland habitats (Wetland), barren and other open habitats (Barren), mixed and coniferous open stand (CO), mixed and coniferous dense stand (CD) and a category (Other) comprised of rarer habitats such as broadleaf stands, herbs, bryoids and open water (Wulder *et al.* 2008). Anthropogenic disturbances are limited in caribou range in Newfoundland but consist of logging, hydroelectric development, and roads. We restricted our analysis to five important migratory herds located south of the main east-west highway that crosses the island (Fig. 6-1).

Animal capture and monitoring

During 2006-2010, more than 200 caribou were captured, principally during winter, and fitted with global positioning system (GPS) collars that obtained locations every 2 hours. We focused on 114 adult females (271 caribou-years and 384,764 locations) that were followed during 2007-2010 and that resided in 5 distinct herds (Buchans [*n*=17 caribou], Lapoile [*n*=19], Middle Ridge [*n*=28], Pot Hill [*n*=18] and Gaff Topsails [*n*=32]). We limited our movement analysis to the crucial, post-migratory period of calving and post-calving (1 May - 1 August) when most caribou neonate mortalities occur. We also used GPS locations of 66 adult male and female black bears (125 bear-years and 96,531 locations) and 47 adult male and female coyotes (59 coyote-years and 18,842 locations) followed during the same period in the vicinity of our study area. Although most of the study area contained radio-collared predators, the central portion of our study area was under-represented in terms of predator locations, most notably for bears. We therefore did not use the density of locations as a measure of predation risk (e.g. kernel density estimate), but rather sought to quantify predation risk via habitat selection approaches.

We used caribou GPS locations to create a 95% bivariate kernel density estimate using an *ad hoc* approach to estimate the smoothing parameter to roughly delineate the areas used during calving and post-calving (hereafter, “calving grounds”) for each herd (see Worton 1989). We then created a general study area of availability that encompassed these five herds that was generally delineated by the Trans-Canada Highway to the north, east and west, and by the coast to the south (Fig. 6-1). The study area and the herd calving ground delineations represented our two levels of availability (second and third-order selection, respectively; Johnson 1980).

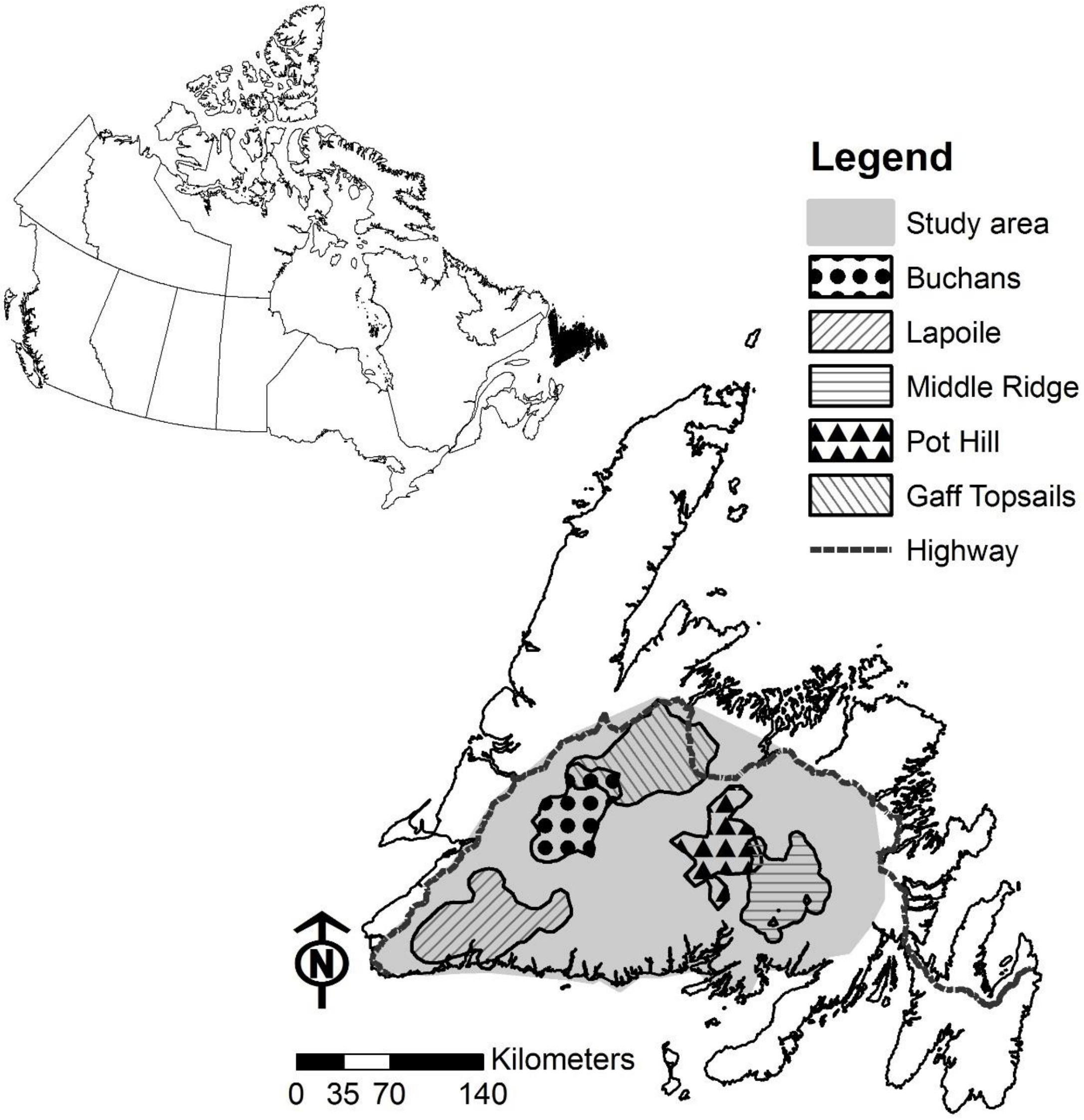

Figure 6-1. Calving grounds and the larger study area for five caribou herds in Newfoundland, Canada. These delineations were used to define habitat availability.

Definitions of availability

1- Random model

Most resource selection analysis involving radio-telemetry is based on the use-versus-availability design, where availability is sampled from locations drawn within an area assumed to define what actually is available to the animal. However, defining habitat availability has constituted a longstanding challenge in ecology (Beyer *et al*. 2010). Specifically, 'availability' usually is identified by sampling habitats randomly within the defined area and relying on the assumption that accessibility of different habitats is similar across all individuals. This assumption depends on habitat connectivity and animal movement (Dancose, Fortin & Guo 2011) and is less likely to be satisfied at higher orders of selection (Johnson 1980). Our first definition of availability was based on this simple definition (hereafter, "random model"). We generated 5 million random locations within the study area and assigned each location evenly to one of 15,000 virtual individuals. We also generated 1 million random locations within each herd's calving ground and equally associated them with one of 3,000 virtual individuals. We randomly assigned each location to a specific day and each individual to a specific year (2007-2010 [2009-2010 for Middle Ridge]) corresponding to the radio-telemetry data for each herd. Associating random locations to an individual, day, and year was necessary for subsequent analyses.

2- Mechanistic model

For fine-scale analyses of resource selection, realistic and restrictive definitions of availability based on movement properties have been proposed (Hjermann 2000; Matthiopoulos 2003; Fortin *et al.* 2005; Fieberg *et al.* 2010; Aarts *et al.* 2013; Avgar *et* *al.* 2013), but for broad-scale analyses, alternatives are still limited (see Arthur *et al.* 1996). Ecologists generally view habitat selection as a hierarchical process; it is well accepted that fine-scale selection is a function of resource availability at the same level, yet availability is defined by broad-scale habitat selection (Schaefer & Messier 1995; Mysterud & Ims 1998; DeCesare *et al.* 2012). The consequence of such a view is that, when inferring motivation behind selection, each level is viewed as independent. This view has been reinforced by the hierarchical habitat selection hypothesis (HSS) proposed by Rettie & Messier (2000), where broad-scale selection reflects the most relevant limiting factors (but see Dussault *et al*. 2005, Hebblewhite & Merrill 2009 for a critical discussion of this hypothesis). Use of specific resources, in addition, should be seen as a summation of multiple processes operating at different scales adding to the difficulty of interpreting scale-specific selection. Therefore, inferring motivation behind such patterns often can be challenging (Beyer *et al*. 2010).

To understand the motivation behind caribou migration or other broad-scale habitat selection patterns, researchers might compare locations used by animals to a set of random locations within a larger area. However, mammals, and notably ungulates, are known to display movements that balance both long-term and short-term motivations (Mueller, Fagan & Grimm 2011), and therefore a more refined analysis should reflect finer-scale decisions that are made when moving within the larger area. As we seek to understand the motivation behind a level-specific behaviour as well as a realistic estimate of habitat availability, we need to control for the influence of fine-scale selection patterns. This can be achieved by refining our definition of availability to consider fine-scale movements. At first glance, inclusion of information related to mechanisms of selection at fine-scales may not seem appropriate for studying broad-scale processes. However, for the purpose of our study it is necessary to determine whether observed differences between used and available locations result from actual differences in broad-scale space-use or as an artefact of fine-scale movement patterns. Refining the definition of availability would therefore allow a more conservative estimate of broad-scale selection that considers fine-scale movement and improves the distinction between levels of selection, allowing for a more rigorous test of selection itself, as well as a refined approach to evaluate novel hypotheses.

To get a more realistic (and restrictive) view of availability that considers fine-scale animal movements, we built a spatially-explicit, mechanistic model that represented between-patch transition in areas that could be occupied by caribou. At a minimum, a suitable model of fine-scale movement should include step lengths and turning angles, but also could incorporate a weighting function representing preference for specific resources (Rhodes *et al.* 2005). Such a model would therefore include both reduction of movement and biased movement to inform on fine-scale selection patterns (Moorcroft & Barnett 2008; Bastille-Rousseau, Fortin & Dussault 2010).

We used a spatially-explicit mechanistic model, based on a step-selection function, to provide our second definition of availability (hereafter, "mechanistic model"). We randomly initiated this model within the study area to investigate selection of caribou calving grounds (second-order selection) and to study third-order selection within each of the five calving grounds. This model included movement parameters (step length and turning angles) derived from collared caribou combined with a weighting function translating between-habitat preference in inter-patch movements. Full details regarding model formulation and estimation of parameters can be found in Potts *et al.* (2014). We initiated 15,000 virtual individuals within the broader areas and 3,000 within each calving ground, which were assigned locations every 2 hours and then processed similarly to locations from the random model.

Predation model

We used a resource selection function (RSFs; Boyce *et al.* 2002; Manly *et al.* 2002) to describe the spatial relationship between the probability of occurrence of coyotes and black bears according to landscape attributes. We estimated RSFs by comparing habitat characteristics at observed and random locations with mixed-effects logistic regression models, with individual as random factor (i.e., random intercept; Gillies *et al.* 2006; Hebblewhite & Merrill 2008) to account for spatial autocorrelation and differences in sample size. We drew random locations for a given individual within the 99% utilization distribution evaluated from a Brownian bridge kernel approach (Horne *et al.* 2007). Random locations were drawn at a density of 2 points/km^2. Observed and random locations were characterized by dummy variables representing landcover types (with Wetland as the reference category), as well as elevation, slope, and proportion of each habitat category within a 5-km radius (except habitats classified as ‘Water’ and ‘Other’). Proportion of habitat within a buffer was used to account for the presence of a functional response in habitat selection (Mysterud & Ims 1998; Moreau *et al.* 2012), which may improve model fit, especially over large areas (Aarts *et al*. 2013). We therefore added an interaction term between coefficients for a specific habitat and its proportion (McLoughlin *et al.* 2010; Aarts *et al.* 2013).

