GENERAL PATTERNS AMONG GENERALISTS: WHAT IS REVEALED BY SPATIAL MODELS OF COYOTES?

ANTHONY J. McCUE

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by

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ABSTRACT

Colonization of insular Newfoundland by coyotes (*Canis latrans*) coincided with declines in woodland caribou (*Rangifer tarandus caribou*) populations, generating public outcry to reduce coyote predation on this iconic species. My research was focused on the Maritime Barrens Ecoregion of Newfoundland, which is more akin to an arctic habitat than the desert, plains, or forest habitats typically occupied by coyotes. I investigated both habitat associations and spatial stability of coyotes in relation to short-distance migratory caribou. I compared efficacy between statistical and algorithmic spatial models incorporating relatively static habitat and environmental data for predicting patterns of use. The algorithmic model was superior for predicting future use with the limited background data. However, the best predictive model showed substantial individual variation, possibly reflecting local availability of food resources emphasizing the need to collect these data. Coyote home ranges were relatively static across seasons and years. Overall coyotes appeared to exhibit adaptive and opportunistic behaviour common throughout the species range.

Keywords: boosted regression trees; *Canis latrans*; coyote; geographic information system; Global Positioning System; Maritime Barrens Ecoregion; mixed-effects model; Newfoundland; resource selection model

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I began my Master of Science program in 2007 with grand plans for uncovering truths regarding coyotes, caribou, and the boreal forest ecosystems of insular Newfoundland. A few heartbreaks, a function of unforeseen circumstances in both field and laboratory, and nearly as many subsequent research proposals culminate in this thesis.

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List of Abbreviations and Symbols

AIC – Akaike's information criterion

AUC – area under the curve

BRT – boosted regression trees

CMA – caribou management area

Δ_i – AIC differences relative to the smallest AIC value among candidate models

DEM – digital elevation model

DOP – dilution of precision

EOSD – Earth Observation for Sustainable Development of Forests

GIS – geographic information system

GLMM – generalized linear mixed-effects model

GPS – Global Positioning System

K – number of estimated parameters in the model

KDE – kernel density estimation

$\mathcal{L}(g_i|x)$ – discrete likelihood of model g_i, given the data x

MBE – Maritime Barrens Ecoregion

ROC – relative operating characteristic

RSF – resource selection function

RSM – resource selection model

SDM – species distribution model

TCI – topographic convergence index

UD – utilization distribution

w_i – Akaike weights, a measure of probability that model i is the best model considered

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CHAPTER 1. INTRODUCTION AND OVERVIEW

1.1. Eastern Coyote

Coyotes (*Canis latrans*) are possibly the most thoroughly studied carnivores in North America (Voigt and Berg 1987; Bekoff and Gese 2003). While much of this research has been conducted in western desert, mountain, and plains habitat, there has been substantial research following coyote range expansion eastward across the continent. It is well documented that the coyote niche differs both in eastern populations (Parker 1995; Gompper 2002) and in the absence of wolves (Bekoff and Gese 2003; Berger and Gese 2007). Most of the research in eastern coyote range has occurred in areas where wolves are in low density or absent, as is the case for my research in insular Newfoundland. Eastern coyotes are considered distinct from western populations in both genetic make-up, which has led to increased body size and possibly the ability to hunt larger prey (Kays *et al*. 2010), and ecological role as a predator/scavenger of larger mammals (Harrison 1992). Although eastern coyotes typically represent the largest canine predator on the landscape, they are not the functional ecological equivalent of wolves (Crête *et al*. 2001). Eastern coyotes do not show consistent preference for particular habitats, but anthropogenic landscapes tend to be more productive and occupied in greater density than forested areas (Ray 2000; Gompper 2002). Community-level effects following coyote colonization can be far-reaching (Gompper 2002).

The coyotes inhabiting northeastern North America are a genetically distinct population segment descended from dispersers that immigrated north of the Great Lakes from western portions of the continent over the course of the past century (Kays *et al.* 2010). Parker (1995) outlined the colonization history of the species through the mid-western states and Ontario, and into New England and the Maritime provinces. The final major hurdle in the eastward colonization was cleared in the mid-1980s when the first coyotes reached the island of Newfoundland, purportedly crossing Cabot Strait over sea ice (Moore and Parker 1992). The first confirmation of breeding success on the island was a juvenile coyote killed by a vehicle near Deer Lake in 1987. Northward colonization of the continent continues (Chubbs and Phillips 2002, 2005; Cluff 2006), though at a slower rate, likely due to the continued presence of wolves and less intensive anthropogenic landscape change north of all current coyote range (Moore and Parker 1992).

In addition to this ecological distinction, eastern coyotes seem to be more maligned than their western counterparts. This public perception and fear may be a consequence having to deal with a largely unknown predator on the landscape (e.g., Kellert 1985; Linnell *et al.* 2003; Andersone and Ozolinš 2004; Røskaft *et al.* 2007). Researchers throughout the eastern coyote range have commented on public fears and hatred following successful colonization (e.g., Hilton 1992; Moore and Parker 1992; Stevens *et al.* 1994; Parker 1995; Ray 2000; Gompper 2002). Sutherland (2010) focused specifically on this issue in insular Newfoundland and discovered public perceptions and emotions similar to those experienced elsewhere. Specifically, individuals in her survey indicated that negative feelings may be a result of lack of familiarity with coyotes compared to other predators that have been on the landscape since pre-colonial times. Attitudes toward coyotes in Newfoundland also followed demographic and experiential parameters in the same way as elsewhere across North America, such as more negative attitudes among older and more rural people along with those unfamiliar with the species in their area (Kellert 1985). Research indicates that education programs may improve attitudes for co-existence with coyotes (Stevens *et al.* 1994; Baker and Timm 1998; Fox 2006), a necessity for successful management of a species that is relatively immune to population control measures (Voigt and Berg 1987; Parker 1995).

1.2. Natural History of Newfoundland

My research focuses on spatial aspects of coyote ecology in a landscape that appears dramatically different from everywhere else coyotes have been studied. The Maritime Barrens Ecoregion (MBE) of Newfoundland (Figure 2.1) is more akin to an arctic habitat than the desert, plains, or forest habitats typically occupied by coyotes (Figure 2.3). In addition to the landscape, coyotes in the MBE interact with a unique assemblage of prey.

The terrestrial ecosystems of the island of Newfoundland, historically characterized by depauperate native fauna, have undergone numerous redefining events. This native assemblage was heavily unbalanced with 7 carnivores, 3 rodents, 1 lagomorph, and 1 ungulate representing the entire suite of quadrupedal mammals (Bangs 1913). In the period following European settlement, numerous modifications of the natural system have occurred both accidentally and intentionally (Table 1.1). Fires have resulted in drastic changes to the landscape, most notably the development of the entire Maritime

Barrens Ecoregion as a primarily non-forested landscape (Meades 1983). Faunal changes include extinction of the endemic Newfoundland wolf (*Canis lupus beothucus*; Allen and Barbour 1937) following decades of bounty, and introductions of 2 galliform birds (Tuck 1968), 7 rodents, 1 lagomorph, and 1 ungulate. All of these ecosystem and community changes may have substantial importance for the naturally colonized population of coyotes.

Many far-reaching direct and indirect impacts of these ecosystem changes have been observed or hypothesized. Introduction of the snowshoe hare (*Lepus americanus*) has been implied as the indirect cause of range restriction and population declines of the Arctic hare (*Lepus arcticus*; Bangs 1913; Bergerud 1967). Similarly it has been hypothesized that red-backed vole (*Myodes gapperi*) introductions will eventually cause range restriction and reduced populations of the endemic meadow vole (*Microtus pennsylvanicus terraenovae*; Hearn *et al*. 2006). Increases in the accidentally introduced mink (*Mustela vison*) populations have been considered the likely cause of observed declines in muskrat (*Ondatra zibethicus obscurus*) populations (Soper and Payne 1997). Possible extinction of the endemic Newfoundland crossbill (*Loxia curvirostra percna*) has been attributed to establishment of the red squirrel (*Tamiasciurus hudsonicus*; Benkman *et al*. 2008). The woodland caribou is among the latest species that may be suffering adverse effects of faunal changes.

Insular caribou herds of Newfoundland have been intensively studied during the past 60 years due to importance as a cultural and economic resource. Woodland caribou are the only ungulate species native to Newfoundland (Bangs 1913). Unmonitored hunting of the population led to precipitous declines in the early 20th century limiting total numbers to 1000-2000 (Bergerud 1971). This was followed by a period of restriction on harvest and more directed management leading to steady growth of herds (Bergerud 1971) and eventual exponential growth (Mahoney and Schaefer 2002a) resulting in a population peak of approximately 96 000 in 1996 (NLDEC 2009a). Since that time caribou have entered another period of precipitous decline with a current population estimate of 32 000 (NLDEC 2009a). During this decline, behavioural changes have been observed including more dispersed calving (NLDEC 2009b) and changes in core areas of use (Stantec Consulting Ltd. 2011). Numerous hypotheses have been suggested as to the causal factors in the recent decline, including density-dependent nutritional limitation (Mahoney and Schaefer 2002a), anthropogenic disturbance leading to habitat loss (Chubbs *et al*. 1993; Mahoney and Schaefer 2002b; McCarthy *et al*. 2011), and predation by endemic lynx (*Lynx canadensis subsolanus*; Bergerud 1971), endemic black bear (*Ursus americanus hamiltoni*; Mahoney and Virgl 2003), and recently colonized coyote (NLDEC 2008). Thomas and Gray (2002) indicate that interplay among these factors may make it difficult to identify the factors regulating caribou populations.

1.3. Coyotes in Newfoundland

Coyote predation may be contributing to caribou population declines with varying levels of impact in time and space. It has been suggested that, following colonization in Québec, coyotes have contributed to increased caribou calf mortality and consequent population declines (Crête and Desrosiers 1995). However, predation may be a proximate rather than ultimate cause for decline in caribou numbers, mediated by habitat change and alternate prey species (Festa-Bianchet *et al.* 2011). Since coyotes first arrived in Newfoundland, *ca.* 1985, the population has rapidly increased and expanded across the island (McGrath *et al.* 2010). Increased coyote observations (McGrath 2004) and harvest (McGrath *et al.* 2010) coincided with caribou declines, but this correlation is not sufficient evidence to constitute causality. Although it is likely that coyotes are playing a significant role in caribou mortality, the determination of proximate versus ultimate factors is likely to be less clear and of great importance in the long term management of the ecosystem. Determination of which factors affect coyote temporal use of space within this system should provide further insight to the mechanisms underlying associated trophic interactions.

The potential prey component for coyotes in the MBE is composed of seasonally migratory caribou, moose (*Alces amricanus*; as carrion), beaver (*Castor canadensis*), muskrat, snowshoe hare, grouse, ptarmigan (*Lagopus* spp.), red squirrel, and voles. Interspecific competition in this landscape is limited. Bears and red foxes represent the primary mammalian competition. Lynx are also present, but typically occur at lower density in this open landscape compared to forested regions to the north (*M.J. McGrath, personal communication*). Additional ecological knowledge in the form of spatial dynamics should provide valuable insight to this relatively simplified predator-prey system.

In a multi-prey system, adaptive predation can have dramatic population level effects (Owen-Smith and Mills 2008). This is largely a result of prey switching due to changes in relative vulnerability with changes in environmental conditions and prey demographics. In a simple wolf-elk-bison system in Yellowstone National Park, prey abundance, size, defensive behaviour, seasonal vulnerability, and predator preference all played roles in switching behaviour of wolves (Garrott *et al*. 2007). Owen-Smith and Mills (2008) conclude that the higher the diversity of prey, the harder to tease apart factors affecting prey demographic response to predation. This suggests that identifying factors promoting prey switching in MBE coyotes would be extremely difficult given the range of prey sizes and their contrasting ecology. One approach to begin this process of investigation is through identification of spatial patterns. Home range has been shown to reflect variability of resources within an animal's territory, but other factors work to confound this relationship (Börger *et al*. 2006). Additionally, individuals each select from a different set of options given variation across the landscape, particularly when territoriality exists.

1.4. Modelling Space Use

In ecology, we strive to explain processes through various means across a continuum of complexity. Many of these analyses of ecological study are conducted within each investigator's realm of knowledge and comfort (Ellison and Dennis 2010). One of the challenges to modern ecologists is adapting approaches to use the best available methods allowing for a greater depth of scientific enquiry. This will often require researchers to push their personal limitation into new realms of statistical and theoretical knowledge to enhance the understanding of systems and allow ecology to progress beyond the basic questions that have dominated ecological journals and manuscripts for the entire history of the discipline.

The concept of delineating spatial parameters that correspond to wildlife behaviour is by no means new. For centuries, natural historians and biologists have endeavoured to understand space use by animals (Burt 1943). Refinements of the concepts of home range and territory to include various stages of life history and temporal scale have advanced our understanding of animal behaviour from the individual and population perspectives. In recent decades, advances in technology (i.e., radio- and satellite-telemetry, satellite imagery) have dramatically increased the temporal and spatial resolution and extent of data available to scientists and led to a proliferation of new techniques for modelling animal space use.

Technological advances allow us to apply spatial theory to research questions concerning ecology of wide-ranging carnivores (Young and Shivik 2006). Basic use-availability models were enhanced by consideration of the effects of spatial scale (Johnson 1980). Geographic information systems (GIS) coupled with remotely-sensed data from satellite images greatly expanded the scope of background data available for building spatial models. Individual-based spatial models were further advanced with the resource selection function (RSF) typically implemented as a generalized linear model (Boyce and McDonald 1999; Manly *et al*. 2002). By the turn of the century Global Positioning System (GPS) collars were becoming more prevalent as a means of collecting high frequency location data and bringing the issue of spatial autocorrelation to the forefront (Otis and White 1999; Rodgers 2001). At this same time new approaches based on machine learning algorithms were entering the field of habitat modelling (Guisan and Zimmermann 2000; Scott *et al*. 2002). Despite this, the RSF approach to modelling has persisted for many years as the primary tool for modelling habitat associations. Modifications to the RSF have evolved to improve our knowledge of systems based on remotely collected data. Most of this model evolution has focused on serial autocorrelation associated with high-frequency data for a small sample of individuals. Generalized additive models, generalized estimating equations, generalized linear mixed-effect models, and generalized additive mixed-effect models have all been applied and advocated for modelling resource selection in the past decade (e.g., Gillies *et al*. 2006; Guisan *et al*. 2006; Aarts *et al*. 2008; Koper and Manseau 2009).

Alternative methods to statistical data models – known as algorithmic modelling, data mining, or machine learning – are rapidly increasing with advances in computing technology (see Hastie *et al*. 2009). The use of machine learning techniques for species distribution modelling continues to be promoted (e.g., Elith *et al*. 2006; Hochachka *et al*. 2007; Marmion *et al*. 2009; Drew *et al*. 2011), but is yet to enter the mainstream of resource selection modelling. Machine learning often outperforms traditional statistical approaches in identifying patterns in biogeographical space (Cushman *et al*. 2007). Machine learning approaches are especially suited to situations where the data do not necessarily represent mechanisms generating the observed patterns. Specific strengths of machine learning include no *a priori* assumptions regarding relationship between response and predictor variables, variable selection is built into the algorithms, non-linear and hierarchical structure are easily modelled, and high-order interactions can be included (Craig and Huettmann 2009). Model interpretation is generally very difficult with many machine learning implementations, but exceptions do exist. For example, boosted regression trees provide model output that is easy to visualize, similar to traditional linear approaches (Elith *et al*. 2008). A disadvantage of machine learning models is the lack of mechanistic tie between predictor and response variables (Cushman *et al*. 2007). While these rule-based algorithms excel at finding patterns in data and predicting throughout parameter space, there is no link to explaining the underlying process. Therefore the value may be in identifying thresholds and targets for additional exploration (Hochachka *et al*. 2007).

Resource selection models typically require some assessment of the background environment in which individuals are making behavioural choices of selecting among available options. Large GIS data sets allow for ease of sampling background data and hence the use of pseudo-absence data (i.e., a random sample of points representing the available environmental conditions) to incorporate in presence-absence models. There is a vast literature dealing with potential issues of contamination in pseudo-absence data as well as alternative approaches when reliable absence data are not available (e.g., Keating and Cherry 2004; Pearce and Boyce 2006; Phillips *et al*. 2009). Failure to adequately deal with the contamination issue can lead to biased parameter estimates in resource selection functions. Therefore, evaluating outputs is imperative when using the model for predictive purposes (Rykiel 1996; Guisan and Zimmermann 2000). This procedure provides some level of credibility regarding model accuracy as well as a measure of comparison among candidate models, particularly when an independent test set is used for evaluation (Araújo and Guisan 2006).

1.5. Thesis Overview

The MBE is a unique system within the coyote's current range. Coyotes in the MBE exhibit the largest home ranges among all populations studied in North America (Blake 2006) reflecting the low net primary productivity of the ecoregion (Liu *et al.* 2002). The MBE has undergone rapid change following the arrival of coyotes, most notably the reduction in caribou abundance. Research has shown that coyotes are contributing to the high mortality rate of caribou calves in central Newfoundland (Blake 2006; Trindade *et al.* 2011). An ongoing diet study has also shown a high proportion of ungulate biomass (i.e., moose and caribou) is consumed by coyotes during the winter (McGrath *et al.* 2010). This baseline information supports the idea that coyote foraging efforts may be focused on abundant migratory caribou when they are at highest density in the MBE during the winter season. The dramatic reduction in caribou population numbers and changes in calving distribution (NLDEC 2009b) may somewhat reflect the establishment of coyotes, but continued predation pressure is the greatest concern for my research. Additional over-winter mortality or reduced fitness due to predation risk could significantly impact the already stressed caribou population. Clarifying the ecological niche of coyotes in the MBE will provide insight to the dynamic processes among predator and prey species.

