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Integrating functional connectivity and climate change in the design of protected area networks

Thèse

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Doctorat en sciences forestières

Philosophiæ doctor (Ph.D.)

Québec, Canada

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Résumé

Le rapide déclin actuel de la biodiversité est inquiétant et les activités humaines en sont la cause directe. De nombreuses aires protégées ont été mises en place pour contrer cette perte de biodiversité. Afin de maximiser leur efficacité, l'amélioration de la connectivité fonctionnelle entre elles est requise. Les changements climatiques perturbent actuellement les conditions environnementales de façon globale. C'est une menace pour la biodiversité qui n'a pas souvent été intégrée lors de la mise en place des aires protégées, jusqu'à récemment. Le mouvement des espèces, et donc la connectivité fonctionnelle du paysage, est impacté par les changements climatiques et des études ont montré qu'améliorer la connectivité fonctionnelle entre les aires protégées aiderait les espèces à faire face aux impacts des changements climatiques.

Ma thèse présente une méthode pour concevoir des réseaux d'aires protégées tout en tenant compte des changements climatiques et de la connectivité fonctionnelle. Mon aire d'étude est la région de la Gaspésie au Québec (Canada). La population en voie de disparition de caribou de la Gaspésie-Atlantique (*Rangifer tarandus caribou*) a été utilisée comme espèce focale pour définir la connectivité fonctionnelle. Cette petite population subit un déclin continu dû à la prédation et la modification de son habitat, et les changements climatiques pourraient devenir une menace supplémentaire. J'ai d'abord construit un modèle individu-centré spatialement explicite pour expliquer et simuler le mouvement du caribou. J'ai utilisé les données VHF éparses de la population de caribou et une stratégie de modélisation patron-orienté pour paramétrer et sélectionner la meilleure hypothèse de mouvement. Mon meilleur modèle a reproduit la plupart des patrons de mouvement définis avec les données observées. Ce modèle fournit une meilleure compréhension des moteurs du mouvement du caribou de la Gaspésie-Atlantique, ainsi qu'une estimation spatiale de son utilisation du paysage dans la région. J'ai conclu que les données éparses étaient suffisantes pour ajuster un modèle individu-centré lorsqu'utilisé avec une modélisation patron-orienté. Ensuite, j'ai estimé l'impact des changements climatiques et de différentes actions de conservation sur le potentiel de mouvement du caribou. J'ai utilisé le modèle individu-centré pour simuler le mouvement du caribou dans

des paysages hypothétiques représentant différents scénarios de changements climatiques et d'actions de conservation. Les actions de conservation représentaient la mise en place de nouvelles aires protégées en Gaspésie, comme définies par le scénario proposé par le gouvernement du Québec, ainsi que la restauration de routes secondaires à l'intérieur des aires protégées. Les impacts des changements climatiques sur la végétation, comme définis dans mes scénarios, ont réduit le potentiel de mouvement du caribou. La restauration des routes était capable d'atténuer ces effets négatifs, contrairement à la mise en place des nouvelles aires protégées. Enfin, j'ai présenté une méthode pour concevoir des réseaux d'aires protégées efficaces et j'ai proposé des nouvelles aires protégées à mettre en place en Gaspésie afin de protéger la biodiversité sur le long terme. J'ai créé de nombreux scénarios de réseaux d'aires protégées en étendant le réseau actuel pour protéger 12% du territoire. J'ai calculé la représentativité écologique et deux mesures de connectivité fonctionnelle sur le long terme pour chaque réseau. Les mesures de connectivité fonctionnelle représentaient l'accès général aux aires protégées pour le caribou de la Gaspésie-Atlantique ainsi que son potentiel de mouvement à l'intérieur. J'ai utilisé les estimations de potentiel de mouvement pour la période de temps actuelle ainsi que pour le futur sous différents scénarios de changements climatiques pour représenter la connectivité fonctionnelle sur le long terme. Le réseau d'aires protégées que j'ai proposé était le scénario qui maximisait le compromis entre les trois caractéristiques de réseau calculées.

Dans cette thèse, j'ai expliqué et prédit le mouvement du caribou de la Gaspésie-Atlantique sous différentes conditions environnementales, notamment des paysages impactés par les changements climatiques. Ces résultats m'ont aidée à définir un réseau d'aires protégées à mettre en place en Gaspésie pour protéger le caribou au cours du temps. Je crois que cette thèse apporte de nouvelles connaissances sur le comportement de mouvement du caribou de la Gaspésie-Atlantique, ainsi que sur les actions de conservation qui peuvent être prises en Gaspésie afin d'améliorer la protection du caribou et de celle d'autres espèces. Je crois que la méthode présentée peut être applicable à d'autres écosystèmes aux caractéristiques et besoins similaires.

Abstract

The world is facing worrisome declines in biodiversity. Species extinction rates have increased as a direct consequence of human activities. Protected areas have been implemented around the world in an effort to counter biodiversity loss. Although protected areas are part of the solution, they should be designed systematically in a way to maximize their effectiveness. Enhancing functional connectivity between protected areas is one way to increase their effectiveness. Climate change is disrupting environmental conditions globally. It is a threat to biodiversity that until recently was not often integrated into protected area design. Climate change has been shown to impact species movements, and therefore landscape functional connectivity. Some studies have suggested that enhancing functional connectivity between protected areas can also help species cope with climate change impacts.

My thesis presents a methodology to design protected area networks while accounting for climate change and functional connectivity. My study area is located in the natural region of Gaspésie in Québec (Canada). The endangered Atlantic-Gaspésie population of woodland caribou (*Rangifer tarandus caribou*) was used as the focal species to define functional connectivity. This small population is in long-term decline due to predation and habitat change, but climate change may become an additional threat. First, I built a spatially explicit individual-based model to explain and simulate caribou movement. I used sparse VHF data available at the time of the study to select and parameterize a movement model using a pattern-oriented modeling strategy. My best model reproduced most of the movement patterns defined from the observed data. This model improved the understanding of the movement drivers for the Atlantic-Gaspésie caribou. It also provided spatial estimates of caribou landscape use in the Gaspésie region. I concluded that sparse data were sufficient to fit individual-based models when coupled with a pattern-oriented modeling strategy. Second, I estimated how climate change and conservation activities may impact caribou movement potential. I used the individual-based model to simulate caribou movements in hypothetical landscapes representing the impacts of various climate change scenarios and conservation activities. Conservation activities represented the implementation of new protected areas in Gaspésie, according to the scenario developed by

the government of Québec, and the restoration of secondary roads inside protected areas. Climate change impacts on vegetation, as defined in my scenarios, reduced caribou movement potential. Road restoration was able to mitigate these negative effects whereas the implementation of the new protected areas did not improve caribou movement potential. Third, I presented a methodology to design effective protected area networks and proposed new protected areas to implement in Gaspésie to conserve biodiversity in the presence of climate change. I created a large sample of protected area networks expanding the existing network to reach an areal target of 12%. I then calculated an ecological representativeness index and two measures of functional connectivity over time for each network. Functional connectivity measures represented the overall access to the protected areas and the movement potential in them for the Atlantic-Gaspésie caribou. I used movement potential estimates for the current time period and for the future under different climate change scenarios to represent functional connectivity. The protected area network I proposed maximized the trade-off between the three network features I calculated.

In this thesis I examined Atlantic-Gaspésie caribou movements under different environmental conditions, including climate change impacted landscapes. These results helped define new protected areas for the Gaspésie region that will protect the caribou population over time. I believe this thesis gives new insights on the Atlantic-Gaspésie caribou movement behavior, as well as on the management actions that could be taken in Gaspésie to improve conservation of caribou and of other species. I believe this methodology could be applied to other ecosystems with similar characteristics and needs.

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Abbreviations

AAC: annual allowable cut

AD: absolute deviation

ANOVA: analysis of variance

Area$_{HMP}$: area of high movement potential

BEACONs: Boreal Ecosystems Analysis for Conservation Networks

BFEC: Bureau du Forestier en Chef du Québec

CC (CC0, CCMin, CCMed, CCHigh): climatic scenarios (CC0 = no climate change, CCMin = minimum climate change impacts, CCMed = medium climate change impacts, CCHigh = high climate change impacts)

COSEWIC: Committee on the Status of Endangered Wildlife in Canada

GIS: geographical information system

good-HQ: good habitat quality

GPS: global positioning system

hm-BCRW: habitat-mediated biased correlated random walk

hm-FL: habitat-mediated foray loop

hm-RW: habitat-mediated random walk

IBM: individual-based model

IPCC: Intergovernmental Panel on Climate Change

IUCN: International Union for Conservation of Nature

low-HQ: low habitat quality

M1 to M6: model 1 to model 6

MAD: mean absolute deviation

MDDELCC: Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques du Québec

MFFP: Ministère des Forêts, de la Faune et des Parcs du Québec

ODD: overview, design concepts, and details

PA (PA0, PA+): protected area network scenarios (PA0 = current protected areas, PA+ = current protected areas coupled with the biodiversity reserves from the scenario proposed by the government of Québec (MDDELCC))

POM: pattern-oriented modeling

R. t. c.: *Rangifer tarandus caribou*

Road (Road0, Road50, Road100): road restoration scenarios (Road0 = no restoration, Road50 = restoration of 50% of the secondary roads, Road100 = restoration of all secondary roads)

RSF: resource selection function

SE-IBM: spatially explicit individual-based model

VHF: very high frequency

Remerciements

Je tiens à remercier tout d'abord mes trois directeurs qui m'ont guidée et encouragée pendant toutes ces années. Merci à Steve Cumming de m'avoir accueillie dans son laboratoire. Merci de l'aide apportée, de m'avoir fait confiance et laissé prendre mes décisions dans ce projet. Merci à Eliot McIntire pour son aide, autant à distance que lors de mes visites au Pacific Forestry Centre. L'énorme travail effectué ensemble lors de mon premier passage à Victoria aura été déterminant pour ma thèse et son passage à la vitesse supérieure. De plus, mon temps passé à Victoria aura été un magnifique séjour dans l'Ouest. Merci à Martin-Hugues St-Laurent qui, aussi malgré la distance, a toujours été là pour m'aider. Merci d'avoir toujours été rapide et efficace à me répondre, pour mes corrections et tous mes questionnements.

De l'Université Laval, je tiens à remercier particulièrement Pierre Racine qui m'a été d'une grande aide pour mes débuts avec ArcGIS. Merci à mes collègues de bureau d'avoir rendu les journées plus agréables; ceux du 2111 : Aude Corbani, Toshinori Kawaguchi et Jean Marchal (merci aussi pour son aide avec R et l'informatique en général); ainsi que ceux du 2107 : Flavie Noreau, Mathieu Paradis et Mélina Houle. Merci aux Cool Kids de m'avoir intégrée dans leur cercle : Christian Roy, Nicole Barker, Sébastien Renard, Josh Nowak (merci de m'avoir fait découvrir le hockey !) et Jerod Merkle. Merci aux membres du Métalab, présents entre autres pour m'aider dans la préparation de mes présentations orales. Merci à François Fabianek, Renée Roy et Julie Faure-Lacroix d'avoir fait des diners une pause divertissante dans la routine du travail. Merci à Louis Bélanger et à tous les Beavers de m'avoir accueillie dans la secte du castor, pour tous les moments (sérieux ou de détente) partagés ensemble. Je pense particulièrement à ceux avec qui tout a commencé : Amélie Denoncourt, Marie-Ève Deshaies, Victor David, et Eric Domaine, ainsi que Papy-Claude Bolaluembe Boliale et Michel Babalé.

Du Pacific Forestry Centre, je ne remercierai jamais assez Alex Chubaty d'avoir mis au point Condor, avec Eliot, pour faire tourner mes simulations. J'ai tant fait appel à Alex pour réparer et ajuster Condor et mon projet ne serait rien sans la capacité informatique à laquelle j'ai eu accès grâce à lui. Merci à Julia Chacón et Alana Clason pour le temps passé

Avant-propos

La thèse présentée comporte trois chapitres. Ils sont rédigés sous la forme d'article scientifique pour des fins de publication. Je suis l'auteure principale de chaque article. J'ai réalisé avec l'aide de mes coauteurs : la définition des objectifs et des hypothèses, l'établissement de la méthodologie et l'interprétation des résultats. J'ai réalisé seule : la construction des modèles, la réalisation des analyses statistiques et la rédaction des manuscrits. Les étapes réalisées seules ont été revues et corrigées par mes coauteurs. La version présentée des articles dans cette thèse est la version soumise, ou à être soumise, excepté pour les résumés. Les résumés ont été raccourcis pour répondre aux critères de la Faculté des études supérieures et postdoctorales pour le dépôt de la thèse.

L'article du premier chapitre s'intitule « *Overcoming challenges of sparse telemetry data to estimate caribou movement* ». Il a été réalisé en collaboration avec Eliot McIntire, Martin-Hugues St-Laurent et Steve Cumming. L'article a été accepté pour publication dans la revue Ecological Modelling en mai 2016.

L'article du second chapitre s'intitule « *Reducing movement barriers mitigates negative effects of climate change on caribou movement potential* ». Il a été réalisé en collaboration avec Eliot McIntire, Martin-Hugues St-Laurent et Steve Cumming. L'article a été soumis à la revue Journal of Applied Ecology en mai 2016.

L'article du troisième chapitre s'intitule « *Maximizing ecological representativeness and functional connectivity over time when designing protected area networks* ». Il a été réalisé en collaboration avec Steve Cumming, Martin-Hugues St-Laurent et Eliot McIntire. L'article sera prochainement soumis à Landscape Ecology.

General introduction

Global biodiversity decline

Biodiversity decline is currently a global phenomenon (Pereira *et al.* 2010; Ceballos *et al.* 2015). Even with conservative assumptions, modern rates of extinction for vertebrate species are 8 to 100 times higher than the background rates (Ceballos *et al.* 2015). Among the various ecosystem functions contributing to human well-being, more than half are declining due to a loss of biodiversity (Millennium Ecosystem Assessment 2005). Five major drivers of biodiversity decline have been identified, affecting differently the various ecosystems on the planet. These drivers are habitat change, climate change, invasive species, over-exploitation, and pollution (Secretariat of the Convention on Biological Diversity 2006). All are direct consequences of human activities.

Habitat change, through landscape modification and habitat fragmentation, has the greatest impact on biodiversity decline on a global scale (Secretariat of the Convention on Biological Diversity 2006). The conversion of species' habitats into landscapes adapted for human needs has driven past extinctions of species and continues to be a current threat. In Canada, most of the caribou populations (*Rangifer tarandus*) are declining (Vors & Boyce 2009; Festa-Bianchet *et al.* 2011). For boreal populations of woodland caribou (*R. t. caribou*), alterations of caribou habitat by forestry is recognized as a major driver of trends in population demographics (Leclerc, Dussault & St-Laurent 2014; Losier *et al.* 2015). Another example refers to the modern decline of the Atlantic-Gaspésie caribou population (*R. t. c.*) in Québec, which is largely related to higher predation pressure exacerbated by anthropogenic disturbances. Indeed, predator populations are sustained by other prey species that are favored by young forests resulting from intense forestry activities in the region. This is referred as apparent competition (St-Laurent *et al.* 2009; Boisjoly, Ouellet & Courtois 2010).

Climate change is affecting all of the planet's ecosystems. Rapid shifts of species range to higher latitudes or elevation are occurring in order to keep pace with changing climate (Loarie *et al.* 2009; Chen *et al.* 2011). In eastern North America, boreal forest tree

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species are likely to be impacted by climate change (Périé *et al.* 2014). Some southern hardwood species may find better environmental conditions in the future. They may be able to expand their range into more northern latitudes or higher elevations. However, modeling studies suggest that some conifer species common in the boreal region, such as Jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), eastern larch (*Larix laricina*) or balsam fir (*Abies balsamea*) may suffer significant declines over more than 20% of their current range (Périé *et al.* 2014).

The concept of protected area networks

Protected areas have been implemented in many parts of the world to counter the loss of biodiversity (Ervin 2003; Coetzee, Gaston & Chown 2014). The IUCN Protected Areas Categories System defines different levels of protection for these areas limiting the human activities permitted inside (Dudley 2008). Single protected areas mostly reduce the threats of habitat change and over-exploitation inside their boundaries. However, they cannot alone solve all the negative impacts of these two threats. For examples, some habitat changes outside protected areas can still modify the ecosystem functions inside them by contamination (Hansen & DeFries 2007). Also, poaching and illegal fishing inside protected areas are hard to control (Agnew *et al.* 2009). The impacts of climate change, invasive species and pollution on biodiversity are less, or not at all, mitigated by individual protected areas as these threats do not stop at human-delineated boundaries.

A protected area network is a group of single protected areas (i.e., cores of the network) which are functionally connected between each other (Bennett & Mulongoy 2006; Ervin *et al.* 2010). Functional connectivity is "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1993), as perceived by a particular species or population (Baguette & Van Dyck 2007; Kadoya 2009). The enhancement of functional connectivity in landscapes is beneficial for species conservation (Bennett 2003; Rudnick *et al.* 2012), particularly when enhanced between protected areas (Bennett & Mulongoy 2006; Andrello *et al.* 2014). High functional connectivity allows individual movement or dispersal between protected areas. It increases the effective protected surface available for an individual or a population (Di Minin *et al.* 2013). A

connected protected area network can help counter the negative impacts from habitat change and over-exploitation that cannot be solved within single protected areas. For example, strong connectivity between protected areas can help reduce the impacts of land use contamination from outside, as individuals are more able to travel further to find resources and avoid disturbances (Bennett & Mulongoy 2006). Connectivity could also help reduce poaching as animals could have better access to refuges. Protected area networks could also decrease accessibility by poachers if landscape fragmentation due to trails and road networks is reduced (Linkie *et al.* 2006). A connected network of protected areas can also help species better cope with climate change and reduce invasive species impacts. Climate change disturbs environmental conditions (Loarie *et al.* 2009) and therefore resource distribution, potentially driving some species out of the protected areas where they currently live (Araújo *et al.* 2004). Populations moving to follow their optimal environmental conditions (Chen *et al.* 2011) could still remain partly protected if they can easily move from one protected area to another through a connected network. Functional connectivity is enhanced in the protected area network for some particular species. If invasive species have different needs (e.g., open vs closed areas), suitably designed networks could delay the spread of these species while favoring the sustainability of the focal ones (Bakker & Wilson 2004).