The global RSF took the form:

$$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_{\mathrm{u}} x_{\mathrm{uij}} + \beta_{\mathrm{u\_5k}} x_{(\mathrm{u\_5k})\mathrm{ij}} + \ldots + \beta_{\mathrm{u}} x_{\mathrm{u}} * \beta_{\mathrm{u\_5k}} x_{(\mathrm{u\_5k})\mathrm{ij}} + \gamma_{0j}) \qquad (1)$$

where *w(x)* represented the RSF scores, β_{u} was the selection coefficient for resource $x_{\underline{u}}$ or for the elevation and the slope, $\beta_{\mathrm{u\_5k}}$ was the selection coefficient for proportion of the resource within a 5-km buffer $x_{(\mathrm{u\_5k})}$, and γ_{0j} was the random intercept for animal *j*. We tested for collinearity using the variance inflation factor (Graham 2003) and used $\mathrm{AIC_c}$ selection criteria to identify the most parsimonious model (Burnham & Anderson 2002) within the global model and subset of simpler models (Table S1, Supplementary material, Appendix E). We then used k-fold cross validation to evaluate the robustness of RSFs (Boyce *et al.* 2002). An RSF model based on 80% of the data was estimated, withholding the remaining 20% for evaluation. Predicted scores of the model were placed in ten bins of equal size that represented the percentile range of predicted scores. We then determined the frequency of locations in the withheld data (20%) that fell into each bin. To evaluate model performance, we calculated a Spearman rank correlation (r_s) between the frequency of occurrence for the withheld 20% and the ranked RSF-availability bins (Boyce *et al.* 2002). The process was repeated 20 times and we report the average r_s. We used the validated RSFs to build island-wide maps of relative occurrence probabilities, which we used to estimate encounter risk with both predator species. RSFs were calculated using R statistical software (ver. 2.15.0, R

Development Core Team 2008) with the package lme4 (Bates *et al.* 2014) and adehabitatHR (Calenge 2006).

Forage model

To study caribou use of vegetation-rich areas, we created a spatiotemporally dynamic model of forage biomass (similar to Hebblewhite, Merrill & McDermid 2008). This model was based on the five habitat categories, and field vegetation surveys linked to a temporally dynamic forage availability model using MODIS Terra NDVI 250 m every 16 days. Complete details of this model are given in Supplementary material, Appendix E.

Statistical analysis

For every set of caribou locations (observed, random, and mechanistic), we extracted habitat category, relative probability of occurrence of black bears and coyotes, and vegetation biomass based on timing of the location. We estimated selection for each habitat by computing resource selection ratios (w_i) and tested for overall selection using a Chi-square test (Manly *et al.* 2002). We assessed selection for vegetation at a given scale by comparing the yearly between-individual average value of vegetation biomass of each herd with the average value for the set of available locations based on the random and mechanistic models. For locations representing use, confidence intervals around the average provide an indication of individual variation. Similarly, we tested for avoidance of predation by comparing the average probability of occurrence of bears and coyotes for each herd at actual caribou locations with average availability observed from each of our four models of availability.

Lastly, to gain insight into the behavioural motivation behind migration, we assessed trade-offs between vegetation and predation faced by caribou at the second-order level of selection. We used the following linear model:

$$Biomass\ (x) = \beta_0 + \beta_{Bear} * x_{Bear} + \beta_{Coyote} * x_{Coyote} + \beta_{Interaction} * x_{Bear} * x_{Coyote} \qquad (2)$$

where Biomass(x) represents the vegetation biomass in a given location, β_0 represents the intercept, $\beta_{Predators}$ represents the slope between the risk from a predator $x_{Predators}$ and biomass. A positive and statistically significant coefficient β indicates that caribou would face a trade-off between the specific cause of predation and forage. An interaction between bear and coyote relative probability of occurrence was added to account for the presence of non-linearity in the influence. We estimated this model using the actual set of locations, but also using the availability models generated within the general study area based on the random and mechanistically simulated models. We used bootstrapping to get more robust standard error estimates for the two availability models, since these models are biased due to arbitrary determined sample sizes. More precisely, we performed these regressions with a sub-sample of the random and mechanistic datasets of available locations, sampling the same amount of individuals as the actual data (*n*=271 individual-years). We repeated these steps 1000 times and used the average standard errors in confidence interval calculation.

Results

Predator occurrence and vegetation abundance

For both black bears and coyotes, AIC_c model selection showed that the global model with all habitat categories and presence of functional responses was most parsimonious

(AIC_c weights > 0.99, Table S1, Appendix E). Both black bears and coyotes displayed a functional response in habitat selection, where selection for most habitats decreased as the proportion of a given habitat in the area surrounding a location increased as revealed by the negative coefficient for interactions terms. This response was stronger for coyotes than for bears in the selection of Barren and Wetland habitats (Table 6-1). The two predators responded differently to elevation and slope, with black bears avoiding sites with higher elevations, but selecting sites with steeper slopes, and coyotes displaying the opposite pattern, with selection favouring higher elevation and low slope. *K*-fold cross-validation indicated these models were robust, with r_s= 0.979 for black bears and r_s = 0.930 for coyotes.

During the same period, Wetland and Coniferous Open supported the highest vegetation biomass, followed by Barren and Coniferous Dense (Table 6-2). Correlations between increases in NDVI Modis Tera satellite index and vegetation growth were strong (average conditional R^2 = 0.920). As revealed by the magnitude of the slopes, changes in NDVI had the strongest impact on changes in vegetation growth in Wetland and Barren habitats, while having smaller influence in Coniferous Dense (Table 6-2). Complete details of the spatio-temporal vegetation model are given in Appendix D.

Table 6-1. Mixed-effects RSFs for black bears and coyotes, Newfoundland, 1 May - 1 August, 2008-2010. Parameter estimates (β), standard errors (SE), and variance estimates of the random intercept are presented.

	Black bear		Coyote	
Variables	*β*	SE	*B*	SE
Water	-1.103	0.035	-1.395	0.050
Barren	-0.113	0.032	-0.257	0.049
Coniferous Dense (CD)	0.799	0.024	0.331	0.038
Coniferous Open (CO)	0.570	0.017	0.195	0.028
Other	0.641	0.051	0.288	0.091
Elevation	-0.178	0.010	0.081	0.023
Slope	0.243	0.009	-0.105	0.012
Wetland within 5 km	0.050	0.014	-0.248	0.022
Barren within 5km	0.112	0.013	-0.255	0.023
Coniferous Open within 5km	-0.031	0.017	-0.345	0.025
Coniferous Dense within 5km	-0.074	0.016	-0.552	0.023
Wetland within 5km * Wetland	-0.146	0.014	-0.135	0.029
Barren within 5km * Barren	-0.264	0.020	0.023	0.030
Coniferous Open within 5km * CO	0.012	0.014	-0.076	0.023
Coniferous Dense within 5km * CD	-0.159	0.015	-0.350	0.032
Random effect	Variance: 1.168		Variance: 1.506	

Table 6-2. Relative abundance indices of vegetation biomass from vegetation surveys by landcover type. The slope and coefficient of determination (conditional R^2) represent the relationship between vegetation biomass and NDVI values. See Appendix D.

Habitat	Index of biomass	Slope	Conditional R^2
Barren	0.734	4.541	0.932
Wetland	1.000	4.877	0.930
Coniferous Open	0.990	2.276	0.945
Coniferous Dense	0.458	0.665	0.870

Habitat selection

Based on the random model of availability, female caribou (except for Pot Hill) displayed selection for Barren and Wetland habitats at both second- and third-order levels. Conversely, caribou tended to avoid Coniferous Open and Dense stands as well as Water, at both scales. Surprisingly, the Pot Hill herd displayed the opposite pattern, with preference for Coniferous Open stands and general avoidance of other habitats at both scales (Table 6-3). Patterns of selection were qualitatively similar to those from the mechanistic sampling model, although the proportion of statistically significant selection ratios across habitats decreased from 68% to 53%. This decrease in statistical significance would lead to different inferences regarding selection due to the more conservative nature of the comparison between used- and mechanistically defined availability locations.

Response of caribou to forage and predation

All herds except Pot Hill displayed selection for sites with higher forage both when choosing their calving grounds and subsequently when moving within the calving grounds. Interestingly, the mechanistic model of availability indicated greater access to forage than the random model, a pattern that was consistent across scales. This indicates that no matter where caribou were moving, interpatch movement rules were already providing access to sites with greater forage, but that the choice of calving grounds and core areas within caribou calving grounds reinforced this selection (Fig. 6-2).

Only two herds (Buchans and Gaff Topsails) appeared to reduce risk of encountering coyotes by migrating to their calving grounds. These two herds and the Middle Ridge herd were also able to further reduce risk when moving within their calving grounds. Individuals from two herds (Buchans and Lapoile) appeared to reduce risk of encountering bears when migrating to their calving ground but when considering carefully their potential exposure based on their fine-scale movement (mechanistic model), all herds except Pot Hill appeared to reduce predation risk from bears via second-order selection. Three herds also enhanced risk reduction when choosing core areas within calving grounds. In all cases, the mechanistic model of availability showed higher risk of predation than the random model, indicating that fine-scale movements could increase risk for caribou (Fig. 6-2).

Trade-offs between predation risk and forage

If areas with high forager availability are associated (positively correlated) with an increased risk of predation, caribou will face a trade-off between the two. In general, available locations with higher forage based on the random model were associated with less risk from bears (negative coefficient) but reflected a trade-off with respect to coyote predation (positive coefficient). Available locations based on mechanistic modeling also indicated a trade-off between foraging and coyote predation (Fig. 6-3). However, caribou were able to reduce exposure to predation in their actual use of habitat, most notably regarding the relationship between foraging sites and black bear predation risk.

Table 6-3. Selection ratios (± 95% CI) of 134 female caribou from five caribou herds, Newfoundland, 1 May - 1 August, 2007-2010. Selection ratios higher than one indicate preference for a given resource whereas values lower than one indicate avoidance of the resource. Selection ratios were computed at two different levels: second-order and third-order (within calving grounds), using the general random model of availability and a mechanistic model of availability. Chi-square values indicating overall presence of selection are also given. Statistically significant values (α=0.05) are presented in bold.

Random model

Herd	Level	Water	Barren	Wetland	Coniferous Open	Coniferous Dense	Other	Chi^2
Buchans	3rd-order	**0.264 ± 0.178**	**1.971 ± 0.376**	**1.531 ± 0.262**	**0.700 ± 0.129**	**0.622 ± 0.276**	0.929 ± 2.238	**82.48**
	2nd-order	**0.242 ± 0.163**	**3.366 ± 0.642**	**1.700 ± 0.291**	**0.603 ± 0.111**	**0.652 ± 0.290**	**0.251 ± 0.605**	**157.18**
Lapoile	3rd-order	**0.308 ± 0.201**	**1.377 ± 0.278**	**1.236 ± 0.222**	0.971 ± 0.154	**0.458 ± 0.275**	0.87 ± 1.244	**37.04**
	2nd-order	**0.257 ± 0.167**	**3.103 ± 0.626**	**1.589 ± 0.285**	**0.738 ± 0.117**	**0.368 ± 0.221**	0.71 ± 1.015	**130.66**
Middle Ridge	3rd-order	**0.414 ± 0.191**	**2.215 ± 0.862**	**1.492 ± 0.219**	**0.817 ± 0.121**	0.877 ± 0.445	2.724 ± 3.158	**51.60**
	2nd-order	**0.497 ± 0.229**	1.027 ± 0.400	**2.061 ± 0.303**	**0.809 ± 0.120**	**0.509 ± 0.258**	1.075 ± 1.247	**68.69**
Pot Hill	3rd-order	**0.337 ± 0.236**	0.488 ± 0.892	**0.680 ± 0.269**	**1.171 ± 0.071**	0.826 ± 0.322	1.225 ± 2.171	**24.02**
	2nd-order	**0.224 ± 0.157**	**0.051 ± 0.093**	**0.431 ± 0.171**	**1.634 ± 0.099**	0.832 ± 0.324	0.463 ± 0.820	**133.7**
Gaff Topsails	3rd-order	**0.147 ± 0.138**	1.119 ± 0.288	**1.372 ± 0.250**	1.016 ± 0.142	0.898 ± 0.348	0.392 ± 0.804	**42.54**
	2nd-order	**0.125 ± 0.118**	**2.117 ± 0.545**	**1.558 ± 0.284**	**0.861 ± 0.121**	0.843 ± 0.326	0.346 ± 0.710	**81.91**

Table 6-3 (continued)