Coyotes in the MBE were instrumented with GPS collars and tracked from 2005-2009 by the Newfoundland and Labrador Wildlife Division. I used these GPS data to develop resource selection models for coyotes based on available GIS data that characterize environment and habitat across the entire ecoregion. I then tested the predictive accuracy of both a traditional statistical approach and a machine learning approach as a means of determining (1) whether one approach is superior with the limited available background data, (2) the value of indirect measures in modelling a generalist, and (3) the best model for further analyses (Chapter 2). Additionally, I investigated seasonal and annual shifts in individual home range utilization in an attempt to identify any patterns in shifting prey focus based on over-winter presence of migratory caribou (Chapter 3). I interpreted the best predictive model (from Chapter 2) and used this model to generate predictive distribution maps for coyotes across the central portion of the MBE (Chapter 3). Finally, I attempted to fill another knowledge gap with a preliminary assessment of coyote summer diet (Appendix A) as a potential path forward for coyote research into mechanisms of observed spatial patterns.

This thesis continues to build upon research directed toward understanding the ecological niche of coyotes in this novel insular landscape. Specifically, my research adds a spatial component to the understanding of coyote ecology and how this fits with implications that coyotes are responsible for the decline in caribou populations. It also identifies an alternate approach to resource selection modelling and the merits of data mining given limited ecological knowledge or data, concepts broadly applicable to ecological research.

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Table 1.1. Notable terrestrial animals of the island of Newfoundland.

Order	Scientific Name[1,2]	Common Name	Origin	Status	References
Carnivora	*Canis latrans*	coyote	colonized, *ca.* 1985	ubiquitous	Moore and Parker (1992) Blake (2006)
	Canis lupus beothucus	Newfoundland wolf	native	endemic, extinct, *ca.*1930	Allen and Barbour (1937) Maunder (1991)
	Lontra canadensis	North American river otter	native	ubiquitous	Dodds (1983) Larivière and Walton (1998)
	Lynx canadensis subsolanus	Newfoundland lynx	native	endemic, ubiquitous	Bangs (1913) Anderson and Lovallo (2003)
	Martes americana atrata	Newfoundland marten	native	endemic, threatened	Bangs (1913) COSEWIC (2007)
	Mustela ermina	ermine	native	ubiquitous	Dodds (1983) Eger (1990)
	Neovison vison	American mink	introduced, *ca.* 1934	ubiquitous	Northcott *et al.* (1974a)
	Ursus americanus hamiltoni	Newfoundland black bear	native	endemic, ubiquitous (exc. Avalon Pen.)	Cameron (1956) Marshall *et al.* (2011)
	Vulpes vulpes deletrix	red fox	native	endemic, ubiquitous	Bangs (1913) Larivière and Pasitschniak-Arts (1996)
Artiodactyla	*Alces americanus*	moose	introduced, 1878 and 1904	ubiquitous	Pimlott (1953)
	Rangifer tarandus	woodland caribou	native	declining (60% since 1996)	Thomas and Gray (2002) NLDEC (2009a)
Lagomorpha	*Lepus americanus*	snowshoe hare	introduced, *ca.* 1864	ubiquitous	Dodds (1965)
	Lepus arcticus	arctic hare	native	limited distribution (alpine)	Bergerud (1967) Best and Henry (1994)

[1] Mammalian taxonomy follows Wilson and Reeder (2005).

[2] Sub-species is included when this taxonomic level is considered endemic to the island of Newfoundland.

Table 1.1 (continued).

Order	Scientific Name[1,2]	Common Name	Origin	Status	References
Rodentia	*Castor canadensis caecator*	Newfoundland beaver	native	endemic	Bangs (1913) Dodds (1983)
	Microtus pennsylvanicus terraenovae	Newfoundland meadow vole	native	endemic, ubiquitous	Bangs (1913) Folinsbee *et al.* (1973)
	Myodes gapperi	southern red-backed vole	introduced, *ca.* 1998	expanding range	Hearn *et al.* (2006)
	Mus musculus	house mouse	introduced, *ca.* 1500s	limited distribution (settlements)	Dodds (1983)
	Ondatra zibethicus obscurus	Newfoundland muskrat	native	endemic, suppressed	Bangs (1913) Soper and Payne (1997)
	Peromyscus maniculatus	North American deermouse	introduced, 1968	limited distribution	Gould and Pruitt (1969) Tucker *et al.* (1988)
	Rattus norvegicus	brown rat	introduced, *ca.* 1500s	ubiquitous	Dodds (1983)
	Tamias striatus	eastern chipmunk	introduced, 1962	limited distribution (hardwood stands)	Northcott *et al.* (1974b)
	Tamiasciurus hudsonicus	red squirrel	introduced, 1963	ubiquitous	Payne (1976)
Soricomorpha	*Sorex cinereus*	masked shrew	introduced, 1958	ubiquitous	MacLeod (1960) Whitaker (2004)
Galliformes	*Lagopus muta welchi*	rock ptarmigan	native	limited distribution (alpine and barrens)	Montevecchi and Tuck (1987) Warkentin and Newton (2009)
	Lagopus lagopus alleni	willow ptarmigan	native	common (primarily barrens)	Montevecchi and Tuck (1987) Warkentin and Newton (2009)
	Bonasa umbellus	ruffed grouse	introduced, 1956	ubiquitous	Inder (1967) Tuck (1968)
	Falcipennis canadensis	spruce grouse	introduced, 1964	ubiquitous	Tuck (1968)

Co-authorship Statement

The following two manuscript chapters of this thesis were co-authored by Michael J. McGrath and Yolanda F. Wiersma. I was the principal contributor to project design, proposal, data analyses, and manuscript preparation for all chapters of the thesis. Mr. McGrath contributed design and implementation of coyote location data collection, ecological knowledge of coyotes in Newfoundland, logistical support, and constructive feedback regarding project design and manuscript drafts. Dr. Wiersma provided critical support in the form of research guidance throughout the process from initial design through manuscript completion. This includes constructive feedback at all levels of the work and manuscript writing process.

Both Chapters 2 and 3 are written for submission to journals with only minor modification. Thus, it was necessary to repeat some information from Chapter 1 as well as study area descriptions and data collection procedures between Chapters 2 and 3. I also anticipate submitting the material in Appendix A for publication with co-author contributions from Michael J. McGrath and Rick Curran.

CHAPTER 2. CREATING HABITAT MODELS FOR A GENERALIST PREDATOR: APPROACHES AND ISSUES

2.1. Introduction

Species distribution models (SDMs) are widely used in ecology, both for development of theoretical frameworks and application to conservation problems. Despite the plethora of models that have been developed, there remains a relatively limited suite of analytical methods used to construct the majority of these models. Researchers have noted that ecology as a field may lag behind other areas of scientific endeavour because we fail to apply more powerful and more appropriate techniques that remain outside of our comfort zone (O'Connor 2002; Hochachka *et al.* 2007). This situation is not limited to ecology alone; Breiman (2001) challenged the statistical community to expand their knowledge and practice by including the techniques of machine learning in the suite of tools for data analysis, citing various scenarios where stochastic data models failed to meet the capabilities of algorithmic models.

Resource selection models (RSMs), the subset of SDMs typically developed with repeated observations from a limited number of individuals, remain firmly entrenched in the linear stochastic data model approach (Hegel *et al.* 2010). Manly *et al.* (2002) promoted logistic regression as a resource selection function, which has become the norm for identifying spatio-temporal associations of animals in their environment. Modellers facing budget and time constraints are often challenged to meet assumptions of this approach. The combination of increased location frequency available with Global Positioning System (GPS) tracking technology, opportunistic field data collection and common practice of using readily available datasets (e.g., satellite image, forest inventory, and topographic data) exacerbate these issues when modelling species response to their environments.

Advances have been made in the more traditional approach to resource selection modelling by incorporating hierarchical structure to account for random effects. These advances in RSM structure help to address some major issues, such as correlation, unbalanced samples, and unaccounted variability (Gillies *et al*. 2006; Cressie *et al*. 2009; Fieberg *et al*. 2010). Additionally, numerous researchers have shown how explicitly accounting for random effects in stochastic data RSMs can enhance the explanatory power of these models (e.g., Gillies *et al*. 2006; Hebblewhite and Merrill 2008; Godvik *et al*. 2009). However, the mixed-effects modelling approach does come with its own assumptions, namely distribution of the random effects, that can be both a strength (e.g., predicting to new situations) and weakness (e.g., no individual exhibits the mean response; Fieberg *et al*. 2009; O'Hara 2009).

Stochastic data models in ecology typically focus on identifying explained variance in a functional form. This procedure requires clearly defined hypotheses of the relationship between variables. When the goal of modelling is focused on using the best available data to predict scenarios beyond the original data without inferring process or functional association, other methods, particularly algorithm-based approaches (a.k.a. data mining, machine learning), may be more appropriate (Hochachka *et al*. 2007). The design of machine learning algorithms is such that the goal of the resulting model is prediction rather than explanation (De'ath 2007; Hochachka *et al*. 2007; Hastie *et al*. 2009). This is a fuzzy distinction from a mixed-effect stochastic data model, which has a similar predictive attribute inherent in the random-effect structure, but is one that may have practical implications.

The limitations of linear approaches for constructing SDMs have been highlighted in recent years, but this has primarily transpired in the area of species occurrence modelling. Maximum entropy, artificial neural networks, genetic algorithms, decision trees, and support vector machines have all been shown to improve predictive performance when compared to logistic regression and other forms of stochastic data models when applied to occurrence-based SDMs (Elith *et al*. 2006; Cutler *et al*. 2007; De'ath 2007). The greatest predictive performance has been consistently achieved with ensemble learning methods (i.e., bagging, boosting, random forests; Caruana and Niculescu-Mizil 2006; Olden *et al*. 2008) that build upon basic machine learning algorithms by incorporating a randomization component (Hastie *et al*. 2009). The call by O'Connor (2000, 2002) to advance the field of ecology with models that identify constraints rather than correlates in an attempt to find causal relationships by incorporating analytical advances advocated by Breiman (2001) remains largely unfulfilled fully a decade later (but see Guilford *et al*. (2009), Monterroso *et al*. (2009), Oppel *et al*. (2009), Jiguet *et al*. (2010), and Kuemmerle *et al*. (2010) for examples of ensemble learning methods applied to RSMs).

Finally, and not of least importance, is the underlying theory regarding best modelling practices. For years theoretical habitat ecologists have advocated for the use of indirect (environmental), direct (habitat), and resource gradient data for constructing both *a priori* hypotheses and the models to test them (Guisan and Zimmermann 2000; Austin 2002; Scott *et al.* 2002). In practice, RSMs are typically parametrized with readily available data. These data are commonly derived from remote sensing applications and interpretation of the resulting data within an ecological context (Kerr and Ostrovsky 2003; Cohen and Goward 2004). What is commonly missing in this approach is the explicit data relating resource gradients to animal space use (e.g., spatially and temporally dynamic food resources). From an individual animal viewpoint these resources largely affect the behavioural response we are trying to model at the individual level (e.g., Creel and Christianson 2008; Kanarek *et al.* 2008; Moorcroft and Barnett 2008).

In this chapter, I attempt to address some of these issues through application of emerging analytical approaches to model habitat use by a generalist predator in a relatively monolithic and depauperate landscape. Specifically I investigate whether models parametrized with only environmental and habitat gradient data may be insufficient to accurately predict habitat use for a generalist carnivore, indicating a need for more resource data (i.e., prey availability). This is based on my hypothesis that appropriate driver data will allow for effective modelling using diverse approaches (i.e., model convergence). I predict that a resource selection function designed to explain patterns of coyote (*Canis* *latrans*) space use should highly correlate to the prediction of an ensemble learning model, given adequate correlative data.

2.2. Methods

2.2.1. Study Area

I obtained coyote data from the central portion of the Maritime Barrens Ecoregion (MBE) of the Island of Newfoundland, Canada (Figure 2.1). The entire MBE encompasses some geographically disjunct units (i.e., Avalon Peninsula, Burin Peninsula, eastern peninsulas, and coastal strip extending westward from White Bear River). Based on spatial connectivity and caribou migratory patterns, these peninsular areas will not be considered hereafter. However, the discontinuous portions of Central and Western Newfoundland Ecoregions located entirely within the MBE are included in the study area. The MBE represents the primary historical wintering area for six of the province's woodland caribou "herds" (Bergerud 1971), as defined by Caribou Management Areas (i.e., Buchans Plateau, Gaff Topsails, Grey River, Middle Ridge, Mount Peyton, and Pot Hill; Figure 2.2; NLDEC 2010a, 2010b, 2010c, 2010d, 2010e, 2010f). Under the current management regime, the MBE contains roughly one-third of Newfoundland's primary core area for caribou and a comparable proportion of secondary core area (Stantec Consulting Ltd. 2011).

The MBE is characterized by heath barrens interspersed with peatlands and dense patches of stunted balsam fir and spruce. The climate exhibits thin winter snow cover, high wind exposure, and regular, dense fog (Damman 1983). Summers are cool and wet;

winters are mild relative to surrounding ecoregions. Frequent soil frost and a history of fire prevent substantial forest regeneration in this area (Meades 1983). Existing forested areas are typically restricted to the steep sided valleys and some hill slopes (Figure 2.3).

2.2.2. Data Sources

Data for my research originated from two general sources, coyote captures to deploy GPS tracking collars and publicly available environmental datasets (Table 2.1). Point data representing the response variable in all models were derived from GPS collar locations (n = 30 788) combined with a random sample of points (n = 61 576) representing available habitat by individual for 17 coyotes (8 females, 9 males). Global Positioning System collars were deployed by Newfoundland and Labrador Wildlife Division personnel during mid-winter from 2005 to 2008. These GPS collars were programmed with a variety of location recording schedules, which I filtered to a standardized, continuous interval (see Chapter 3 for additional details). I generated utilization distributions (UDs) via kernel density estimation for each individual for the entire study period using Hawth's Tools (Beyer 2007) within the ArcGIS (v. 9.3; ESRI 2008) geographic information system (GIS). Random points were selected within a buffered 99% volume contour of each individual UD at a 2:1 ratio with location points (see Chapter 3 for additional details).

I used sixteen explanatory variables to parametrize coyote RSMs with the two methods outlined below. Newfoundland and Labrador Wildlife Division personnel assigned the individual identifier, and determined age and sex at capture. I delineated year and season (based on caribou migration dates; Table 2.1) from date information collected by GPS collars. Land cover classification followed the Earth Observation for Sustainable Development of Forests system (Wulder *et al.* 2004). I generated distance rasters from water features (NRC 2007a) and road features (NRC 2007b) using the GIS. A digital elevation model (DEM) based on the Canada3D product (NRC 2001) originally derived from the Canadian Digital Elevation Data (NRC 2000) was used to sample elevation. Slope and aspect (absolute deviation from north) were derived from the DEM within the GIS. Both slope and aspect were treated as continuous variables. Additionally, a topographic convergence index (TCI) developed by Skinner (2011) replaced elevation, slope, and aspect in some candidate models. The TCI is a proxy for surface moisture based solely on DEM components slope, aspect, and steepness. High values of TCI represent highly drained areas and low values represent areas of moisture collection. Resource data were not available at the scale of the models and hence were not included.

2.2.3. Data Analyses

I employed two approaches to modelling coyote response to environment and habitat variables; a stochastic data model and an algorithmic model. Generalized linear mixed-effect models (GLMMs) were used in the stochastic data approach. With this structural framework I was able to account for autocorrelation within individuals and within years by assigning these as random effects.

I constructed 26 candidate GLMMs for each season using a variety of explanatory variable groupings to assess various hypotheses of coyote ecology and potential interaction with caribou and anthropogenic disturbance (Table 2.2, Appendix B). Each model included parameters to consider year (slope) dependent upon individual (intercept) as random effects, following implementation methods of Bates (2010a, 2010b, 2010c). I fit the fixed-effects portion of each GLMM with a binary logistic regression function using the lme4 package (Bates and Maechler 2010) in R (v. 2.11.1; R Development Core Team 2010). Following standard practices, all explanatory variables were assessed for collinearity. All variables in any model had reasonably low Pearson correlations (≤0.41). Residual plots were used to assess assumptions of linear models including homogeneity, independence, normality and link function (Breslow 1996). I assessed each suite of candidate models using Akaike's Information Criterion (AIC) to select the "best" summer and winter models based on the training data (Burnham and Anderson 2002). Model averaging was not necessary due to high Akaike weights of leading candidate models for each season.

As an alternative to the more common stochastic data modelling approach, I modelled the same data using boosted regression trees (BRT). This algorithmic model from the field of machine learning was developed by Friedman (1999a, 2001) and later refined to incorporate randomization leading to a more robust and less computationally intensive algorithm (Friedman 1999b, 2002). The base algorithm of BRT is a decision tree. An ensemble of trees is built in a forward, stagewise series and optimized by stochastic gradient descent of the "pseudo"-residuals (Ridgeway 2007; Elith *et al*. 2008). The theory behind ensemble methods is that a committee of weak learners will be far more robust than a single complex decision tree in predicting outside the range of training data (Hastie *et* *al*. 2009). Tree-based algorithmic models are able to handle missing values, incorporate interactions among predictor variables, and identify natural breaks in the data to model non-linear response (De'ath and Fabricius 2000).

In my implementation of BRT for a coyote RSM, I followed recommendations of Hastie *et al*. (2009) for setting algorithm parameters. The size of constituent trees (nodes; *J*) was set to 6 (Hastie *et al*. 2009:363); learning rate (shrinkage; ν) was set at 0.1 (Hastie *et al*. 2009:620); subsample of training data observations in each iteration (bag fraction; η) was 0.5 (Ridgeway 2007; Hastie *et al*. 2009:620); an additional regularization parameter, number of trees in final model (λ) was determined by minimizing the cross-validation deviance following the code of Elith *et al*. (2008:supplementary material). Boosted regression tree implementation was conducted using the gbm package (Ridgeway 2010) in R. Following initial BRT model development, I ran a simplification procedure (Elith *et al*. 2008) to reduce model complexity by sequentially dropping the least important variable while maintaining predictive deviance based on 10-fold cross-validation. This simplified BRT model was assessed for overall performance compared with other models.