Protected area networks can decrease the rate at which species are going extinct (Geldmann *et al.* 2013; Andrello *et al.* 2014). However, the protection they provide is limited to certain biodiversity threats and is ineffective for most of the species living outside of their boundaries. Protected area networks are part of the solution to counter biodiversity loss but they cannot solve it alone. A global conservation effort is required, including a better management of the surrounding matrix (i.e., outside of the networks) (Ervin *et al.* 2010; Hansen *et al.* 2011; Lesmerises *et al.* 2013), as well as actions aimed towards reducing the causes of biodiversity decline (Secretariat of the Convention on Biological Diversity 2006).

Building effective protected area networks

There are many approaches to designing protected areas systems so that they form a cohesive, functionally connected network which would be effective, currently and in the future, at protecting the biodiversity in a defined region (Heller & Zavaleta 2009). Here, I present a three-step method: 1) defining the current and future environmental conditions in the focal region taking into account projected climate change; 2) defining the movements for the focal species which require(s) protection, for the same time periods as the environmental conditions; 3) defining a set of protected areas to create a network that achieves ecological representativeness and functional connectivity for the focal species, now and under projected future conditions.

Understanding the current state of the regional landscape requires defining the current climate, vegetation and terrain conditions (e.g., elevation, cover types). This is usually done by remote sensing and data can be obtained from research and governmental agencies (e.g., Hijmans *et al.* 2005; Dupigny-Giroux *et al.* 2007; Xie, Sha & Yu 2008). To define the future environmental conditions in a context of climate change, scenarios and models are required. The Intergovernmental Panel on Climate Change (IPCC 2007) established various climate scenarios which lead to predicted future climates (Randall *et al.* 2007). Given climate, future vegetation can be predicted in several ways. For example, bioclimatic envelope models are fit from empirical data to describe the realized niche of a target species. The species' future distribution is then projected using the future climate predicted and the current species-climate relationship (Heikkinen *et al.* 2006). These models assume a consistency over time of the observed species-climate relationship (equilibrium assumption), as well as a strong adaptive capacity of the species to the new environmental conditions (Araújo & Peterson 2012). Individual-based models are more mechanistic. They can define the potential location of a population based on its life cycle and different types of interactions, such as with climate, landscape conditions, or with other species (e.g., Wiegand *et al.* 2006). While complex mechanistic models require more data and knowledge about the species ecology than species distribution models, they can overcome empirical model limitations by adapting the species behavior to different environmental conditions.

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Focal species movement through time needs to be described to account for functional connectivity between the protected areas. First, the choice of the focal species needs to accord with regional conservation needs. The focal species needs to be either of high importance for conservation (e.g., high cultural value, important for ecological processes) or an umbrella species (Roberge & Angelstam 2004; Baldwin *et al.* 2010). Movement pattern of the focal population can be modelled from telemetry data (e.g., VHF or GPS collars) or field observations (Movebank 2015). Not all individuals can be monitored at all times; thus models must be developed from the observation data. There are many kinds of movement models (Turchin 1998). The choice depends, among other things, on the population movement assumptions, the data available and the goal of the study. If the movement models include climatic or climate-dependent variables (e.g., vegetation cover), it is then possible to predict potential future movement of populations by inserting the variable predicted value under climate change (e.g., Lawler *et al.* 2013).

Protected area networks need to preserve a representative set of the regional biodiversity. Protecting most of the undisturbed habitat types according to their original proportions in the landscape is expected to protect the majority of the regional biodiversity (Hunter 1991; Dudley & Parish 2006). To be robust to climate change, and ensure protection over time, landscape changes need to be planned for in advance (Hannah *et al.* 2007). While protected areas should maximize ecological representativeness over time, they should also be located in a way that the focal species can easily move from one area to another, considering its current movement patterns and the predicted ones for the future (Nuñez *et al.* 2013; Andrello *et al.* 2014).

Case study: the Gaspésie peninsula

The present thesis was originated as part of a bigger project initiated by the Québec government. It aimed to adapt the design and the management of the protected area networks in Québec to climate change (Bélanger *et al.* 2013). Two study areas were identified because of their ecological challenges regarding climate change: one of which is my study area, the natural region of the Gaspésie peninsula (MDDELCC 2014).

The natural region of the Gaspésie covers about 25,000 km² at the tip of the Gaspésie peninsula. Most of the area, except for the coasts, belongs to the balsam fir - white birch bioclimatic domain (Saucier *et al.* 2003). It is a mountainous area with open alpine tundra on mountain tops mostly maintained by wind (Renard, Isabel & McIntire 2015). The tundra may be threatened by vegetation colonization due to climate change (Logan 2012; Dumais *et al.* 2014); though there is also some evidence that it may not change (Renard, McIntire & Fajardo 2015). The main natural disturbance in the region is spruce budworm outbreaks (*Choristoneura fumiferana*). Future spruce budworm impacts could be less important than they are currently since spruce budworm growth rate is predicted to decrease with climate change (Gray 2008; Régnière, St-Amant & Duval 2012). A large portion of the Gaspésie is public land. Forestry activities, with their associated road network, are the main human disturbances in the area (MDDELCC 2014).

Currently, the existing protected areas cover 5.5% of the region (Fig. 3.1). Most of these areas are small but the biggest protected area, the Gaspésie National Park, covers 802 km² (LeSage & Paquin 2000). This park helps the conservation of several endangered species among which are two endemic taxa, the Atlantic-Gaspésie caribou population and the green-scaled willow (*Salix chlorolepis*) (MDDELCC 2014). A gap analysis of the current network showed that several environmental features were poorly represented in the existing protected areas (MDDELCC 2014). The Québec government aims to protect 12% of its territory (Brassard *et al.* 2010). The "Comité sur les aires protégées terrestres de la Gaspésie" (Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques du Québec, MDDELCC) proposed a scenario of new protected areas (Fig. 3.1), which when associated with the existing ones, would protect a total of 12.3% in the natural region of the Gaspésie peninsula (MDDELCC 2014).

Focal population: the Atlantic-Gaspésie caribou

The Atlantic-Gaspésie caribou was used as the focal population for measuring functional connectivity of protected area networks. This caribou population belongs to the mountain ecotype (COSEWIC 2011) of the woodland caribou subspecies (Banfield 1961). In 1850, the southern limit of the caribou range went as south as Vermont, USA (Courtois *et al.*

2003). The caribou range has shrunk over time and now the Atlantic-Gaspésie population is the last one surviving south of the St. Lawrence River. The population mostly occupies the Gaspésie National Park (Mosnier *et al.* 2003; Lalonde 2015). Population surveys began in the 1980s and estimated the population to be around 200 (Fournier & Faubert 2001). The population has declined continually since then. The last survey in 2015 estimated the herd size of around 100 individuals (Lalonde 2015). The population was identified as a Designatable Unit for the caribou species in Canada (COSEWIC 2011) and it is listed as endangered since 2000 (Environment Canada 2015).

The Atlantic-Gaspésie caribou is mostly threatened by human disturbances. The proximate cause of the population decline is predation, mostly by coyotes (*Canis latrans*) which first appeared in the Gaspésie National Park in the early 1980s, and black bears (*Ursus americanus*) (Crête & Desrosiers 1995). The predation pressure is driven by apparent competition due to a large abundance of alternative prey, mostly moose (*Alces americanus*), which can sustain large predator populations. These alternate prey species are themselves sustained by the large areas of young forests produced by forestry activities which seem the ultimate cause of caribou decline (St-Laurent *et al.* 2009; Boisjoly, Ouellet & Courtois 2010). Forestry activities also decrease the area of mature fir forests on which caribou rely during winter to feed on arboreal lichen (Mosnier *et al.* 2003). Aside from habitat change, climate change may become a threat to this population in the future. Indeed, the population inhabits the alpine tundra in the Gaspésie National Park and relies on fir stands (Mosnier *et al.* 2003), two ecosystems potentially threatened by climate change (Loarie *et al.* 2009; Périé *et al.* 2014; Dumais *et al.* 2014).

The future of the Atlantic-Gaspésie caribou population is at risk due to its long-term consistent population decline and its uniqueness, making it a primary target for conservation measures. This population is also sensitive to human disturbances and is therefore a good indicator of the health of the ecosystems in Gaspésie. I assumed that conservation measures directed towards the caribou population would also protect the other local species affected by the same disturbances or sharing the same habitat preferences, making the Atltantic-Gaspésie caribou a potential umbrella species (Bichet 2014) and therefore a relevant focal species.

Thesis outline

The aim of this thesis is to propose a methodology to define effective protected area networks by integrating functional connectivity and climate change into their design. This thesis is composed of three chapters.

The first chapter shows that sparse data, when used with individual-based models and pattern-oriented modeling, can be sufficient to understand and simulate potential animal movement. I modeled Atlantic-Gaspésie caribou movement using sparse VHF telemetry data available for this population. I parameterized individual-based models that included environmental and intrinsic variables with a pattern-oriented modeling strategy to reproduce the movement patterns from telemetry data. Then, I simulated caribou movement to define the potential landscape use of the Gaspésie region by the caribou.

In the second chapter, I show that decreasing movement barriers through road restoration can mitigate the predicted loss of movement potential for caribou under climate change. It was beyond the scope of this project to build robust vegetation-landscape models to predict the potential future state of the environmental conditions in Gaspésie. Therefore, I built possible future landscapes under various climate change scenarios from the literature. I included in these scenarios the outcomes of alternate conservation activities including new protected areas and road restoration. I used the individual-based model from the first chapter to predict the movements of the Atlantic-Gaspésie caribou in the scenario created landscapes. I estimated the caribou movement potential by comparing the movement model outputs to those produced by a null model, defined as a random walk in a homogeneous landscape. Scenarios with road restoration inside the protected areas led to an increase of the area of high movement potential for caribou, compensating for losses induced by climate change.

In the third chapter I present a strategy for designing effective protected area networks and illustrate it for the Gaspésie region. I built multiple protected area networks and quantified the degrees to which they achieved current ecological representativeness and functional connectivity over time. I could not measure ecological representativeness over

time as no models were available to predict detailed landscapes under climate change. I used the methodology and results of the second chapter to measure network functional connectivity over time using estimates of caribou movement potential. I used quantile-based criteria to select the optimal protected area network scenario that simultaneously achieved high degrees of ecological representativeness and functional connectivity. I also compared the performances of the network proposed by the government with the networks I created.

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Chapter 1: Overcoming challenges of sparse telemetry data to estimate caribou movement

Résumé

Les modèles individu-centré spatialement explicites peuvent reproduire le mouvement des espèces. Lorsqu'ils sont couplés avec une modélisation patron-orienté, ils peuvent être paramétrés et évaluer différentes hypothèses de mouvement en comparant leurs résultats avec les patrons des données de mouvement. Nous l'avons illustré en utilisant les données VHF (« Very High Frequency ») éparses de la population en voie de disparition de caribou de la Gaspésie-Atlantique. Notre meilleur modèle a pu reproduire avec succès la plupart des patrons de mouvement dérivés des localisations VHF. Nous avons utilisé le modèle pour estimer et cartographier l'utilisation potentielle du paysage par le caribou. Nous avons conclu que les données éparses, comme les localisations VHF, peuvent être utilisées pour ajuster des modèles de mouvement dont les paramètres ne peuvent pas être estimés directement des données observées. Ces modèles peuvent s'avérer utiles dans la gestion du paysage afin d'identifier les régions où développer des stratégies de conservation pour assurer la persistance de populations menacées.

Abstract

Spatially explicit individual-based models (SE-IBMs) can simulate species' movement behaviors. Coupled with a pattern-oriented modeling strategy, SE-IBMs can be parameterized and assess alternate hypotheses on movement behaviors by comparing simulated to observed patterns of movement. We illustrated this with the endangered Atlantic-Gaspésie caribou population while using sparse Very High Frequency (VHF) telemetry data. The best fitted model we built successfully reproduced most of the movement patterns derived from the VHF locations. We used the model to estimate and map potential landscape use by the Atlantic-Gaspésie caribou. We concluded that sparse data sets, such as VHF collar locations, can be used to fit movement models whose parameters could not be estimated directly from the data. SE-IBMs coupled with pattern-oriented modeling can reveal new insights about landscape use and can identify habitat locations where management actions could be taken to facilitate persistence or recovery of endangered populations.

Introduction

Quantitative models of animal movement and landscape use can make important contributions to our understanding of animal fitness (Cagnacci *et al.* 2010). Individuals must move through their landscape to access food resources (Turner *et al.* 1994), to find a mate (Hooker *et al.* 2002), to reach suitable natal habitat (Richardson, Stirling & Hik 2005), or to escape predators (Forester *et al.* 2007). Understanding the mechanisms behind animal movement, quantifying how the landscape is used, and identifying potential movement corridors or barriers are therefore key to understanding on how species interact with their environment (Gibeau *et al.* 2002; Marucco & McIntire 2010). This information is crucial when land management is aimed at protection or recovery of endangered populations (Dyer *et al.* 2002; Gibeau *et al.* 2002). In this context, a deeper understanding of animal movement and spatial estimates of population landscape use, would allow managers to identify, more precisely or with greater certainty, areas in need of protection from human disturbances, or of restoration to enhance individual movement and thereby population viability. One way to gain such an understanding is through movement models.

Individual-based models treat individuals as unique, autonomous entities with state-dependent behaviors, which interact with their environment and/or with each other. Population-level patterns emerge from these interactions (Railsback & Grimm 2012). Spatially explicit individual-based models (SE-IBMs) simulate individual movements over landscapes (McIntire, Schultz & Crone 2007; Grosman *et al.* 2011) and are particularly useful in forecasting landscape use (Gustafson 2013). SE-IBMs are abstract representations of movement in terms of statistical processes governing the distances moved and the choice of direction between consecutive moves. These components need to be parameterized correctly. Usually, only some parameter values are known in advance, and others must be estimated from data (Wiegand *et al.* 2004; Marucco & McIntire 2010).

For many animal populations, available telemetry data are obtained from transponders attached to the individuals (collars), with locations estimated by triangulation of the Very High Frequency (VHF) radio signal or, more recently, from Global Positioning System (GPS) fixes taken by the collars themselves. VHF location recording requires observers to find collared animals in the field (e.g. by aerial survey) which leads to several

complications. Individuals outside the usual population range at the time of survey will rarely be detected because observers survey the commonly used areas for reasons of cost. Observers need to see the animals to record their position, but environmental conditions (e.g., landscape cover, weather, low light) can hide some of them. Then, because surveys are costly and time consuming, time lags between consecutive VHF locations are often long and irregular. For these reasons, VHF collar data are usually too sparse in time to permit direct estimation of movement parameters. That is, the frequency with which individual locations are obtained is too low compared to the rates of movement. For example, step selection functions assume straight line steps between consecutive observed locations (Fortin *et al.* 2005) and state-space models require observed movement metrics like speeds or turning angles (Patterson *et al.* 2008). Such prerequisites cannot be fulfilled by VHF data. GPS collar data can have a much higher frequency of data capture but are still limited by relatively small sample sizes (Hebblewhite & Haydon 2010). Despite their more advanced technology and greater capacity, GPS collars remain more expensive than VHF collars, and they have a shorter battery life (Latham *et al.* 2015). Also, not all studies require GPS locations; for some ecological questions, VHF locations are sufficient (Latham *et al.* 2015), so the method is expected to remain in use for some time. Finally, VHF technology is decades older than GPS technology. Thus, we have access to animal behavior for time periods before the advent of GPS collars (Hebblewhite & Haydon 2010). Historical VHF data are available for many species (e.g., Gibeau *et al.* 2002; Weerakoon *et al.* 2004; Arraut *et al.* 2010; Forero-Medina, Cárdenas-Arevalo & Castaño-Mora 2011; Lewis, Cain III & Denkhaus 2014) and despite their above-mentioned limits, they represent an important resource for conservation applications. For example, they could be used to inform about movement behaviors under historical landscape conditions less affected by human disturbances than today, provided that the challenges of estimating movement parameters from sparse data are overcome.

Pattern-oriented modeling (POM) is a strategy to estimate unknown model parameters that could not be directly measured, by adjusting a model to reproduce patterns which are features of the available data (Grimm *et al.* 2005; Grimm & Railsback 2012). The first step is to identify suitable patterns from the data. Large numbers of simulations are then run with different values for the unknown parameters sampled from their expected

ranges. For each simulation, the selected patterns are derived from model outputs. Finally, best parameter values are identified by minimizing a measure of the difference between the simulated patterns and the patterns in the data. The POM strategy is particularly useful to parameterize SE-IBMs from sparse data when paired with a robust, hypothesis-driven methodology (McIntire & Fajardo 2009).

We built SE-IBMs to understand the movements and to predict the potential landscape use of an animal population from sparse VHF telemetry data. Our case study was the Atlantic-Gaspésie caribou population, *Rangifer tarandus caribou*, in Québec, Canada. First, we proposed several movement hypotheses based on the literature, representing different movement mechanisms. We tested if caribou movements were homogeneous or heterogeneous in space, if inter-patch movements were best represented by a random walk, a biased correlated random walk, or a foray loop (Conradt *et al.* 2003), and if there was a mating site fidelity. We translated these various movement behavior hypotheses into a SE-IBM and calibrated each model with the VHF data using a POM strategy. We then selected the best model using a similar POM strategy, and validated the model against the VHF data. The model was then used to simulate individual movements from which we estimated and mapped the population's potential landscape use. Finally, we compared the estimated landscape use with a habitat selection study done for the same caribou population.