Mechanistic model

Herds	Scale	Water	Barren	Wetland	Coniferous Open	Coniferous Dense	Others	Chi2
Buchans	3rd-order	0.663 ± 0.445	**2.137 ± 0.408**	**1.493 ± 0.255**	**0.605 ± 0.112**	**0.572 ± 0.254**	1.031 ± 2.486	**79.49**
	2nd-order	0.601 ± 0.404	**3.412 ± 0.651**	**1.610 ± 0.275**	**0.533 ± 0.098**	**0.630 ± 0.280**	0.315 ± 0.760	**144.08**
Lapoile	3rd-order	0.633 ± 0.412	**1.396 ± 0.281**	1.180 ± 0.212	0.866 ± 0.138	**0.457 ± 0.274**	0.954 ± 1.364	**21.73**
	2nd-order	0.638 ± 0.416	**3.144 ± 0.634**	**1.506 ± 0.27**	**0.653 ± 0.104**	**0.356 ± 0.214**	0.892 ± 1.275	**115.61**
Middle Ridge	3rd-order	1.005 ± 0.464	**2.289 ± 0.891**	**1.420 ± 0.209**	**0.703 ± 0.104**	0.877 ± 0.445	3.819 ± 4.428	**42.60**
	2nd-order	1.232 ± 0.568	1.041 ± 0.405	**1.952 ± 0.287**	**0.715 ± 0.106**	**0.492 ± 0.250**	1.352 ± 1.567	**62.43**
Pot Hill	3rd-order	0.882 ± 0.617	0.561 ± 1.026	**0.673 ± 0.267**	**1.080 ± 0.065**	0.862 ± 0.336	1.622 ± 2.876	6.66
	2nd-order	**0.556 ± 0.389**	**0.051 ± 0.094**	**0.408 ± 0.162**	**1.444 ± 0.087**	0.805 ± 0.314	0.582 ± 1.031	**90.99**
Gaff Topsails	3rd-order	**0.356 ± 0.335**	1.148 ± 0.295	**1.312 ± 0.239**	0.898 ± 0.126	0.864 ± 0.334	0.448 ± 0.919	**15.65**
	2nd-order	**0.311 ± 0.292**	**2.145 ± 0.552**	**1.476 ± 0.269**	**0.761 ± 0.107**	0.815 ± 0.315	0.435 ± 0.893	**52.95**

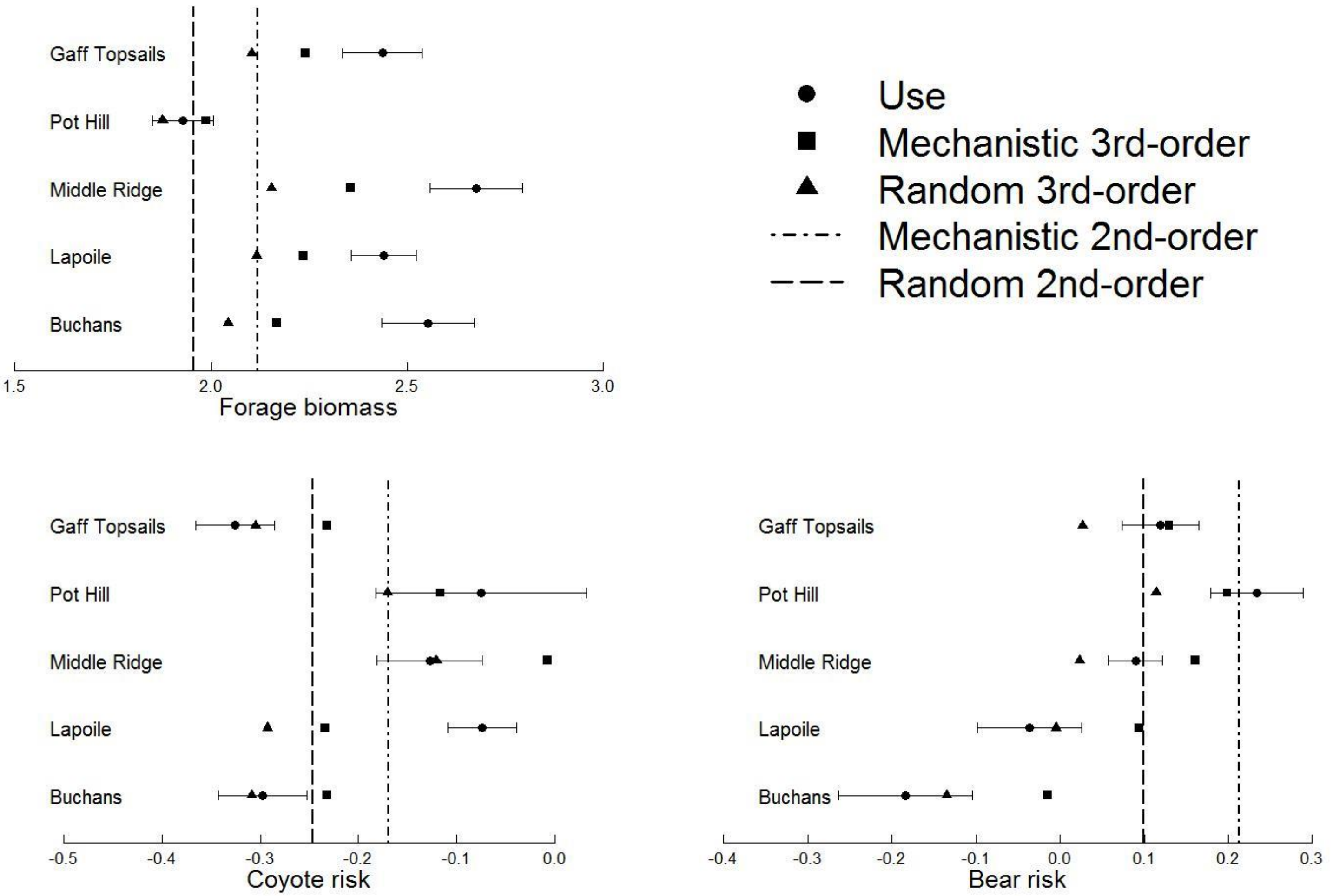

Figure 6-2. Average (± 95% CI) exposure to forage biomass, coyote encounter risk and bear encounter risk for female caribou from five herds, Newfoundland. Actual exposure (Use) is compared to availability represented by two scales of movement: (i) Selection of a calving ground (2^nd-order) and (ii) within calving-ground (3^rd-order). Availability at each scale was also defined using two approaches: (i) a random model (Random) and (ii) simulated locations based on mechanistic modelling of fine-scale movement (Mechanistic). Overall, preference is inferred when use is higher than availability while avoidance is inferred as the converse.

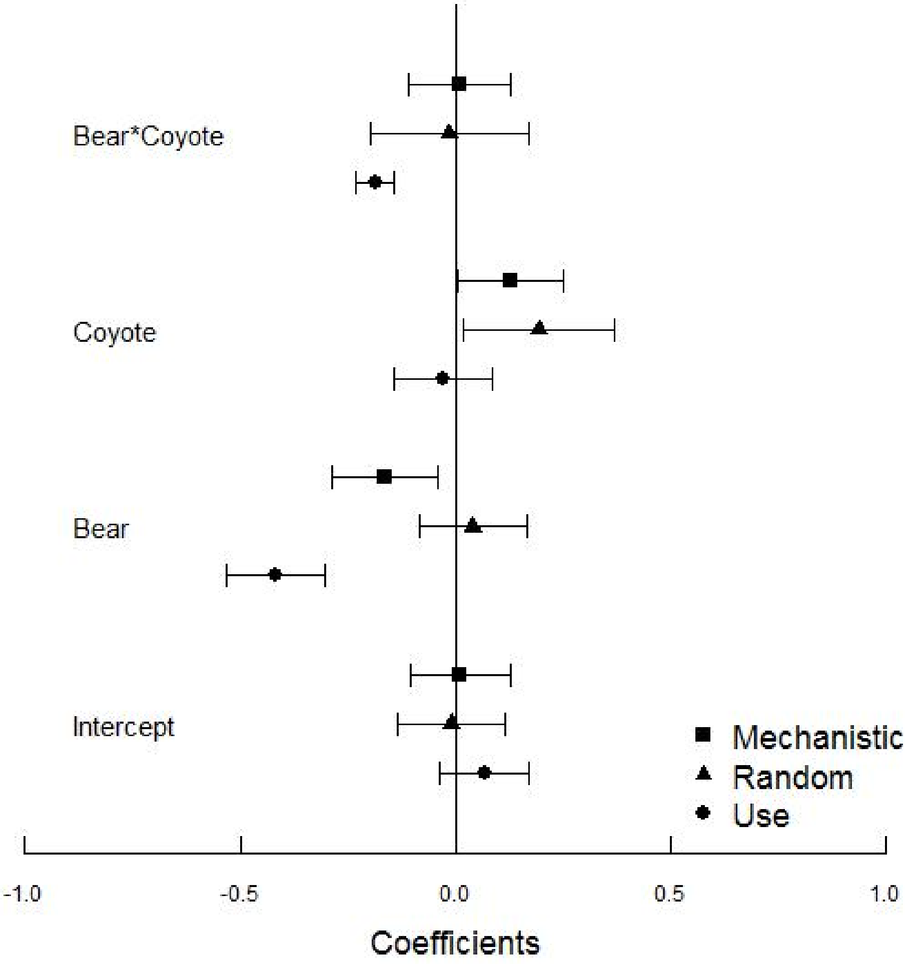

Figure 6-3. Linear models between vegetation biomass and predation risk from bear, coyote and the interaction of the two showing potential trade-offs for caribou when choosing their calving grounds. Models estimates are given with 95% confidence intervals. Models were performed using the actual caribou locations (Use), but also using random sample of availability (Random) within the study area and a simulated sample based on a mechanistic model (Mechanistic) of fine scale movement for caribou.

Discussion

Using an extensive dataset of telemetry locations of caribou and their predators, we studied broad-scale habitat selection of five caribou herds with an emphasis on the trade-offs between food acquisition and predation risk. We found that caribou movements at both selection levels are oriented mainly toward increased access to forage and also reduction of encounter risk with bears, and to a lesser extent, coyotes. This was somewhat contrary to our original predictions in that we expected third-order selection would be driven by an avoidance of predation risk. Our refined definition of habitat availability, based on a mechanistic model of caribou movements, provided different insights into the food-predation trade-off faced by caribou and allowed us to consider behavioural motivation as a level-specific driving force behind habitat selection. The fact that this refined analysis revealed patterns of forage selection and predator avoidance that would not have been revealed using more traditional approaches, speaks to the subtle factors underlying caribou movements and the need to better identify what is considered as 'available' in use-availability studies. Ultimately, our findings reveal how prey can integrate multiple levels of selection to balance the importance of predation risk on foraging behaviour.

Our results showed that, except for the Pot Hill herd, caribou select calving grounds on the basis of the foraging opportunities that they provide. This observation is reinforced by evidence of habitat selection at both the finer-scale within calving grounds, as well as the movement paths between habitat patches (as shown by the difference in vegetation exposure between our two models of availability). Following

Rettie & Messier's (2000) hypothesis that a hierarchy in limiting factors matches the hierarchy in habitat selection, it appears that foraging access is likely to be an important limiting factor for caribou during the critical period of calving and post-calving, with the cost of lactation for ungulate females and associated increasing need in foraging (Hamel & Côté 2008). However, predation risk avoidance is not as clear in that some herds were more responsive to risk exposure than were others, perhaps reflecting local differences in cause-specific predation risk across the broader caribou population, although evidence in previous chapters indicate little variation. For instance, recent coyote colonization in Newfoundland may explain why caribou tended to display less avoidance of this predator. The lack of response to either food or predation risk in Pot Hill animals is problematic but may relate to between-herd differences in habitat selection determinants or localized error in the Landsat TM classification. Notwithstanding this, we contend that our approach offers transparent and conservative results regarding selection because the analyses summarized individual selection and then pooled the individual responses into herds rather than a more uniform (and less appropriate) multi-herd pooling.