2.2.4. Model Evaluation

The objective of this research was to develop an operationally valid predictive model of coyote space use across seasons and years within the MBE. I evaluated the "best" models from each approach using a temporally-independent data set of GPS locations (n = 11 195) and random points (n = 22 390) obtained from 7 individuals (3 female, 4 male). Three of the individuals (1 female, 2 male) in the evaluation dataset were also monitored within the training dataset. Sensitivity (proportion of observed positive cases correctly classified) and specificity (proportion of observed negative cases correctly classified) of model output are commonly used metrics for assessment of prediction to new data (Fielding and Bell 1997). Specifically, relative operating characteristic (ROC) curves are a derived graphical representation of model discrimination across the range of threshold values (Swets 1988; Pearce and Ferrier 2000). I considered predictive capability for both GLMM and BRT modelling approaches using area under the ROC curve (AUC) with the ROCR package (Sing *et al.* 2009) in R. Assessment with AUC comes with some inherent pitfalls concerning model accuracy, especially for models of generalists and models built from pseudo-absences (Lobo *et al.* 2008; Hand 2009). Despite this, Lobo *et al.* (2008) note that AUC scores complemented with sensitivity and specificity values are useful for discriminating among models for a single species within the same extent.

2.3. Results

2.3.1. Stochastic Data Models

Within each season a single "best" model emerged from among the 26 candidate GLMMs based on Akaike weights (Table 2.2, Appendix B). The summer and winter models diverged substantially. The summer GLMM was a simplified version of the winter GLMM with 2 fewer explanatory variables. Also of note is the drastic difference in variability among the random effects. Variance of the random effects of individual and year was 1.78×10^7 and 4.38, respectively, in the summer GLMM; whereas, the same random effects in the winter GLMM had a variance of only 1.07×10^{-3} and 3.02×10^{-10}. These accumulated differences are readily apparent in the spatial predictions of coyote use (Figure 2.4).

Due to the high variance among individuals in the summer GLMM, I parametrized the "best" model for each of the 17 individuals in the training dataset. Year was retained as a random effect in individual GLMMs. Nearly all coefficient estimates ranged widely among individuals and had inconsistent directionality of effect (Table 2.3). This diffuse variation among individuals is important to consider within the framework of prediction, as any averaging across individuals is likely to give an inaccurate representation of individual behavioural response.

2.3.2. Algorithmic Models

The BRT model was optimized over 6500 forward, stagewise iterations using 14 predictor variables (Table 2.1). Following initial model development, a simplification procedure was conducted to drop variables that did not contribute to the overall model predictive performance within the training dataset. The final simplified model contained 12 of the original 14 predictor variables. Season and sex were determined to be unnecessary by the algorithm. The relative influence of individual variables changed from the original BRT to the simplified BRT, but rank order of variables retained in the simplified BRT remained the same (Table 2.4). Both the original BRT and simplified BRT performed very well in predicting outcomes within the training dataset (Table 2.5). This is notable because the training data are resampled at each iteration with 50% of the data remaining "out-of-bag".

There is distinct dissimilarity with GLMM predictions for either season (Figure 2.4). Whereas, the two BRTs exhibit similar spatial predictions when projected in geographical space (Figure 2.5). This incongruity among models indicates that one or both modelling approaches is ineffective in achieving the desired level of predictive accuracy.

2.3.3. Model Evaluation

Predictive performance was extremely low for most of the evaluation dataset following both modelling approaches. Boosted regression trees outperformed GLMMs, but limited inference can be gained from any of the coyote RSMs based on environment and habitat gradient data alone. Area under the curve values ranged from 0.517 to 0.746, broken down by data domain of biological interest. Many of my RSM predictions can be considered no better than random. Generalized linear mixed-effect models were particularly poor with all AUC < 0.6 (Figure 2.6). Only BRTs predicting to future years for individuals within the training dataset had reasonable predictive success (i.e., AUC > 0.7 (Pearce and Ferrier 2000); Figure 2.7). Relative operating characteristic plots show that BRT outperformed the best GLMMs across the entire range of classification thresholds, indicating superior predictive capability.

2.4. Discussion

The results of my research have shown that BRT can provide better model structure for predicting to new data than traditional stochastic data modelling approaches, even those adapted to deal with unaccounted random variation. The superior performance of BRT compared with GLMM shown in predicting new locations of individual coyotes is testament to the power of ensemble methods in resource selection modelling. Similar results of algorithmic models outperforming stochastic data models have been well documented in species occurrence modelling (e.g., Elith *et al*. 2006; Guisan *et al*. 2007; Marmion *et al*. 2009; Zurell *et al*. 2009) as well as other natural and social science applications (e.g., Berk 2006; Abeare 2009; Siroky 2009; Ahmed *et al*. 2010), but not in resource selection modelling.

In general, stochastic data models can be interpreted as our attempt to "summarize the understanding of a phenomenon" (Breiman 2001:227). The structure of a GLMM as applied herein accounts for individual and annual variability. Marginal (population-level) inference from this GLMM fixed-effect structure provides an estimate of "typical" response within a RSM framework (Gillies *et al*. 2006; Aarts *et al*. 2008; Hebblewhite and Merrill 2008). However, Fieberg *et al*. (2009) suggested that application of mixed-effects models averaged across random effects will weaken marginal predictions. This averaging effect may have been partially responsible for the poor performance of GLMMs, particularly the summer models where there was extreme variability observed within the random effects. Specifically, the differences among individual availability when averaged over the population may have been a major contributor to the poor performance of the summer models (Beyer *et al*. 2010). Winter models likely indicate other issues with the data as random-effect variability was quite low.

Ensemble methods of machine learning, particularly tree based methods, focus on prediction without implying mechanism (Breiman 2001). These models do not require prior understanding of the system based on available data. Araújo and New (2007) also note that in the absence of idealized data for model parametrization, ensemble models may provide more robust predictions than any single "best" model. Though ensemble methods are often seen as "black box" approaches, information can be extracted *post hoc* regarding model structure that directly relates how individual variables affect the ensemble model (Hastie *et al.* 2009:620). In addition, data mining can lead to new hypotheses when unexpected evidence for variables appears (Hochachka *et al.* 2007; Aarts *et al.* 2008). It follows that my BRT models may indicate areas for future ecological research (see Chapter 3). The ability to interpret the structure of BRT combined with the robust predictive capability makes this analytical method appealing for a wide variety of modelling applications (Elith *et al.* 2008). Therefore, this method should be applicable to RSMs where little is known, or in situations limited by data or other constraints (e.g., broad niche that is logistically unquantifiable, areas inaccessible for the purpose of data collection, historical data that cannot be augmented, and financial or time limitations).

Model validation, as conducted in this research, seeks to convey confidence in resulting predictions (Rykiel 1996). Wiens (2002:744) referred to model prediction and accuracy as "the holy grail of wildlife biology". Importantly, where increasing geographic prevalence has been shown to reduce model accuracy (Marmion *et al.* 2009), AUC scores are essentially independent of prevalence (Manel *et al.* 2001; McPherson *et* *al*. 2004) making this measure valid for comparison of models developed with the same data. Failure of most of my models to predict well in a limited domain of parameter space according to AUC values indicates that little information was gained from any of the approaches. Although the models were not validated, they are not necessarily entirely invalid either. The true operational validity lies in model accuracy, which spans a greater gamut of evaluation criteria (Lobo *et al*. 2008). The highly vagile and generalist nature of the species, use of pseudo-absence data (with inherent contamination), and lack of temporal variability in the predictors will have limiting effects on the value of raw AUC scores. Low discrimination ability of model predictions does not necessarily indicate low accuracy. In this case ranking of raster values (Figures 2.4 and 2.5) may be correct, whereas identifying a threshold value for predicting presence/absence remains inappropriate. Regardless of the absolute AUC scores, it can be noted from the ROC plots (Figures 2.6 and 2.7) that BRTs outperformed GLMMs across the entire range of possible threshold values.

The limitation of all models in my research for predicting to new individuals represents the inherent issues with indirect gradient data for species distribution modelling. The lack of standard correlations between these indirect gradients and causal gradients is likely restricting any generalization of RSM results (Guisan and Zimmermann 2000; Austin 2002). In this case, the RSM may be applicable only at the local scale of observed individuals due to variation in behavioural response to causal gradients. Because indirect gradients provide only correlative structure to the model, variability within any system or population will reduce the predictive capacity of the models. More explicitly incorporating ecological theory in the form of causal predictors will likely lead to more robust predictions (Guisan and Zimmermann 2000; Austin 2002; Austin 2007).

Predictive and mechanistic modelling typically diverge in their conceptual design where causality is not necessarily fundamental to accurate prediction. Surrogate variables are often adequate for valid prediction and may be preferred (Guisan and Zimmermann 2000). The lesser detail required in collection of surrogates to behavioural response often result in time and monetary savings while achieving the desired outcome of accurate prediction within the spatio-temporal scope of research objectives. However, my research has shown that readily available remotely sensed data is largely inadequate when developing a generalist carnivore RSM for management purposes. Although setting the proximal goal of accurately predicting ecological phenomena will guide better management practice, we as ecologists continue to strive for understanding process that leads to observed patterns (Beyer *et al*. 2010). When designing research to develop a RSM for coyotes or similarly adaptable species I would highly recommend *a priori* cost assessment through a pilot project or other means to determine whether tradeoffs are manageable within the greater constructs of the research program and make direct gradient and resource measurement a top priority for implementation.

Data available for this research lacked a mechanistic tie at the scale of individual behavioural response, therefore the RSM approaches investigated with these data were weak in predictive power. Insight to resources as the fundamental drivers of coyote ecology requires further investigation (see Appendix A). Additional financial and human resources would need to be dedicated for future research to attain improved model performance. The high costs of collecting resource data for terrestrial carnivore RSMs (i.e., prey availability) due to both high spatio-temporal variation and associated labour requirements for adequate sampling typically preclude this type of modelling effort (Austin 2002).

Many resource selection studies are now making use of advancing technology for increased location frequency available with GPS collars (Hebblewhite and Haydon 2010). Additional large volume data sources are becoming more available through other monitoring devices and remote sensing (Hooten 2011). Pairing these technological advances with continuously improving computational technology is imperative to gain the greatest insight to ecological phenomena (Green *et al*. 2005; Cagnacci *et al*. 2010). Data mining should offer opportunities to explore these profuse data without the assumptions, both biological and statistical, inherent in the stochastic data modelling approach. It is important to consider that differences in parametrization of modelling approaches may lead to spurious conclusions regarding performance comparisons (Araújo and Guisan 2006). While algorithmic models can find correlations and high order interactions within the data, stochastic data models may perform as well given this prior knowledge to incorporate in models. Therefore, we must remember that improved modelling techniques are not a substitute for best practices of study design and data collection, but can be powerful tools to learn more about systems of interest.

2.5. References

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Table 2.1. Data used to generate models of coyote space use in the Maritime Barrens Ecoregion of the island of Newfoundland. Use was modelled as the response variable with binary input values for coyote locations and random points within home range. All other variables are candidate predictors.

Variable Name	Description	Data Source
Use	GPS locations / Random points	GPS collar / Hawth's Tools
ID	Individual identifier	Assigned
Sex	Female / Male	Determined at Capture
Age	Pup / Yearling / Adult	
Year	Calendar Year 2005 - 2008	GPS collar
Season[1]	Winter / Summer = November 1 / May 10	
CovTyp	Land cover classification (LCC; 18 categories)	Earth Observation for Sustainable Development (Wulder *et al.* 2004)
CovT[2]	Generalized LCC (12 categories)	
Cov[2]	Generalized LCC (7 categories)	
dRoad	Distance to Nearest Road (m)	National Road Network (NRC 2007b)
dWater	Distance to Nearest Water (m)	National Hydro Network (NRC 2007a)
dWater1ha	Distance to Nearest Water ≥1ha (m)	
dWater5ha	Distance to Nearest Water ≥5ha (m)	
Elev	Elevation (m)	Digital Elevation Model (NRC 2001)
Slope	Steepness of Land Surface (degrees)	
Aspect	Horizontal Direction of Slope (degrees from North)	
TCI	Topographic Convergence Index	Modelled (Skinner 2011)

[1] Season delineation based on mean caribou migration dates reported by Mahoney and Schaefer (2002).

[2] Not included in boosted regression tree models as the decision trees of BRT will automatically create groups of categories.

Table 2.2. Candidate generalized linear mixed-effect models to describe coyote habitat by season in the central Maritime Barrens Ecoregion of the island of Newfoundland[†].

	Model Formula	$\mathcal{L}(g_i \mid x)$	K	AIC	Δ_i	w_i
Winter	Use~CovTyp+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	1	8	38171.85	0.00	1
	Use~CovT+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	4.38×10^{-20}	8	38261.00	89.15	4.38×10^{-20}
	Use~Cov+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	3.76×10^{-23}	8	38275.12	103.27	3.76×10^{-23}
	Use~CovTyp+dRoad+dWater+Aspect+(Year|ID)	1.38×10^{-28}	6	38300.15	128.30	1.38×10^{-28}
	Use~CovTyp+dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	4.02×10^{-31}	8	38311.83	139.98	4.02×10^{-31}
	Use~CovTyp+dRoad+dWater5ha+Elev+Slope+Aspect+(Year|ID)	1.83×10^{-39}	8	38350.24	178.39	1.83×10^{-39}
Summer	Use~CovTyp+Elev+Slope+Aspect+(Year|ID)	1	6	20853.32	0.00	1
	Use~Elev+Slope+Aspect+(Year|ID)	2.50×10^{-37}	5	21021.88	168.56	2.50×10^{-37}
	Use~CovTyp+TCI+(Year|ID)	0	4	23459.45	2606.13	0
	Use~CovT+Elev+Slope+Aspect+(Year|ID)	0	6	32706.57	11853.25	0
	Use~CovTyp+dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	0	8	35933.24	15079.92	0
	Use~CovTyp+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	0	8	35961.04	15107.72	0

[†] Only the top 6 models for each season are presented here due to the extremely low Akaike weights of all but the top model. A full list of candidate generalized linear mixed-effect models in rank order can be found in Appendix B.

Table 2.3. Parameter coefficient estimates (bold) and number of occurrences (below) from generalized linear mixed-effect models of coyote resource selection during summer in the Maritime Barrens Ecoregion of Newfoundland.

	ID	EOSD Land Cover Classification														Elev (m)	Slope (°)	Aspect (deviation from N°)
		Unclassified	Broad Leaf	Coniferous Dense	Coniferous Open	Coniferous Sparse	Exposed	Grass/ Herb	Mixed Wood Dense	Mixed Wood Open	Rock	Shrub	Water	Wetland Herb	Wetland Shrub			
Female	102	*na*	*na*	**-7.09**	**-6.86**	**-6.36**	**-6.53**	**-4.37**	**-19.31**	*na*	**-6.21**	**-5.35**	**-6.09**	**-21.03**	**-6.38**	**0.03**	**-0.38**	**0**
		0	0	136	73	647	488	1316	6	0	80	19	773	31	1321	4890	4890	4890
	105	*na*	*na*	**-10.33**	**-9.45**	**-14.03**	**-14.92**	**-14.48**	**-25.29**	*na*	**-15.12**	**-15.35**	**-15.44**	**-26.47**	**-14.59**	**0.01**	**-0.15**	**-0.01**
		0	0	4	4	404	354	277	3	0	75	8	207	7	988	2331	2331	2331
	106	**0.47**	**19.19**	**2.55**	**15.08**	**21.87**	**22.74**	**22.27**	**1.61**	*na*	**22.62**	**21.62**	**20.72**	**2.84**	**22.33**	**-0.03**	**-0.45**	**0**
		22	2	79	62	777	479	698	9	0	120	23	533	27	1244	4075	4075	4075
	107	**-14.6**	**-29.93**	**-20.38**	**-15.74**	**-19.59**	**-18.51**	**-18.89**	**-29.43**	*na*	**-20.41**	**-19.33**	**-19.35**	**-17.56**	**-18.49**	**0.01**	**0.2**	**0.01**
		31	2	108	91	592	135	421	7	0	25	24	286	91	647	2460	2460	2460
	108	**-36.84**	*na*	**-27.76**	**-27.59**	**-26.83**	**-29.1**	**-26.9**	**-40.31**	*na*	**-40.62**	**-26.98**	**-26.5**	**-26.53**	**-26.52**	**0.07**	**-0.14**	**0**
		6	0	45	58	944	94	224	4	0	22	26	465	31	718	2637	2637	2637
	109	**-26.39**	*na*	**-27.14**	**-13.1**	**-12.65**	**-14.51**	*na*	*na*	**4.38**	**-27.01**	**-13.08**	**-15.16**	*na*	**-13.56**	**0**	**-0.03**	**0**
		20	0	11	99	1445	234	0	0	1	18	126	157	0	244	2355	2355	2355
	110	**-8.99**	*na*	**-10.29**	**-9.13**	**-10.99**	**-14.34**	**-12.7**	**-23.35**	*na*	**-27.22**	**-12.13**	**-13.15**	**-12.04**	**-12.06**	**0**	**-0.36**	**0.01**
		7	0	51	219	855	162	206	3	0	35	12	312	9	664	2535	2535	2535
	111	**-19.75**	**-1.05**	**-3.98**	**-3.4**	**-2.18**	**-3.78**	**-18.32**	**-3.35**	**-2.55**	**-18.12**	**-2.52**	**-4.67**	**-2.59**	**-4.48**	**0**	**0.08**	**0**
		117	8	44	67	1103	43	18	50	3	1	54	158	3	115	1784	1784	1784

Table 2.3 (continued).