Material and methods

Case study: the Atlantic-Gaspésie caribou population

Our study area was the Gaspésie peninsula in Québec, Canada (Fig. 1.1), defined as the Gaspésie natural region (MDDEP 2012). The area is mountainous and forms the northeastern limit of the Appalachian range. The study area falls within the boreal biome (Brandt 2009) and, except for the coast, is part of the balsam fir-white birch bioclimatic domain (Saucier *et al.* 2003). The area is home to the small, relict Atlantic-Gaspésie caribou population ("caribou", hereafter), which is associated with alpine tundra habitats on high-elevation sites. The study area is surrounded by water on three sides while the western boundary adjoins a region highly modified by agriculture, industry and urban areas

(Wildlife Conservation Society Canada 2015) which we considered effectively impermeable to caribou movement. This caribou population is thus effectively isolated.
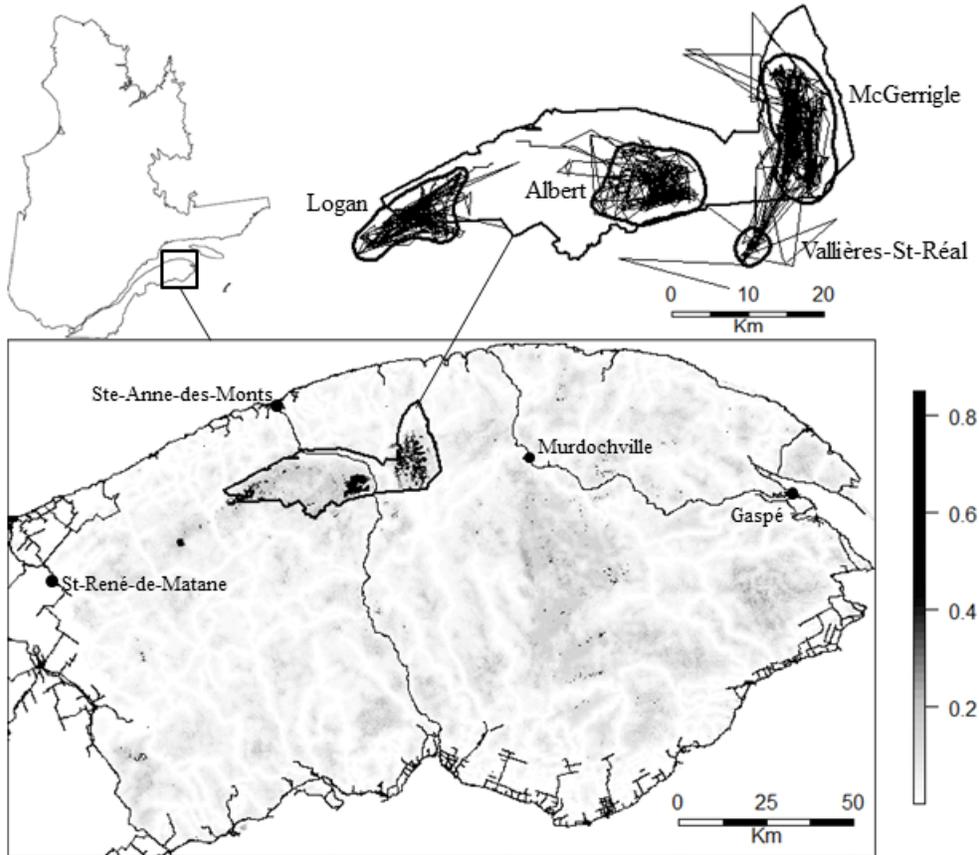
Figure 1.1: Left inset: The province of Québec (Canada), with study area, the Gaspésie natural region, outlined. Lower map: Summer resource selection function for the Atlantic-Gaspésie caribou (Gaudry 2013) applied over our study area. Paved roads are shown in thin lines and the boundary of Gaspésie National Park is the thick outline. The four towns nearest to recent caribou sightings distant from the park are indicated (St-Laurent, unpublished data). Right inset: Caribou movement paths defined from consecutive VHF locations, with the park boundary and subpopulation ranges outlined.

The caribou population belongs to the mountain ecotype (COSEWIC 2011) of the woodland caribou subspecies (Banfield 1961). When population surveys began in the 1980s, the population size was estimated to be around 200 (Fournier & Faubert 2001).

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Numbers have declined steadily since that time, and, as of 2014, the estimated herd size was 94–100 individuals (Lalonde 2015). The population was designated as endangered in 2000, a status re-examined and confirmed in 2002 and in 2014 (Environment Canada 2014). The population was recently identified as a Designatable Unit for the caribou species in Canada, which is a "both discrete and significant unit that is an irreplaceable component of Canada's biodiversity" (COSEWIC 2011). This status confers on the population priority for conservation action.

The proximate cause of the Atlantic-Gaspésie caribou decline is predation, mostly by coyotes (*Canis latrans*) and bears (*Ursus americanus*) (Crête & Desrosiers 1995), but the ultimate cause is land-use changes, primarily due to forest harvesting. Forest harvesting increases the area of young forests, leading to increased abundances of alternate prey species such as moose (*Alces americanus*) and their predators (St-Laurent *et al.* 2009). Caribou telemetry locations suggest that individuals are mostly restricted to the Gaspésie National Park (Fig. 1.1). The population appears to be divided into three groups, gathered on Mts. Logan, Albert and McGerrigle (Mosnier *et al.* 2003) (Fig. 1.1), with very few individual exchanges. There is no evidence that the Atlantic-Gaspésie caribou is a metapopulation (*sensu* Hanski & Hanski 1999) but, for the purpose of this study, we considered these groups as three subpopulations. We referred to them as the Logan, the Albert and the McGerrigle (caribou) subpopulations. Recent caribou sightings at unexpectedly distant locations (Fig. 1.1) and the 1997 colonization of Mt. Logan, probably by Albert caribou (Fournier & Faubert 2001), show that long-distance movements and re-establishments are possible. A mechanistic understanding of caribou movements is essential to understand and facilitate colonization processes to secure the recovery of this population.

To develop movement models, we used VHF telemetry data from 35 adult caribou (20 females, 15 males) that were collared and followed from 1998 to 2001 (Mosnier *et al.* 2003). Periodic aerial surveys of the known population range located collared animals by their signal and recorded their position. Flights were conducted, on average, every two weeks (mean = 17 days, SD = 17 days). The mean number of locations per individual was 45 (SD = 20). Because of the small dataset, we did not differentiate males from females. Some movement behavior may differ between sexes, such as an anti-predator strategy

stronger for the females after calving. However, we did not think this abstraction would impact our models as we studied caribou movement over the whole year at a medium spatiotemporal scale. We used a kernel density at 80% on the VHF locations to delineate subpopulation ranges (Fig. 1.1). Due to the low number of individuals per subpopulation, the value of 80% was the largest that identified three subpopulation ranges without depending on uncommon behavior of a single caribou. Ranges for the Logan and Albert subpopulations are each represented by single contiguous areas, whereas the McGerrigle range is represented by two areas, one centered on the McGerrigle mountains and a smaller, less frequently used one, around the Vallières-St-Réal (Fig. 1.1).

Spatially explicit individual-based model

To simulate caribou movement, we built SE-IBMs that incorporated temporally varying behavioral responses to spatially varying environmental conditions (Hanks *et al.* 2011; Hanks, Hooten & Alldredge 2015). The models run on a grid of 75 x 75 m cells covering the study area. Model time steps are daily, indexed by calendar days; the large temporal scale of the telemetry dataset precluded finer resolution. Simulated individuals have a fixed name and mating area associated, two movement states, and a behavioral state. The movement states are the coordinates of the individual current positions on the landscape (i.e. the currently occupied cell) and a heading or direction of last movement. The behavioral state can change depending on time and location. All individuals move once per time step according to the current landscape conditions and their behavioral state. Alternate hypotheses on the processes governing movement in this population were expressed as alternate model formulations (McClintock *et al.* 2012) or spatial constraints on movement. A complete description of the SE-IBMs following the Overview, Design concepts, and Details protocol of Grimm *et al.* (2006, 2010) is available in Appendix 1.A. The model was written in R 3.1.0 (R Core Team 2014) using the following packages: adehabitatHR (Calenge 2006), CircStats (Rao Jammalamadaka & SenGupta 2001), data.table (Dowle *et al.* 2015), maptools (Bivand *et al.* 2016), PBSmapping (Schnute *et al.* 2015), Pomic (Piou, Berger & Grimm 2009), raster (Hijmans *et al.* 2016), rgeos (Bivand *et al.* 2016), sp

(Pebesma & Bivand 2005; Bivand, Pebesma & Gomez-Rubio 2013), and spatstat (Baddeley, Rubak &Turner 2015).

Each landscape cell had three spatial characteristics that drive movement: the habitat quality, the presence or absence of paved roads and whether or not it is located within a seasonal mating area. Habitat quality was predicted using two seasonal resource selection function (RSF) models (Manly *et al.* 2002) developed for the Atlantic-Gaspésie caribou (Gaudry 2013) (Fig. 1.1). The RSF models were built with four habitat types (alpine tundra, mature fir stands, regenerating stands and other forest stands) and three linear anthropogenic features. There were three classes of these linear features: paved roads, gravel/secondary roads, and hiking trails, with mean densities in the study areas of 0.32, 1.79, and 0.04 km/km², respectively. One RSF was developed for the winter period (November 16th to April 30th) and the other RSF for the snow-free period, hereafter called "summer" (May 1st to November 15th). As in Gaudry (2013), we classified forest stands in our study area using the 1:20,000 digital ecoforestry map of the 3rd forest inventory program (source: Ministère des Forêts, de la Faune et des Parcs du Québec, MFFP) updated in 2001 and the linear anthropogenic structure data published by the MFFP. Using the RSF models developed by Gaudry (2013), we obtained two seasonal maps of relative probabilities of caribou occurrence. We use these probabilities as surrogates for habitat quality (Hebblewhite *et al.* 2011). Roads are known to be significant barriers to caribou movement (Dyer *et al.* 2002; Beauchesne, Jaeger & St-Laurent 2013) so we defined the major paved roads which is a subset of the main roads defined as "paved roads" (Fig. 1.1, density in the study area equal to 0.09 km/km²) as semi-permeable barriers to movement (Kramer-Schadt *et al.* 2004; Wiegand *et al.* 2004). All types of road decreased habitat quality, but only the major paved roads acted as barriers that impeded caribou movement. The presence or absence of paved roads was determined at the cell level. Finally, many caribou populations exhibit fidelity to various sites, among which breeding and mating sites (Metsaranta 2008; Faille *et al.* 2010; Schaefer & Mahoney 2013). The mating season for the Atlantic-Gaspésie caribou is defined from September 15th to November 1st (Bergerud 1973; Lalonde & Michaud 2013). VHF data showed caribou clustering at high-elevation sites during the peak of the mating season. We defined three mating areas, using a 50% kernel density on subpopulation locations during the mating season.

Ungulates exhibit multiple-behavior movement which can be distinguished as intra-patch or inter-patch movements (Johnson *et al.* 2002), possibly corresponding to "encamped" and "exploratory" behavioral states (Morales *et al.* 2004). We assumed these behaviors to be related to habitat quality. Therefore in our model, we distinguished "good habitat quality" (good-HQ) movements from "low habitat quality" (low-HQ) movements. Empirical kernel density functions of quality values at recorded VHF locations were bimodal within seasons (Fig. 1.2). We defined the minimum density between the two peaks as the quality threshold between the low-HQ and the good-HQ behaviors. The estimated summer and winter thresholds were 0.290 and 0.382, respectively (Fig. 1.2). During the simulation, at locations with quality value above or equal to the threshold, individuals followed a good-HQ movement behavior; otherwise individuals follow a low-HQ movement behavior. Above-threshold quality habitat is mostly found within the subpopulation ranges (around 67% of it), although it does exist elsewhere in the area.
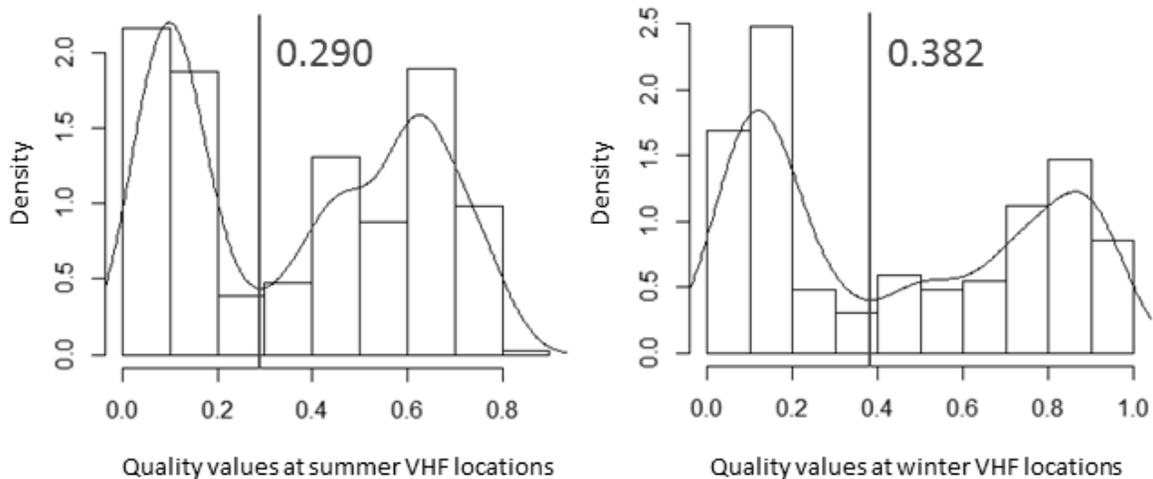
Figure 1.2: Kernel density estimates of habitat quality values at VHF locations for summer (800 locations) and winter (770 locations). The thresholds separating good and low habitat quality behaviors are shown.

We created 35 adult individuals (no sex assigned) to represent the VHF-collared caribou and randomly placed them inside their own mating area. A complete simulation

lasted four years of 365 days. In each time step, Julian date was incremented and landscape quality values were updated if the season changed. Individuals were then assigned a movement model according to their location, and the hypothesis under test (see below *Movement models*). Then, a step length was sampled independently for each individual from a lognormal distribution with state-dependent parameters; the parameter for mean step-length varied with habitat quality (Table 1.1). To avoid unrealistically large daily movements, step-lengths were truncated at 20 km. Each individual identified all unique locations at the selected step length from its current position (Fig. 1.3a), and thus the potential pathways it could follow (Fig. 1.3b). Each pathway was evaluated and assigned a numeric index value for each movement characteristics (Table 1.2), depending on the model being evaluated (see below *Movement models*). For each index, the values were rescaled across all pathways to sum to 1 (see Appendix 1.A for more details). These rescaled indices were interpreted as the probabilities for the individual to choose a pathway based on that particular movement characteristic (e.g. habitat quality, paved road presence). The product of the rescaled indices was then calculated for each path, and rescaled to sum to 1 over all paths. The results were finally interpreted as per-pathway movement probabilities. Finally, one pathway was randomly drawn based on these probabilities (Fig. 1.3c) and the individual moved at the end of this pathway (Fig. 1.3d). This straight line was not intended to represent an exact caribou trajectory at fine scale, but rather an emergent net displacement over a day with habitats that caribou potentially went through (Fortin *et al.* 2005). At the end of a run, we produced a map of landscape use as the number of caribou visits per cell over the last three years of the simulation. The maps were created by counting all cells intersecting the straight-line pathways of each movement. The first year of movement was not included so as to limit the effect of initial conditions.

Parameter to be estimated		Range tested	Unit
$\mu_{sl.good}$	Mean of the lognormal distribution for the step length simulation in good quality habitat	[3;8]	log(m)

$\mu_{sl.low}$	Mean of the lognormal distribution for the step length simulation in low quality habitat	[3;8]	log(m)
σ_{sl}	Standard deviation of the lognormal distribution for the step length simulation	[0.5;1.5]	log(m)
p_{cross}	Probability for a caribou to cross a paved road	[0;1]	
σ_{ma}	Standard deviation of the truncated Normal distribution for the mating area attraction	[0;180]	degree
σ_c	Standard deviation of the truncated Normal distribution for the correlation movement	[0;180]	degree
$max_{dist.bias}$	Maximum distance for the bias between the individual position and the closest habitat of good quality	[0;50]	km
σ_b	Standard deviation of the truncated Normal distribution for the biased movement	[0;180]	degree
$max_{steps.loop}$	Maximum step length of the outgoing portion of the foray loop	[0;20]	steps
σ_{fl}	Standard deviation of the truncated Normal distribution for the foray loop movement	[0;180]	degree

Table 1.1: Model parameters to be estimated with the range of values tested within the pattern-oriented modeling strategy and their unit.
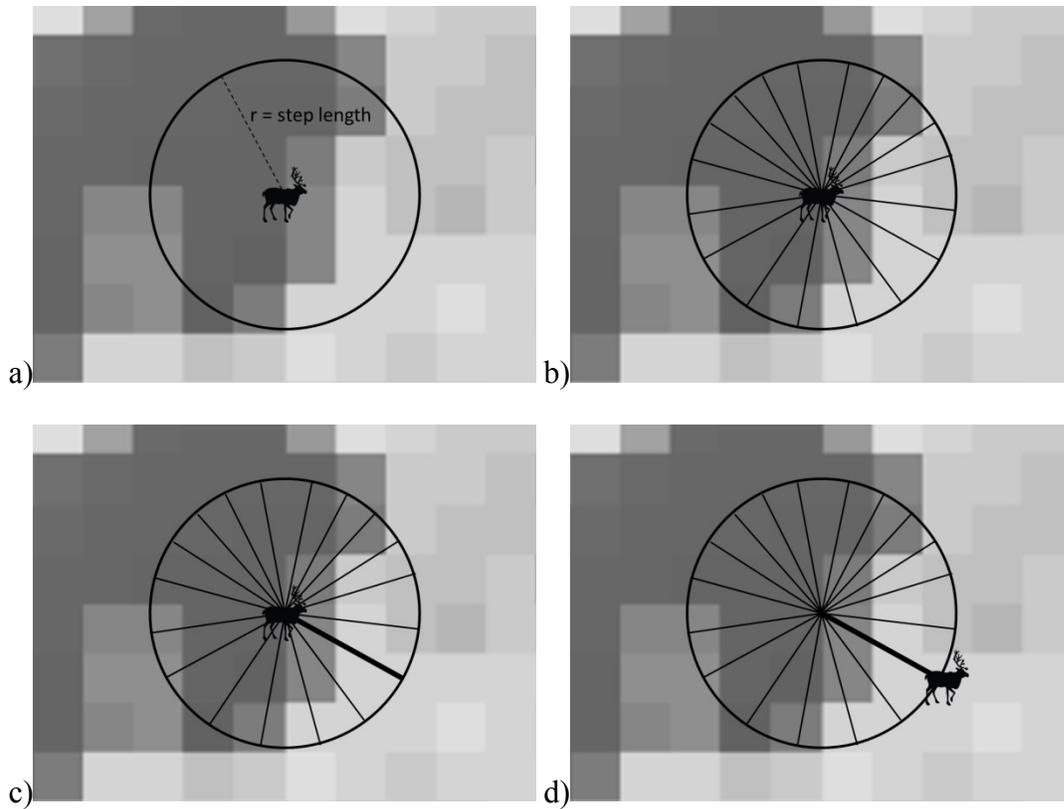
Figure 1.3: Movement illustrations of one daily time step for one individual. a) A step length is sampled. b) All unique pathways are identified, going from the individual current position to every unique cell of the gridded landscape at the sampled distance. c) One pathway is selected (thick line) based on probabilities derived from the characteristics of the movement model followed by the individual. d) The individual moves to the end of the selected pathway. The underling grey-scale grid represents the habitat quality layer.