The Buchans herd appeared to be the most effective at avoiding predation, which is interesting given that it is the herd that undergoes the longest annual migration to calving grounds (Mahoney & Schaefer 2002b). This suggests that migratory caribou may face a trade-off between migration distance and its expected benefit in terms of reduced predation risk and increased foraging opportunities (Gunn, Poole & Nishi 2012); such a trade-off is likely to exist in terrestrial species given the high costs associated with migratory behaviour (Alerstam, Hedenstrom & Akesson 2003). Considering the observed variability in Newfoundland caribou migratory movements (Rayl *et al.* 2014), it appears that this trade-off may lead to variable migratory behaviour across herds. Some ungulates such as elk (*Cervus elaphus* L.) and caribou exhibit partial migration with some populations migrating and others being sedentary (Mahoney & Schaefer 2002b; Hebblewhite & Merrill 2009; Festa-Bianchet *et al.* 2011; Middleton *et al.* 2013a), but results from Rayl *et al.* (2014) as well as those herein reveal a likely gradient of migratory behaviour in Newfoundland caribou. Bergerud *et al*. (2008) concluded that migration for caribou herds in North America was associated with wolf (*Canis lupus* L.) avoidance because migrating females typically had access to lower quality forage than sedentary males. In addition, elsewhere in caribou range, movements away from tree line likely reduce risk of wolf predation (Heard & Williams 1992; Bergerud *et al.* 2008). However, the relatively small size of Newfoundland island may impose spatial constraints on migrating caribou compared to other populations, thereby reducing their ability to escape predation by wolves (historically) or other carnivores (currently). Indeed, migration in Newfoundland caribou may have originated both as a predation- and foraging-oriented behaviour, which is supported by the observed behaviour among female caribou in this study, almost a century after wolves were extirpated from the island.

During the past 50 years, caribou herds on Newfoundland have undergone marked changes in abundance, with population sizes being notably low during the 1960s and 1970s, increasing rapidly during the 1980s to mid-1990s, and declining precipitously following the mid-late 1990s (Mahoney & Schaefer 2002a; Mahoney et al. 2011). These fluctuations seem to be driven by a combination of factors, including decadal trends in winter severity, density-dependent nutrition during summer, and predation on neonates (Bastille-Rousseau et al. 2013; Schaefer & Mahoney 2013). However, if migratory behaviour or habitat selection are mismatched with current predation risk and forage availability, then reductions in productivity and survival are expected (Hebblewhite & Merrill 2011; Middleton et al. 2013a). To date, this potential source of caribou population decline in Newfoundland had yet to be fully understood. Our results do not support this hypothesis but rather show that habitat selection is driven primarily by improved foraging opportunities implying that food has been limiting, at least during the period of decline (see Fryxell & Sinclair 1988; Fryxell & Avgar 2012). Yet, although we did not detect clear trade-offs between predation and foraging in our study (Fig. 6-3) at the migratory level, it seems that fine-scale interpatch movements may have increased caribou exposure to predation risk while also providing increased access to forage. It is understood that most prey species, notably ungulates (Creel et al. 2005), avoid forage-rich areas when such areas also confer higher risk (leapfrog effect; Sih 1998; Laundré 2010). Because Newfoundland caribou do not avoid such habitats, this disconnect may explain why high calf predation seems to be the main proximate factor limiting the Newfoundland caribou population (Mahoney & Weir 2009).

Refining the definition of availability to study behavioural trade-offs

Habitat selection studies usually describe an animal as using certain areas within a rather specific and narrow set of rules. Yet this approach can be problematic because it fails to provide an appropriate mechanism explaining habitat use patterns relative to what is actually available to the animal (Aarts *et al*. 2013). We showed how a mechanistic model of availability, mimicking fine-scale inter-patch movements, can be used to study broad-scale selection and thereby improve our understanding of how caribou trade off food acquisition versus predation risk. Our mechanistic model allows us to draw inferences about multiple and perhaps paradoxical motivations, as was evident by the revelation that female caribou make habitat-related decisions on the basis of foraging opportunities despite resultant increase in predation risk. Specifically, we would have missed that caribou are able to adjust their movements to reduce bear predation risk; such an interpretation would not have been possible in the absence of our mechanistic model, since we would not have detected that the majority of the herds displayed bear avoidance. Accordingly, we suggest that our model offers an improvement over the random model by restricting habitat availability to areas that are potentially usable by an individual on the basis of its movement decisions. Other approaches have been proposed in this vein (see notably Avgar *et al*. 2013), but our approach is unique in that we used a mechanistic model of movement capturing fine scale selection to study broader scale patterns. Spatially-explicit modelling therefore allowed us to isolate the selection process occurring at a specific level, clarifying inferences about the motivation behind selection and providing a refined understanding of how caribou handle food versus safety trade-offs across levels of selection. Therefore, we infer that this refined assessment of habitat availability will open up additional opportunities for testing new hypotheses related not only to predator-prey interactions but to the general behavioural process of habitat selection in relation to the several competing behavioural motivations underlying it.

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Chapter 7 – General discussion

Synthesis

The goal of this thesis was to further our understanding of the demography and habitat selection of Newfoundland caribou, especially in the context of their decline. In chapter 2, we tested hypotheses that have been proposed to explain long-term fluctuations in migratory caribou abundance (Crête *et al.* 1993; Bergerud 1996; Mahoney & Schaefer 2002a; Gunn 2003). We found that herd trajectories correlated in a time-delayed manner with winter severity and also found a signature of delayed density-dependence in caribou morphometrics. These findings collectively pointed to winter severity and density-dependent decline in summer range as providing partial explanation for the observed patterns of population change.

In chapter 3, we investigated how density-dependence interacts with predation and climatic processes to influence the demography of caribou, through changes in mortality of neonates. We tested the hypothesis that climatic conditions during the calving period are more important for predator-driven neonate mortality when individuals are already under nutritional stress caused by food limitation. Our results supported this hypothesis. When caribou populations were increasing (and food was presumably abundant), coyote and bear predation of neonates was most strongly influenced by the summer and winter conditions preceding calving (maternal condition mechanism); when populations began to decline from nutritional stress, weather conditions during calving (current condition mechanism) influenced survival as well.

In chapter 4, we demonstrated that current weather patterns in Newfoundland have differential effects on caribou calf vulnerability to predation. Indeed, the influence of most climatic variables was antagonistic between coyotes and black bears, such that weather patterns promoting increased risk from coyote predation reduced risk from bear predators and vice-versa. We then investigated the influence of climate change on cause-specific survival. Climate projections indicated that the current, largely antagonistic pattern of cause-specific predation may not be retained into the future as conditions will become more conducive to higher coyote predation. The implications for future caribou populations could be important as reduction in survival may be sufficient to limit future population increase.

In chapter 5, we explored spatial interactions between predators and prey at the population and individual level, to improve our understanding of hunting behaviour in incidental predators. We explored seasonal patterns of space-use for each species, and determined that annual niche overlap with caribou was slightly higher for coyote than for bear. For coyote, seasonal changes in niche overlap mirrored variation in hazard risk, but had less association with co-encounter rate. In contrast, changes in niche overlap during the calving season for black bear had little association with either co-encounter patterns or overall risk for caribou neonates. These differences in space use overlap between two predators and a potentially incidental prey species speak to a higher level of variability that is likely driven by other considerations (alternate prey, intraspecific competition) in the spatial game of predator-prey interactions.

In chapter 6, we studied broad-scale habitat selection of Newfoundland caribou with an emphasis on potential trade-offs between food acquisition and predation risk. Despite wolf disappearance a century ago, we found adaptive value in caribou movements as they are oriented mainly toward increased access to forage and also reduction of encounter risk with bears, and to a lesser extent, coyotes. Our findings reveal how prey can integrate multiple levels of selection to balance the importance of predation risk on foraging behaviour.

Collectively, these findings imply that the decline of Newfoundland caribou was ultimately driven by extrinsic and intrinsic elements related to density-dependence and resource limitation. Although predation may appear to be the main proximate cause of mortality for calves (Weir *et al.* 2014), and coyote colonization appeared to have amplified this declining trend, nutritionally stressed female caribou produce calves that have lower overall survival, whether it be due to coyote predation or not. Further, despite the fact that caribou overlapped weakly with their predators and their broader-scale movements were oriented toward partial reduction of predation risk, at a finer scale, females foraged in richer, yet riskier habitat. This is the mechanistic link between the ultimate and proximate causes of Newfoundland caribou decline.

Scientific significance

Results in this thesis offered new insights and perspectives into several aspects of population and behavioural ecology. Our results in chapter 2, 3, and 4 provided a basis for further tests of the natural processes affecting animal population numbers, notably in regard to the relative roles of extrinsic and intrinsic drivers affecting population dynamics and the several interactions among these elements. With respect to animal survival, numerous studies have examined interactions between intrinsic and extrinsic factors, but our work is among the first to look at interactions between density-dependence, climate and predator-driven mortality (but see Lima *et al.* 2002; Wang *et al.* 2009). We also formalized a new mechanism linking these elements: density-dependence climate predator (DDCP) interactions, where maternal body condition influences susceptibility to climate-related events and, subsequently, risk from predation. As discussed in chapter 3, DDCP interactions may be more apparent on neonate survival than adults (Festa-Bianchet *et al.* 2003). DDCP interactions are also likely to be variable in magnitude among species (Stearns 1992) and across a species' range (Bjørnstad *et al.* 1995; Stenseth *et al.* 1998). Future work will be needed to confirm the generality of the DDCP hypothesis, but this framework is particularly useful as it provides predictions regarding how these elements interact (Lima *et al.* 2002; Wilmers *et al.* 2007).

Multiple studies have reported influence of climate on predation risk, but few have acknowledged that weather patterns can differentially alter risk from specific predators (Post *et al.* 1999; Yasué *et al.* 2003; Griffin *et al.* 2011). Our analyses in chapter 3 and 4 clearly illustrated that a given set of climatic variables can increase risk from a specific predator. Based on these findings, we provided a new mechanism for how future climate change may alter predator-prey interactions, with subsequent repercussions on population dynamics.

Despite confusing nomenclature in regard to compensatory mortality, our work illustrated that non-independence among causes of mortality can be observed at different levels. Two causes of death may be dependent on each other without the implication of an external factor, in this case referring to the general definition of compensatory mortality (Heisey & Patterson 2006). A similar mechanism of compensation, that we coined antagonistic interactions, can also exist when the effect of an external element, such as climate, has an opposite effect on risk among different causes of mortalities. Antagonistic interactions among predators in response to environmental factors have not been discussed previously in the literature, despite great attention devoted to additivity and compensation in mortality causes (Murray *et al.* 2010; Griffin *et al.* 2011; Sandercock *et al.* 2011). Our work provides strong support for the presence of such interactions and also provided a methodological way of detecting them (see next section).

A great deal of literature on predator-prey interactions has focused on systems involving specialist predators. Detailed spatial models of the behavioural games for both species, or formulations of several types of functional responses, greatly improve the study of predator-prey interactions involving specialists (Vucetich *et al.* 2002; Hebblewhite *et al.* 2005; Laundré 2010). The behavioural strategies of generalist consumers are, however, not easily captured by these theoretical models. Our work reinforced this gap in knowledge by illustrating that incidental predators sharing a prey species can have markedly different strategies regarding patterns in niche overlap and encounter, notwithstanding high levels of within-species variation. Despite this variation, coyote and bear had a similar impact on prey mortality.

Methodological contribution

Cause-specific survival analysis

Cause-specific survival analysis provides a powerful, and yet underused, approach in ecology (Murray & Bastille-Rousseau, in review). Cause-specific analysis allowed us to independently quantify the impact of weather conditions on risk for each predator. In chapter 3 and 4, these analyses provided us with a refined understanding of how variables associated with weather can differentially influence predator-specific mortalities and allowed us to assess the presence of antagonistic interactions among causes of death and climatic variables. More importantly, by adding interactions between cause of death and climatic variables, we not only doubled our model fit (R^2) compared to the single-cause-model, but we were also able to find an influence of climate on mortality patterns that the single-cause model would not have detected (Table 4-2). It follows that cause-specific survival analysis is an effective tool to understand how changes in climate or predator community govern population dynamics.