	ID	EOSD Land Cover Classification														Elev (m)	Slope (°)	Aspect (deviation from N°)
		Unclassified	Broad Leaf	Coniferous Dense	Coniferous Open	Coniferous Sparse	Exposed	Grass/ Herb	Mixed Wood Dense	Mixed Wood Open	Rock	Shrub	Water	Wetland Herb	Wetland Shrub			
Male	201	*na*	**-24.53**	**-25.14**	**-12.3**	**-11.81**	**-12.64**	**-12.41**	*na*	*na*	**-12.41**	**-12.31**	**-12.79**	**-25.31**	**-12.31**	**0.01**	**-0.17**	**-0.01**
		0	1	4	5	438	422	359	0	0	78	23	274	13	1116	2733	2733	2733
	202	**10.74**	**8.66**	**11.15**	**11.23**	**12**	**11.84**	**-20.51**	**9.64**	**-4.75**	**10.08**	**12.56**	**11.39**	**11.07**	**11.62**	**0**	**0.05**	**0**
		73	5	71	114	1440	197	86	38	1	30	63	208	13	373	2712	2712	2712
	203	**-16.7**	**-18.07**	**-1.17**	**-0.78**	**-1.12**	**-1.36**	**-18.73**	**-2.68**	**-1.18**	**-18.68**	**-3.82**	**-3.13**	**-0.98**	**-2.58**	**0.01**	**-0.08**	**-0.01**
		28	7	34	85	623	99	59	10	2	8	30	198	14	156	1353	1353	1353
	206	**-29.87**	*na*	**-24.33**	**-23.03**	**-21.98**	**-21.7**	**-20.03**	**-19.8**	*na*	**-22.1**	**-22.63**	**-21.53**	**-23.25**	**-21.57**	**0.04**	**-0.67**	**0**
		22	0	44	47	377	189	704	9	0	34	20	411	25	632	2514	2514	2514
	212	**-27.43**	*na*	**-32.32**	**-31.61**	**-31.18**	**-33.44**	**-31.8**	**-39**	**-44.02**	**-48.11**	**-30.62**	**-31.16**	**-30.33**	**-30.77**	**0.08**	**-0.48**	**0**
		36	0	40	34	864	140	289	5	1	28	33	351	22	701	2544	2544	2544
	214	*na*	**-27.93**	**-15.73**	**-17.58**	**-15.01**	**-14.59**	**-14.69**	**-26.45**	*na*	**-14.84**	**-28.38**	**-15.05**	**-17.06**	**-15.02**	**0.02**	**-0.22**	**0**
		0	2	64	50	561	338	522	2	0	61	13	380	60	851	2904	2904	2904
	215	**-15.44**	*na*	**-15.77**	**-0.46**	**0.26**	**-0.71**	**-15.38**	*na*	**1.47**	**-15.6**	**-0.37**	**-0.56**	**-16.04**	**-0.58**	**0**	**0.03**	**0**
		8	0	10	70	1075	117	4	0	3	4	75	142	1	222	1731	1731	1731
	216	**-7.74**	**-5.4**	**-24.78**	**-24.15**	**-12.12**	**-12.03**	**-11.79**	**-12.18**	**-23.37**	**-11.79**	**-13.45**	**-12.96**	**-7.56**	**-12.08**	**0**	**-0.26**	**0**
		15	2	17	17	695	343	540	13	1	89	11	240	2	1004	2989	2989	2989
	217	**-14.63**	*na*	**-15.84**	**-15.53**	**-15.63**	**-17.11**	**-34.36**	**-16.69**	*na*	**-36.11**	**-15.18**	**-15.76**	**-15.49**	**-16.01**	**-0.01**	**-0.16**	**-0.01**
		5	0	88	96	959	73	24	7	0	11	17	306	10	267	1863	1863	1863

Table 2.4. Relative contribution (% of constituent trees) of predictor variables from boosted regression tree models of coyote resource selection in the Maritime Barrens Ecoregion of Newfoundland.

Predictor	**Base Model**	**Simplified Model**
ID	33.95	35.17
dRoad	19.93	21.59
Elev	10.03	9.71
dWater1ha	5.97	6.32
CovTyp	5.97	5.61
dWater5ha	5.66	4.64
Slope	3.99	4.11
Aspect	3.90	3.69
dWater	3.44	3.20
TCI	2.95	2.73
Year	2.13	2.25
Season	1.07	
Age	0.98	0.96
Sex	0.03	

Table 2.5. Boosted regression tree model performance assessed via 10-fold cross-validation of the training data.

	Source	**Base Model**	**Simplified Model**
No. trees		6500	5250
No. predictors		14	12
Deviance	Total	0.92	0.92
	Residual	0.32	0.34
	C.V. est.[1]	0.473 ± 0.001	0.483 ± 0.002
Correlation	Training	0.84	0.82
	C.V. est.	0.719 ± <0.001	0.711 ± 0.001
AUC[2]	Training	0.97	0.97
	C.V. est.	0.921 ± <0.001	0.918 ± 0.001

[1] Cross-validation values are mean ± standard deviation

[2] Area under the relative operating characteristic curve

Figure 2.1. Maritime Barrens Ecoregion of Newfoundland (highlighted) with the central portion representing the study area for this research outlined in red. The island of Newfoundland is highlighted in the inset map of Canada.

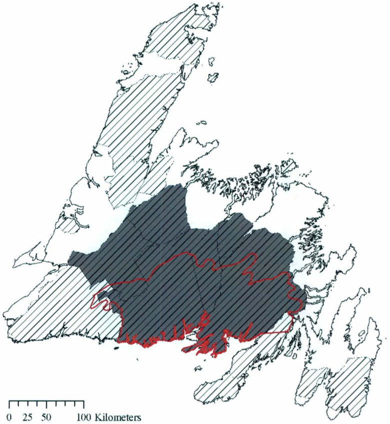

Figure 2.2. Caribou Management Areas (CMA) of the island of Newfoundland designated by the Department of Environment and Conservation, Wildlife Division. Highlighted CMAs (Buchans [Bu], Gaff Topsails [GT], Grey River [GR], Middle Ridge [MR], Mount Peyton [MP] and Pot Hill [PH]) are included in this research as representative of caribou populations that overlap with GPS monitored coyotes.

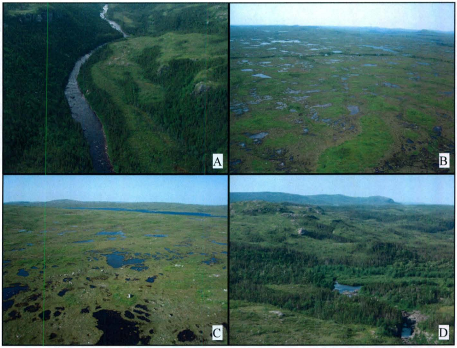

Figure 2.3. Aerial view of forest and barrens typical of the central Maritime Barrens Ecoregion of Newfoundland. Forested areas are generally restricted to steep-sided valleys (a) and protected slopes (d). Barrens (b, c) make up the majority of the study area composed of heathlands and peatlands interspersed with water bodies of various sizes.

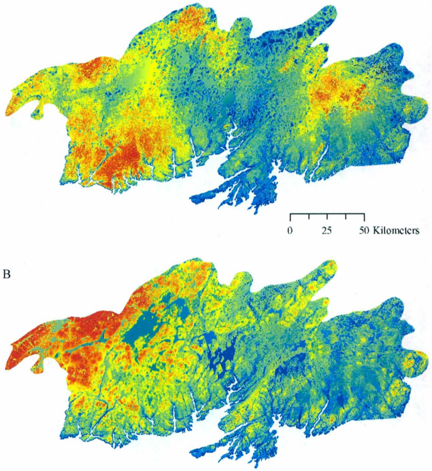

Figure 2.4. Spatial predictions of generalized linear mixed-effect models for coyotes in the central Maritime Barrens Ecoregion of Newfoundland. Differences between winter (a) and summer (b) projections are easily visible with the effect of roads and water incorporated in the winter model. Blue and red colours represent predicted areas of low and high coyote use, respectively.

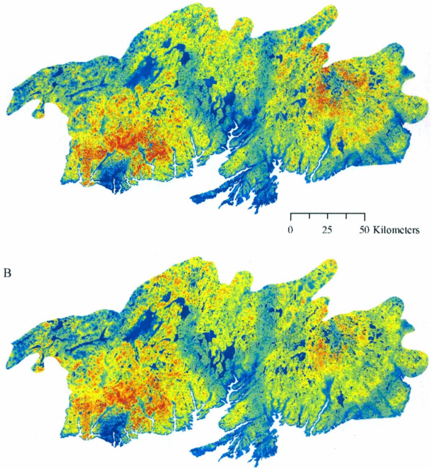

Figure 2.5. Spatial predictions of boosted regression tree (BRT) models for coyotes in the central Maritime Barrens Ecoregion of Newfoundland. Only the model for adult females during summer is shown (a) among the projections for the original model containing all 14 predictors. The simplified BRT model is shown for adult coyotes (b). Other age, sex and season projections show only minor deviations not easily differentiated at this scale in graphical format. Blue and red colours represent predicted areas of low and high coyote use, respectively.

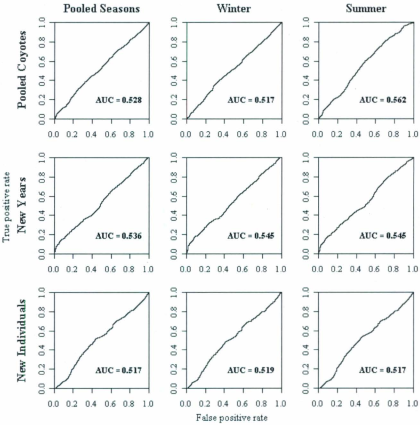

Figure 2.6. Relative operating characteristic (ROC) plots for prediction to an independent evaluation dataset from generalized linear mixed-effect models of coyote resource selection within the central Maritime Barrens Ecoregion of Newfoundland. Area under the ROC curve (AUC) values provide of measure of reliability for model predictions under various conditions (i.e., all coyotes pooled, coyotes from the training data in a different time period, and new coyotes in a different time period) for each seasonal model and pooled predictions from both seasonal models.

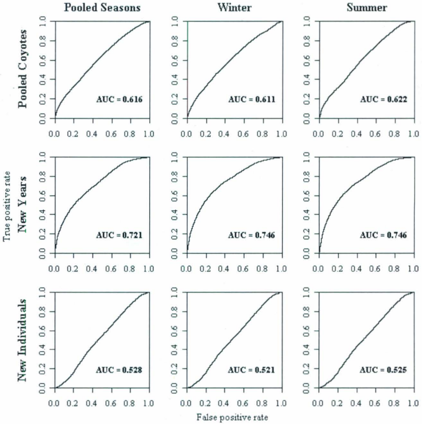

Figure 2.7. Relative operating characteristic (ROC) plots for prediction to an independent evaluation dataset from a boosted regression trees model of coyote resource selection within the central Maritime Barrens Ecoregion of Newfoundland. Area under the ROC curve (AUC) values provide of measure of reliability for model predictions under various conditions (i.e., all coyotes pooled, coyotes from the training data in a different time period, and new coyotes in a different time period) for each season and pooled predictions from both seasons.

CHAPTER 3. NEARING THE ECOLOGICAL LIMIT: COYOTE ADAPTABILITY PRODUCES INDIVIDUALISTIC SPACE USE PATTERNS

3.1. Introduction

Predators are often implicated when socio-economically important prey species decline (e.g., Matte 2007; Jacques and Van Deelen 2010; Stansell *et al.* 2010). Thus, it is not surprising that coyote (*Canis latrans*) predation has been asserted as the cause for woodland caribou (*Rangifer tarandus caribou*) population declines on the island of Newfoundland (NLDEC 2008). Coyotes first arrived in Newfoundland *ca.* 1985 (Moore and Parker 1992) and have since expanded across the island. Increased coyote observations and harvest (McGrath *et al.* 2010) coincided with caribou declines, but this correlation is not sufficient evidence to constitute causality. Although it is likely that coyotes are playing a significant role in caribou mortality, the determination of proximate versus ultimate factors is likely to be less clear and of great importance in the long term management of the ecosystem. Herein I seek to delineate a framework of implied coyote predation risk for caribou in time and space.

In this context I want to determine whether coyote home range attributes imply a temporal increase in predation risk for woodland caribou. The home range as defined by Burt (1943) is an often-studied construct in spatial ecology of animals. This region defined by an animal's regular movements encompasses the space required to gather food, acquire mates, and rear young. Home range size within eastern coyote range varies both seasonally and geographically with food availability (Gompper 2002). Within a region, coyote home range size reflects density of available food resources (Mills and Knowlton 1991; McLoughlin and Fergusson 2000; Young *et al*. 2008). Consequently, coyotes may shift use patterns within their home range through time as a response to changes in food distribution (Mills and Knowlton 1991; Kitchen *et al*. 2000).

Seasonality and patchiness of food resources is known to be a primary driver of carnivore spacing behaviour (McLoughlin *et al*. 2000). Coyotes in Newfoundland may respond to highly variable prey density (i.e., seasonally migratory caribou) by shifting home ranges to adapt to this variability. Research in Colorado has shown that coyotes will shift core areas of use possibly in response to changing resources (Kitchen *et al*. 2000). Shifting spatial patterns have also been observed in other carnivores where patterns reflected changes in prey density or availability (e.g., (Logan and Irwin 1985; Lovallo and Anderson 1996). Coyotes on Cape Breton Island, Nova Scotia exhibited no territorial shift during winter in response to congregations of ungulate prey (Patterson and Messier 2001). However, in southeastern Québec, coyote relocation frequency increased in a deer wintering area within existing home ranges (Crête *et al*. 2001). In cases of extremely low food resource density, territoriality will break down due to costs of large area defence (McLoughlin *et al*. 2000). This strategy may be most appropriate in Newfoundland where observed coyote home ranges are far larger than elsewhere within the species range and may represent the maximum extent possible. Therefore, shifting or expansion-contraction of seasonal home ranges may be the most effective adaptation to exploit seasonal prey abundance.

Differential use of space within an individual's home range is the subject of resource selection modelling (RSM). Habitat data typically represent the biophysical environment that an individual encounters during its lifetime. For the purposes of modelling, we are commonly limited by available habitat data that provide a snapshot of this environment. Spatial extent and resolution of these data may affect model outcomes (Guisan *et al*. 2007; Zuckerberg *et al*. 2011). Lack of temporal congruence of datasets may also introduce errors in prediction dependent on the level of change across time periods spanning data collection. Guisan and Thuiller (2005) provide a more thorough list of considerations for building and evaluating species distribution models. Of the three idealized types of spatial gradients identified by Austin (1980), many available habitat datasets function as indirect gradients. These indirect gradient data will likely limit geographical scope of predictions (Austin 2002). It is important to note that even less than ideal data can still provide useful information for modelling species' distributions (Zuckerberg *et al*. 2011). At a minimum, successful predictive models based on surrogate data should provide information to target future research.

A plethora of coyote RSMs have been created throughout the species range, but due to their generalist nature the ecological niche of this species varies geographically and with differing community composition (Voigt and Berg 1987). Gompper's (2002) summary of northeastern coyote populations indicates that home ranges reflect food availability and vary both geographically and seasonally. Plant community structure largely influences animal distributions, particularly herbivorous mammals and birds (e.g., St-Georges *et al*. 1995; Mayor *et al*. 2009), that represent the majority of coyote diets in insular Newfoundland (McGrath *et al*. 2010; Appendix A). Large, deep water bodies may function as escape terrain for caribou during the summer (Bergerud 1985; Bergerud *et al*. 1990). Deer and elk in Yellowstone have been observed using water bodies as an effective means to escape coyote predation (Gese and Grothe 1995). Conversely, caribou may be more susceptible to coyote predation on these large water bodies when they are frozen (*M.J. McGrath, personal communication*). Roads commonly represent increased human impact due to traffic levels and access opportunity leading to negative consequences for wildlife (Fahrig and Rytwinski 2009). Topography may function as a surrogate for microclimatic variation that is not otherwise quantified (Guisan and Zimmermann 2000). All of these biological, physical, and anthropogenic factors may play into the way coyotes make use of their home ranges.

In this chapter, I attempt to provide insight toward the issue of coyote predation on migratory woodland caribou through an assessment of coyote space use during seasons of high and low relative caribou abundance. Specifically I investigate whether coyote home ranges shift coincident with over-winter aggregations of caribou in the MBE. My hypothesis is that coyotes in Newfoundland are food limited and will adapt space use to exploit available resources. I predict that if coyotes are targeting caribou as a primary winter food source, then territories will break down and significant shifts in home ranges will be observed across seasons. Relatively static home ranges will indicate that coyotes are acquiring sufficient food resources within their territories throughout the year irrespective of large caribou aggregations occurring within any individual territory. I also investigate habitat features that coyotes select within their home range across seasons and years. This addresses my hypothesis that coyotes are selecting habitat within territory based on relative primary food resource availabilities by season. I predict that if coyotes are selecting habitat based on similar habitat attributes believed to be important to caribou, then open cover types, areas near large water bodies, and high elevation sites will be selected for by coyotes. However, if coyote space use is a function of human influence and individual adaptation to locally available food resources then roads, developed areas and dense cover types should be more influential for coyote habitat selection.

3.2. Methods

3.2.1. Study Area

I obtained coyote data from the central portion of the Maritime Barrens Ecoregion (MBE) of the Island of Newfoundland, Canada (Figure 3.1). The entire MBE encompasses some geographically disjunct units (i.e., Avalon Peninsula, Burin Peninsula, eastern peninsulas, and coastal strip extending westward from White Bear River). Based on spatial connectivity and caribou migratory patterns, these peninsular areas will not be considered hereafter. However, the discontinuous portions of Central and Western Newfoundland Ecoregions located entirely within the MBE are included in the study area. The MBE represents the primary historical wintering area for 6 of the province's woodland caribou "herds" (Bergerud 1971), as defined by Caribou Management Areas (CMAs; i.e., Buchans Plateau, Gaff Topsails, Grey River, Middle Ridge, Mount Peyton, and Pot Hill; Figure 3.2; NLDEC 2010a, 2010b, 2010c, 2010d, 2010e, 2010f). Under the current management regime, the MBE contains roughly one-third of Newfoundland's primary core area for caribou and a comparable proportion of secondary core area (Stantec Consulting Ltd. 2011).