Movement characteristic	Index value
Habitat quality	Mean quality value for the cells composing the pathway
Paved road presence	Probability p_{cross} of crossing a paved road for a caribou raised to the number of road crossing the pathway
Mating area	Probability from a truncated Normal distribution (-180° and 180°)

attraction	with mean equal 0 and standard deviation σ_{ma} of the angle between the pathway direction and the direction towards the individual mating area
Correlation	Probability from a truncated Normal distribution (-180° and 180°) with mean equal 0 and standard deviation σ_c of the angle between the pathway direction and the individual current heading
Bias	Probability from a truncated Normal distribution (-180° and 180°) with mean equal 0 and standard deviation σ_b of the angle between the pathway direction and the direction towards the closest habitat of good quality
Foray loop	Probability from a truncated Normal distribution (-180° and 180°) with mean equal 0 and standard deviation σ_{fl} of the angle between the pathway direction and the direction away or towards the loop starting location

Table 1.2: Movement characteristic and index values used to assign pathway probabilities (see Appendix 1.A for more details).

Movement models

We simulated good-HQ movement behavior using a habitat-mediated random walk model (hm-RW) to represent low correlation movements (e.g. foraging; Morales *et al.* 2004). To explain the caribou low-HQ movement behavior we tested three alternative movement hypotheses: a hm-RW, the same as the good-HQ movement to represent a single-behavior movement strategy; a habitat-mediated biased correlated random walk (hm-BCRW) (Van Moorter *et al.* 2009); and a habitat-mediated foray loop (hm-FL) (Conradt *et al.* 2003). To test these as alternative models, one of the three low-HQ movement behaviors was chosen to apply to all individuals throughout a simulation run.

To test which behavior hypothesis best represents the caribou movement displayed in our telemetry data, we created six different alternative SE-IBMs (M1 to M6). M1 was a single movement-behavior model where individuals followed a hm-RW for the good-HQ and low-HQ movement behaviors. M3 and M5 were two-behavior movement models; individuals followed a hm-RW for the good-HQ movement behavior and either a hm-BCRW (M3) or a hm-FL (M5) for the low-HW movement behavior. M2, M4 and M6 were respectively the same as M1, M3 and M5 where we added the mating area attraction. Movement characteristics (Table 1.2) for the different models applied as following:

- M1 ~ habitat quality + paved road presence

- M2 ~ M1 + mating area attraction

- $M3_{good}$ ~ M1;

  $M3_{low}$ ~ habitat quality + paved road presence + correlation + bias

- $M4_{good}$ ~ $M3_{good}$ + mating area attraction;

  $M4_{low}$ ~ $M3_{low}$ + mating area attraction

- $M5_{good}$ ~ M1;

  $M5_{low}$ ~ habitat quality + paved road presence + foray loop

- $M6_{good}$ ~ $M5_{good}$ + mating area attraction;

  $M6_{low}$ ~ $M5_{low}$ + mating area attraction

Using these models, we tested three different mechanisms to explain caribou range fidelity and extra-range movement: an attraction to a mating area during mating season, a bias toward close areas of good quality and a foray loop movement starting from good quality location. If mating area attraction occurred (M2, M4 and M6), we assumed that individuals favored pathways leading towards their mating area during mating season. Under the bias models (M3 and M4), pathways leading individuals towards the closest habitat of good quality were preferred. The bias relies on some combination of habitat sensing at shorter ranges and of memory at longer ranges. Because the biases are implemented as probability distributions on movement angles, there is no supposition that sensing is necessarily of high accuracy or that recall is total. We included a parameter

30

$max_{dist.bias}$ for the maximum distance from good habitat for which bias occurred (Schultz and Crone, 2001). We further included a correlation in the biased movement; individuals should also tend to continue moving in the same direction by favoring pathways minimizing rotation of their current heading. Under the loop models (M5 and M6), we assumed that individuals started from a place of good quality to explore their surroundings and chose pathways going away from their starting point. If the individual did not find a good habitat on its outward path within a maximum number of steps $max_{steps.loop}$, it moved back towards its starting point.

Model parameterization

We estimated the unknown parameters for each model (Table 1.1) with a POM strategy. POM requires the identification of emergent patterns produced by the model which can be compared to the observed data. We identified three such patterns: emergence of subpopulations, frequency of road crossings, and distributions of distances moved. Simulated caribou locations were extracted at time steps corresponding to the dates of VHF locations for each individual.

Each simulated caribou had a mating area associated and therefore belonged to the subpopulation which had its range containing the individual mating area. For each subpopulation range, we counted the number of simulated locations from individuals belonging to that subpopulation which occurred inside the associated range. These were compared with the corresponding values from the observational VHF data by taking the absolute deviations (ADs=|x-y|). We obtained four ADs for this pattern, one for the Logan caribou, one for the Albert caribou and two for the two parts McGerrigle range (Fig 1.1). Similarly, we calculated three ADs of the number of road crossings events, one for each subpopulation. A crossing was defined when consecutive locations were on opposite sides of a paved road (Fig. 1.1). As an AD statistic approached zero, the pattern emerging from the simulation approached the pattern in the observed data. Finally, we compared the distributions of distances between consecutive locations for each subpopulation, as follows. We first calculated the POMDEV statistics between the distributions of simulated and observed distances. A POMDEV statistic indicates a relative deviance between two

distributions "[correponding] to [minus] twice the sum of the log of an approximate likelihood given by the approximating function of density from the simulation results applied on the field data" (Piou, Berger & Grimm 2009). We then calculated null indices by comparing the distributions of observed movement distances with distributions obtained by drawing random points inside the 100% minimum convex polygon of the telemetry data. A POMDEV index is dependent on the distribution used as a comparison. Therefore, to put all subpopulation indices of this pattern on the same scale, we calculated three McFadden's R^2 as 1 minus the ratio of simulated and null deviance statistics (McFadden 1974). As McFadden's R^2 statistic approached 1, the pattern of distances in the simulation approached the equivalent pattern in the observed data.

We used a best-fit calibration method (Railsback & Grimm 2012) to estimate model parameters (Table 1.1). We ran 100,000 simulations for each model using a HTCondor cluster (Thain, Tannenbaum & Livny 2005). While more simulations may have resulted in more precise parameter estimates, ours appeared adequate to obtain parameter estimates with reasonable confidence intervals regarding computation time. For each simulation, parameter values were sampled independently from uniform distributions (Table 1.1). For each model, we selected a subset of the runs whose outputs best reproduced all the patterns simultaneously. We used thresholds to define that a pattern was reproduced. We created a quantile value Q which we incremented from 0 to 1 by 0.01. At each Q value tested, we identified, independently for each pattern, the Q-ile simulation run and its pattern statistic associated which stood for the pattern threshold. For example, at Q=0.01, the threshold for the Logan subpopulation emergence pattern is equal to the AD statistic of that pattern for the (Q*100,000=) 1000th simulation when ranked for this particular statistic from low to high. For a simulation to be selected, the AD statistic for each subpopulation range patterns (n=4) and for each road crossing patterns (n=3) must be lower than the defined thresholds and the McFadden's R^2 statistics for each distance moved patterns (n=3) must be above the thresholds. We increased Q until at most 500 of the 100,000 simulations were selected. The number of simulations selected was a trade-off between too few simulations to obtain reliable parameter estimates and too many that included noise. From this selection, we removed simulations where individuals were stuck on a single landscape cell, an infrequent occurrence. We identified these situations from the output maps of landscape use. We

defined a cell in a map as an outlier when its number of visits was greater than 10 times the 0.975 quantile number of visits for that map as the difference between a cell repeatedly visited by caribou and one where an individuals was "stuck" was obvious from inspection of plotted maps. We removed simulations from the previous selection where their output map contained such outlier cells. We used kernel density estimators to determine the mode of the parameter values from the selected simulations. We interpreted these modes, which are, values close to the ones most commonly used in the selected simulations, as the parameter estimates. We estimated 95% confidence intervals of the parameter estimates with an Efron bootstrapping method. We re-sampled with replacement the parameter values from the selected simulations and defined the new mode. We iterated this step 10,000 times for each parameter. The 2.5[th] and 97.5[th] percentiles of the mode distributions obtained by bootstrap defined the confidence intervals of the parameters.

Movement hypothesis testing

Using the six fitted models, we assessed which model, and which corresponding hypothesis was best supported by the observational data, again using a POM strategy (Railsback & Grimm 2012). We ran each model 10,000 times, sampling parameters from the empirical density functions defined over the 95% confidence intervals of the bootstrapped estimates. Fewer simulations were needed than for model parameterization. We used the same 12 comparison statistics as described above and we calculated the mean statistic values across the 10,000 runs (i.e., mean absolute deviations (MADs) and McFadden's R^2 means) for each model. Then, we summed the statistic means for each global pattern and we selected the model with the lowest MAD sum for the emergence of subpopulations, the lowest MAD sum for road crossing and the highest McFadden's R^2 mean sum for the distances moved as our best supported hypothesis.

Model validation

We conducted an internal validation to test the ability of the best model to reproduce the data with which it was parameterized. We ran the model 10,000 times and, for each

simulation, recorded the values for the subpopulation emergence and road crossing patterns. We recorded the actual pattern values (e.g., number of location inside a range), not the AD statistics. AD statistics were useful to compare models but cannot be used to test for the robustness of a single model. We tested if the empirical pattern values fell within the pattern's simulated 95% coverage (Wiegand *et al.* 2004; Kramer-Schadt *et al.* 2007). The distances moved recorded per simulation were distributions, not single values. We therefore could not apply the same test as for the other two patterns, and so did not use it in model validation.

Landscape use estimate and comparison with habitat selection model

Using the selected best movement model, we ran 10,000 simulations, with 20 individuals created in each subpopulation to reduce dependency on the current population distribution. We summed the resultant landscape use maps to represent the potential landscape use by caribou during the period of the VHF surveys. A seasonally averaged map of relative occurrence probabilities from the two RSF models was constructed as an alternate estimate of potential landscape use. To summarize the differences between the two measures, we calculated the mean landscape use as a function of distance from the nearest subpopulation range (results within the ranges were not included). We rescaled values to the range [0,1] to facilitate comparisons.

Results

Model parameterizations and selection

For all six models, estimates of mean step length were higher in good habitats than in low quality habitats (Table 1.3). In good habitats, mean daily net distance moved ranged from 350.0 m to 997.1 m whereas in low quality habitats, estimates ranged from 103.9 m to 345.4 m. Estimated road crossing probabilities were low for all models, ranged from 0.12 to 0.51 (Table 1.3).

	$\mu_{sl.good}$	$\mu_{sl.low}$	σ_{sl}	p_{cross}	σ_{ma}	σ_c	$max_{dist.bias}$	σ_b	$max_{steps.loop}$	σ_{fl}
M1	5.00 [4.68;6.09]	4.11 [3.92;4.27]	1.31 [1.03;1.36]	0.14 [0.10;0.79]						
M2	5.66 [5.39;6.35]	4.09 [3.90;5.27]	1.10 [0.89;1.31]	0.51 [0.09;0.57]	31.00 [21.49;51.43]					
M3	5.48 [5.29;6.20]	4.41 [4.23;4.59]	1.14 [0.78;1.37]	0.20 [0.12;0.51]		86.65 [79.96;98.28]	25.64 [11.84;41.39]	87.01 [58.47;143.37]		
M4	5.97 [5.17;6.38]	4.59 [3.68;5.25]	1.34 [0.96;1.37]	0.17 [0.13;0.35]	85.95 [20.08;105.68]	113.42 [91.94;139.14]	20.45 [18.30;43.54]	121.53 [97.93;153.94]		
M5	5.53 [5.26;6.72]	3.85 [3.54;5.19]	1.26 [1.05;1.33]	0.14 [0.10;0.20]					3.53 [2.82;14.09]	124.70 [76.09;141.25]
M6	5.98 [5.81;6.39]	4.92 [3.87;5.17]	1.36 [1.02;1.39]	0.12 [0.09;0.18]	144.77 [26.42;150.76]				5.68 [4.64;16.80]	134.91 [74.32;151.12]

Table 1.3: Parameter estimates with 95% confidence intervals for each model.

Model M6, with a foray loop behavior in low quality habitat and a mating area attraction was the most consistent with the caribou VHF data. M6 yielded the lowest MAD sum for the subpopulation range pattern, the second lowest MAD sum for road crossings, and the highest McFadden's R^2 mean sum for the distribution of distances moved (Table 1.4). M5, with the foray loop behavior as in M6, but without mating area attraction, also performed well (Table 1.4). It was the best model with respect to road crossings and the second best for the subpopulation range pattern.

	MAD SR$_L$	MAD SR$_A$	MAD SR$_{McG}$	MAD SR$_{Vall}$	Sum MADs SR	MAD Xing$_L$	MAD Xing$_A$	MAD Xing$_{McG}$	Sum MADs Xing	McF.R^2_L mean	McF.R^2_A mean	McF.R$^2_{McG}$ mean	Sum means McF.R^2
M1	134.99	71.48	85.85	49.82	342.14	0.04	2.36	0.35	2.75	0.55	0.58	0.49	1.62
M2	81.11	54.49	84.70	52.53	272.83	0.08	2.27	0.55	2.90	0.58	0.62	0.52	1.72
M3	84.48	95.16	115.32	47.96	342.92	0.04	2.15	0.88	3.07	0.57	0.61	0.51	1.69
M4	**74.22**	70.87	98.87	**47.60**	291.56	0.04	2.10	0.82	2.96	0.59	**0.63**	0.53	1.75
M5	77.46	60.06	72.04	50.16	259.72	**0.02**	2.14	**0.20**	**2.36**	0.59	0.62	0.53	1.74
M6	80.07	**53.09**	**60.69**	48.86	**242.71**	0.04	**2.04**	0.30	2.38	**0.60**	**0.63**	**0.54**	**1.77**

Table 1.4: Pattern statistics for the model selection process. White columns are the statistic means over the 10,000 simulations and grey columns are the sum of these statistic means over each of the three global patterns. Bold values highlight the model which performed the best for that statistic. SR=subpopulation range pattern, L=Logan, A=Albert, McG=McGerrigle, Vall= Vallières-St-Réal, Xing=road crossing pattern, McF.R^2= McFadden's R².

Model validation

The best model (M6) was consistent with the data, according to internal validation tests. For six out of the seven patterns tested, values derived from the VHF data fell within the 95% coverages of the simulation output values (Table 1.5). The presence of McGerrigle caribou in the Vallières-St-Réal part of the subpopulation range was under-represented by the simulations; simulated 95% coverage of [0;34] did not include the total of 56 occurrences in the VHF survey data (Table 1.5). However, some of the 10,000 simulations did reproduce or exceed this indicator; the maximum number of McGerrigle caribou locations simulated in the Vallières-St-Réal area was 93.

	SR_L	SR_A	SR_{McG}	SR_{Vall}	$Xing_L$	$Xing_A$	$Xing_{McG}$
VHF data	266	279	357	56	0	3	0
95% range	[77;334]	[139;430]	[236;592]	[0;34]	[0;1]	[0;8]	[0;4]

Table 1.5: Pattern values from the VHF data and 95% coverages from simulation outputs with the best model. SR=subpopulation range pattern, L=Logan, A=Albert, McG=McGerrigle, Vall= Vallières-St-Réal, Xings=road crossing pattern.