Refining definition of availability

We showed in chapter 6 how a mechanistic model of availability, mimicking fine-scale inter-patch movements, can be used to study broad-scale selection and thereby improve our understanding of how caribou trade-off food acquisition with predation risk. Our mechanistic model allowed us to draw inferences about multiple and paradoxical motivations behind habitat selection. We proposed that our model offers an improvement over the random model by restricting habitat availability to areas that are potentially usable by an individual on the basis of its movement decisions. Spatially-explicit modelling therefore allowed us to isolate the selection process occurring at a specific level, clarifying inferences about the motivation behind selection and providing a refined understanding of how caribou handle food versus safety trade-offs across levels of selection. We believe a mechanistic definition of habitat availability will open up additional opportunities for testing new hypotheses for habitat selection in relation to the several competing behavioural motivations underlying it.

Newfoundland caribou: New findings and conservation implications

All caribou populations on Newfoundland underwent a dramatic increase and decline during the last 40 years, a pattern that was highly synchronous island-wide. These populations have been in a state of protracted decline since the mid-1990s following an increase initiated at least by the 1970s. During this decline, coyotes colonized the island and became widespread, adding to the complexity of disentangling potential causes behind this decline. It had been previously speculated that fluctuations among migratory caribou in eastern North America emerge from time-delayed density-dependence and cyclic pattern in winter severity (Messier *et al.* 1988; Gunn 2003; Bergerud *et al.* 2008). Time-delayed density-dependence may arise from forage deterioration on calving grounds, which could be driven by overgrazing and trampling of vegetation (Messier *et al.* 1988; Bergerud 1996; Mahoney & Schaefer 2002a; Schaefer & Mahoney 2013). Our analyses in chapter 2 revealed support for density-dependence in the absence of evidence of either direct or interactive effects of calving range decline, and also support for cyclic trends in winter severity that correlated with population abundance. These findings indicated that to an extent fluctuations in Newfoundland caribou are independent of predators or human interventions and the situation is likely to be reversed as forage availability improves (Figure 3-2; Schaefer & Mahoney 2013).

It remains that the principal proximate cause behind caribou decline is an increase in calf mortality during the period of population decline. Our findings in chapter 3 indicated that variation in risk from black bears and coyotes through time were surprisingly consistent between species during the period they coexisted (Figure 3-3). The striking difference in cumulative risk was rather in the shape of the curves between the population periods of increase and decline for black bear. Cumulative risk from bear also increased significantly, nearly doubling during the period of caribou population decline and following coyote appearance. This interesting difference in cumulative hazards might be attributable to multiple causes. One possibility is that calves born to nutritionally stressed dams are smaller and there is a corresponding delay in improved calf mobility or that these dams are foraging in riskier habitat (Brown *et al.* 1999; Taillon *et al.* 2012). Predators may also interact in a synergistic way leaving fewer predator-free refugia for caribou (Holt & Lawton 1994; Schmidt 2004). As discussed in chapter 3, there is partial support for each possibility underlying the decline of neonate survival in Newfoundland. Nevertheless, it is evident that in Newfoundland coyotes are responsible for calf mortality that is at least partly additive to other causes, and that their appearance worsened the declining trend.

We have little knowledge of the functional response of predators toward caribou neonates and we assumed that the rate was constant in our projections in chapter 4. Findings in chapter 3 suggested that mortalities are not currently density-dependent but rather that caribou are one of many food items consumed by bears and coyotes (Matt Mumma unpublished; Bridger 2005). In this instance, predation should have a stabilizing role on caribou population abundance (Fryxell & Lundberg 1994) as this would mean that per-capita predation is unlikely to be reduced following further decrease in abundance. We, however, do not know if predators could functionally increase their response to caribou as the population increases. Actually, our population projections in chapter 4 indicated that, relative to black bears, coyotes may be favoured as the climate changes, potentially causing predation risk to increase independently of caribou density. As the possibility of increase in the functional response of predators was not accounted for in our previous climate projection modelling, it made our approach more conservative regarding future persistence of caribou in Newfoundland. These findings also may represent a dire prognosis for the future of Newfoundland caribou recovery, meaning that the population will need to be closely monitored through the coming decades.

The interplay between Newfoundland caribou and its predators is extremely complex. Many of our findings provided support for the possibility that predation risk may increase in the future. Increasing risk from coyotes with climate change is predicted to become important following the mid-21st century. More importantly, however, our results indicated that the decline is not solely caused by coyote colonization of Newfoundland, but ultimately is a result of both long-term abiotic and biotic factors affecting caribou body condition. Predator removal is therefore not a suitable solution for caribou population increase in the long-term, at least not as a widely applied strategy for increasing calf survival. (See Lewis *et al*. 2014 for a further analysis of the cost-benefits of predator removal.) Rather, it is more important that support for caribou conservation be oriented toward monitoring caribou population trends and demography through time; targeted actions should be postponed to when habitat conditions will be more conducive to support an increase in caribou numbers.

Finally, chapter 6 tested another possible reason for decline in caribou. When migratory behaviour or habitat selection become mismatched with predation risk and forage availability, reductions in productivity and survival result (Hebblewhite & Merrill 2011; Middleton *et al.* 2013a). Migration in woodland caribou is normally assumed to be adaptive in response to wolf predation (Bergerud *et al*. 2008), yet wolves have been extinct in Newfoundland island for almost a century, a potential mismatch may result from such strereotypical behaviour. Our results in chapter 6 showed that habitat selection is driven primarily by improved foraging opportunities and therefore appear to be adaptive to current constraints faced by Newfoundland caribou (Fryxell & Sinclair 1988; Fryxell & Avgar 2012).

Future directions

Fine scale habitat selection of female caribou

There is much empirical evidence supporting lower recruitment as the main proximate cause of decline in Newfoundland caribou (Lewis & Mahoney 2014, Weir *et al*. 2014).

One of the main hypotheses behind our work was that parturient females under nutritional stress forage in riskier habitat, and therefore predation risk for neonates is increased. Although we did not detect clear trade-offs between predation and foraging at the broader levels in chapter 6, it seemed that fine-scale interpatch movements increased caribou exposure to predation risk while also providing increased access to forage. Most prey species, notably ungulates (Creel *et al.* 2005), avoid forage-rich areas when such areas also afford higher risk (leapfrog effect; Sih 1998). Because Newfoundland caribou do not avoid such habitats at the fine scale, this disconnect could explain why high calf predation seems to be the main proximate factor limiting the Newfoundland caribou population (Lewis & Mahoney 2014; Weir *et al.* 2014). Further analysis of fine-scale space-use patterns linking foraging with predation risk of parturient and non-parturient females and their predators is the logical next step toward a better understanding and potential innovative conservation measures.

Foraging strategies of predators

In comparison to other ungulate systems, Newfoundland caribou neonates are exposed solely to generalist and omnivorous predators. The behavioural strategies of generalist predators are not easily captured by theoretical models regarding space-use and functional response curves that are typically developed for specialist predators (see chapter 5). This leaves ecologists ill-equipped to examine predator-prey interactions involving generalist consumers. It is therefore crucial that we establish a more robust theoretical foundation for predator-prey interactions involving generalist predators, to better predict future influences on ecosystem function.

As discussed in chapter 5, generalist predators focus on multiple prey species, preferring the more profitable ones, but nevertheless orienting their foraging behaviour toward multiple resources (Smout *et al.* 2010). This flexibility in searching behaviour increases the opportunity for incidental predation, resulting in the consumption of prey that are unintentionally encountered (Schmidt *et al.* 2001; Schmidt 2004). We concluded in chapter 5 that the small overlap between bear and coyotes with caribou indicated that caribou are unlikely to be a primary prey item for both species. It was unclear, however, whether these predators are actively searching for neonates or are simply incidentally encountering them. This can have implications regarding possible mitigation measures to reduce predation, as human intervention to lure predators away from caribou may alleviate incidental predation (Bastille-Rousseau *et al*. 2011). This could be achieved by diversionary feeding of predators away from the calving ground, a strategy that was attempted for the Middle Ridge herd in 2010 and 2011, with little success (Lewis *et al.* 2014). However, further assessment of resource selection, foraging strategies and functional response of coyotes and black bears towards caribou calves are needed to provide a more robust understanding of the role caribou play in predator diet and searching behaviour.

Adult demography

The demographic aspect of this thesis focused on calf survival and population abundance even if a plenitude of demographic parameters has been recorded since the 1980s for adult and neonate caribou in Newfoundland. Caribou age structure, percentage of males, female productivity, birth weight of calves, adult body size, and tooth wear (an indication of food quality) all have fluctuated to some degree over the last 30 years (Weir *et al*. 2014). These long-term time-series data offer valuable information to test how nutritional stress and density-dependence is apparent in adult demography and how these parameters may affect each other mechanistically, ultimately leading to a reduction in neonate survival.

Despite tremendous fluctuations in abundance and variation in several demographic parameters, adult caribou survival remained high and constant throughout the period of increase and decline, arguably because of the absence of wolves. It is well accepted that ungulate population fluctuations are mostly driven by variation in calf survival, with relatively constant adult survival (Gaillard *et al.* 2000). However, it is interesting to note that adult survival was unaffected by density-dependence during the decline in Newfoundland caribou. This may provide some insights into how caribou balance long-term reproductive success and survival with current reproductive success, and thereby address issues touching upon caribou life history strategy and evolutionary ecology. This avenue would be a particularly fascinating one to pursue in terms of future research.

Epilogue

"Statistics is the grammar of science".

- Karl Pearson

"Doubt is the beginning, not the end, of wisdom".

- George Iles

I spent a great deal of time over the past 4 years thinking about caribou and their ecology, sometimes to the limit of my own sanity. This thesis represents the main outcome of this journey, a journey filled with challenges, but also with rewarding scientific discoveries. Throughout this quest, modelling and statistics have been invaluable tools allowing me to discover glimpses of insights into data, where patterns had been previously well-hidden. Spending this amount of time focusing on this project, however, came with a cost; it compromised my ability to accurately and objectively self-assess my own conclusions. For this problem, transparency is the main cure. My goal throughout this thesis has been to clearly articulate the decisions I made in choosing my analyses and drawing my conclusions. But as much as I believe that strong statistical analyses are needed to make strong ecological insights, I also believe that the way forward in science requires that we remain humble and critical about our own results, inviting people to challenge our perspective. The invitation is on the table…

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Appendices

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Appendix B. Supplementary material for chapter 2

Supplementary Information 1 – Herd fidelity of Newfoundland caribou populations during calving season

Methods

To verify the assumption of independence between caribou herds and thus allow us to consider each herd as a replicate, we evaluated caribou site-fidelity to specific calving ground and the overlap in calving grounds between herds. Caribou display their highest level of philopatry during calving and post-calving seasons; herd characteristics and their dynamics are therefore largely shaped by movements to and from calving grounds. It follows that if individuals visit a single calving ground either during a year or between consecutive years, the assumption that herds are independent should be upheld.

Telemetry locations were obtained from 715 female caribou in 16 different herds that had received VHF (60%), GPS (15%) and ARGOS (25%) radio-collars and whose movements had been tracked. We used caribou locations from June to delineate core areas of calving for each herds using a fixed kernel density estimator (Worton 1989). We used the same approach that we used to produce the core calving areas to produce kernels, but instead used a smoothing parameter value of 2500m and isopleth value of 80%.

Using this delineation, we evaluated every telemetry location inside each core area. We then evaluated the percentage of caribou from each herd with locations falling into multiple pre-determined calving grounds. Only 9 of 175 individuals (1.3%) had telemetry locations that were included within the range of multiple herds. Each of the 9 individuals had been fitted with a VHF transmitter (i.e., thus leading to high location error and infrequent relocation) and occurred in the same 2 herds (Grey River and Pot Hill). Between those 9 individuals (<1%), no more than one or two locations were found in the second calving ground, implying that the observed use of multiple calving grounds likely was due to location error. In contrast, the sample of 15% and 25% of animals receiving GPS and ARGOS collars, respectively, did not show temporal overlap with multiple herds. Therefore, we were justified in using each herd as an independent unit in our analyses.