The MBE is characterized by heath barrens interspersed with peatlands and dense patches of stunted balsam fir and spruce. The climate exhibits thin winter snow cover, high wind exposure, and regular, dense fog (Damman 1983). Summers are cool and wet; winters are mild relative to surrounding ecoregions. Frequent soil frost and a history of fire prevent substantial forest regeneration in this area (Meades 1983). Existing forested areas are typically restricted to the steep sided valleys and some hill slopes (Figure 3.3).

3.2.2. Coyote Location Data

Researchers with the Newfoundland and Labrador Wildlife Division instrumented 26 coyotes with Lotek GPS 4400 Global Positioning System (GPS) collars (Lotek Wireless, Inc., Newmarket, ON) between 2005 and 2009 within the MBE. I censored coyotes with less than 100 days of successful monitoring from all analyses. Global Positioning System recording schedules varied among individual collar deployments, so I filtered the entire dataset to a 4-hour relocation schedule. This schedule represents the highest standardized relocation frequency across all individuals. Standardized sampling is important to control for effects of autocorrelation within the dataset (Otis and White 1999; de Solla *et al.* 1999; Fieberg 2007a). Fix rates at this interval were 88.1 ± 1.6% ($\bar{x}$ ± SE) among individual coyotes. Two coyotes had respective gaps in GPS records of 9 and 68 days due to collar failure prior to replacement. Both individuals were retained for analysis, but it should be noted that this may affect results for early-winter space use especially concerning the 68-day data gap. The 4-hour relocation data were then filtered to remove the most likely erroneous data based on limited information (D'eon and Delparte 2005; Lewis *et al*. 2007; Tobler 2009). All locations with ≥ 4 satellite vehicles (3-dimensional) were filtered to a maximum dilution of precision (DOP) allowance of 10; locations with 3 satellite vehicles (2-dimensional) were filtered to a maximum DOP of 5. Quality filtering resulted in an additional 5.8 ± 0.7% data loss among individuals. Fix success rate and location quality were highly correlated ($R^2 = 0.499$) within individual collar deployments. The data retained for these analyses (41,983 locations) included 10 female and 11 male coyotes; 18 adults (≥ 2 years old), 13 yearlings (1-2 years old) and 2 pups (< 1 year old). Some individuals are represented in multiple age classes as they transitioned from pups to yearlings and yearlings to adults (Table 3.1). Monitoring for each individual ranged from 140 to 758 days.

3.2.3. Home Range Overlap

In order to assess whether coyotes maintained seasonal home range fidelity, I calculated home range similarity across seasons on an individual basis using Bhattacharyya's affinity. Bhattacharyya's affinity is a function of the product of two distributions that can be used to quantify the degree of similarity between utilization distributions (UDs; Bhattacharyya 1943; Fieberg and Kochanny 2005). Values of Bhattacharyya's affinity range from 0 (no overlap) to 1 (identical distributions). Seasons were delineated based on caribou migration trends (Mahoney and Schaefer 2002) with designated cutoff dates of May 10 and November 1. Summer represents the calving and post-calving period for caribou when calf predation is known to be high (Blake 2006; Trindade *et al.* 2011). Winter represents the period of large-scale aggregation with anecdotal evidence that predation may be causing significant added mortality. Beginning of summer as designated here also corresponds with approximate parturition date of coyotes in Newfoundland (Blake 2006). Where I am primarily concerned with the influence of coyotes on overwintering caribou populations, this biological discretization is most informative (Kie *et al.* 2010). I developed individual seasonal UD estimates of home range using kernel density estimation (KDE) procedures with the adehabitatHR package (Calenge 2011) in R (v. 2.11.1; R Development Core Team 2010). In most cases the least-squares cross-validation KDE method failed to converge, a situation that has been noted by other researchers with high volume location data (e.g., Hemson *et al.* 2005; Gitzen *et al.* 2006). Therefore, I used the reference smoothing parameter for all KDE home range calculations to maintain consistency among individuals. Although the reference method tends to over-smooth data, it provides a more conservative estimate of home range (Börger *et al.* 2006). I expect the over-smoothing tendency to minimize KDE differences across seasons leading to a more conservative estimate of possible shifting patterns of use. For my purposes, actual home range size was not an issue, but rather the changes in shape and extent of the home range over time. I calculated Bhattacharyya's affinity of pooled and chronological seasonal UDs for each individual using the adehabitatHR package. I also evaluated home range similarity within each season (i.e., summer and winter) across years as a measure of spatial stability for each individual.

3.2.4. Random Location Data

In addition to temporal changes in space use, I investigated the specific habitat associations of coyotes in the MBE. Utilization distributions have been suggested as an effective approach to define availability in habitat studies (Kie *et al.* 2010) in order to limit bias in the pseudo-absence sample (Phillips *et al.* 2009). Following this premise, I generated random points within the 99% volume contour of each individual's UD plus a buffer area equal to the 95th percentile 4-hour movement distance over the entire monitoring period. This area was selected to represent the entire area with which each coyote had experience and reasonable opportunity to select spatial locations for continued use within the sampling period. I used least-squares cross-validation smoothing parameters to develop the individual KDE-based UDs for random point selection. The least-squares cross-validation method has lower bias (Seaman and Powell 1996), but is likely to produce fragmented UDs due to under-smoothing with large data sets (Kie *et al.* 2010). Fieberg (2007b) recommended less smoothing with large sample size, something that is accomplished with least-squares cross-validation relative to the reference method. The fragmentation issue disappeared following the buffering procedure in all but 3 cases (transient individuals). I implemented UD methods for these habitat analyses with Hawth's Tools (Beyer 2007) in ArcGIS (v. 9.3; ESRI 2008).

Within each buffered UD, I generated twice as many random points as there were filtered GPS telemetry locations. Random points were distinct for each individual regardless of buffered UD spatial overlap. Data masking (i.e., portions of GIS layers excluded from sampling) was limited to raster pixels representing ocean (i.e. random points that were classified as ocean from land cover and shoreline data were excluded as valid locations because the ocean in this region is free from ice cover throughout the year). Points on freshwater bodies were retained as these areas are commonly used during the winter months (i.e. when ice covered) by coyotes for travel and possibly for hunting ungulate prey.

3.2.5. Landscape Data

I followed the general approach to habitat modelling of using readily available datasets to rank likelihood of use by coyotes in the MBE. Topographic parameters often function as surrogates for more direct gradient variables due to micro-climatic and biotic community associations, but tend to limit functional geographic extent of models (Guisan and Zimmermann 2000). I extracted elevation, slope, and aspect data from the Canada3D digital elevation model (NRC 2001). As an alternative means of classifying topography, I incorporated topographic convergence index (TCI) values generated by Skinner (2011) for the island of Newfoundland. The TCI is a proxy for surface moisture based solely on DEM components slope, aspect, and steepness. High values of TCI represent highly drained areas and low values represent areas of moisture collection. I used land cover classification values from the Earth Observation for Sustainable Development of Forests

(EOSD) dataset (Wulder *et al.* 2004) to represent plant communities in the MBE. It has been noted that the EOSD data may not be as reliable as provincial forest resource inventory data for the island of Newfoundland (Saunders 2010), but the EOSD dataset is the most comprehensive for classifying land cover in the MBE, due to the lack of forest cover in this region. Following previously stated hypotheses of caribou refugia and coyote hunting success, I created distance rasters from nearest water body of 5 ha, 1 ha, and any surface water as delineated in the National Hydro Network (NRC 2007a). I assessed potential avoidance of higher human use areas by creating a distance from nearest road raster using the National Road Network (NRC 2007b). These layers were sampled at all random and GPS telemetry locations using the GIS.

3.2.6. Predictive Distribution Models

Point attributes from the habitat data described above were used to determine the best predictive model of coyote habitat use from the existing data. I explored both generalized linear mixed-effect models and boosted regression trees (BRT) to maximize predictive success with the available habitat data for the MBE. Boosted regression tree models outperformed generalized linear mixed-effect models based on predictive performance with an independent dataset (see Chapter 2). In fact, the mixed-effect model predictions were no better than random, indicating limited explanatory power at the population level. Therefore, in this chapter I report only BRT results.

Boosted regression trees are algorithmic models for identifying patterns in data. This exploratory approach makes no assumptions about data structure or underlying distributions. The BRT model is a forward, stagewise series of decision trees constructed from the pseudo-residuals of the preceding tree (see Friedman (2001, 2002), Ridgeway (2007), and Elith *et al.* (2008) for complete details). This type of tree-based algorithmic model is robust to missing data, non-linear response, and high-level interactions (De'ath and Fabricius 2000) while predicting beyond the range of training data (Hastie *et al.* 2009).

I followed the recommendations of Hastie *et al.* (2009) and Ridgeway (2007) to set BRT algorithm parameters (see Chapter 2 for details). The BRT model was implemented in R using the gbm package (Ridgeway 2010) with additional code (Elith *et al.* 2008) to minimize the cross-validation deviance as a means to optimize number of trees in the final model.

3.2.7. Model Evaluation

Model evaluation was incorporated at two stages. During model calibration, 10-fold cross-validation of the bag fraction (subset of data used to construct the decision tree) was used to assess predictive performance at each iteration. In addition, I withheld approximately 25% of the location data for evaluation purposes. These evaluation data were temporally independent of the calibration data and composed of locations from 3 individuals within the training data and 4 new individuals (see Chapter 2 for details). A new set of random locations was generated to correspond to this withheld evaluation data following the same procedures as above. I assessed predictive performance of the BRT model using this temporally independent data with the area under the relative operating characteristic curve (AUC) using the ROCR package (Sing *et al.* 2009).

I also assessed accuracy across the range of values with correct classification rate using the ROCR package. This metric was employed to quantify the ability of the model to distinguish between binary classes, not to determine any threshold value for classification of sites. Threshold values are often misleading in that correct classification rate is dependent on prevalence (Fielding and Bell 1997). The design of this study dictated a prevalence of 33% within the dataset. Thus, any point where accuracy is above 67% indicates an improvement over random chance.

3.3. Results

3.3.1. Home Range Overlap

There was substantial spatial flux in coyote seasonal home ranges through the study period. Values of Bhattacharyya's affinity ranged from 0.23 to 0.96 across all seasons and individuals (Appendix C). Individual coyote home range overlap did not differ significantly ($F_{4, 180} = 0.14$, $p = 0.97$) between seasons (0.784 ± 0.037 ($\bar{x} \pm$ SE); summer and winter locations pooled across years), within seasons across years (winter = 0.748 ± 0.030; summer = 0.765 ± 0.111), through consecutive seasons (0.763 ± 0.022), and among all seasons (0.765 ± 0.017). Two outliers in the dataset were both second year males that may have been transient rather than territorial.

3.3.2. Predicting Coyote Distribution

The BRT model that I developed indicates that unmeasured quantities have a strong effect on coyote space use in the MBE as indicated by the variable for individual being most influential (Table 3.2). Among measured quantities, distance to nearest road, elevation, distance to water body (≥ 1 ha), EOSD land cover class, and distance to large water body (≥ 5 ha) were most influential to the BRT model (Figures 3.4-3.8). Each of these predictors was incorporated in more than 5% of the 6500 boosted trees that made up the final model.

Other predictors included in the BRT model were not very influential. These include calendar year as a means to control for annual variations, coyote age class to determine if pups or likely dispersing juveniles used the landscape in a different manner from adults, and sex. Each of these 3 "control" predictors was selected in fewer than 2.5% of constituent trees. The topographic components – slope, aspect, and TCI – along with distance to surface water each contributed less than 4% (Figures 3.9-3.12). Distance to surface water has a very limited range of values in this wet climate and poorly drained landscape. Most important from a caribou ecology perspective was the effect of season on space use. Somewhat surprisingly, season was included in just over 1% of trees in the model. Interestingly, sex and season were found to have no "significant" contribution according to the simplification process of Elith *et al*. (2008; see Chapter 2 for simplified BRT model results).

3.3.3. Model Evaluation

The strong relative influence of individual in the BRT model indicated that I was missing important predictors for characterizing coyote space use. Within the training data, the BRT performed extremely well (10-fold cross-validation AUC = 0.92). Independent test data indicated much higher uncertainty in predictions. When accounting for known individual variation in space use, the model reliably predicted future coyote locations ($AUC > 0.7$), whereas model predictions for previously unknown individuals were no better than random ($AUC \approx 0.5$; Figure 3.13). Thus, my BRT model results are likely limited in inferential power to assess predictions outlined in the introduction. Cutoff values varied over the possible range of values and exhibited a peak correct classification rate near 68% (Figure 3.14). This measure indicates little improvement over random chance as the peak in accuracy is only slightly above prevalence within the dataset. Again, the modest success of the BRT model is likely a product of insufficient causal input data.

The BRT model predicted 2 primary areas of coyote use in the central MBE (Figure 3.15). The central portion of the Middle Ridge CMA contained a concentration of relatively high-use predictions, although the area to the east of Eastern Meelpaeg in the Bay du Nord Wilderness Reserve was predicted as low relative use. An even greater concentration of high-use was predicted in the central Grey River CMA across the plateau from the head of Bay de Vieux to the head of Facheux Bay. Interestingly, while both of these areas are historically important caribou wintering areas, the intensity of coyote use is more dispersed during the winter period. Relative low-use areas were predicted along the immediate coastline and through the centre of the study area. These low-use predictions likely reflect the negative association of coyotes to both roads and developed areas shown in the partial dependence plots (Figures 3.4, 3.7). Large lakes also stand out as predicted low-use during all seasons. Besides these areas there was a general pattern of moderate use across the MBE, interspersed with both high and low use patches. Little difference can be seen between seasons or sexes as indicated by the relative influence measures (Table 3.2) and spatial predictions of use (Figure 3.15).

3.4. Discussion

My research focused on the individual scale of coyote spatial dynamics to address the question of response to seasonal caribou abundance. Results indicated that a certain level of change is constant and no seasonal oscillation of space use occurs in relation to prey influx in the form of wintering caribou. Similarity in home range overlap through time suggests that some constant level of spatial flux to exploit resources in specific areas occurs within the MBE coyote population rather than distinct seasonal shifts. In particular, Bhattacharyya's affinity identified changes in distributions (i.e., KDE of use) that translate to the combined effects of changes in home range boundaries and intensity of use. Likely what I observed was individuals tracking changes in resource availability through time similar to other coyote populations (e.g., Kitchen *et al*. 2000). I did not specifically investigate age or social class as factors influencing individual home range overlap. Thus, it is likely that transient individuals were also monitored during this study and may account for the extremely low Bhattacharyya's affinity values seen in a few cases (Appendix C). While there may have been some adjustment to boundaries, most of the shifts were more likely due to within territory changes reflecting local resource availability. This is based on casual observation as I did not quantify absolute size of home ranges or proximity of conspecifics. The high degree of individual overlap indicated that coyotes were not making major shifts to congregate in areas of high caribou density. Coyotes in other areas have been found to alter use patterns within territories when concentrated and abundant food resources are present (Crête *et al*. 2001; Young *et al*. 2008). Though it is notable that highest ungulate density does not always indicate highest hunting effort by coyotes (Patterson *et al*. 1998), I did not have spatial data regarding caribou density to test this possible correlation specifically. In either possible scenario I cannot exclude the hypothesis that coyotes are focused on hunting caribou during winter in the MBE with these data alone.

The more influential BRT model predictors may provide useful insight to how and why coyotes are using the MBE landscape. Coyotes monitored for this research exhibited a negative response to roads within 8 km (Figure 3.4). Part of this response may be related to the limited number of roads within the MBE, basically representing the perimeter of the study area. However, these roads do provide human access to the MBE and may truly be avoided due to harvest pressure on coyotes. Elevation response was also determined to be negative below 150 m (Figure 3.5). Elevation may function as a surrogate for proximity to coastline where small communities exist within the MBE. Alternatively, coyotes may be selecting for high points within home ranges for calling, territory marking, or visual opportunity. Coyotes in this study tended to be found closer to water bodies thought to be large enough to provide escape opportunity for caribou in the ice-free period (≥ 1 ha; Figure 3.6). Land cover class was equally important to distance to water body in predicting where collared coyotes would be found. Coyotes in this study showed an affinity for tall shrub, herbaceous ground cover, dense broad-leaf forest, and dense and open mixed-wood forest cover types (Figure 3.7). Finally, proximity to large water bodies (≥ 5 ha) seemed to only have an effect at distances greater than 3 km (Figure 3.8). Coyotes tended to avoid locations at this greater distance possibly showing a preference for these larger water bodies for travel and hunting of caribou when they are ice covered.

Effects were also found among some of the less influential linear predictors of coyote space use. While these predictors did not contribute information to many of the trees in the BRT model, their effect on classifying coyote spatial distribution may still be important. Coyotes in the central MBE appeared to avoid slopes steeper than 17 degrees (Figure 3.9). Among the lower slope angles, the model indicated that use was highest up to 5 degrees and tended to decrease up to 17 degrees before a sharp decline. This may reflect both the ease of locomotion on lower angle slopes as well as the limited availability of higher angle slopes on the landscape. Steep slopes are often densely forested in the case of the river valleys or largely devoid of vegetation as rocky outcroppings and cliffs within the MBE. No apparent trend was found in coyote response to aspect of slope (Figure 3.10). The low influence on the model and wildly fluctuating response likely reflected random use of all aspects as a result of coyote association with low slope angles. In terms of proximity to all mapped surface water (i.e., lakes, ponds, rivers, and streams), coyotes tended to be located nearer to water with a steady decline to a distance of 500 m (Figure 3.11). This was similar to the trend noted for proximity to small water bodies and may also reflect a preference for flat areas that tend to accumulate water in small ponds and pools. Coyote response to TCI was highly varied, but exhibited a gradual positive trend throughout the range of values (Figure 3.12). Additionally, it appeared that coyotes avoided areas with TCI below 1, possibly due to these locations representing standing water.