Landscape use estimate

The highest simulated landscape use rates were concentrated in the center of each subpopulation range, with a very low potential landscape use outside these ranges (Fig. 1.4). Potential landscape use outside the Gaspésie National Park was also low. These results were expected and were already displayed by the VHF locations themselves. However, there was the suggestion of two corridors between the Logan and Albert subpopulation ranges, indicating possible movements of individuals between the two subpopulations (Fig. 1.4). This was not revealed by the VHF data. The model also identified areas of high potential use south of the Albert subpopulation range, where one VHF location was

recorded, and to the west and north of the Logan subpopulation range where no locations were recorded (Fig. 1.4).
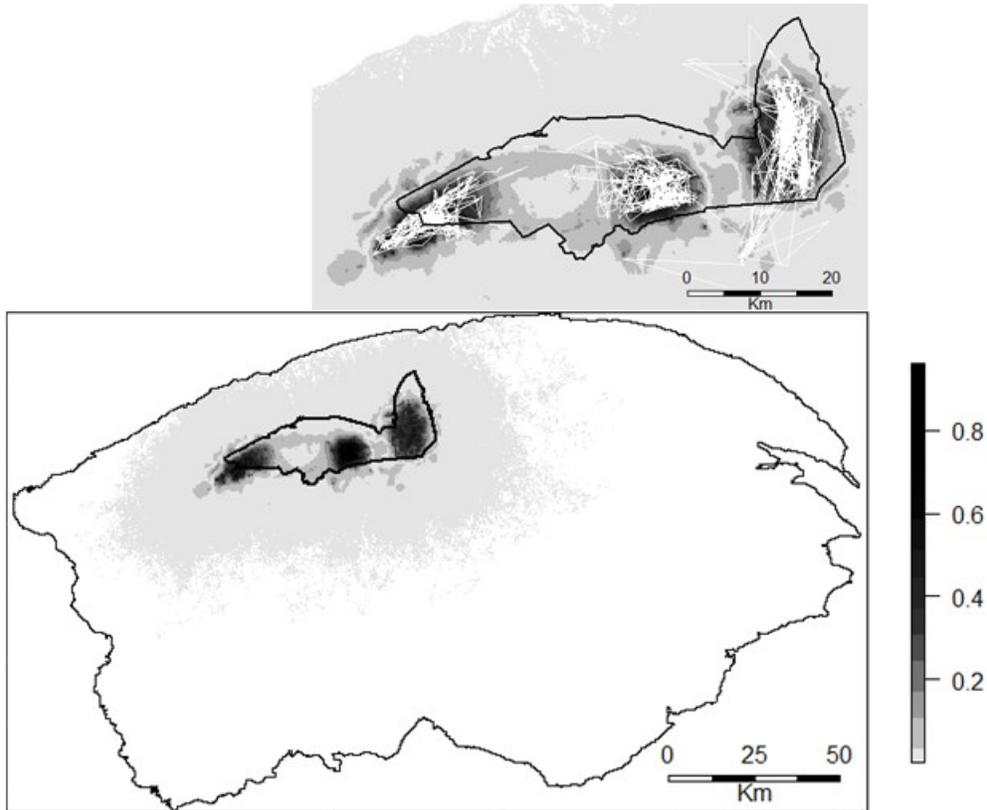
Figure 1.4: Lower map: Atlantic-Gaspésie caribou predicted landscape use for the time period of the VHF data surveys with the Gaspésie National Park boundary overlaid. Inset: Landscape use in the vicinity of the park with caribou paths inferred from VHF data (Fig. 1.1) shown as thin white lines.

Comparison of SE-IBM and RSF landscape use estimates

According to both movement and RSF models, caribou landscape use decreased sharply with distance from the nearest subpopulation ranges (Fig. 1.5). The models behaved similarly for distances up to 3 or 4 km. At greater distances, SE-IBM landscape use rates decreased rapidly, approaching 0 at a distance of 15 km. In contrast, RSF landscape use

estimates remained relatively high, between 0.18 and 0.53, at distances of up to 100 km from the subpopulation ranges.
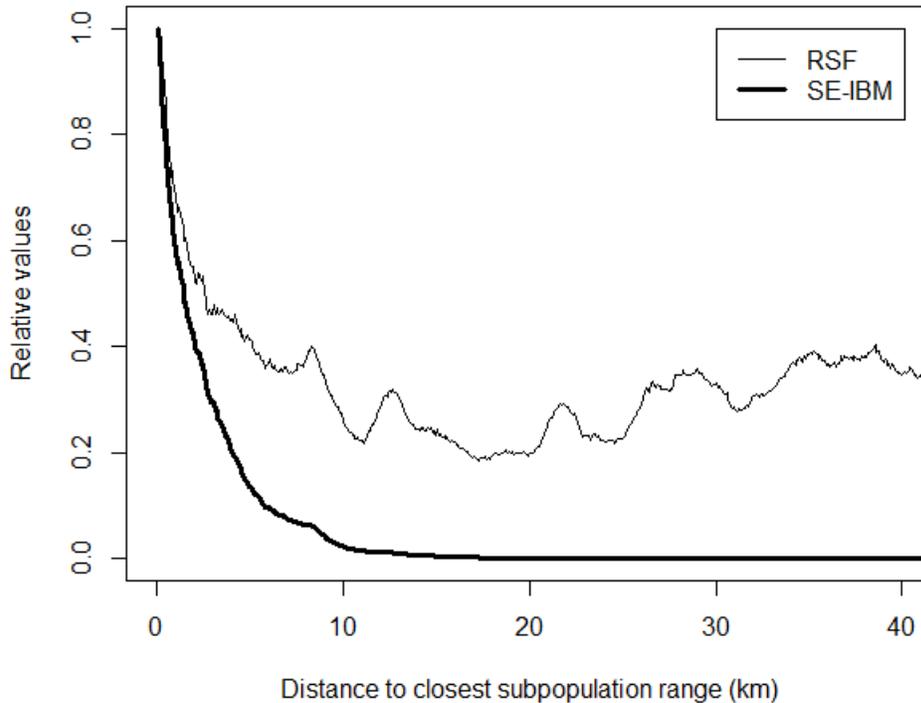
Figure 1.5: Atlantic-Gaspésie caribou relative landscape use as a function of distance to the nearest subpopulation range, calculated from resource selection function (RSF) and spatially explicit individual-based model (SE-IBM).

Discussion

By using spatially explicit individual-based models coupled with a pattern-oriented modeling strategy and spatially and temporally sparse data obtained from VHF surveys, we were able to build a robust movement model for the Atlantic-Gaspésie caribou population and estimate its landscape use. All the movement patterns defined with the telemetry data, except one, were commonly reproduced by simulations. The one exception, namely the number of individual occurrences in a small, disjunct component of one of the three subpopulation ranges, was reproduced by the best supported model, but with low

probability. The patterns used for model parameterization and selection represented three distinct and characteristic features of the observed movements of the Atlantic-Gaspésie caribou: distinct subpopulation ranges associated with site fidelity, road avoidance, and daily movement distances. They also seemed the most informative that could be derived from the VHF locations. Using multiple independent patterns ensured a strong filtering of the different model parameterizations and movement hypotheses when selecting our best model (Latombe, Parrott & Fortin *et al.* 2011; Grimm & Railsback, 2012).

VHF data contained enough information to clearly discriminate between alternate movement models. The data supported a model with two distinct movement behaviors for this caribou population, similar to a result found using GPS data for another caribou population (Johnson *et al.* 2002) and for elk (Morales *et al.* 2004). The two behaviors we identified were dependent on habitat quality. The VHF data was further able to discriminate between two hypotheses on movement behavior in low quality habitats. Foray loop behavior better reproduced characteristics of the data than did a biased correlated random walk. This suggests that caribou voluntarily moved away from good quality habitats to explore their surroundings, possibly in search of new resources (e.g., food, space, shelter, other individuals, etc.) embedded within relatively hostile or low quality habitats (Conradt *et al.* 2003). When such forays were unsuccessful, individuals returned to the good quality areas, which were mostly located inside the subpopulation ranges. The estimated number of daily time steps per foray loop was six steps (Table 1.3). Thus, the transit returning to high quality habitat, the second phase of an unsuccessful foray loop, would be better explained by memory rather than by a perceptual process leading to directional bias (Van Moorter *et al.* 2009; Fagan *et al.* 2013). The VHF data also sufficed to identify a temporal component to caribou behavior. Adding mating season range attraction improved the model ability to replicate patterns in the data. The model mechanisms suggested that Atlantic-Gaspésie caribou fidelity to their range was based at least in part on intrinsic behavior and not solely on responses to spatially varying habitat quality (Faille *et al.* 2010). Finally, the VHF data led to low estimates of paved road crossing probabilities which is consistent with known road avoidance behavior for this species (Dyer *et al.* 2002; Leblond, Dussault & Ouellet 2013; Beauchesne, Jaeger & St-Laurent 2013), as well for this population (Gaudry 2013).

Estimated mean step lengths were larger in good quality than in low quality habitats, which was counter-intuitive. Indeed, several sources have shown the opposite pattern; animals remain for shorter times, and thus to travel faster, within low quality habitats, and remain longer in good quality habitats to benefit from better environmental conditions (Johnson *et al.* 2002; Morales *et al.* 2004). However, our findings may reflect characteristics of the Gaspésie landscape. The tops of the mountains, where much of the good quality, safer habitats for caribou are found, have very low tree cover (i.e., alpine tundra) and moving around is easy. Valley bottoms, which are considered low quality habitats, have dense tree covers of balsam fir and other tree and shrub species (Nadeau Fortin 2015), potentially slowing or inhibiting caribou movement.

The landscape use map derived from the movement simulations provides a spatial understanding of where the population potentially moved through and interacted with its landscape, over the time period of the dataset. High landscape use was predicted, as expected, for the areas where VHF locations were recorded; in this case, at high elevation sites where we defined the subpopulations ranges (Mosnier *et al.* 2003). But the more interesting results were where high landscape use was predicted from environmental conditions and individual movement behavior in areas where no caribou were observed (Marucco & McIntire 2010). Such predictions can only be obtained by simulations. Our models seemed to reveal movement corridors between the Logan and the Albert ranges, even though no individual exchange was recorded between the two subpopulations in these data. Clearly, because the current Logan population was established by recolonization from the Albert population during the late 1990s, such connections exist. A better connectivity analysis would be needed to explore if individual exchanges were likely or, even though these areas were likely used, individuals were still faithful to their subpopulation (Lookingbill *et al.* 2010). Some areas outside the Gaspésie National Park, where no VHF locations were recorded, nevertheless showed a high potential for landscape use; these areas were reachable by the caribou. These regions could indicate specific opportunities for expanding the park or at least for adding some measures of habitat protection outside the park to improve caribou conservation (as suggested in St-Laurent *et al.* (2009)).

Defining good quality areas that individuals have access to is one of the main differences between the outputs from the spatially explicit individual-based model and the

results from the empirical habitat selection model (i.e., RSF). The RSF model suggested large areas of usable, but sub-optimal, habitats distant from the current subpopulation ranges. The spatial constraints added by the individual-based model (e.g., roads as movement barriers), as well as the spatial and temporal components of individual movement behavior, had the effect of making it extremely improbable that members of the existing population would reach these more distant areas (Marucco & McIntire 2010; Grosman *et al.* 2011). Movement simulations therefore showed very low potential landscape use at distance above a few kilometers from the subpopulation ranges. This will be further exacerbated because we found two behavioral reasons for this limitation, namely return to mating area and foray loops. In other words, they may be compelled to return even if good habitat were found outside. The movement model, if tied to a demographic population model (Wiegand *et al.* 2004; Marucco & McIntire 2010), could be used on a longer time scale to identify stepping stones that enable the population to reach more distant, high quality, habitats within the peninsula.

Conclusion

Identifying mechanisms of animal movement and estimating potential landscape use does not require large amounts of high resolution telemetry data, provided some basics of species habitat preferences are known. However, the spatial and temporal resolution of the movement sought must be commensurate with the data: for example, one should not try to recreate hourly movements from weekly data. The complexity of the behavioral model should also be adapted to the resolution of the data, to avoid overfitting. Using spatially explicit individual-based models and pattern-oriented modeling techniques, we identified and quantified drivers of individual movement behaviors, and thus simulated spatial landscape use at the population level, using only relatively few locations obtained by VHF telemetry. These models can identify landscape features that could be modified by managers to improve population movement (e.g., paved roads), as well as intrinsic behavioral characteristics that must be accommodated (e.g., mating site fidelity). Estimating potential landscape use of the animal population gives managers a spatial reference of where movement is facilitated or impeded, defining priority areas to work on

for the protection or recovery of endangered populations. For example it can help to define areas to apply new protection rules or to design movement corridors for the studied species. Despite the above-mentioned limits of the VHF data, they represent an important resource for conservation applications, especially when immediate actions are needed. The methods used in this study could be applied on other populations or species, facilitating conservation studies when observational data are few.

Acknowledgements

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Appendix

Appendix 1.A: Movement model for the Atlantic-Gaspésie caribou: Overview, Design concepts, and Details protocol.

Overview

Purpose

We developed spatially explicit individual-based models for the Atlantic-Gaspésie caribou (*Rangifer tarandus caribou*). The purpose of the models was to understand caribou movement and estimate its potential landscape use. Our focus was on movements outside subpopulation ranges, identifying the mechanisms that lead individuals to return to their ranges and simulating these behaviors in relation to landscape features. The primary challenge was the sparseness of the available data. We used a pattern-oriented modeling strategy for parameter estimation and model selection. In this document, we present the details of the SE-IBMs according to the ODD protocol (Grimm *et al.* 2006, 2010).

Entities, state variables, and scales

The mobile entities in the SE-IBMs represented the 35 collared caribou in the telemetry dataset. Individuals had five state variables:

name: individual's name taken from the telemetry data;

mating area: one of three mating areas, defined by spatio-temporal analysis of the telemetry data;

position: coordinates of the individual current location;

heading: individual current heading;

behavior: if the individual would follow a "good habitat quality" or a "low habitat quality" movement model.

Simulation time step was daily; positions and headings were updated at each time step. A complete simulation ran four years to cover the telemetry survey period. Individual movements were simulated over a landscape which extent covered the whole Gaspésie natural region (MDDEP 2012). The landscape was represented as a regular grid of 75 x 75 m cells (0.5625 ha). Landscape characteristics were represented by the following cell-level state variables:

quality: a measure of caribou selection. Values were relative probabilities of occurrence calculated from the resource selection function models for the same caribou population (Gaudry 2013); values ranged from 0 (avoided) to 1 (selected). We used two seasonal RSF models, one for summer and one for winter. Thus, habitat quality changed over time within years.

road: a binary value indicating if the cell was intersected by a paved road.

mating area: a code identifying cells within each of the three mating areas.

Process overview and scheduling

At each time step, the Julian date is updated. If the season changes, cell quality values are updated. Individuals select a pathway based on environmental characteristics and the movement model they followed. First, individuals checked the quality value of their current location and followed a good-HQ behavior movement model if the value was equal or above a certain threshold or a low-HQ movement behavior model otherwise. A step length for the next move was sampled per individual. Individuals identified all possible pathways around them, defined as the list of cells on the straight lines going from their current position to every unique cell of the landscape located at their step length distance (Fig. 1.3a and 1.3b). For each available pathway, index values were calculated based on the different movement characteristics (Table 1.2). These indices were based on: the quality value of the cells on the pathway (Fig. 1.A.1a), the presence of paved road on the pathway (Fig. 1.A.1b), the deviation of the pathway with the direction towards the individual mating area (Fig. 1.A.1c), the deviation of the pathway with the individual current heading (Fig. 1.A.1d), the deviation of the pathway with the direction towards the closest area of good quality (Fig. 1.A.1e), and the deviation of the pathway with the direction away from (Fig. 1.A.1f) or towards (Fig. 1.A.1g) the individual loop starting point. Indices were then rescaled independently to sum to 1 to represent the probabilities of choosing a pathway based on a particular movement characteristic. A final probability for each pathway was calculated using some of the rescaled indices, depending on the particular movement model followed by the individual and therefore the movement characteristics included (as described in the main text *Spatially explicit individual-based model*). Finally, one pathway was probabilistically selected among the ones available and the individuals moved at the end of their pathway (Fig. 1.3c and 1.3d).

a)

$$P \sim \frac{1}{N}\sum_{i=1}^{N} quality.cell_i$$

b)

$$P \sim (p_{cross})^{\#roads}$$

$P \sim N(\mu = 0, \sigma = \sigma_{ma})$

$P \sim N(\mu = 0, \sigma = \sigma_{c})$

c)

d)

$P \sim N(\mu = 0, \sigma = \sigma_{b})$

$P \sim N(\mu = 0, \sigma = \sigma_{fl})$

e)

f)

$P \sim N(\mu = 0, \sigma = \sigma_{fl})$

g)
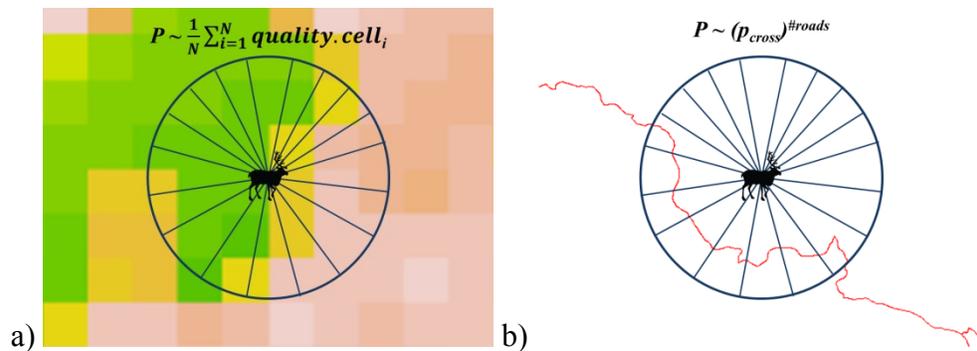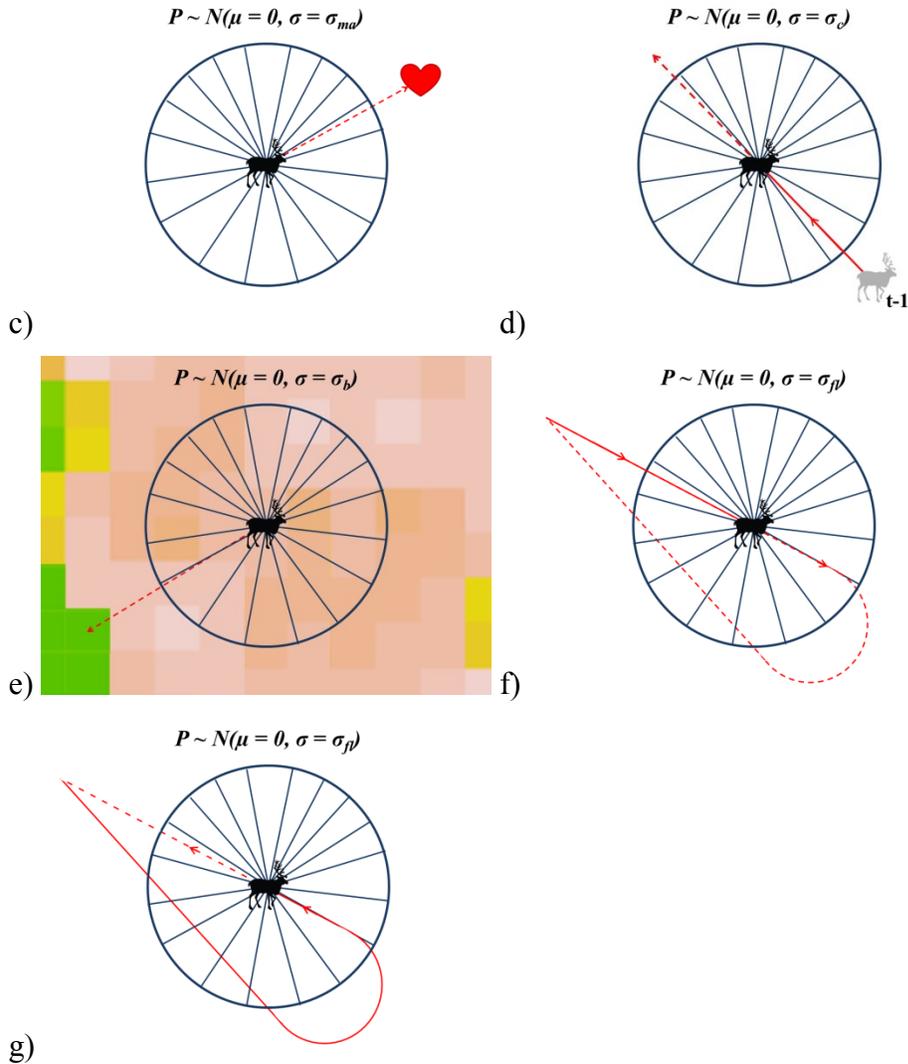
Figure 1.A.1: Illustration of how pathway index values, which are then rescaled into probabilities, were calculated for each movement characteristic. a) Probabilities based on landscape quality. The colors represent quality values with green/yellow for high values (good quality habitats) and pink for low values (low quality habitats). b) Probabilities based on the presence of paved road on the pathways and the crossing probability p_{cross} (Table 1.1) for an Atlantic-Gaspésie caribou. c) Probabilities based on the deviation of the pathways with the direction towards the individual mating area (i.e., heart shape). d) Probabilities based on deviation of the pathway with the current individual's heading defined with the location at the previous time step (t-1). e) Probabilities based on the deviation of the pathways with the direction towards the closest area of good quality (i.e., green area). f) Probabilities based on the deviation of the pathway with the direction away from the individual loop starting point. g) Probabilities based on the deviation of the pathway with the direction towards the individual loop starting point.