Supplementary Information 2

Table S1. Pairwise correlation coefficients for morphometric characteristics (a) Male jaw length, b) female jaw length, c) male diastema, d) female diastema, e) molar row, f) male antler points, g) female antler points) relative to current and delayed caribou population size. Significant correlations (P<0.10) are represented in bold and were adjusted using Bonferroni correction.

a) Male jaw length:

Age	N	N_{t-1}	N_{t-2}	N_{t-3}	N_{t-4}	N_{t-5}
0	0.102	0.076	-0.185	-0.204	-0.221	-0.237
1	-0.366	-0.179	-0.034	0.075	0.401	0.485
2	-0.231	-0.229	-0.220	-0.124	-0.022	0.101
3	0.085	0.126	0.154	0.189	0.120	0.123
4	0.237	0.256	0.263	0.300	0.349	0.350
5	-0.308	-0.274	-0.240	-0.113	-0.093	-0.115
6	-0.194	-0.164	-0.137	-0.327	-0.253	-0.166
7	-0.083	-0.024	0.023	0.141	0.303	0.211
8	-0.119	-0.109	-0.097	0.016	0.007	-0.078
9	-0.176	-0.186	-0.187	-0.149	-0.144	0.058
10	-0.076	-0.137	-0.180	-0.221	-0.212	-0.173

b) Female jaw length:

Age	***N***	***N_{t-1}***	***N_{t-2}***	***N_{t-3}***	***N_{t-4}***	***N_{t-5}***
0	0.987	1.000	1.000	1.000	1.000	1.000
1	-0.671	-0.562	-0.477	-0.410	-0.357	-0.313
2	-0.495	-0.588	-0.622	-0.632	-0.632	-0.628
3	-0.234	-0.274	-0.298	-0.526	-0.643	-0.618
4	-0.313	-0.375	-0.412	-0.669	**-0.765**	**-0.756**
5	-0.398	-0.444	-0.469	-0.595	**-0.746**	**-0.752**
6	-0.270	-0.360	-0.417	**-0.738**	**-0.748**	**-0.751**
7	-0.741	**-0.789**	**-0.798**	**-0.792**	**-0.782**	**-0.879**
8	-0.166	-0.252	-0.304	-0.332	-0.347	-0.354
9	0.230	0.104	-0.002	-0.081	-0.140	-0.184
10	-0.288	-0.356	-0.398	-0.662	-0.663	-0.658

c) Male diastema:

Age	***N***	***N*** $_{t-1}$	***N*** $_{t-2}$	***N*** $_{t-3}$	***N*** $_{t-4}$	***N*** $_{t-5}$
0	0.395	0.380	0.362	0.137	-0.148	-0.162
1	0.124	-0.072	-0.212	-0.305	-0.368	-0.412
2	-0.255	-0.314	-0.350	-0.399	-0.409	-0.405
3	0.016	-0.004	-0.020	-0.073	-0.121	-0.202
4	-0.202	-0.143	-0.094	-0.195	-0.305	-0.203
5	0.040	0.117	0.172	0.266	0.259	0.211
6	0.121	0.143	0.156	0.004	-0.153	-0.016
7	0.522	0.578	**0.605**	0.595	0.595	0.520
8	0.363	0.381	0.384	0.336	0.195	0.151
9	0.341	0.353	0.352	0.349	0.265	0.333
10	0.416	0.432	0.432	0.374	0.355	0.330

d) Female diastema:

Age	***N***	***N$_{t-1}$***	***N$_{t-2}$***	***N$_{t-3}$***	***N$_{t-4}$***	***N$_{t-5}$***
0	0.419	0.194	-0.222	-0.242	-0.262	-0.281
1	-0.703	-0.559	-0.448	-0.363	-0.297	-0.243
2	-0.135	-0.217	-0.266	-0.296	-0.314	-0.415
3	-0.250	-0.283	-0.301	-0.408	-0.490	-0.469
4	-0.343	-0.380	-0.398	-0.584	-0.704	-0.625
5	-0.303	-0.351	-0.378	-0.492	**-0.668**	**-0.663**
6	-0.291	-0.370	-0.417	**-0.694**	**-0.691**	**-0.683**
7	-0.388	-0.410	-0.414	-0.537	-0.518	-0.584
8	-0.453	-0.568	**-0.627**	**-0.654**	**-0.666**	**-0.669**
9	-0.152	-0.238	-0.290	-0.318	-0.331	-0.336
10	-0.023	-0.070	-0.104	-0.209	-0.372	-0.371

e) Molar row:

Age	N	N_{t-1}	N_{t-2}	N_{t-3}	N_{t-4}	N_{t-5}
0	0.506	0.511	0.516	0.521	0.526	0.530
1	-0.620	-0.521	-0.413	-0.319	-0.244	-0.184
2	-0.474	-0.335	-0.209	-0.111	-0.038	0.018
3	**-0.641**	-0.451	-0.281	-0.149	-0.050	0.026
4	-0.560	-0.406	-0.265	-0.155	-0.071	-0.008
5	-0.567	-0.439	-0.315	-0.216	-0.139	-0.079
6	-0.481	-0.382	-0.285	-0.205	-0.143	-0.094
7	-0.582	-0.531	-0.459	-0.393	-0.338	-0.293
8	-0.578	**-0.635**	**-0.639**	-0.621	-0.597	-0.574
9	-0.368	-0.373	-0.353	-0.327	-0.302	-0.279
10	-0.423	-0.569	-0.643	**-0.676**	**-0.687**	**-0.689**

f) Male antler points:

Age	***N***	**$N_{t\text{-}1}$**	**$N_{t\text{-}2}$**	**$N_{t\text{-}3}$**	**$N_{t\text{-}4}$**	**$N_{t\text{-}5}$**
0	-0.459	-0.472	-0.482	-0.489	-0.495	-0.501
1	0.189	0.107	0.051	0.014	-0.012	-0.030
2	-0.172	-0.227	-0.250	-0.259	-0.263	-0.265
3	-0.374	-0.428	-0.438	-0.436	-0.430	-0.424
4	-0.723	-0.772	-0.762	-0.740	-0.718	-0.699
5	**-0.841**	**-0.845**	-0.804	-0.761	-0.725	-0.696
6	**-0.800**	**-0.849**	**-0.835**	**-0.810**	-0.785	-0.763
7	**-0.797**	-0.733	-0.656	-0.594	-0.547	-0.510
8	-0.589	-0.681	-0.701	-0.698	-0.689	-0.679
9	-0.063	0.089	0.170	0.215	0.242	0.259
10	-0.656	-0.379	-0.185	-0.066	0.011	0.065

g) Female antler points:

Age	N	N_{t-1}	N_{t-2}	N_{t-3}	N_{t-4}	N_{t-5}
0	.	.	.	.	.	.
1	0.173	0.170	0.166	0.162	0.159	0.155
2	-0.977	-0.978	-0.979	-0.980	-0.981	-0.981
3	-0.742	-0.783	-0.791	-0.791	-0.789	-0.787
4	-0.947	-0.959	-0.960	-0.959	-0.957	-0.955
5	-0.930	-0.939	-0.927	-0.914	-0.903	-0.894
6	-0.829	-0.890	-0.907	-0.912	-0.913	-0.913
7	-0.451	-0.390	-0.361	-0.344	-0.333	-0.324
8	-0.759	-0.833	-0.856	-0.866	-0.870	-0.872
9	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000
10	.	.	.	.	.	.

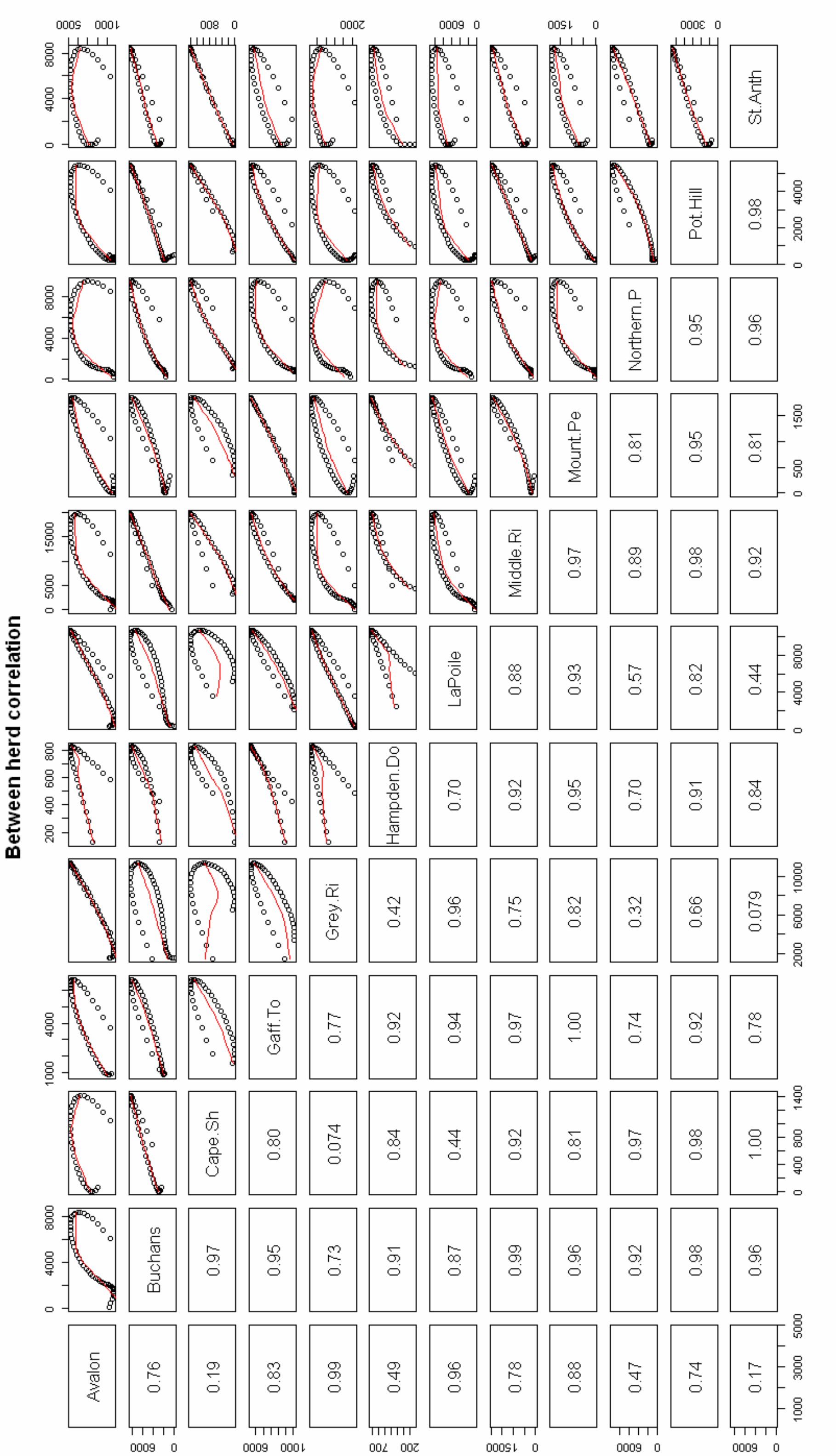

Figure S1. Between-herd correlation for 12 caribou populations on Newfoundland. The lower panel represents Pearson correlation coefficients and upper panel represent actual population estimates.

Appendix C. Supplementary material for chapter 4

Details of the population viability analysis

The population viability analysis (PVA) was parameterized with island-wide data collected by the Department of Environment and Conservation, Government of Newfoundland and Labrador spanning 1979-2010. Data were obtained from herd composition surveys, radio-telemetry studies and harvest records, and have been presented in the comprehensive summary by Randell et al. (2012). We used Vortex 10.0 with a population-level algorithm that did not consider some variables available in the software (e.g. of inbreeding depression).

Initial population size, productivity and adult mortality

Female productivity and adult survival were variable between the three stages of population fluctuations; low density, increase and decrease period and are presented in Table S1. Initial population size for the low density and increase period were based on current estimate of population size, while initial population size was based on the last estimate of population peak based on mark-recapture surveys. Productivity rates were estimated during spring herd composition surveys. Adult survival rates were calculated using telemetry data, using Heisey-Fuller estimates (Heisey and Fuller 1985). Demographic parameter estimates were kept constant between the compensatory and additive versions of each modeled scenarios.