The four lowest ranked predictors represented a combined influence of less than 5% in my BRT model. Demographic groups (sex and age) are unlikely to provide insight to space use by coyotes at the population level in the MBE. Eastern coyotes in particular tend to form cohesive family groups that travel and forage as a unit (Harrison 1992; Patterson and Messier 2001). This behaviour should mean that all individuals within any family group will have very similar patterns of resource utilization at the scale of this study. Variation in the MBE is likely occurring at a finer scale than the temporal partitions (season and year) used in this model. Spatial variation at the ecoregional scale probably determines more of the direct individual response.

Many habitat models developed for coyotes and other carnivore species focus largely on land cover types. Much of this research has taken a coarse-grained approach to classification and has found that rural agricultural areas provide superior coyote habitat compared to forested areas (Crête *et al.* 2001; Gompper 2002). Finer-grained approaches to modelling habitat within individual home ranges generally incorporate a wider array of potential variables. These include proximity to roads, structures and water, precipitation, topography, anthropogenic disturbance history and structural vegetation metrics (Gompper 2002; Kays *et al.* 2008; Boisjoly *et al.* 2010). The importance of these various metrics in predicting coyote habitat are often in opposition within the literature depending on the researchers' definitions and level of resolution. For example, roads may be negatively associated with coyote use when defined as high traffic corridors (Gompper 2002; Kays *et al.* 2008), but positively associated when they are used by coyotes for travel in more remote settings (Gompper 2002; Kolbe *et al.* 2007).

Another confounding factor in coyote habitat modelling has been the changing predictor associations through time, for example varied responses to land cover (Litvaitis and Harrison 1989; Person and Hirth 1991). Often these variations have been attributed to either changes in density of the primary prey (Murray *et al.* 1994; Carroll *et al.* 2000), the generalist diet of coyotes (Litvaitis and Harrison 1989), or annual life cycle requirements (Person and Hirth 1991). One approach to accounting for these changes has recently emerged in the form of mechanistic models. Moorcroft *et al.* (2006) found that prey abundance in a spatially explicit model provided significantly better predictions than a model with a more common proxy measure of terrain.

Available data often limit the applicability of any RSM. The landscape data I used for this study were no exception. Minimal gradient range, patchy distribution of gradients on the landscape, and coarse resolution of data relative to fine scale of the actual gradient all proved to restrict the insight into individual behavioural response. The minimal gradient ranges can be visualized in the random point attributes (decile plots in Figures 3.4 – 3.12). Surrogate data such as I used for the BRT model are likely to be less successful with these shallow gradients (Austin 2002). Extensive forest cover, slope, and range in elevation are concentrated in the major river valleys (Figure 3.3). These predictors exemplify patchy distribution of gradients on the landscape. Many habitat features influencing coyote behavioural responses (e.g., topographic features) are likely not captured at the coarse resolution of available datasets. Saunders (2010) describes how this could be the case with EOSD classification of the ecosystem in Newfoundland.

Forest structural components are not as refined in satellite image based EOSD as the provincial forest inventory (Saunders 2010). This may affect modelled outcomes where reflectance values fail to provide distinction among habitat that are perceived very differently by animals on the landscape. For example, Kays *et al*. (2008) showed the importance of the structural components of forest stands in predicting coyote use. The structural components such as stem density, fine scale edges, and tree height are possibly influential factors affecting coyote movements. Further refinements or increased coverage of existing land cover datasets could dramatically improve model performance with inclusion of these variables.

Evaluation criteria underscored the idea that the most important factors determining coyote space use are missing. Unmeasured influences were strongest in this coyote

RSM (e.g., individual behavioural response, relative prey density within home range). Area under the curve values indicate that overfitting may have been an issue with my BRT model (Vaughan and Ormerod 2005). Cross-validation prediction estimates performed very well; prediction of known individuals in a new time period were moderate; and predictions to new individuals were poor. This further implies that gradient data were inadequate for prediction rather than model overfitting *per se*.

Generalist species represent particularly challenging subjects for modelling in a novel landscape (Seoane *et al.* 2005; Evangelista *et al.* 2008). Defining the ecological niche for coyote in the MBE follows this pattern. Home-range-level habitat modelling with landscape-level GIS data tends to limit ecological insight, but can provide a useful starting point for directing further research efforts. Ground-truthing remotely-sensed datasets can be labour intensive and financially prohibitive, particularly in remote locations where individual animals roam over expansive areas. Focusing efforts with baseline models should facilitate targeting of sampling efforts to refine resource selection models. The "hot spots" identified in my BRT model of coyote habitat (i.e., Middle Ridge and Grey River CMAs) could be used as focal areas to collect more detailed data concerning potential drivers of coyote space use in the MBE. These hot spots may correspond to historical calving grounds, but recent information indicates that calving has become much more dispersed in recent years (NLDEC 2009).

Factors other than those I investigated in creating this BRT model are likely affecting coyote space use in the MBE. One major influence that was omitted due to lack of existing data was resource density. It has been shown that coyotes spatial patterns often mirror those of their primary prey species (Carroll *et al.* 2000; Kays *et al.* 2008). Complementary to this similarity in spatial patterns is the idea that coyote space use may also reflect prey density across the landscape and through time (Mills and Knowlton 1991; Patterson and Messier 2001). As a generalist predator, coyotes regularly alter their diets dependent on available foods. This dietary shift may be seen both seasonally (Appendix A) and throughout cycles of prey abundance (O'Donoghue *et al.* 1998a,b; Stoddart *et al.* 2001). Therefore, I would expect that some of the predictive power lacking in my final RSM may be attributed to spatio-temporal variability in diet composition and prey abundance.

Coyote habitat is known to reflect prey habitat coupled with vulnerability (O'Donoghue *et al.* 1998a; Patterson *et al.* 1998). The current lack of knowledge concerning prey habitat in the MBE added another layer of challenge to modelling. While limited prey species are available to coyotes in Newfoundland (see review in Chapter 1), these prey also occupy non-typical habitats. The patches of stunted conifer growth common throughout the MBE are generally quite small, often highly dispersed, and uncharacteristic of habitats occupied by snowshoe hare (*Lepus americanus*) or red squirrel (*Tamiasciurus hudsonicus*). Regardless, these two species were frequently seen in coyote diets in the MBE (Appendix A). Voles also appeared in the summer diet of coyotes. Due to a recent introduction and population expansion of red-backed voles (*Myodes gapperi*) in Newfoundland, native meadow vole (*Microtus pennsylvanicus terraenovae*) ecology is likely in a state of dramatic change (Hearn *et al.* 2006). Overall this lack of prey knowledge fails to inform a more detailed model of coyote habitat.

Prey density does not necessarily imply hunting success. Variation in prey vulnerability due to vegetation structure, snowpack, and landscape geomorphology can also play an important role (Murray *et al.* 1994; Kays *et al.* 2008). Individual coyotes will likely modify their behaviour to have the highest success rate of acquiring food items balanced with the reward of those items (Patterson *et al.* 1998). This again leads to a dynamic spatial process through time dependent on relative density of food items coupled with their accessibility.

Additional factors that may be affecting coyote space use in the MBE include environmental conditions and competitive interactions. Snow depth and hardness can alter coyote habitat use in both restricting movements (Murray *et al.* 1994; Gese *et al.* 1996) and increasing prey vulnerability (Patterson and Messier 2003). These effects can interact to complicate the observed response at different scales (Kays *et al.* 2008). Negative interspecific interactions observed in western North America (Carroll *et al.* 2000; Berger and Gese 2007) may be somewhat limited in Newfoundland due to the absence of wolves. However, dietary overlap with lynx, foxes, and black bears may have some level of influence on coyote movements. Conspecific avoidance is likely more important in the MBE as this type of interaction has been shown to shape coyote spatial dynamics throughout their range (e.g., Messier and Barrette 1982; Patterson and Messier 2001; Moorcroft *et al.* 2006).

Cosmopolitan habits of the coyote may represent a rare ecological case of the extreme generalist, but therefore make a useful case study in modelling. A species native to the western United States, coyotes have expanded and thrived across the continent following the widespread extirpation of wolves and habitat fragmentation as a result of agricultural and forestry development (Moore and Parker 1992; Gompper 2002; Boisjoly *et al*. 2010). Newfoundland is no exception to this, but does provide another example of the species' adaptive capabilities, both crossing sea ice in what was likely a multi-day trek (Moore and Parker 1992) as well as inhabiting a landscape depauperate in typical prey. The extreme home range sizes reported for Newfoundland (Blake 2006) are likely a reflection of the limited resource availability that coyotes have encountered since colonizing the island. This may again lead to a necessity in being a generalist. It has been observed that even Canada lynx, one of North America's most studied specialists (Aubry *et al*. 1999; Mowat *et al*. 1999) have taken on more of a generalist role on the island of Newfoundland, including exploitation of abundant caribou calves during the summer months (Saunders 1963; Bergerud 1971).

Based on landscape geometry, RSMs can incorrectly define selection of locations used in transition only (Moorcroft *et al*. 2006). Coyotes by nature are cursorial animals, a trait that may be magnified in the MBE where home ranges are expansive. Potential for patchy distribution of prey or long distance movements between prey encounters due to low density of food items will compound any effects of improper identification of sites selected by coyotes. Repeated observations of coyotes within the MBE travelling long distances (several kilometres) in a straight-line path (*J. Neville, personal communication*) support this concept. In light of this lack of information regarding behaviour at any given location, inference to selection at that location is limited. Diet analyses suggest the importance of ungulate carrion in coyote diets. This food source is likely discovered from extensive olfactory searching (Wells and Bekoff 1982) and not necessarily tied to any particular landscape feature if the carrion is a result of the recreational hunting season. Relative abundance of carrion on the landscape may also alter coyote hunting behaviour and thus any assessment of space use.

3.4.1. Management Implications

This research has shown that coyote predation risk for overwintering caribou is likely much less than what has been suggested from anecdotal evidence. While I cannot rule out intense localized effects, I did not find evidence to support the hypothesis that coyotes are actively targeting winter aggregations of caribou to the point of altering coyote territorial structure. Instead I found that individual variation is extremely high, indicating that individual coyotes are adapting to localized conditions and likely exploiting the most abundant and vulnerable food resources at a finer scale. This fits with what others have found regarding exploitation of highly vulnerable neonate caribou calves (Trindade *et al*. 2011).

What all of this may mean for management of a true generalist in this landscape is the necessity to track prey availability in one form or another. Ongoing autumn and winter diet analysis suggests a dynamic response both seasonally and across years by coyotes (McGrath *et al.* 2010). Additional data collected as part of this study investigated summer coyote diet and further highlights the breadth of seemingly opportunistic food exploitation (Appendix A). This dynamic response to food availability implies a necessarily spatio-temporal response to management of coyotes dependent on ecological and societal goals. A relatively static habitat model will be of limited value compared to the much more difficult and costly option of dynamic resource modelling. While determining mechanisms of coyote spatial associations may be challenging, the information gained for adaptively managing impacts on prey populations may prove worthwhile.

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Table 3.1. Individual GPS collared coyote age class representation in the central Maritime Barren Ecosystem of Newfoundland during the study period, 2005-2009.

Individual[1]	Seasons Monitored	Age Classes[2]
102	5	A
105	3	A
106	4	Y, A
107	3	Y, A
108	3	A
109	5	Y, A
110	3	P, Y
111	3	P, Y
112	3	A
113	3	A
201	3	Y, A
202	3	Y, A
203	2	Y, A
206	3	A
212	3	A
214	3	Y, A
215	4	Y, A
216	5	Y, A
217	3	Y, A
218	3	A
221	2	P, Y

[1] Each coyote was given a unique identifying number; 100 series for females, 200 series for males.

[2] Age classes were assigned as P = pup (< 1 year), Y = yearling (1-2 years), and A = adult (> 2 years) based on estimated birth date of April 1.

Table 3.2. Relative contribution of predictor variables from boosted regression tree model of coyote resource selection in the central Maritime Barrens Ecoregion of Newfoundland.

Predictor	Relative Influence (%)
ID	33.95
dRoad	19.93
Elev	10.03
dWater1ha	5.97
CovTyp	5.97
dWater5ha	5.66
Slope	3.99
Aspect	3.90
dWater	3.44
TCI	2.95
Year	2.13
Season	1.07
Age	0.98
Sex	0.03

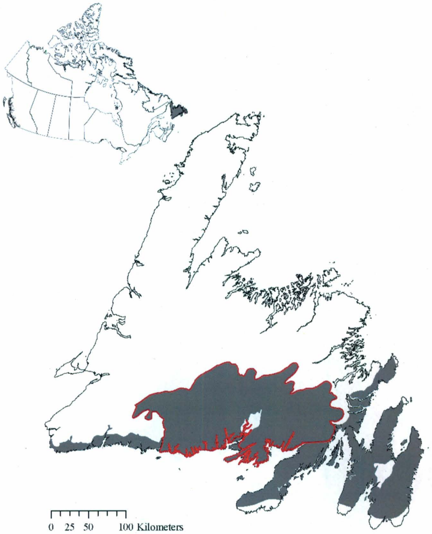

Figure 3.1. Maritime Barrens Ecoregion of Newfoundland (highlighted) with the central portion representing the study area for this research outlined in red. The island of Newfoundland is highlighted in the inset map of Canada.

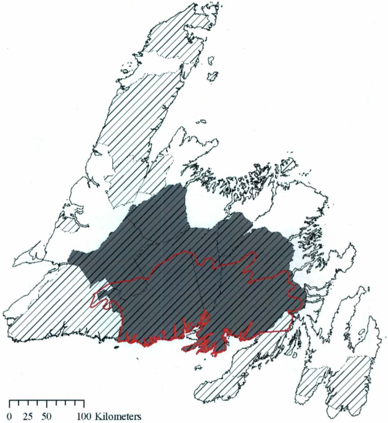

Figure 3.2. Caribou Management Areas (CMA) of the island of Newfoundland designated by the Department of Environment and Conservation, Wildlife Division. Highlighted CMAs (Buchans [Bu], Gaff Topsails [GT], Grey River [GR], Middle Ridge [MR], Mount Peyton [MP] and Pot Hill [PH]) are included in this research as representative of caribou populations that overlap with GPS monitored coyotes.

Figure 3.3. Aerial view of forest and barrens typical of the central Maritime Barrens Ecoregion of Newfoundland. Forested areas are generally restricted to steep-sided valleys (a) and protected slopes (d). Barrens (b, c) make up the majority of the study area composed of heathlands and peatlands interspersed with water bodies of various sizes.

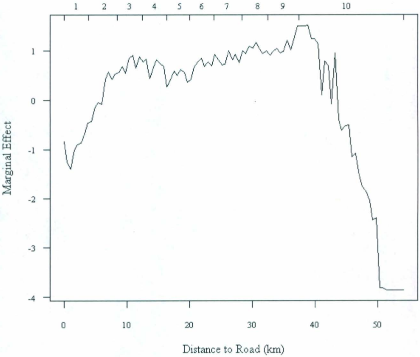

Figure 3.4. Partial dependence plot for distance to nearest road as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Distance to nearest road was included by the regression tree algorithm in 19.9% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

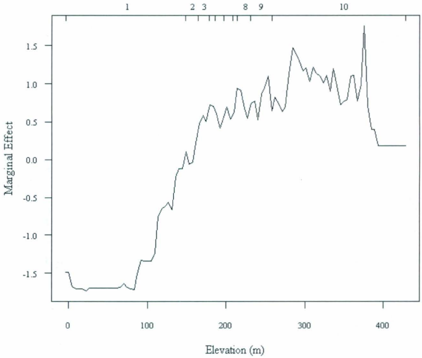

Figure 3.5. Partial dependence plot for elevation as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Elevation was included by the regression tree algorithm in 10.0% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

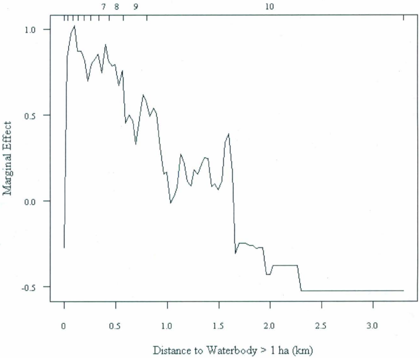

Figure 3.6. Partial dependence plot for distance to nearest body of water ≥ 1 ha as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Distance to nearest body of water ≥ 1 ha was included by the regression tree algorithm in 6.0% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

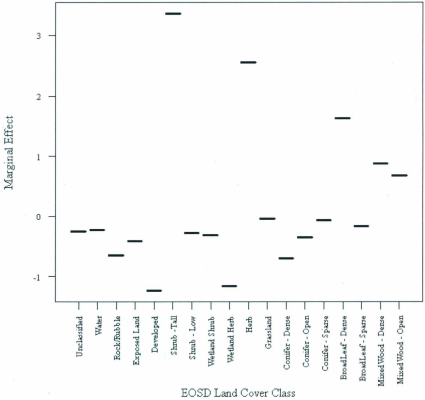

Figure 3.7. Partial dependence plot for Earth Observation of the Sustainable Development of Forests (EOSD) land cover class as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. EOSD land cover class was included by the regression tree algorithm in 6.0% of 6500 trees in the model.