Design concepts

Basic principles

The main assumption of the SE-IBMs was that caribou can sense their environment and use this information to make movement decisions. Atlantic-Gaspésie caribou (and of other populations) do not move randomly. Different habitats are over-used (i.e. selected) or under-used (i.e. avoided) relative to their availability (Ouellet, Ferron & Sirois 1996; Mosnier *et al.* 2003). The different usage of available habitats, in combination with observed movements of radio-collared individuals, was the empirical foundation for our models.

We tested single- and two-behavior movement strategies (Johnson *et al.* 2002; Morales *et al.* 2004). Johnson *et al.* (2002) differentiated "intrapatch" from "interpatch" movements, and Morales *et al.* (2004) differentiated "encamped" and "exploratory" states. We used the quality values at caribou telemetry locations to define a threshold between two movement behaviors. Quality values for the VHF locations followed a bimodal distribution (Fig. 1.2) and the quality value for which the density function was the lowest was chosen as the threshold. Separate thresholds were defined for winter and summer. The threshold separated habitats of higher quality (mostly inside the subpopulation ranges and which can be related to an "intrapatch" or "encamped" movement) from habitats of lower quality (which can be related to the "interpatch" or "exploratory" movement). In a two-behavior model, the good-HQ or low-HQ movement behavior was selected by comparing the quality of the individual current location to the threshold at the current date.

We used one movement model to represent good-HQ movement behavior: a habitat-mediated random walk. We tested three movement models for the low-HQ movement behavior: a hm-RW (i.e., same as the good-HQ behavior, the individuals therefore followed a single-behavior strategy), a habitat-mediated biased correlated random walk and a habitat-mediated foray loop. All models were habitat mediated so they all accounted for habitat quality (Fig. 1.A.1a) and road presence (Fig. 1.A.1b). The relative probability of caribou occurrence derived from the RSF was used to calculate the relative probability of choosing a pathway based on landscape quality. Roads have been recognized as strong barriers for caribou movements (Dyer *et al.* 2002; Leblond *et al.* 2011; Fortin *et al.* 2013; Beauchesne, Jaeger & St-Laurent 2013). A model parameter p_{cross} (Table 1.1), the probability of crossing a paved road given it was encountered (Dyer *et al.* 2002) was estimated for each movement model.

We tested the impact of mating area attraction on caribou movement (Fig. 1.A.1c). Caribou populations are faithful to their home ranges (Metsaranta 2008; Faille *et al.* 2010) and our telemetry data showed a strong fidelity from the Atlantic-Gaspésie caribou to a single subpopulation range, especially during the peak of the mating season. If we included mating site fidelity during the mating season (defined from September 15th to November 1st; Moisan 1958; Bergerud 1973; Lalonde & Michaud 2013), simulated individuals preferred pathways that lead them towards their own mating area.

When individuals followed a hm-BCRW, they chose their next pathway based on a correlation with their previous movement (Fig. 1.A.1d) and a bias towards habitats of good quality (Fig. 1.A.1e). Individuals favored pathways with the least deviation from their current heading (i.e., correlated movement; Bergman, Schaefer & Luttich 2000; Latombe

2013), but they also favored pathway that lead them towards nearby habitats of good quality. The bias effect occurred over a certain distance from the closest habitat of good quality ($max_{dist.bias}$), assuming that caribou could sense their environment over that certain distance.

When individuals followed a hm-FL, they chose their next pathway based on a looping pattern (Conradt *et al.* 2003). In this pattern, individuals moved away from a cell of good quality, considered as the starting point of their loop, to explore their surroundings (Fig. 1.A.1f). Therefore they favored pathways going away from this location. If during the looping pattern individuals did not find a new good cell and they reached a maximum number of steps allowed for this exploratory loop ($max_{steps.loop}$, Table 1.1), they went back to their starting point (Fig. 1.A.1g). They favored pathways going towards this location on the way back. The definition of a good area/cell for the hm-BCRW and the hm-FL was based on the same quality threshold as to differentiate the two movement behaviors.

To test which mechanisms best represented caribou movement displayed in our telemetry data, we created six different models (M1 to M6). M1 was a single movement-behavior model where individuals followed a hm-RW for the good-HQ and low-HQ movements. M3 and M5 were two-behavior movement models; individuals followed a hm-RW for the good-HQ movement and either a hm-BCRW (M3) or a hm-FL (M5) for the low-HW movement behavior. M2, M4 and M6 were respectively the same as M1, M3 and M5 where we added the mating area attraction to both the good-HQ and low-HQ movement models (see main text *Movement models*).

Emergence

Four movement patterns were identified in the Atlantic-Gaspésie caribou telemetry data and we sought to recreate these patterns in the simulation outputs. First, simulated caribou should have recreated the three subpopulation ranges, located on the three mountains ranges in the Gaspésie National Park as identified with the VHF locations (Latombe 2013; Beauchesne, Jaeger & St-Laurent 2013). Second, a paved road crosses the population range and the telemetry data showed few crossings of that road. Thus, simulated caribou should have crossed the paved roads at a similar low rate in the simulations. Third, the measured walked distances between the consecutives recorded locations should have matched with the distances walked by the simulated individuals for the same time lags. And fourth, the data showed no individuals with repeated VHF locations at the exact same position. Thus, we expected a continued movement of the individuals. A lack of motion from individuals pointed out some unrealistic parameter values. We used these four patterns to parameterize the SE-IBMs using the POM strategy and the first three patterns were used for model selection (Grimm *et al.* 2005; Kramer-Schadt *et al.* 2007; Railsback & Grimm 2012).

Adaptation

Individuals were simulated in a heterogeneous landscape and they made decisions about their next move based on a new set of information at each time step. Their environment influenced the movement model they followed (good-HQ or low-HQ movement) which included different movement characteristics. They adapted their next movement based on

the landscape surroundings (e.g., habitat quality, road presence, bias towards good areas), the time period (e.g., reaching their mating area during mating season), and/or their previous movement (e.g., correlated movement, looping movement).

Objectives

Individuals did not have a global objective such as a fitness measure, or need to fulfill over a long time period (Semeniuk *et al.* 2012). Their objectives were a daily search for their next move. They selected a pathway among the ones available based on probabilities dependent on the specific movement model they followed. The models represented various hypotheses: individuals moved through high quality cells, they avoided paved roads, they oriented towards mating area during the mating season, they kept a constant heading, they oriented towards nearby locations of high quality habitat, or they performed loop patterns when exploring the surroundings.

Learning

Individuals did not have a learning behavior which changes their decision process over time; the rules followed for each movement model were constant over the course of a simulation.

Prediction

There was no prediction in the model, individuals sensed the current environmental conditions around them but they could not predict future conditions. For example, individuals did not anticipate mating season, but simply changed their behaviors with the seasons.

Sensing

Individuals had knowledge of the state variables for the cells they could sense, which were the cells within their step length distance, or within the maximum distance for the bias to occur ($max_{dist.bias}$, Table 1.1). Individuals also knew the location of their mating area and when it was mating season.

Interaction

There was no interaction in the model either between individual caribou, or between caribou and the environment (e.g., there was no quality decrease through food depletion; Semeniuk *et al.* 2012).

Stochasticity

Step lengths were sampled from a distribution, and the choice for the pathway to follow was according to probabilistic simulations and would have not necessary selected the best one.

Collectives

There were no groupings of individuals in this model as there were no individual interactions.

Observation

We used a POM strategy to parameterize the models and to select the best one among the six models tested to explain caribou movement. We compared emergent patterns from the simulated outputs to the patterns of the telemetry data. To define patterns from the simulated outputs, we sampled simulated individual locations by extracting locations at the dates caribou were recorded in our telemetry data. This method ensured similar sample sizes for the simulated and telemetry data. Independently for each model, we searched for parameter values that minimized the deviation between output and telemetry patterns, over a large number of random samples of parameter values (see main text *Model parameterization*). We then used the optimal parameterization of each model to select the best one with the same deviance criteria (see main text *Movement hypothesis testing*). Using the selected model, we simulated caribou movement to produce a map of the Atlantic-Gaspésie caribou landscape use. To do so, we mapped the number of caribou visits at each cell for the last three years of simulation (the first year was removed to limit the influence of initial positions).

Details

Initialization

The landscape included a landscape quality layer, the designated mating areas, and the road network. For each simulation, 35 caribou were created corresponding to the unique collared caribou. Individuals were assigned a name and mating area from the telemetry data. An initial position was drawn randomly within their mating area, with a random heading. The maximum value allowed for step length simulation with the lognormal distribution was set to 20 km to avoid unrealistic large daily step. Simulations started at Julian day 1 of year 1. Quality values of the landscape cells were assigned according to the winter RSF (Gaudry 2013). The mating season was defined between Julian day 258 (September 15th) and Julian day 305 (November 1st) (Moisan 1958; Bergerud 1973; Lalonde & Michaud 2013).

Input data

Cell quality values were updated the first day of winter and summer of each year with the seasonal RSF values. Winter was defined from November 16th to April 30th; summer was from May 1st to November 15th (Gaudry 2013). The quality threshold was updated at the

same time; it equaled to 0.382 in winter and 0.290 in summer (see main text *Spatially explicit individual-based model*).

Submodels

Submodels were executed in the following order during the simulation.

date: Julian date increased by one. After Julian date reached 365, it went back to one and the number of simulated year increased by one. The simulation stopped at the end of the time step Julian day 365 year 4.

update-quality: At Julian date 121 (May 1st), the cell's quality was assigned RSF summer values and the quality threshold value was updated with the summer value. At Julian date 320 (November 16th), the RSF winter values were assigned and the quality threshold value was updated with the winter value.

sim-step-length: Step length values were sampled from a lognormal distribution, one per individual. The mean of the distribution depended on the quality of the cell at the individuals' current location ($\mu_{sl.good}$ or $\mu_{sl.low}$, for good and low quality habitats, respectively; Table 1.1). The means and standard deviation σ_{sl} (Table 1.1) of the distributions were parameters to be estimated. Maximum step-lengths were enforced by rejection sampling.

id-pathways: Individuals identified all the unique pathways around them based on the grid landscape. Pathways were defined as lists of cells on the straight lines going from the current location to all unique cell's at distance of a given step length.

Then, six different probabilities were calculated for each pathway based on the index values of the movement characteristics (Table 1.2). The following six submodels detail each probability.

quality-prob: The quality value of all cells along each available pathway for the individual was extracted and the mean along each pathway was calculated (Fig. 1.A.1a). The path means were standardized to sum to 1 and then stood as probabilities based on landscape quality. The rescaling so that index values of all pathways sum to 1 was done for each movement characteristic independently (i.e., in the submodels *quality-prob*, *road-prob*, *mating-prob*, *corr-prob*, *bias-prob,* and *fl-prob*.); index values were then considered as probabilities.

road-prob: If there was a paved road crossing for one of the available pathways for the individual, the pathways index values were equal to the probability of crossing a paved road for an Atlantic-Gaspésie caribou p_{cross} (Table 1.1) raised to the number of cells crossed by a road on the pathways (Fig. 1.A.1b). The road crossing probability was a parameter to be estimated (Table 1.1).

mating-prob: During mating season, at locations outside an individual's mating area, the bearing between each pathway and the mating area was calculated. Index values were calculated for these bearings from a Normal distribution truncated to -180° and 180° with direction to mating area equal to 0° (Fig. 1.A.1c). The standard deviation σ_{ma} (Table 1.1) of the distribution was a parameter to be estimated.

corr-prob: The rotation angle between each pathway and the current heading of the individual was calculated. Then index values were calculated for each angle from a Normal distribution truncated between -180° and 180° with current heading equal to 0° (Fig. 1.A.1d). The standard deviation σ_c (Table 1.1) of the distribution was a parameter to be estimated.

bias-prob: If the individual was within the bias distance $max_{dist.bias}$ (Table 1.1) of a good quality habitat, movement in this direction was favored. The rotation angle between each pathway and the direction of this good location was calculated. Then index values were calculated from a Normal distribution truncated between -180° and 180° with direction to good habitat quality equal to 0° (Fig. 1.A.1e). The bias distance and the standard deviation σ_b (Table 1.1) of the distribution were parameters to be estimated.

fl-prob: Foray loop behavior was defined by movements away from starting location in search of new high quality habitat. There was a maximum of movement steps permitted $max_{steps.loop}$ (Table 1.1). If a new high quality cell was found within that many movement events, it became the starting location for a new foray loop and the movement counter was reset to 0. Otherwise, the caribou began to move towards the starting location of the current foray loop. Then, a new loop started from this location in another direction. When moving away from the loop starting location, the rotation angle between each pathway and the opposite direction to the loop starting location was calculated. If the caribou was moving back, the rotation angle between each pathway and the direction towards the loop starting point was calculated. Pathway index values were then calculated using a Normal distribution truncated between -180° and 180°, centered on the direction away from, or towards the current foray loop starting location (Fig. 1.A.1f and 1.A.1g). The maximum number of steps allowed in the loop pattern away $max_{steps.loop}$ (Table 1.1) and the standard deviation σ_{fl} (Table 1.1) of the distribution were parameters to be estimated.

pathway-prob: The model-dependent probabilities for each pathway (see main text *Movement models*) were multiplied to obtain a single probability per pathway, according to the movement characteristics included in the model followed. In the two-behavior movement model, the individual first checked the quality value of its current position and followed either a good-HQ movement model (i.e., a hm-RW) if the quality value was above or equal the threshold, or it followed a low-HQ movement model otherwise (either a hm-BCRW or a hm-FL).

choose-pathway: One pathway was chosen probabilistically using the final pathway probabilities. Probabilities were transformed into a cumulative sum, and then scaled to range from 0 to 1. A uniform random number was then sampled between 0 and 1 and used to select a pathway according to the ranges of the cumulative sums.

move: The individual oriented along its chosen pathway and moved on it by the chosen step length. The individual's location was then recorded.

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Chapter 2 : Reducing movement barriers mitigates negative effects of climate change on caribou movement potential

Résumé

Les activités anthropiques et les changements climatiques peuvent perturber le mouvement des animaux et détériorer leur potentiel de mouvement dans le paysage. Quantifier et cartographier le potentiel de mouvement des populations peut aider les prises de décision en gestion du paysage en identifiant les barrières au mouvement qui peuvent être aménagées. Nous avons utilisé un modèle individu-centré spatialement explicite développé pour la population de caribou de la Gaspésie-Atlantique pour tester l'impact des changements climatiques et de différentes mesures de conservation sur son potentiel de mouvement. Les changements climatiques ont réduit le potentiel de mouvement du caribou. Restaurer les routes secondaires dans les aires protégées a maintenu plus efficacement le potentiel de mouvement du caribou que ne l'a fait l'ajout des nouvelles aires protégées actuellement proposées. Les modèles individu-centré spatialement explicite couplés avec des scénarios de paysage peuvent efficacement prédire le potentiel de mouvement et évaluer l'efficacité potentielle de mesures de conservations.

Abstract

Human land use and climate change can disrupt individual movements of terrestrial animals and therefore degrade population movement potential over a landscape. Quantifying and mapping movement potential can support management decision-making by identifying and locating movement barriers. Once identified, resulting negative impacts may be mitigated. We used a spatially explicit individual-based model previously developed for the Atlantic-Gaspésie caribou population to test the impact of climate change and conservation measures on the caribou movement potential. Climate change impacts reduced caribou movement potential. Restoring secondary roads inside protected areas more effectively maintained caribou movement potential than did the addition of the new protected areas currently proposed. Spatially explicit individual-based models coupled with landscape scenarios can effectively forecast movement potential and evaluate the potential effectiveness of alternate conservation measures.