Table S1. Input data for the PVA-VORTEX scenarios used to project Newfoundland caribou between 2055-2085

Scenarios	Initial pop. size	Productivity ± S.D.	Adult mortality ± S.D.	Calf mortality – Compensatory ± S.D.	Calf mortality – Additive ± S.D.
Low density	36,000	76.1 ± 4.4	10.2 ± 3.5	69.1 ± 5.2	(0.218*Year - 370.88) ± 5.2
Increase	36,000	83.1 ± 4.4	9.1 ± 3.5	51.6 ± 5.2	(0.223*Year - 381.54) ± 5.2
Decrease	96,000	76.4 ± 4.4	11.6 ± 3.5	68.4 ± 5.2	(0.342*Year - 637.55) ± 5.2

Estimation of calf mortality

Initial estimates of calf survival were determined based on telemetry data and were performed in Program Mark (White and Burnham 1999) using the nest survival model to account for changing risk through time (Lewis & Mahoney 2014). These estimates were used for the compensatory model. During the course of our study, coyotes were responsible for 30% of the mortalities (142 mortalities over 468). Fully additive mortality means that an increase in hazard from coyote will translate into proportional increase in this cause of death and therefore increase total mortality as well. We calculated how total mortality would be increased for 2025, 2055, and 2085, based on change in hazard relative to current hazard. We then proportionally increased or decreased calf survival by relating total number of mortality (i.e. 468) with predicted total and associated calf survival in current year for each scenarios (i.e. Table S1, Calf mortality- Compensatory column) and each projected year (2025, 2055, 2085). We then fitted a linear model between calf mortality through time to estimate an equation predicting calf mortality as a function of year (Table S1) for the different scenarios. Linear models were more parsimonious than polynomial and exponent models based on AIC_c and provided a good fit for the relationship between calf mortality and time ($R^2 = 0.811$).

Other population vital rates

The following are a description of other vital rates and information used to parameterize the model in vortex:

- Sex ratio of calves at birth was set to 50/50%

- The age of reproduction for females was set to a minimum of 2 years and a maximum of 12 years.
- The age of reproduction for males was set to 4 to 9 years. Percentage of males in breeding pool was set to 57.7%
- We did not include harvest in our scenarios.
- We used a stable age distribution when initiating the simulations.

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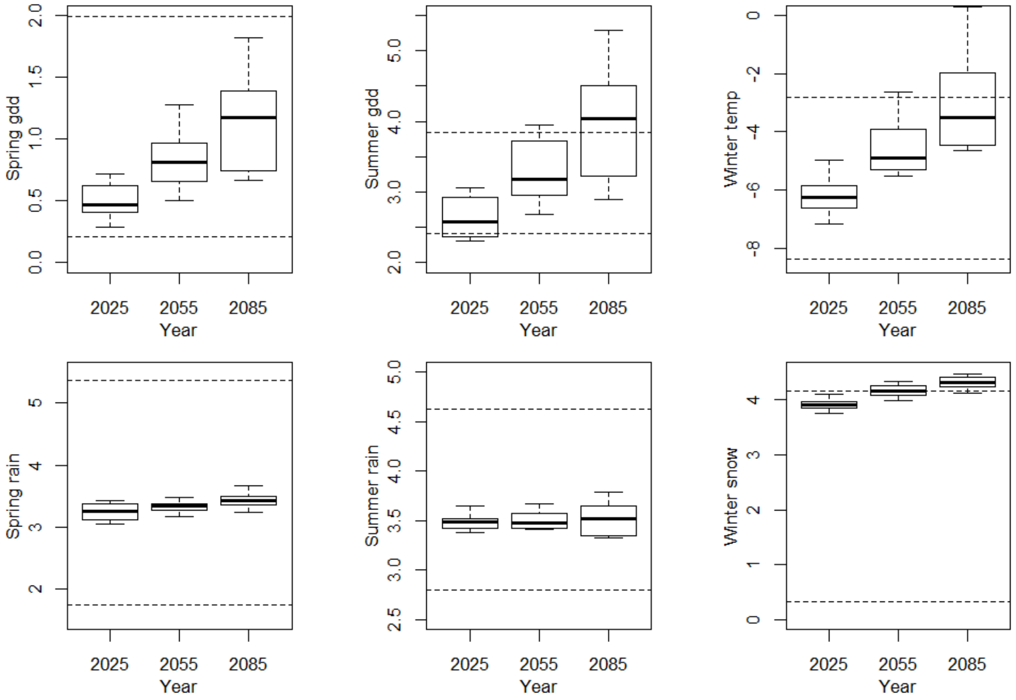


Figure S1. Comparison between climate used in our analysis and bioclimatic projection. Horizontal dashed lines represent the range of variation in historic data while whiskers represent variation between the 8 projected scenarios for each time period.

Appendix D. Supplementary material for chapter 5

Table S1. Linear model between predator individual niche overlap with caribou and predator characteristics for 55 black bears and 47 coyotes, Newfoundland, 2008-2010. Parameters estimates with standard error and model R_2 are presented for models run on each predators-caribou seasons. Differences detected at P = 0.05 are in bold.

Bear

	16/04 - 27/04	28/04 - 30/05	31/05 - 27/06	28/06 - 01/08	02/08 - 10/09	11/09 - 24/09	25/09 - 08/10	09/10 - 28/10
Intercept	0.008	**0.029**	**0.044**	**0.063**	**0.064**	**0.023**	**0.033**	**0.020**
	(0.004)	**(0.010)**	**(0.011)**	**(0.013)**	**(0.011)**	**(0.010)**	**(0.009)**	**(0.004)**
Adult	0.000	0.009	-0.002	-0.013	-0.008	0.011	0.002	-0.007
	(0.005)	(0.012)	(0.013)	(0.016)	(0.013)	(0.012)	(0.011)	(0.005)
Male	0.002	0.011	0.008	0.006	0.005	**0.033**	-0.002	-0.006
	(0.006)	(0.013)	(0.014)	(0.017)	(0.014)	**(0.013)**	(0.012)	(0.005)
Adult: Male	0.006	-0.007	0.002	0.003	-0.006	-0.026	0.002	0.012
	(0.007)	(0.016)	(0.017)	(0.021)	(0.017)	(0.015)	(0.014)	(0.007)
R2	0.096	0.027	0.028	0.037	0.04	0.132	0.004	0.074

Coyote

	18/03 - 14/04	14/04 - 27/04	28/04 - 27/06	28/06 - 12/08	13/08 - 10/09	11/09 - 24/09	25/09 - 05/11	06/11 - 18/02
Intercept	**0.079**	**0.046**	**0.135**	**0.102**	**0.032**	0.018	0.036	0.022
	(0.019)	**(0.019)**	**(0.033)**	**(0.027)**	**(0.019)**	(0.022)	(0.024)	(0.028)
Adult	-0.031	0.000	-0.031	-0.049	0.012	0.009	0.052	0.059
	(0.020)	(0.020)	(0.035)	(0.028)	(0.020)	(0.023)	(0.026)	(0.030)
Male	-0.030	-0.020	-0.059	-0.052	0.008	0.009	0.013	0.065
	(0.022)	(0.022)	(0.037)	(0.030)	(0.021)	(0.025)	(0.027)	(0.031)
Resident	-0.007	-0.008	-0.011	0.011	0.002	0.022	0.015	0.007
	(0.012)	(0.012)	(0.020)	(0.016)	(0.012)	(0.013)	(0.015)	(0.017)
Adult: Male	0.034	0.013	0.055	0.050	-0.016	-0.003	-0.034	-0.044
	(0.025)	(0.025)	(0.042)	(0.034)	(0.024)	(0.028)	(0.032)	(0.036)
R2	0.055	0.035	0.057	0.112	0.012	0.067	0.141	0.155

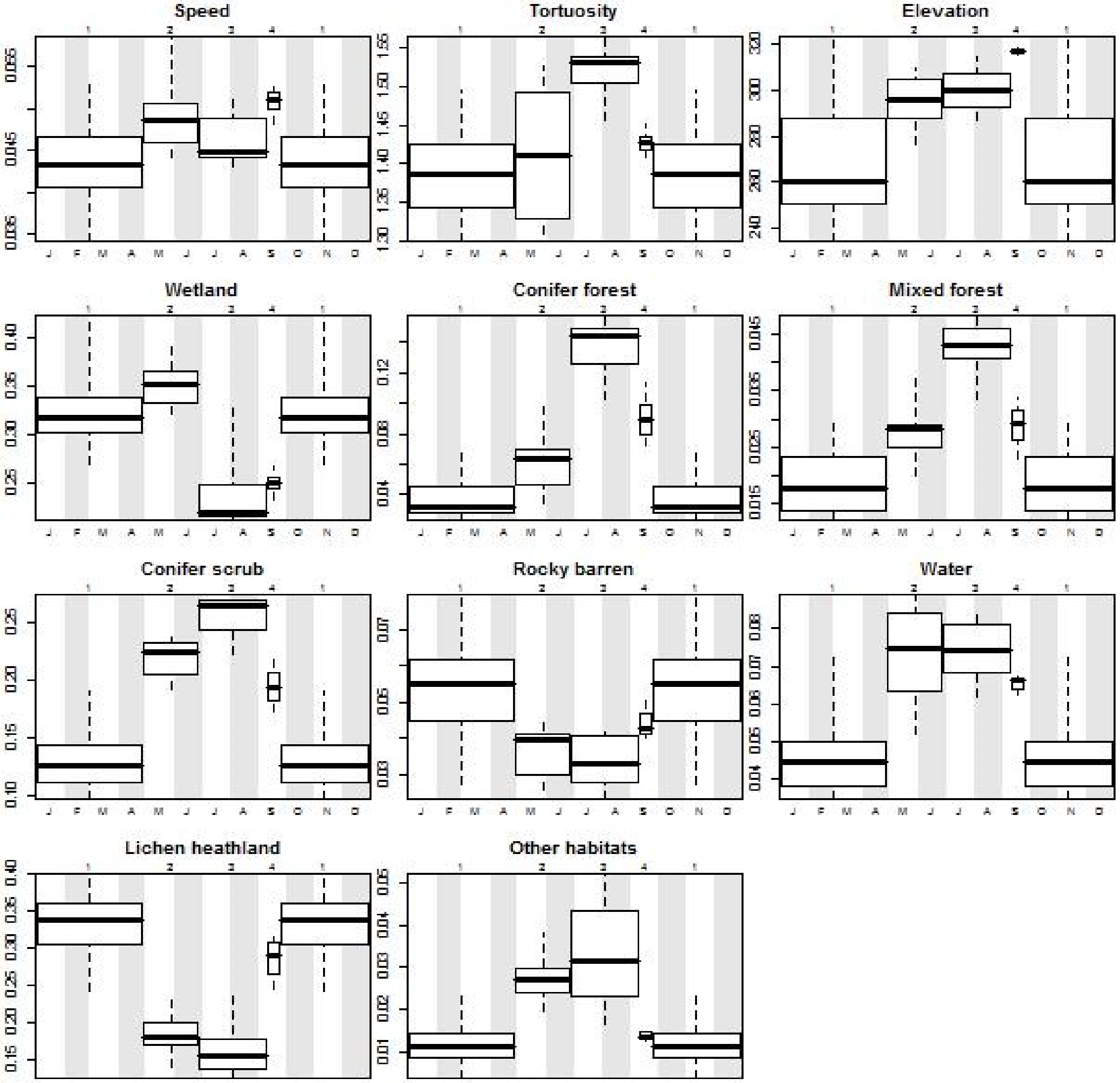


Figure S1. K-means associated with the multi-layer approach during the year for 146 caribous in Newfoundland, 2006-2013. Variation in movement parameters and resource use variables can be seen throughout the year. Note that the winter season overlaps the end and the beginning of the year.