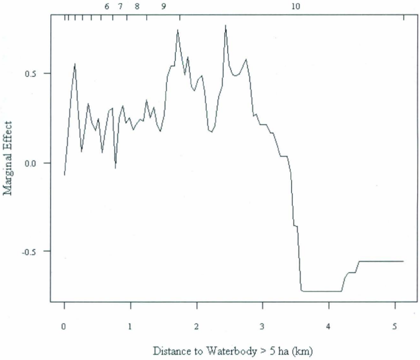

Figure 3.8. Partial dependence plot for distance to nearest body of water ≥ 5 ha as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Distance to nearest body of water ≥ 5 ha was included by the regression tree algorithm in 5.7% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

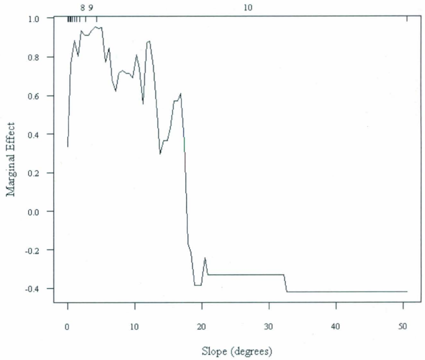

Figure 3.9. Partial dependence plot for slope as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Slope was included by the regression tree algorithm in 4.0% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

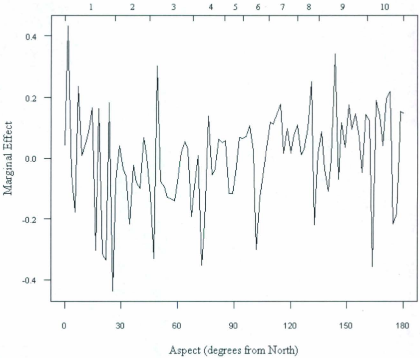

Figure 3.10. Partial dependence plot for aspect of slope relative to north as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Aspect of slope was included by the regression tree algorithm in 3.9% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

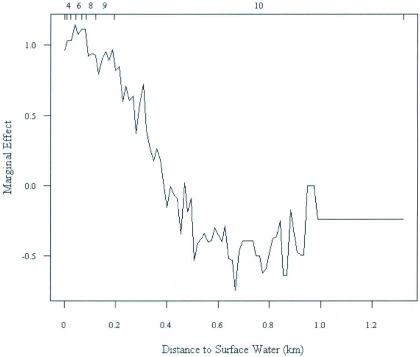

Figure 3.11. Partial dependence plot for distance to nearest surface water as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Distance to nearest surface water was included by the regression tree algorithm in 3.4% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

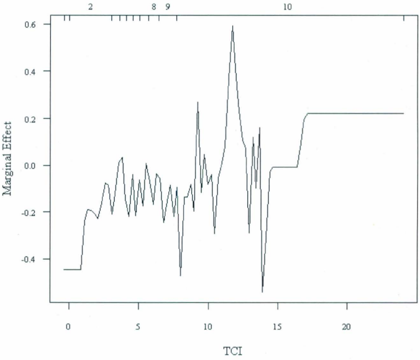

Figure 3.12. Partial dependence plot for topographic convergence index as predictor of coyote space use in the central Maritime Barrens Ecoregion of Newfoundland. Topographic convergence index was included by the regression tree algorithm in 3.0% of 6500 trees in the model. Tick marks at top of plot area represent deciles of data.

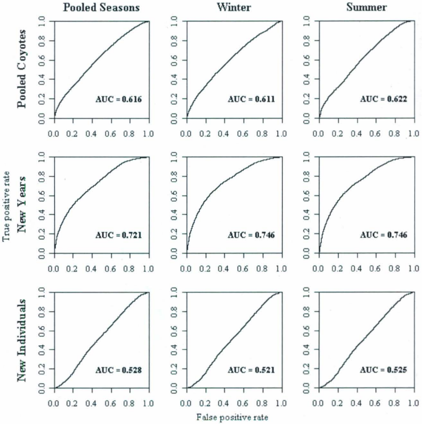

Figure 3.13. Relative operating characteristic (ROC) plots for prediction to an independent evaluation dataset from a boosted regression trees model of coyote resource selection within the central Maritime Barrens Ecoregion of Newfoundland. Area under the (ROC) curve (AUC) values provide of measure of reliability for model predictions under various conditions (i.e., all coyotes pooled, coyotes from the training data in a different time period, and new coyotes in a different time period) for each seasonal model and pooled predictions from both seasonal models.

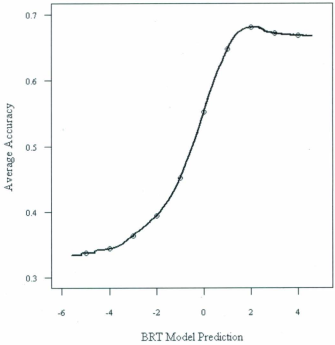

Figure 3.14. Cutoff plot showing the range of modelled response values for differentiating used and non-used geographic locations from a boosted regression tree (BRT) model of resource selection by coyotes in the central Maritime Barrens Ecoregion of Newfoundland.

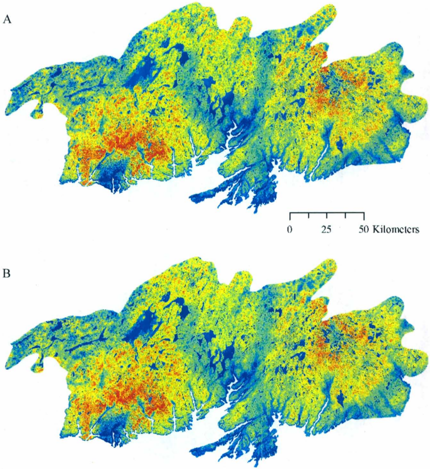

Figure 3.15. Spatial representations of predicted female coyote use during summer (a) and winter (b) from a boosted regression trees model for the central Maritime Barrens Ecoregion of Newfoundland. Blue and red colours represent predicted areas of low and high coyote use, respectively.

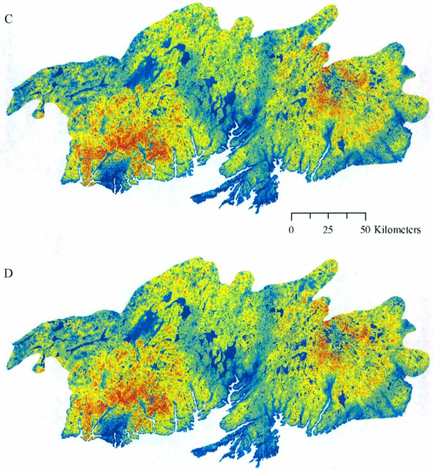

Figure 3.15 (continued). Spatial representations of predicted male coyote use during summer (c) and winter (d) from a boosted regression trees model for the central Maritime Barrens Ecoregion of Newfoundland. Blue and red colours represent predicted areas of low and high coyote use, respectively.

CHAPTER 4. SUMMARY AND CONCLUSIONS

4.1. Spatial Modelling

My thesis has shown that incorporating disparate modelling approaches in the study of a biological system with unknown strength of associations between available habitat data and species response can yield additional insight over a single model approach. In particular, I found that an algorithmic model can provide insight to underlying biological processes beyond the scope of the original dataset by functioning as a tool to refine hypotheses for future research.

Generalized linear mixed-effect models can be highly effective in refining our understanding when basic correlations are known *a priori*. The mixed-effect structure can account for autocorrelation and control for random effects so that we can more readily determine the associations among the effects of interest. However, these models carry some important distributional assumptions (Fieberg *et al.* 2009; O'Hara 2009). There is also the assumption of a linear relationship between response and explanatory variables.

Ensemble decision tree models are free from these assumptions of distribution and linear relationships, but the goal of accurate prediction in no way implies causal mechanism (Breiman 2001). However, accurate predictions can still function to guide short-term management. Resultant model predictions can also be used to focus future efforts designed to identify and quantify the causal mechanisms in a more efficient manner.

Removing as many statistical assumptions as possible will get us closer to identifying limiting factors at a given spatial scale, but we rely on underlying ecological assumptions in the relationship as well (O'Connor 2002). Recursive partitioning as a means of finding patterns in data when mechanism is unknown can provide more information regarding current relationships and directions for future research than making assumptions regarding ecological correlation in building confirmatory statistical models (Hochachka *et al.* 2007; Oppel *et al.* 2009).

Machine learning methods are data hungry and thus may have previously eluded resource selection modellers. We can make use of these emerging techniques now that the availability of data has expanded with GPS collars collecting high volume location data that can be combined with high resolution spatial datasets. Algorithmic models provide us an opportunity to gain insight into spatial processes by identifying important variables. Identifying these important surrogate variables should then allow us to more readily transition from modelling constraints and correlation to modelling causation.

4.2. Modelling Coyotes

I found that individual coyotes in the central Maritime Barrens Ecoregion (MBE) of Newfoundland maintain fairly static spatial patterns (Chapter 3) with home ranges more than 10 times the size of what they are in historical coyote range (Bekoff and Gese 2003; McGrath *et al.* 2010). However, individual adaptability was evident within each home range. I did not find specific within-home-range habitat associations that generalize to the population (see AUC values for prediction to new individuals in Chapter 3). The lack of pattern in my models based on commonly used surrogate data (Chapter 2) is likely due to individual behavioural adaptations to available resources in time and space.

I suggest that direct food resource data are essential to modelling coyotes effectively in this landscape and should lead to improved predictions guiding management action. Within the depauperate ecosystem of Newfoundland there exists a high degree of spatio-temporal flux in food availability. The vast majority of the island's caribou migrate between summer and winter range. Moose and caribou hunting seasons result in a flush of carrion on the landscape. Snowshoe hare populations experience cyclical trends characteristic of the species throughout the boreal region of Canada, though asynchronous with mainland populations and with varying amplitude (Joyce 2001). Coyote populations themselves experience substantial mortality from hunting and trapping (McGrath *et al.* 2010), which opens territories and reduces intraspecific resource competition at local scales.

4.3. Adaptation to Prey Abundance

Coyotes occupy a broad dietary niche throughout their range with Newfoundland being no exception (Appendix A; McGrath *et al.* 2010). The limited diversity of mammalian fauna available as food resources for coyotes (see Chapter 1 for list of Newfoundland mammals) coupled with the extraordinary size of home ranges (McGrath *et al.* 2010) indicates that food limitation may be a significant factor in the ecology of coyotes on the island. Therefore any food resource is likely to be exploited to the greatest extent possible. This may exaggerate community-level effects of predation with temporal variation in prey species distribution and abundance.

Accurate predictive models of prey species may be beneficial as inputs to coyote spatial models (Kays *et al*. 2008). Adaptability is key to success at the most basic level of individual fitness for coyotes likely at the extreme of their foraging niche in the MBE. Generalist predators adapt to changes in prey density and vulnerability through time. The temporal scale of these changes can have significant implications for both predator and prey dynamics (Owen-Smith and Mills 2008).

4.4. Implications for Caribou

Individual variation among coyotes' spatial patterns could mask locally intense caribou calf predation during the early summer months now that calving is more dispersed (NLDEC 2009). The MBE is a novel landscape and biological system for coyotes. However, we know that landscape configuration and habitat interact with prey availability to increase coyote predation pressure on caribou in managed forests (Boisjoly *et al*. 2010). Similar managed landscapes have been shown to be avoided by caribou in Newfoundland irrespective of predation (Schaefer and Mahoney 2007). Calf recruitment is also negatively associated with disturbed forest landscapes (McCarthy *et al*. 2011). While this is not really an issue in the MBE where little to no anthropogenic landscape modification has occurred in the past century, other landscape characteristics may similarly affect caribou predation risk.

Numerous researchers across coyote range have shown the strong association between coyote space use and the availability and vulnerability of prey (e.g., Mills and Knowlton 1991; Murray *et al.* 1994; Patterson and Messier 2001). I did not find any strong indication of the coyote population in the MBE focusing efforts on hunting caribou over other prey during winter months. While herbaceous cover types may have been used for travel or hunting caribou, the association of coyotes with tall shrub and dense broad-leaf cover types (Chapter 3) may correspond with habitat use by snowshoe hares. My preliminary summer diet analysis (Appendix A) supports the idea that coyotes are opportunistic foragers with caribou as a substantial component of early summer diet along with snowshoe hare, birds, berries, and voles.

4.5. Conclusions

In light of the factors outlined above and the fact that populations of coyotes have continued to expand while caribou populations have declined dramatically, we need to identify and quantify mechanisms driving coyote ecology on the island of Newfoundland. Understanding the mechanisms of coyote behaviour will better inform management action. Measuring direct gradients is often considered cost prohibitive, but accounting the cost of GPS monitoring makes prey abundance measures a relatively reasonable addition for the quality of information and resultant models. Determination of community interactions will require following trends through time as prey abundance changes (i.e., snowshoe hare cycle, moose harvest levels, future caribou demography). Once causal mechanisms have been identified and measured, mechanistic models (e.g., Mitchell and Powell

2004; Moorcroft and Barnett 2008) can be developed. This will allow researchers to predict the specific outcome of population perturbations (Moorcroft *et al.* 2006).

If caribou population declines continue, mortality factors will need to be addressed. Simple population control measures for coyotes have been determined ineffective as a long-term solution for alleviating predation on caribou in Québec (Mosnier *et al.* 2008). Therefore, habitat and alternative prey management may represent the most efficacious measures. Considering that habitat alteration is not an issue in the MBE, a focus on the suite of prey species is warranted. Availability of moose carcasses and vulnerability of snowshoe hares may be increasing predation risk for caribou (Boisjoly *et al.* 2010). My research provides a foundation in identifying areas requiring further investigation. Individual variation is strongly affecting space use, but in that context other factors emerge as influential as well. These landscape characteristics may hold more direct keys to coyote resource selection such as food availability and protection from persecution.

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APPENDIX A. SUMMER DIET OF COYOTES IN THE BARRENS OF NEWFOUNDLAND

A.1. Introduction

Coyotes (*Canis latrans*) have recently colonized the island of Newfoundland (Moore and Parker 1992) and may be having profound effects on natural communities. One of the species that may be most negatively affected is the native woodland caribou (*Rangifer tarandus caribou*). Public and management interest follow assertions that coyote predation is a major contributing factor in population declines (NLDEC 2008). While much of the coyote ecological niche remains unknown (Chapter 3), there is some evidence that coyotes are contributing to these dramatic caribou declines via calf mortality (Trindade *et al.* 2011).

While commonly considered to be the consummate generalist (Andelt 1987; Bekoff and Gese 2003), coyotes are not purely opportunistic predators (MacCracken and Hansen 1982). Multiple factors can influence coyote foraging behaviour including type and level of human disturbance (Dumond *et al.* 2001), environmental conditions (Andelt *et al.* 1987; Patterson *et al.* 1998), relative and absolute density of available prey (Bartel and Knowlton 2005; Prugh 2005), and landscape type (Andelt *et al.* 1987; Tremblay *et al.* 1998). Therefore, the interplay of these and other factors affecting coyote foraging behaviour in Newfoundland can lead to dramatically different consequences for caribou.

Diet analysis can provide a basis for understanding the mechanisms driving carnivore ecology. Preliminary investigations of autumn and winter diets of coyotes in Newfoundland from stomach contents of harvested individuals began in 2000 (Bridger 2005) and have been well documented since 2005 (McGrath *et al.* 2010). This research has shown that caribou makes up a significant proportion of coyote diet, particularly during late-winter months, but is declining through time. Yet, there remains a knowledge gap regarding summer diets. This is a period of potentially high prey consumption as new pups are born in a population with high reproductive rates (McGrath *et al.* 2010). Here, I provide a snapshot of coyote summer diet from scat contents analysis. Scats offer opportunity for non-invasive study of carnivore diets throughout the year (Seton 1925) and have been shown to be a reliable indicator of coyote diet when compared with more direct evidence of foraging behaviour (Prugh 2005).

A.2. Methods

The Maritime Barrens Ecoregion (MBE) was selected as a study site by the Newfoundland and Labrador Wildlife Division for deployment of Global Positioning System (GPS) collars on coyotes. This ongoing research project facilitated collection of coyote scats for my research. The MBE is the historical wintering ground for a large proportion of the island's woodland caribou population (Bergerud 1971). Many other potential prey species inhabit the MBE also (Chapter 1). However, prey density estimates were not available for these species across the study area. Thus, I focused solely on consumption irrespective of availability.

Adequate sample sizes are required to develop accurate conclusions regarding diet based on scat contents. These sample sizes typically must be large, particularly for species with more generalist dietary habits (Trites and Joy 2005). I collected more than 83 scats from 21 coyote GPS collar location clusters in the MBE during July 2009. Site visits were conducted in conjunction with Newfoundland and Labrador Wildlife Division efforts to obtain information on den habitat, reproductive success, and predation events. All sites were classified based on evidence collected at the site as either den, feeding, or unknown. The location cluster areas were searched and all putative coyote scats were collected. Scats were individually bagged and stored in a freezer until processing.

Each frozen scat was dried in an oven at 60°C for a minimum of 48 hours. I weighed scats as a means of standardizing content for biomass. I soaked scats in water for 12 hours or longer to aid break down, then rinsed each scat through a 0.5 mm sieve to extract macroscopic contents. I visually sorted contents and estimated percent volume to the nearest 5% based on hair for mammals (Kelly and Garton 1997) or other indigestible material for other items. I selected a representative sample of hairs from each scat and placed these on microscope slides in a thin layer of polyurethane spray. Following room temperature drying, I identified scat contents based on medulla and negative cuticle scale patterns using guide books (Day 1966; Adorjan and Kolenosky 1969; Teerink 1991; Jones *et al*. 2009) and a reference collection. Mammalian food items were categorized to species when possible, except in the case of voles (*Microtus pennsylvanicus terraenovae* and *Myodes gapperi*), which were grouped. Other categories included birds, arthropods, vegetation, and inorganic material.

Various methods exist for diet quantification from scats, each providing somewhat different information based on methodology (Ciucci *et al.* 1996; Cumberland *et al.* 2001; van Dijk *et al.* 2007). Various methods of analysis provide information useful to assess level of bias among methods. Weaver (1993) indicated that differential digestability among food items results in overestimation of relative importance for smaller prey items and underestimation of their numbers based solely on percent volume. Conversion of scat content data to estimate biomass may provide a more accurate assessment of diets than relative occurrence. However, the disparity among age classes, especially of large ungulates, can significantly skew biomass estimates when age of prey can not be determined from hairs (Weaver 1993). Another drawback of estimating biomass of ingested food from scats is the limitation of existing conversion equations to mammalian prey (Ciucci *et al.* 1996).