Introduction

Most animals must move across their landscape to acquire the various requirements of their life cycle. Estimating the movement potential (capacity) of species in fragmented and changing landscapes can help to identify actual and potential movement corridors and barriers (Loarie, Van Aarde & Pimm 2009; Marucco & McIntire 2010). This, in turn, helps estimate mechanisms of landscape use such as functional connectivity between distinct habitats (Taylor *et al.* 1993; Baguette & Van Dyck 2007). These mechanisms of landscape use may be contributing to limit population size or persistence (Holdo *et al.* 2011; Andrello *et al.* 2014). In a context of land management aimed towards endangered species recovery or sustainability, estimates of movement potential throughout a landscape can therefore help managers better allocate resources and identify landscape areas for regulations.

Barriers reduce movement potential by impeding individual movement. Barriers can be human-made, such as roads (Beauchesne, Jaeger & St-Laurent 2013) and fences (Loarie, Van Aarde & Pimm 2009), or natural, such as physical obstacles like rivers (Walker, Novaro & Branch 2007) and topographic features (Graf *et al.* 2007), or behavioral barriers induced by predators (Latombe, Fortin & Parrott 2014). When anthropogenic barriers impede movement so as to threaten a population's survival, it is the managers' task to eliminate or mitigate the negative effects of these structures (Bennett & Mulongoy 2006; Beier, Garding & Majka 2008). Land protection (Andrello *et al.* 2014) or restoration (McIntire, Schultz & Crone 2007; Severns, McIntire & Schultz 2013) are some conservation actions which can restore movement potential.

The effects of climate change have already been observed for some species, with individuals shifting in latitude or elevation to follow their optimal habitat conditions (Chen *et al.* 2011). Climate change impacts environmental conditions in various ways such as the spatial and temporal distribution of resources and species (Walther *et al.* 2002; Chen *et al.* 2011), the magnitude of climatic events (Logan 2012) or the timing in habitat states (e.g., frozen VS flowing river; Leblond, St-Laurent & Côté *et al.* 2016). Some of these changes are expected to alter animal movement patterns (Lawler *et al.* 2013) thereby changing population movement potential (Nuñez *et al.* 2013). Forecasting movement potential on human-modified landscapes under future climate (Hof *et al.* 2011) is useful to forecast

population responses to the expected changes. For example, it can help managers identify mitigation measures to restore lost movement potential, such as new protected area implementation or barrier removal. Incorporating climate change into conservation studies is emerging as a major challenge in designing new protected areas and other conservation measures (Hannah *et al.* 2007; Magness *et al.* 2011).

We used an individual-based movement model to estimate and map the movement potential of the Atlantic-Gaspésie caribou (*Rangifer tarandus caribou*), a relict population now confined to high-elevation habitats within a highly modified, managed boreal forest landscape in Québec, Canada. We evaluated caribou movement in several possible future landscapes, simulating the outcomes of various combinations of climate change and conservation scenarios. The climate change scenarios we used represented a gradient of potential climate change impacts on regional vegetation. Conservation scenarios included proposed, new protected areas and the restoration of secondary roads inside protected areas. We tested if projected climate change would impact the landscape so as to decrease caribou movement potential and which conservation strategy (i.e., new protected areas, road restoration or the combination of both) could best mitigate such effects.

Material and methods

Case study: the Atlantic-Gaspésie caribou

Our study system was the caribou population inhabiting the Gaspésie peninsula of Québec, Canada (Fig. 2.1). The Atlantic-Gaspésie population is the last surviving caribou population south of the St-Lawrence River. Currently, individuals are mostly found within the Gaspésie National Park (Mosnier *et al.* 2003; Lalonde 2015). The population is spatially divided into three subpopulations, associated with breeding grounds on the summits of Mounts Logan, Albert and McGerrigle (Fig. 2.1a). There have been very few recorded exchanges of individuals among subpopulations (Mosnier *et al.* 2003).
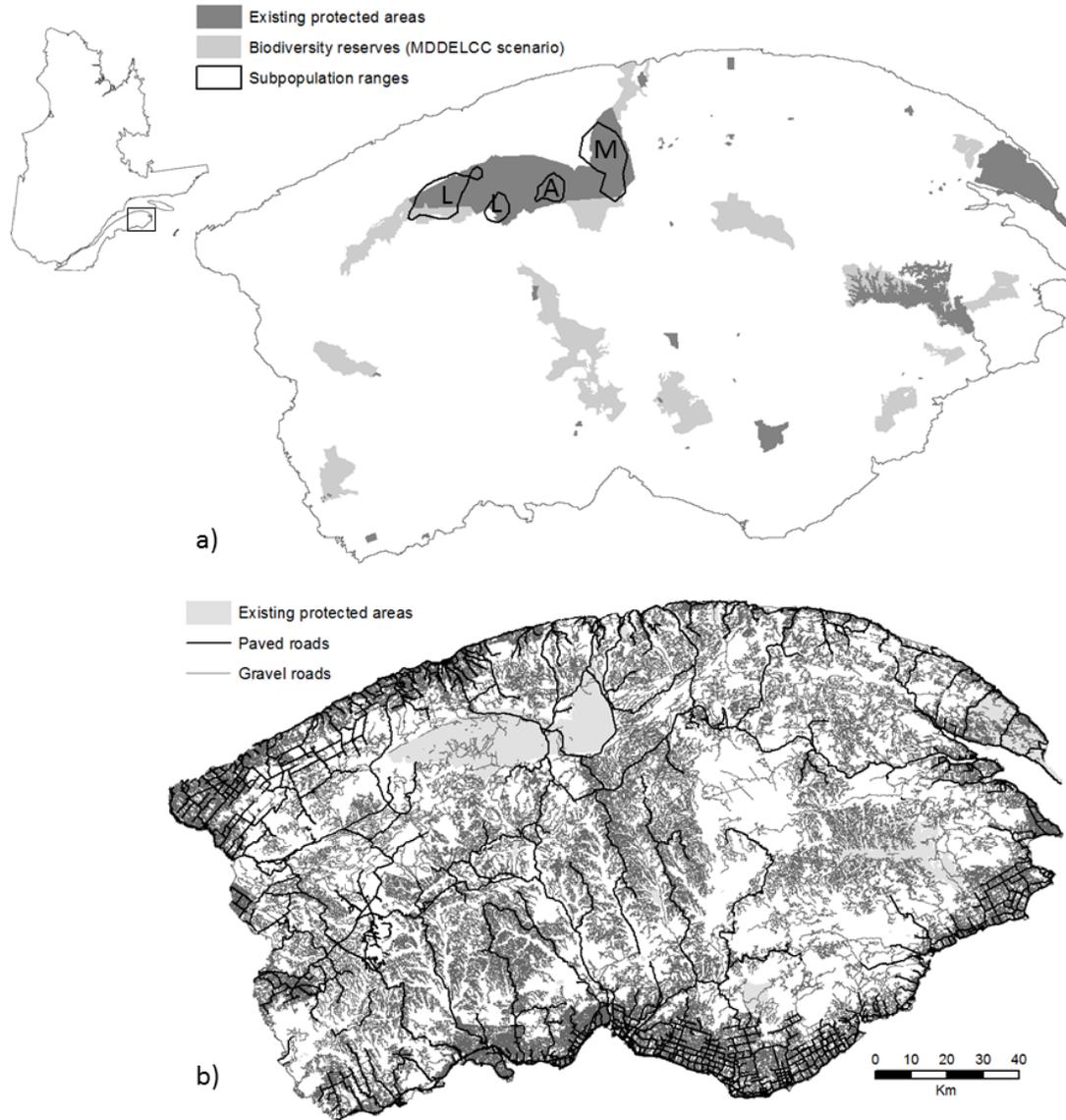
Figure 2.1: Left inset: Province of Québec (Canada) with study area outlined. a) Study area with the existing protected areas and proposed new biodiversity reserves. The largest protected area in the north-west of the study area is the Gaspésie National Park. Subpopulation ranges are delineated by an 80% kernel density using caribou VHF and GPS data (L=Logan, A=Albert and M=McGerrigle). b) Road network in the study area overlaid on the existing protected areas.

The estimated herd size in 2015 was between 94 and100 individuals (Lalonde 2015) and the population is listed as endangered (Environment Canada 2014). The population has

declined in the past several years. Predation by coyotes (*Canis latrans*) and bears (*Ursus americanus*), sustained by abundant alternate prey and forage promoted by forestry activities, seems to be the main cause of recent declines (St-Laurent *et al.* 2009). The caribou population relies on the alpine tundra as an open space to find mating partners and avoid predators. These caribou primarily feed on alpine herbaceous plants and graminoids. In winter, caribou prefer lower elevation, old stands of balsam fir (*Abies balsamea*) and forage on arboreal lichen (Mosnier *et al.* 2003). Both these habitats are threatened by climate change (Loarie *et al.* 2009; Périé *et al.* 2014; Dumais *et al.* 2014), likely decreasing habitat quality for the caribou in Gaspésie and further threaten this fragile population.

The Gaspésie peninsula belongs to the boreal biome. Most of its area, except along the coasts, belongs to the balsam fir - white birch bioclimatic domain (Saucier *et al.* 2003). The forests are dominated by balsam fir and white spruce (*Picea glauca*) stands mixed with white birch on mesic sites (*Betula papyrifera*). On less favorable sites, black spruce *(Picea mariana)*, jack pine (*Pinus banksiana*) and larch are found alongside white birch or trembling aspen (*Populus tremuloides*). The main natural disturbances in this region are spruce budworm (*Choristoneura fumiferana*) outbreaks (Saucier *et al.* 2003), and windthrow (source: ecoforestry maps, Ministère des Forêts, de la Faune et des Parcs du Québec, MFFP). Precipitation is abundant due to the maritime climate and therefore wildfires are infrequent (Saucier *et al.* 2003). Outside protected areas, forestry activities are the main disturbances in terms of annual area affected. Most of the forests are publicly owned and managed by MFFP. A large network of secondary roads, mostly gravel surfaced, has been constructed to support forest harvesting (Fig. 2.1b). Roads can negatively affect the caribou in several ways: as movement barriers, collision risk, disturbance through human presence (Gaudry 2013), or increased predation risk (Whittington *et al.* 2011).

Current protected areas where forestry activities are forbidden (IUCN classes I, II and III; Dudley 2008) cover 1355 km^2 of our study area (~5.5%) (Fig. 2.1a). The "Comité sur les aires protégées terrestres de la Gaspésie" (Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques du Québec, MDDELCC) is working to increase land protection in this region to 12%. According to their scenario of September 2014, they plan to designate an additional 1705 km^2 of

biodiversity reserves that would act as new protected areas (Fig. 2.1a) where no forestry activities would be allowed.

Movement model

We adapted the movement model of Bauduin *et al.* (Chapter 1) to predict and map caribou movement potential under alternate climate and conservation scenarios. The model is a spatially explicit individual-based model (SE-IBM) which simulates daily caribou movement over the landscape as a function of behavioral state, season, and environmental conditions. Bauduin *et al.* (Chapter 1) previously fitted a multiple hypothesis caribou movement model to these landscapes and found best support for caribou that follow either a random walk in high quality habitat or a foray loop (Conradt *et al.* 2003) in low quality habitat. The best habitat-mediated movement hypothesis included a preference for high quality habitat, an avoidance of the major paved roads which are considered as strong movement barriers, and an attraction to individuals' mating area during mating season to represent site fidelity (Bauduin *et al.* Chapter 1).

Habitat conditions were defined by a land cover layer and a linear feature layer. The land cover layer distinguished four classes: alpine tundra, mature fir stands (older than 50 years), regenerating stands (younger than 30 years) and "other." The linear feature layer represented three types of linear structures: paved roads, secondary/gravel roads (Fig. 2.1b), and hiking trails. We used ecoforestry maps (source: MFFP) and the linear anthropogenic structure data published by the MFFP to describe the landscape. The four land cover classes were derived from map attributes of tree species composition, age, and disturbance history. A habitat quality raster layer (75 x 75 m) was predicted from the land cover and linear feature layers using two seasonal Resource Selection Function (RSF) models developed for this caribou population (Gaudry 2013).

The SE-IBM was initially parameterized by pattern-oriented modeling (Grimm *et al.* 2005; Grimm & Railsback 2012) using patterns defined from Very High Frequency (VHF) collar telemetry data. Data represented 35 collared adult caribou (20 females, 15 males) which were located, on average, every two weeks between 1998 and 2001 (Mosnier

et al. 2003). We used the best-supported model structure identified by Bauduin *et al.* (Chapter 1). However, we took advantage of newly available GPS location data of the Atlantic-Gaspésie population to refit the model in order to improve the predictive power. We re-fit the model by adding, to the original VHF patterns, patterns defined from the new GPS locations. The GPS locations came from 22 adult individuals followed from February 2013, and a further 21 followed from February/March 2014, until November 2014 (26 females, 17 males) (source: M.-H. St-Laurent, unpublished data). GPS data were collected in strict accordance with the recommendations of the Canadian Council on Animal Care, and both captures and manipulations of study animals were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate #52-13-112). Captures were conducted on public lands, under the supervision of the Québec government (MFFP), so no land use permissions were required. GPS data were subsampled to match the daily resolution of the SE-IBM. We randomly selected one GPS location per day per individual recorded between 2 pm and 6 pm, the hours when most of the VHF data had been obtained.

We used the best-fit calibration method (Railsback & Grimm 2012), as adapted by Bauduin *et al.* (Chapter 1), for parameter estimation of the movement model. We treated the VHF and GPS collar data as two independent data sets. We generated 100,000 independent random samples of parameter values from the distributions defined by Bauduin *et al.* (Chapter 1) for each parameter to be estimated. For each sample of movement model parameters, we simulated movements of the collared individuals for lengths of time consistent with the two respective survey periods. The seasonal habitat quality layers of the model were predicted using the RSFs and the land cover data that were temporally closest to the times when the data were collected. When recreating movements of the VHF-equipped caribou, we used land cover data from the ecoforestry maps of the 3rd forest inventory program. We used maps from the 4th inventory program when simulating movements of the GPS-equipped caribou. We used the same pattern-oriented modeling strategy and patterns as in Bauduin *et al.* (Chapter 1) to compare simulation outputs to the telemetry data. We selected a subset of at most 500 simulations of the 100,000 runs which produced movement patterns most similar to those defined from the VHF and the GPS data. Parameters and confidence intervals were estimated from these simulations, following

Bauduin *et al.* (Chapter 1). Results are presented in Appendix 2.A. Parameter estimation and all model runs were conducted in R 3.2.0 (R Core Team 2015). Simulation experiments were parallelized using an HTCondor cluster (Thain, Tannenbaum & Livny 2005).

Landscape scenarios

We defined 24 landscape scenarios representing possible conditions in 2080 of climate and conservation effort, under all combinations of four climate change scenarios and six conservation scenarios. We briefly describe these next; a more complete definition of each scenario and of the rules applied to derive the future landscapes from present conditions is presented in Appendix 2.B. We applied rules to generate the corresponding future states of the land cover and linear structures layers used in the RSF models. The different changes applied to the landscape represented a range of potential outcomes for the future environmental conditions. Scenario building was done using ArcGIS 10.2.2 and R 3.2.0 (R Core Team 2015).

> *a) Climate scenarios*

Climate change scenarios were coded as CC0, CCMin, CCMed and CCHigh. CC0 represented a scenario without climate change. The other three scenarios represented increasing impacts of climate change on vegetation and on natural disturbances. We used predictions from literature to generate the future states of each habitat type. Specifically, we created scenarios where climate change reduced the size of tundra patches through vegetation colonization (Logan 2012; Dumais *et al.* 2014), decreased the proportion of fir stands where future habitat conditions for fir tree were predicted to become less suitable (Périé *et al.* 2014) and decreased the proportion of young stands due to decrease of spruce budworm outbreak severity (Gray 2008; Régnière, St-Amant & Duval 2012). We included these climate change impacts in the scenarios (i.e., buffer sizes on the tundra patches, lost proportions of fir stands and lost proportions of young stands) with varying degrees; from minimum in CCMin to high in CCHigh.

> *b) Conservation scenarios*

We created six conservation scenarios as a combination of two scenarios of protected areas and three scenarios of road restoration.

i) Protected area scenarios

PA0 represented the current state with the existing protected areas in the landscape (Fig. 2.1a). In scenario PA+, we added the biodiversity reserves defined by the MDDELCC as new protected areas (Fig. 2.1a). Within protected areas, forest stands were affected by natural disturbances and climate change to predict future conditions. Outside protected areas, forestry activities and climate change impacted forest stands. We applied the governmental forest management plan (source: Bureau du forestier en chef) to predict the future forest cover regarding the proportions of fir stands, old stands and young stands predicted in our study area. Current management actions try to limit natural disturbance impacts on forests outside protected areas and, furthermore, forest management planning implicitly includes them (Bureau du forestier en chef 2013). Thus, we did not explicitly include natural disturbance impacts outside protected areas.

ii) Road restoration scenarios

We tested the potential of land restoration to reduce the barrier effect due to roads as another potential conservation activity. Habitat restoration was applied only to the secondary/gravel road type inside protected areas (Fig. 2.1b); the paved roads were considered too vital to the regional economy to be removed. We defined three road restoration scenarios. No roads were restored in Road0, we reduced road density by 50% uniformly inside the protected areas in Road50 and we completely removed them in Road100.

Movement potential

We used the updated SE-IBM to estimate caribou movement potential for all 24 scenarios. For each scenario, we built the two seasonal habitat quality layers using the RSF models and the scenario's landscape. We then ran 10,000 model simulations, each for four years. In each simulation, we created 20 individuals in each of the three subpopulations to avoid dependency on the current subpopulation size. We summed the last three years of simulated

locations over the 10,000 simulations to create the output map of predicted movement, following Bauduin *et al.* (Chapter 1). We removed the first year to limit the effect of initial positions. Initial tests established that increasing the number of individuals, the number of simulated years, or the number of replicates had minimal effects on the results.