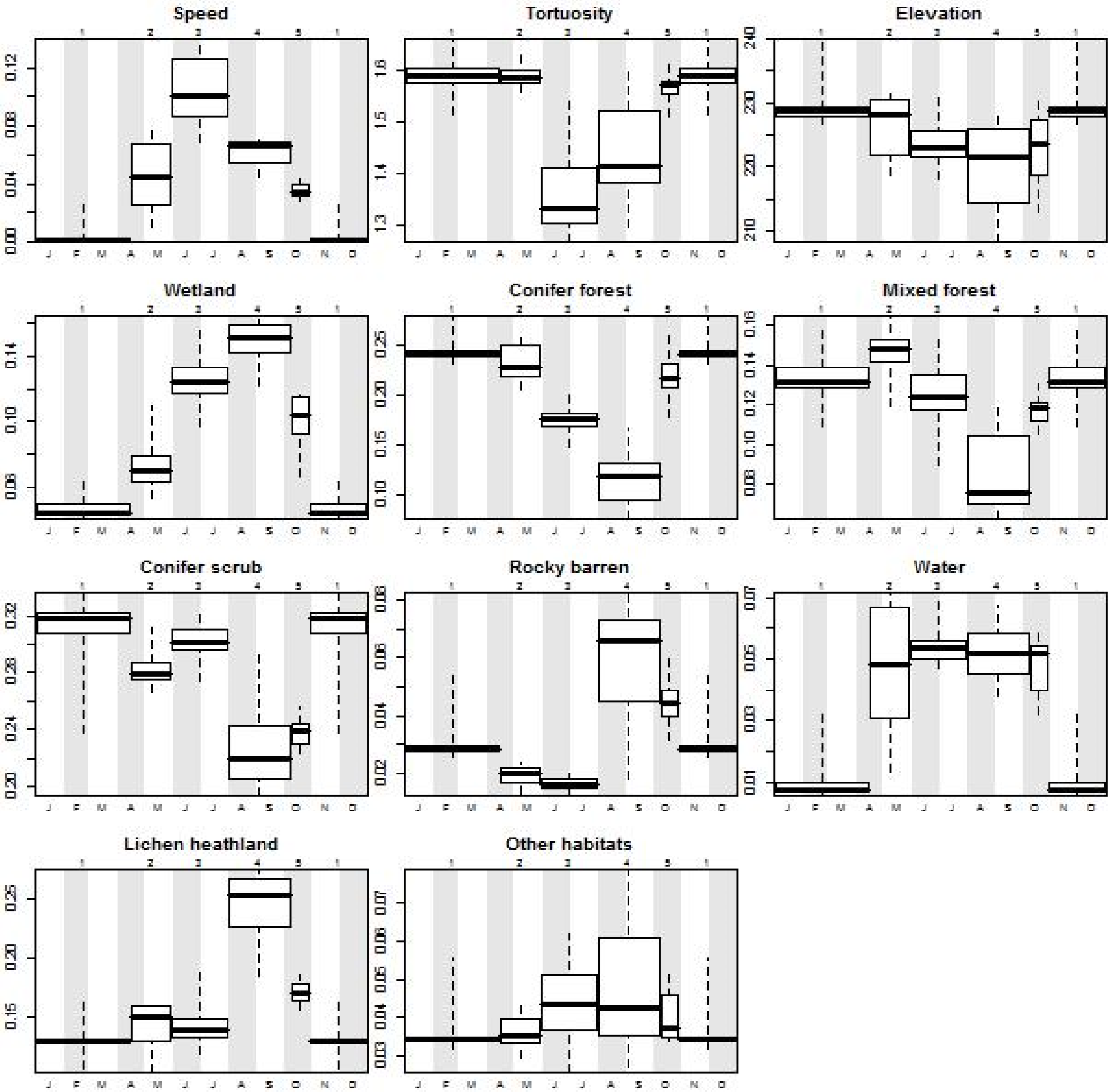
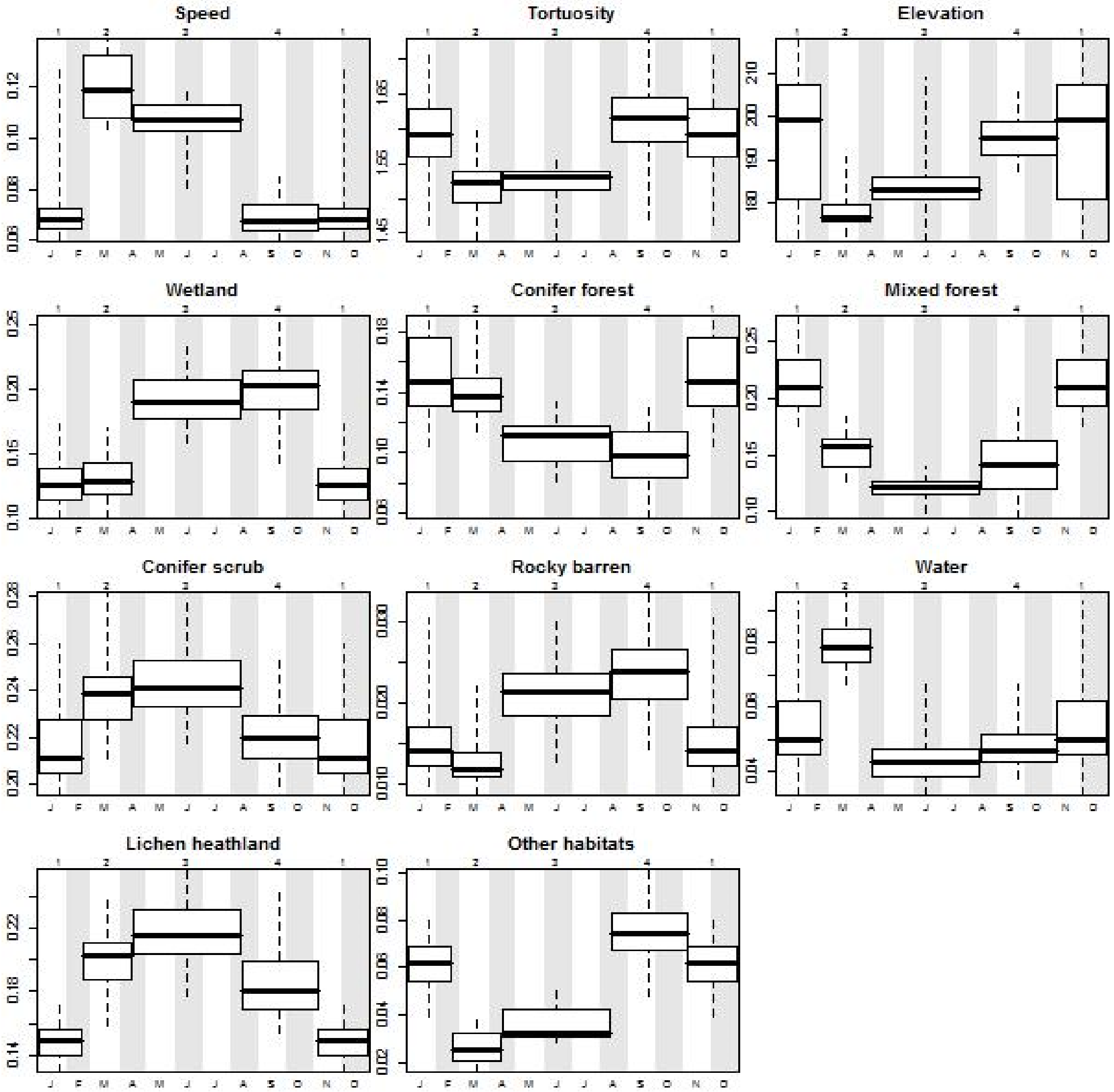


Figure S2. K-means associated with the multi-layer approach during the year for 89 bears in Newfoundland, 2006-2013. Variation in movement parameters and resource use variables can be seen throughout the year. Note that the winter season overlaps the end and the beginning of the year.


Speed

Tortuosity

Elevation

Wetland

Conifer forest

Mixed forest

Conifer scrub

Rocky barren

Water

Lichen heathland

Other habitats

Figure S3. K-means associated with the multi-layer approach during the year for 61 coyotes in Newfoundland, 2006-2013. Variation in movement parameters and resource use variables can be seen throughout the year. Note that the winter season overlaps the end and the beginning of the year.

Appendix E. Supplementary material for chapter 6

Table S1. Candidate models of RSFs for black bears and coyotes, Newfoundland, 1 May - 1 August , 2008-2010. Numbers of parameters (K), second-order Akaike information criteria (AIC_c), delta AIC_c (ΔAIC_c), and AIC weight (ωAIC_c) are presented.

Black bears

Models	K	AIC_c	ΔAIC_c	ωAIC_c
Habitat + Functional response + Elevation + Slope	17	177010.2	0	>0.99
Habitat + Functional response + Elevation	16	177865.4	855.2	0
Habitat + Functional response	15	178748.6	1738.45	0
Habitat	7	179453.3	2443.08	0

Coyotes

Models	K	AIC_c	ΔAIC_c	ωAIC_c
Habitat + Functional response + Elevation + Slope	17	69514.81	0	>0.99
Habitat + Functional response + Elevation	16	69615.21	100.4	0
Habitat + Functional response	15	71850.96	2336.15	0
Habitat	7	72951.27	3436.46	0

Vegetation model

Our forage model linked two components, a dynamically temporal model of vegetation growth and a spatial model based on habitat categories. The approach presented here is similar to the approach presented in Hebblewhite et al. (2008).

Vegetation growth

Changes in forage biomass over the growing season were documented by repeatedly sampling 100 sites in Newfoundland, between May and August 2010-2012; we visited each permanent plot on a mostly bi-weekly schedule. During each sampling period, we recorded total (green and dead) vegetation abundance (% cover) in 8, 1-m^2 quadrats. We classified percent cover into the following categories: Lichen, Grass, Forb, Ericaceous shrub, Fern, Tree, Non-Ericaceous shrub, Crawling species, and Other. We averaged values collected in each quadrat at the site level. Although we merged the habitat class Herbs within Other for our movement analysis, we considered it separately within the vegetation model.

Spatial model

We sampled 309 temporary plots during the peak biomass period (mid-July and August, 2012) distributed into 5 habitat categories to capture variation in peak forage biomass. These plots used the same methodology as the permanent plots, but only had 6 quadrats. For 30 of those quadrats, all vegetation was clipped, dried for 48h at 60°C and weighed. We used this measure of biomass to develop a linear model between observed percent cover and biomass for each vegetation class. Using these equations, we then calculated an average vegetation biomass relative index for each habitat (Table S1).

Table S2. Number of plots in each habitat category with estimates of average biomass for vegetation based on equation between percent cover and dry mass. Relative index was obtained by dividing every biomass by the maximum biomass value (Wetland habitat).

Habitat	N	Biomass	Relative index
Barren	54	42.5742	0.7345
Wetland	101	57.9598	1.0000
Coniferous Open	106	57.4072	0.9904
Coniferous Dense	27	26.5632	0.4583
Herbs	21	53.1574	0.9171

NDVI predictive power

We used the normalized-difference vegetation index (NDVI), a measure of primary productivity frequently used in animal ecology (Pettorelli et al. 2005), from the MODIS Terra satellite (Huete et al. 2002). NDVI predictive power for vegetation growth in the different landcover types was first validated. We extracted values from the NDVI Modis Terra satellite for the pixel corresponding to each permanent plot. We then compared observed patterns in biomass growth to the change in Terra NDVI values to evaluate if the NDVI index represented biomass growth in each landcover type using a linear mixed model without an intercept and with site as a random factor (Hebblewhite et al. 2008). Coefficients of this model and conditional R^2 (Nagakawa 2013) are given in Table S2.

Modelling

Since growth of vegetation in all habitat categories is well predicted by changes in NDVI, we used the following formula to combine our spatial and temporal model of vegetation and to predict Biomass for a specific pixel at a given time (B_{i*T}).

$$B_{i*T} = B_{H_i} * \alpha_{H_i} * \frac{NDVI_{T_i}}{NDVI_{\max_i}}$$

where B_{Hi} is the modeled biomass at peak season in cell i, α_{Hi} is the per habitat slope indicating the rate of change between increase in NDVI and increase in vegetation biomass for a specific habitat, $NDVI_{Ti}$ is the NDVI value for a 250-m2 MODIS pixel encompassing the site pixel i for the 16-d time period T, and $NDVI_{maxi}$ is the maximum NDVI value observed for the pixel during a season.

Table S3. Slope and conditional R^2 for five linear mixed models of the biomass found at 100 sites based on NDVI values of a given pixel between 2011 and 2012 in Newfoundland.

Habitat	N	Slope	Conditional R^2
Barren	19	4.5411	0.9329
Wetland	29	4.8776	0.9306
Coniferous Open	37	2.2766	0.9457
Coniferous Dense	9	0.6658	0.8708
Herbs	6	2.4076	0.5633

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