I estimated dry weight of food items by location cluster and overall percentage of occurrence in summer coyote diet. Items that occurred in trace amounts (i.e., < 5%) were excluded from calculations but reported as present in samples. Percentage of occurrence (PO), calculated as

$$PO_i(\%)=\frac{n_i}{\sum n_i}\times 100 \quad \text{(van Dijk \textit{et al.} 2007)}$$

where n_i is the number of scats containing species i, has been shown high concordance with actual ingested food items, but is still susceptible to the prey size bias (van Dijk *et* *al*. 2007). Ciucci *et al*. (1996) suggested that estimated dry weight (DW), calculated as

$$DW_i = \%\, volume_i \times DW_{scat} ,$$

is less affected by the prey size bias, but differential digestibility remains a concern. The combination of these two metrics provides more accurate qualitative information regarding ingested food items.

A.3. Results and Discussion

Global Positioning System location clusters were biased toward den sites. Eleven of 18 location clusters were determined to be den sites based on field evidence. Samples from seven of these sites included putative pup scats based on size and morphology (Table A1). Feeding sites with remnants of large cervids were also identified, while all other sites were not classified because evidence of other activity (e.g., resting, hunting, and territorial defence) is time sensitive and requires detailed observation beyond the scope of this research.

Coyotes in the MBE exhibited a generalist diet typical of the species. The variety of food items identified from scats included large and small mammals, birds, insects, and berries (Table A2). Bird remains represented a higher proportion of the diet in these data than previous analyses of autumn and winter diet (McGrath *et al*. 2010). Although individual bird species were not identified in scat contents, ptarmigan remains were specifically noted at multiple sites. Plant matter, largely in the form of berries, also represents a higher proportion of coyote diet in the summer, similar to other parts of eastern Canada (Samson and Crête 1997; Patterson *et al*. 1998; Dumond *et al*. 2001). The differences in rank order between percentage of occurrence and estimated dry weight (Table A2) reflect differences in digestibility of food items, diversity of items within samples, size of individual samples (Table A1), and prey size.

Significant interpretation is required to relate scat contents to diet and foraging behaviour. The presence of coyote hair and claws in scats is assumed to be a result of grooming behaviour or inadvertent self-mutilation while restrained in a foot-hold trap. Moose (*Alces americanus*) was likely consumed as carrion, although predation on moose calves cannot be ruled out. Caribou may have been consumed either as carrion or a result of predation; coyote predation on calves is known to occur (Trindade *et al*. 2011). All other animals in the diet are assumed to be a result of direct predation. It should be noted that larger prey items (i.e., caribou and moose) are likely to occur in multiple scats over time and each scat should not be considered equivalent to one animal consumed. As well, some scats will contain multiple individuals of smaller prey species. Remains of smaller prey in scats occur at a higher rate relative to consumed biomass and therefore may be overrepresented in diet analyses without the incorporation of a correction factor (Floyd *et al*. 1978; Weaver 1993).

Combining these data with autumn and winter diet data collected by McGrath *et al*. (2010) provides a more complete picture of coyote dietary niche in Newfoundland. Still missing is the selection behaviour of coyotes in acquiring food items that would provide greater insight to the implication of coyote predation as a contributor to caribou population declines across the range of ecosystem conditions. Biomass estimates of food items across the MBE supplemented to scat content data could provide the necessary information for investigating switching behaviour as abundance of foods changes through time (e.g., Prugh 2005).

Whether coyotes are currently focusing on caribou as a preferred prey species and likely to contribute to further population declines is a matter of ecological and socio-economic importance (Sutherland 2010; Festa-Bianchet et al. 2011). Generalist predators that adapt to prey availability can have destabilizing effects on prey populations where multiple alternative prey provide adequate food for predator subsistence (Fryxell and Lundberg 1994). Research in Québec indicated that changes in coyote diets through time may be affected more by availability of preferred prey than simply by abundance of species consumed (Samson and Crête 1997). Predation on caribou may vary through time as density of moose carrion and snowshoe hare (*Lepus americanus*) changes, or current coyote diets may be a result of the decrease in caribou abundance. The full scope of effects of coyote predation on caribou populations on the island of Newfoundland warrants concern and requires additional research to determine how coyote prey selection is affected by changes in prey densities.

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Table A1. Summary of coyote scats collected during summer 2009 from GPS collar location clusters in the Maritime Barrens Ecoregion of the island of Newfoundland.

Location Cluster ID	**Month of Locations**	**No. Scats**	**Site Type**	**Total Dry Weight (g)**
C3	May	1	*unknown*	20.61
C9	June	1	*unknown*	5.57
C15	June	4	den	40.76
C18	April	1	*unknown*	15.85
C20	April	1	feeding	28.72
C21	May	3	*unknown*	58.01
C24	May	3	*unknown*	57.53
C28	May	2	feeding	20.04
C29[1]	July	11	den	84.79
C30	April	1	den	23.01
C33[1,2]	June	> 5	den	82.56
C34	July	1	den	31.93
C35[1]	July	4	den	26.17
C38[1,2]	July	> 4	den	33.06
C39[1]	June	5	den	22.03
C40	July	1	*unknown*	11.11
C41	June	1	*unknown*	3.59
C43	June	1	*unknown*	16.77
C47	June	4	den	88.87
C48[1]	June	11	den	68.98
C49[1]	July	18	den	98.00

[1] Sample included putative pup scats. Determination was based on scat dimensions and/or presence of pups at site during sample collection.

[2] Numerous scats were amalgamated within a sample; the actual number of scats is unknown.

Table A2. Coyote scat contents from the Maritime Barrens Ecoregion of the island of Newfoundland collected July 2009.

	Percentage of Occurrence		Estimated Dry Weight		Scats with only Trace Amounts (< 5% volume)[1]
	%	rank	g	rank	
Woodland caribou	11.11	5	224.91	1	4
Snowshoe hare	12.96	4	212.69	2	2
Bird *spp.*	14.35	2	136.09	3	15
Vegetation[2]	25.93	1	93.09	4	23
Vole *spp.*	13.43	3	60.20	5	3
Moose	6.02	6	54.51	6	8
Squirrel	4.63	7	24.94	7	1
Mammal	1.39	10	24.88	8	3
Coyote[3]	2.78	9	18.87	9	1
Inorganic material	3.24	8	11.97	10	9
Cervid *spp.*	1.39	10	3.11	11	3
Muskrat	0.46	13	2.43	12	0
Masked shrew	0.46	13	0.79	13	1
Arthropod *spp.*	0.46	13	0.56	14	23
Beaver	1.39	10	0.39	15	2

[1] Food items occurring in trace amounts were not included in calculations for percentage of occurrence or estimated dry weight.

[2] Mostly composed of berries and grasses.

[3] Assumed to be a product of grooming behaviour or inadvertent self-mutilation while restrained in a foot-hold trap.

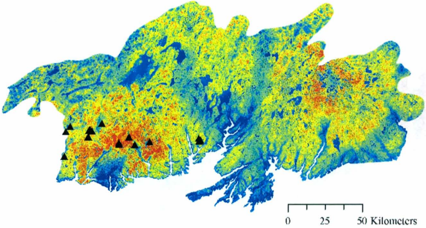

Figure A1. Locations of coyote GPS location clusters where scats were collected (▲) during July 2009 in the Maritime Barrens Ecoregion of Newfoundland. The background represents spatial predictions of relative use for adult female coyotes during summer from a boosted regression tree model (Chapter 3). Blue and red colours represent predicted areas of low and high coyote use, respectively.

APPENDIX B. GENERALIZED LINEAR MIXED-EFFECT MODELS

Table B1. Candidate generalized linear mixed-effect models to describe winter coyote habitat in the central Maritime Barrens Ecoregion of the island of Newfoundland.

Rank	**Model Formula**	**AIC**
1	Use~CovTyp+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	38171.85
2	Use~CovT+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	38261.00
3	Use~Cov+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	38275.12
4	Use~CovTyp+dRoad+dWater+Aspect+(Year|ID)	38300.15
5	Use~CovTyp+dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	38311.83
6	Use~CovTyp+dRoad+dWater5ha+Elev+Slope+Aspect+(Year|ID)	38350.24
7	Use~CovT+dWater+Elev+Slope+Aspect+(Year|ID)	38416.71
8	Use~Cov+dWater+Elev+Slope+Aspect+(Year|ID)	38421.48
9	Use~CovT+dRoad+Elev+Slope+Aspect+(Year|ID)	38456.58
10	Use~Cov+dRoad+Elev+Slope+Aspect+(Year|ID)	38467.66
11	Use~CovT+Elev+Slope+Aspect+(Year|ID)	38677.77
12	Use~Cov+Elev+Slope+Aspect+(Year|ID)	38680.26
13	Use~dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	38750.60
14	Use~Elev+Slope+Aspect+(Year|ID)	39088.50
15	Use~CovTyp+dRoad+dWater+Elev+(Year|ID)	42794.60
16	Use~CovTyp+dRoad+dWater+TCI+(Year|ID)	42834.51
17	Use~CovTyp+dRoad+dWater+(Year|ID)	42919.12
18	Use~CovTyp+dRoad+dWater1ha+TCI+(Year|ID)	42932.50
19	Use~CovTyp+dRoad+dWater5ha+TCI+(Year|ID)	42970.04
20	Use~CovTyp+dRoad+TCI+(Year|ID)	42974.63
21	Use~CovTyp+TCI+(Year|ID)	43394.59
22	Use~CovTyp+(Year|ID)	43513.33
23	Use~Cov+(Year|ID)	43643.90
24	Use~CovT+(Year|ID)	43647.55
25	Use~dRoad+dWater+(Year|ID)	43840.22
26	Use~CovTyp+Elev+Slope+Aspect+(Year|ID)	177363768

Table B2. Candidate generalized linear mixed-effect models to describe summer coyote habitat in the central Maritime Barrens Ecoregion of the island of Newfoundland.

Rank	Model Formula	AIC
1	Use~CovTyp+Elev+Slope+Aspect+(Year|ID)	20853.32
2	Use~Elev+Slope+Aspect+(Year|ID)	21021.88
3	Use~CovTyp+TCI+(Year|ID)	23459.45
4	Use~CovT+Elev+Slope+Aspect+(Year|ID)	32706.57
5	Use~CovTyp+dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	35933.24
6	Use~CovTyp+dRoad+dWater+Elev+Slope+Aspect+(Year|ID)	35961.04
7	Use~CovTyp+dRoad+dWater5ha+Elev+Slope+Aspect+(Year|ID)	36004.11
8	Use~CovT+dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	36020.83
9	Use~Cov+dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	36024.07
10	Use~CovTyp+dRoad+dWater1ha+Aspect+(Year|ID)	36034.44
11	Use~CovT+dRoad+Elev+Slope+Aspect+(Year|ID)	36091.42
12	Use~Cov+dRoad+Elev+Slope+Aspect+(Year|ID)	36093.82
13	Use~Cov+dWater1ha+Elev+Slope+Aspect+(Year|ID)	36129.40
14	Use~Cov+Elev+Slope+Aspect+(Year|ID)	36230.78
15	Use~dRoad+dWater1ha+Elev+Slope+Aspect+(Year|ID)	36520.22
16	Use~CovTyp+dRoad+dWater1ha+Elev+(Year|ID)	39293.16
17	Use~CovTyp+dRoad+dWater1ha+TCI+(Year|ID)	39363.47
18	Use~CovTyp+dRoad+dWater+TCI+(Year|ID)	39392.33
19	Use~CovTyp+dRoad+dWater1ha+(Year|ID)	39393.48
20	Use~CovTyp+dRoad+dWater5ha+TCI+(Year|ID)	39413.70
21	Use~CovTyp+dRoad+TCI+(Year|ID)	39414.44
22	Use~CovTyp+(Year|ID)	39820.43
23	Use~CovT+(Year|ID)	39947.50
24	Use~Cov+(Year|ID)	39965.74
25	Use~dRoad+dWater1ha+(Year|ID)	40682.79
26	Use~CovT+dWater1ha+Elev+Slope+Aspect+(Year|ID)	156971.70

APPENDIX C. BHATTACHARYYA'S AFFINITY MEASURES OF INDIVIDUAL SPATIAL OVERLAP ACROSS SEASONS

Table C1. Bhattacharyya's Affinity values for overlap of seasonal kernel density estimated utilization distributions for individual coyotes in the central Maritime Barrens Ecoregion of Newfoundland.

ID[a] **Age class**[b]		**Season × Season BA**[c]					**Pooled Seasonal BA**[d]
102		W2005	S2005	W2006	S2006	W2007	0.87358
A	W2005		0.90000	0.88924	0.89364	0.77889	
A	S2005			0.87881	0.89194	0.77028	
A	W2006				0.83948	0.88485	
A	S2006					0.69732	
A	W2007						
105		W2005	S2005	W2006			0.89520
A	W2005		0.92789	0.79045			
A	S2005			0.84464			
A	W2006						
106		W2006	S2006	W2007	S2007		0.86966
Y	W2006		0.58424	0.57194	0.55717		
A	S2006			0.92897	0.83070		
A	W2007				0.87183		
A	S2007						
107		W2006	S2006	W2007			0.56978
Y	W2006		0.60816	0.59108			
A	S2006			0.44415			
A	W2007						
108		W2007	S2007	W2008			0.85127
A	W2007		0.77166	0.78147			
A	S2007			0.88276			
A	W2008						

Table C1 (continued).

ID[a]	Age class[b]		Season × Season BA[c]					Pooled Seasonal BA[d]
109			W2007	S2007	W2008	S2008	W2009	0.90103
	Y	W2007		0.92322	0.91475	0.86598	0.84311	
	A	S2007			0.92167	0.90469	0.86693	
	A	W2008				0.84148	0.91215	
	A	S2008					0.74445	
	A	W2009						
110			W2007	S2007	W2008			0.66989
	P	W2007		0.86507	0.49742			
	Y	S2007			0.50567			
	Y	W2008						
111			W2007	S2007	W2008			0.56832
	P	W2007		0.54424	0.57101			
	Y	S2007			0.58227			
	Y	W2008						
112			W2008	S2008	W2009			0.75440
	A	W2008		0.80822	0.71890			
	A	S2008			0.70019			
	A	W2009						
113			W2008	S2008	W2009			0.81272
	A	W2008		0.75809	0.49055			
	A	S2008			0.61244			
	A	W2009						
201			W2005	S2005	W2006			0.94164
	Y	W2005		0.91570	0.74333			
	A	S2005			0.85199			
	A	W2006						
202			S2006	W2007	S2007			0.85095
	Y	S2006		0.67030	0.22790			
	A	W2007			0.59341			
	A	S2007						

Table C1 (continued).

ID[a] Age class[b]		Season × Season BA[c]					Pooled Seasonal BA[d]
203		W2005	S2005				0.25269
Y	W2005		0.25269				
A	S2005						
206		W2006	S2006	W2007			0.78914
A	W2006		0.85276	0.86275			
A	S2006			0.70759			
A	W2007						
212		W2007	S2007	W2008			0.71001
A	W2007		0.78126	0.60326			
A	S2007			0.57609			
A	W2008						
214		W2007	S2007	W2008			0.92498
Y	W2007		0.68340	0.48492			
A	S2007			0.89941			
A	W2008						
215		W2007	S2007	W2008	S2008		0.89522
Y	W2007		0.70872	0.84359	0.87499		
A	S2007			0.83523	0.76842		
A	W2008				0.89037		
A	S2008						
216		W2007	S2007	W2008	S2008	W2009	0.94075
Y	W2007		0.88738	0.87958	0.85977	0.87673	
A	S2007			0.94647	0.96456	0.91333	
A	W2008				0.91544	0.90106	
A	S2008					0.90674	
A	W2009						
217		W2007	S2007	W2008			0.89335
Y	W2007		0.77167	0.81365			
A	S2007			0.90640			
A	W2008						

Table C1 (continued).

ID[a] **Age class**[b]			**Season × Season BA**[c]		**Pooled Seasonal BA**[d]
218		W2008	S2008	W2009	0.64647
A	W2008		0.55940	0.70715	
A	S2008			0.65422	
A	W2009				
221		W2008	S2008		0.84975
P	W2008		0.84975		
Y	S2008				

[a] Females are represented by 100 series identifiers; males are represented by 200 series identifiers.

[b] Age class was determined based on field ageing techniques. Individuals were classified as either pup (P; < 1 year old), yearling (Y; ≥ 1 and < 2 years old), or adult (A; ≥ 2 years old) based on presumed birth date of April 1.

c Bhattacharyya's Affinity (Fieberg and Kochanny 2005) values were calculated for comparison between each pair of seasonal kernel density estimated utilization distributions (KDEs) by individual. Seasons were delineated as summer (S) and winter (W) based on mean date of caribou migration (May 10 and November 1; Mahoney and Schaefer 2002).

[d] Bhattacharyya's Affinity values were calculated for KDE of winter locations pooled across all years compared with KDE of summer locations pooled across all years for each individual.

Table C2. Summary statistics of Bhattacharyya's Affinity values measuring seasonal overlap of coyote kernel density estimated utilization distribution by individual in the central Maritime Barrens Ecoregion of Newfoundland.

	Winter[a]	**Summer**[a]	**Consecutive**[b]	**All**[c]	**Pooled Seasonal**[d]
n	24	6	48	86	21
Mean	0.75	0.76	0.76	0.76	0.78
Standard Deviation	0.15	0.27	0.16	0.16	0.17
Standard Error	0.03	0.11	0.02	0.02	0.04
Minimum			0.25269	0.22790	
Maximum			0.94647	0.96456	

[a] Kernel density estimated utilization distributions (KDEs) were evaluated for overlap of seasonal pairs (i.e., winter or summer) across all year combinations by individual.

[b] KDEs were evaluated for overlap between consecutive seasons only by individual.

[c] All pair combinations of seasonal KDEs were evaluated for the entire monitoring period by individual.

[d] Locations were pooled by season across all years and overlap of pooled KDEs was evaluated by individual.

C.1. References

Fieberg J, Kochanny CO. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69(4):1346-1359.

Mahoney SP, Schaefer JA. 2002. Long-term changes in demography and migration of Newfoundland caribou. Journal of Mammalogy 83(4):957-963.