We defined movement potential for a given landscape as the difference between the predicted movement map according to the SE-IBM and the predictions of a null model. To generate null model predictions, we built a homogeneous habitat quality layer over the whole study area with no roads. We modified the movement model by disabling mating site fidelity and foray loop behavior. Caribou followed a simple random walk during the whole simulation, creating a map that is equivalent to a simple diffusion model (Turchin 1998). Thus, the null model is spatially constrained, with a cost associated to distance from origin. Initial positions of the individuals were randomly assigned inside the subpopulation ranges, as in Bauduin *et al.* (Chapter 1). We ran 10,000 simulations of this null model to predict movement in this homogeneous landscape. We subtracted the values of the predicted movement map for the null model from the ones of the different scenarios tested. Areas not reached by any individual in both the null model and the scenario tested were considered undefined, as potential use was not truly zero. Otherwise, we rescaled the differences to [-1;1]. Positive values represented areas overused relative to the null model, and negative values represented areas of relative underuse. Overused areas were favored by the caribou due to habitat conditions, road absence or site fidelity; movement to those areas was facilitated and movement potential was therefore high. Underused areas were avoided or unreachable by caribou; movement potential was low. We calculated the area of high movement potential (Area$_{HMP}$) in km² for each scenario, defined as the area of relative use greater than 0.01 km². The results were insensitive to choice of cut-off value above 0.01 km² but were highly unstable between 0 km² and 0.01 km². Thus, we selected a cut off of 0.01 km² to remove the noise from the simulation around the zero value where the SE-IBM outputs were similar to the one from the null model. We tested the impact of the different scenarios (CC = climate change scenarios, PA = protected area scenarios, and Road = road restoration scenarios) on Area$_{HMP}$ by a 3-way ANOVA. Due to the low sample size (n = 24), we did not include any interaction terms.

Results

There was a significant effect of climate change scenarios on the area of high movement potential ($Area_{HMP}$) for caribou ($F_{(3, 17)} = 161.88$, $p < 0.001$). As the magnitude of climate change effects increased, $Area_{HMP}$ decreased (Fig. 2.2). There was no significant effect of the protected area scenarios on $Area_{HMP}$ ($F_{(1, 17)} = 3.52$, $p = 0.078$). The slight improvement from the additional protected areas was a side effect of the road restoration impact as more roads were restored. There was a positive impact of road restoration on $Area_{HMP}$ ($F_{(2, 17)} = 362.23$, $p < 0.001$), the more roads were restored, the larger was $Area_{HMP}$ (Fig. 2.2). Only the scenario with a complete restoration of secondary roads (Road100) was able to fully mitigate the impacts of climate change on $Area_{HMP}$ (horizontal dashed line in Fig. 2.2).
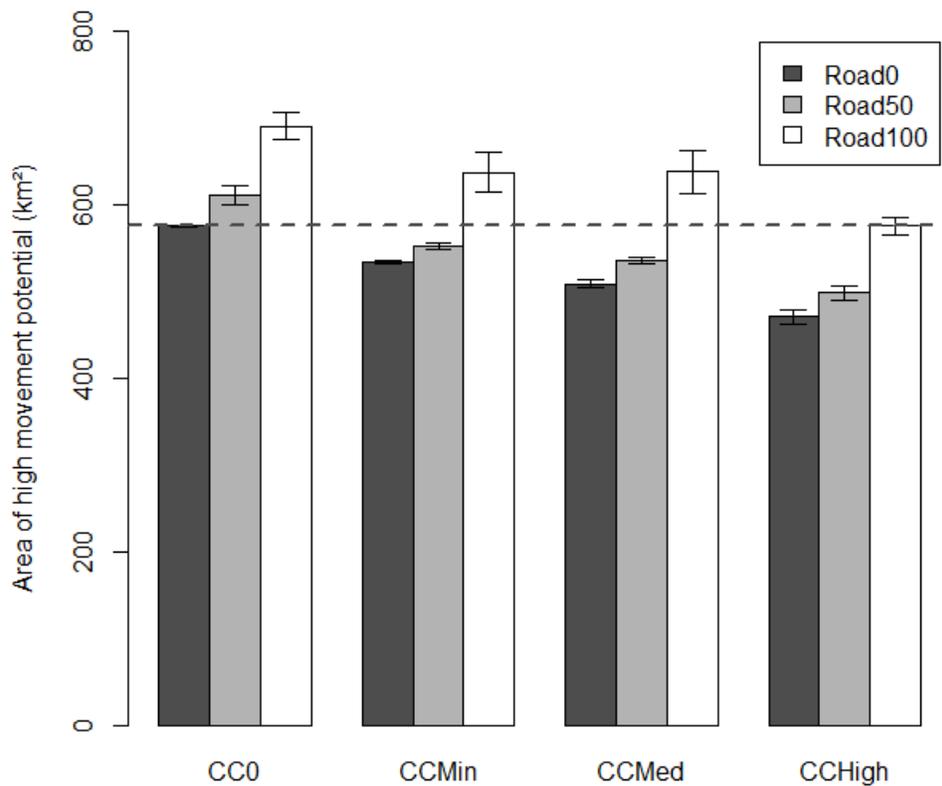
Figure 2.2: Total area of high movement potential ($Area_{HMP}$) under climate change and road restoration scenarios. The bars indicate the means over the two protected area scenarios, with 95 % confidence intervals. The dashed line at $Area_{HMP} = 575.8$ km²

represents the area for the scenario without climate change and road restoration. The values are averaged over the two protected areas scenarios (PA0 and PA+).

In the base case scenario (Fig. 2.3a) areas with high movement potential were mostly located within subpopulation ranges (Fig. 2.1a). Some areas outside the Gaspésie National Park were used more frequently than predicted under the null model, mostly areas south and west of the Logan range. The complete restoration of secondary roads inside protected areas (Fig. 2.3c) increased the area of high movement potential, mostly by reinforcing the travel corridor(s) between the Albert and the Logan subpopulations. Under the most severe climate change scenario, the complete restoration of secondary roads (Fig. 2.3d) was still able to maintain a high movement potential between the Albert and Logan subpopulations, even though movement potential was reduced outside of the park. All scenarios identified the same region of very low movement potential associated with the paved road between the Albert and the McGerrigle ranges (Fig. 2.1 and 2.3). For simplicity, we do not show movement potential maps for other scenarios as they fell between the four extremes presented in Figure 2.3.
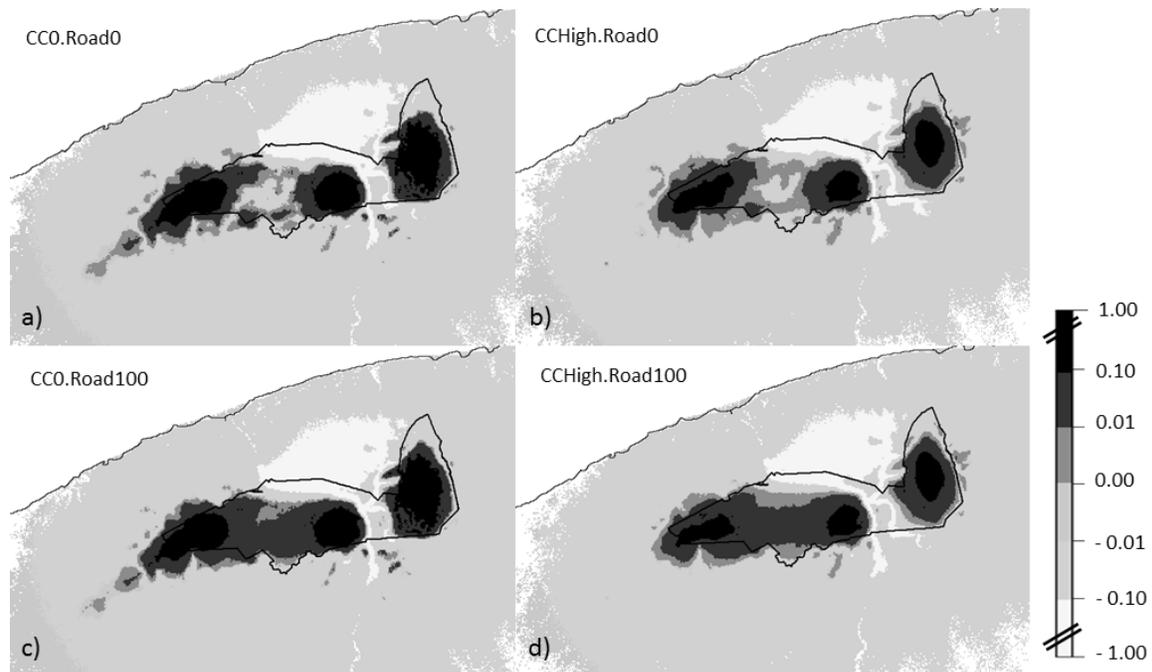
Figure 2.3: Spatial representation of movement potential for the Atlantic-Gaspésie caribou around the Gaspésie National Park (black outline) for the most extreme climate change and road restoration scenarios. The grey scale represents a gradient of movement potential, from high (black) to low (pale grey), measured relatively to a null model. Values are averaged over the two protected area scenarios (PA0 and PA+).

Discussion

The projected effects of climate change on the landscape decreased movement potential for the Atlantic-Gaspésie caribou. Climate change affected the caribou movement through its impact on vegetation cover which induced a reduction of the habitats of high quality for this population. We found that the decrease in caribou movement potential could be mitigated by landscape conservation measures. Simply implementing new protected areas, however, did not enhance movement potential. This is likely because too few of these areas were actually reachable by the caribou given their distances from the Gaspésie National Park; they were too far away for the caribou to benefit. The restoration of secondary roads inside protected areas was the most effective of the mitigation strategies considered. It is interesting that this strategy did not target the landscape features impacted by climate change. However, 50% restoration of roads was not sufficient to fully mitigate the impacts of climate change. Among the alternatives we evaluated, only the scenarios with complete removal of the secondary roads inside the protected areas fully countered the loss of movement potential due to climate change.

The Atlantic-Gaspésie caribou rely mostly on the alpine tundra located on mountain tops of the Gaspésie National Park and the surrounding, lower elevation, mature fir stands (Mosnier *et al.* 2003; Gaudry 2013). Climate change will potentially reduce the area and quality of tundra through shrub colonization due to warmer summer temperatures (Logan 2012; Dumais *et al.* 2014). Climate change may similarly reduce the area of fir stands by decreasing its habitat conditions (Périé *et al.* 2014). Our scenarios simulated the consequences of these impacts on the land cover, both of which reduced the area of high quality habitats. The constriction of individual movements into this smaller area reduced

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movement potential. The maps of movement potential showed that climate change may reduce movements outside of the Gaspésie National Park. This is mostly due to the attraction of individuals towards the remaining good habitats inside the park, where the large tundra areas are located. The map of movement potential could be compared to a map of landscape resistance showing areas where the capacity for movement is facilitated or impeded. However, graph/circuit/network theory could have not been used for this study as they all require nodes to be defined to assess their connectivity (Rayfield, Fortin & Fall 2011). In our case study, we did not want to predefine areas important for the Atlantic-Gaspésie caribou, but let the simulated individuals make the overly-used areas emerged from their movements.

The mating site fidelity feature of the movement model also tended to bring individuals to their mating sites (Bauduin *et al.* Chapter 1) which were these same open alpine tundra patches. This seasonal attraction prevents individuals from exploring the matrix too far from the park, limiting the possibility of establishment elsewhere. In an extreme case of climate change where the tundra are completely colonized by dense vegetation, site fidelity, if not adjusted by the individuals, may result in an ecological trap (Faille *et al.* 2010). Individuals would continue returning to their usual mating sites only to encounter poor habitat conditions for mate selection or predator avoidance, reducing fecundity or survival rates. Since site fidelity for the Atlantic-Gaspésie caribou is an unknown combination of different mechanisms (e.g., open landscape, high elevation, memory, etc.), it is difficult to make more precise predictions at this point.

There was no suitable vegetation dynamics model available to forecast habitat distributions for our study area. Therefore, we used RSF models (Gaudry 2013) to predict the landscapes according to our climate scenarios. The range of existing environmental conditions in the field used to build the RSF models did not cover the climatic and habitat conditions simulated in the scenarios. We are aware this is a limitation of the use of the RSF models (Matthiopoulos *et al*. 2011). A dynamic vegetation model coupled with the movement model would have improved the precision of the movement potential estimates. However we are confident it would not change the conclusions of this study.

The movement model we used did not include any fitness measure, resource intake or depletion through foraging (Semeniuk *et al.* 2012); individuals were not forced to leave small, but good habitats in search of resources elsewhere. The Atlantic-Gaspésie population was almost three times more abundant in the 1980s than today (Fournier & Faubert 2001) so we think it is unlikely that space and resources are the currently limiting factors. Therefore, we are confident that the movement predictions of our model are not compromised by the lack of an explicit mechanism for resource use. We also assumed a constant behavior through time, regardless of the environmental conditions as there was no learning or adaptive behavior in the caribou movement model (Bauduin *et al.* Chapter 1). Because we simulated landscapes while keeping the same basic elements in it (e.g., we did not completely removed the tundra) we felt that movement predictions are still reliable in these simulated environment. For a more precise model adapted for forecasting caribou movement in the future under climate change, behavior responses regarding temperature, plant phenology, insect harassment, predators (i.e., coyotes and bears) and alternative preys (i.e., moose) abundance and distributions, freeze-thawing events, as well as diseases and parasites would need to be included. These elements likely drive caribou movement at some extent and may change under new climate conditions. However, learning and adaptive behaviors are harder to include in models with only a few years of data covering a limited range of environmental conditions and population sizes.

Protecting functional connectivity is an efficient conservation measure to protect species and help their adaptation to the future climate (Rudnick *et al.* 2012; Nuñez *et al.* 2013; Andrello *et al.* 2014). Here, we illustrated the use of individual-based models coupled with different landscape scenarios to anticipate the consequences of climate change on movement potential. This is a first step towards estimating functional connectivity between key locations for the population, such as between protected areas or potential sites for new establishment. Our model also allowed us to identify which conservation measures might best mitigate the negative impacts of climate change. This can be of great help to managers when species are at risk due to climate change and habitat fragmentation.

Management Implications

The Atlantic-Gaspésie caribou population is declining and extirpation is likely unless drastic actions are taken (Lesmerises 2012). The population could be further threatened by habitat disruption caused by climate change if connectivity is reduced through a reduction of movement potential, as our models suggested. The existing network of secondary roads fragmenting the protected areas inhibits caribou movement. Our models suggested that these roads are the most important target for conservation action and the most efficient measure to mitigate reductions in connectivity due to climate change effects on vegetation. The mapping of movement potential showed that it greatly improved the connectivity between the Logan and the Albert subpopulations which can benefit the survival of this population while also increasing genetic diversity. Linear features are also heavily used by predators (Latham *et al.* 2011; Gaudry 2013) and may increase predator-prey encounter rates (Whittington *et al.* 2011). Thus, road restoration could further benefit caribou by reducing predation rates. We tested the removal of half and of all the secondary roads inside the protected areas, and only the scenario of complete restoration was able to counter the reduction of movement potential due to climate change. However, such an extreme restoration of the landscape is unrealistic because of the multiple usages of the secondary roads by people for recreation, so reducing barriers to movement needs to go along with other measures to reduce climate change and its impact on the landscape.

The major paved road crossing the Gaspésie National Park, between Mount Albert and the McGerrigle massif, was an almost impermeable barrier to caribou movement, causing reductions in movement potential on areas much larger than the road itself. This road is regionally too important to be removed for restoration into forest habitat. In similar cases, such as in Banff National Park, crossing structures for highways (over- and underpasses) have proven to be efficient in maintaining connectivity (Sawaya, Kalinowski & Clevenger 2014). We did not test for this type of conservation measure in the present study. However, the simulation tools we used could be applied to identify the best location of such crossing structures (Colchero *et al.* 2011) and predict their effect on movement potential, and potentially their contribution to broader conservation goals.

The addition of new protected areas had little impact on our results. The biodiversity reserves we tested as new protected areas were not designed solely for the purpose of improving movement or connectivity for the Atlantic-Gaspésie caribou. One of the main goals of these new areas is to complete the ecological representation of the region within the protected area network (MDDELCC 2014). Adding new protected areas is certainly part of the solution to improve and secure movement for this caribou population (Bennett & Mulongoy 2006) but their design needs to account for this specific objective. It is likely that an alternate spatial distribution of the biodiversity reserves could secure and improve caribou movement in a context of climate change, while also improving the representativeness of the network.

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Appendices

Appendix 2.A: New parameter estimates (Table 2.A.1) for the caribou movement model. We followed the model parameterization method used in Bauduin *et al.* (Chapter 1). We aimed to reproduce two sets of movement patterns, one defined with VHF data and one with GPS data. These parameter estimates were used to simulate caribou movement for this study.

Parameter	Estimate	95% confidence interval	Unit
Mean step length in good quality habitat $\mu_{sl.good}$	5.47	[5.21;5.65]	log(m)
Mean step length in low quality habitat $\mu_{sl.low}$	5.74	[5.44;6.08]	log(m)
Standard deviation of the step length σ_{sl}	1.20	[0.90;1.43]	log(m)
Probability of crossing a paved road p_{cross}	0.10	[0.09;0.12]	
Standard deviation of the truncated Normal distribution for the mating area attraction σ_{ma}	42.62	[28.18;68.69]	degrees
Standard deviation of the truncated Normal distribution for the foray loop movement σ_{fl}	83.48	[77.85;131.74]	degrees
Maximum step length of the outgoing portion of the foray loop $max_{steps.loop}$	3.16	[2.45;8.44]	steps

Table 2.A.1: Parameter estimates and their 95% confidence interval for the caribou spatially explicit individual-based model.

The main differences between these parameter estimates and those of Bauduin *et al.* (Chapter 1, Table 1.3) were: smaller 95% confidence intervals, $\mu_{sl.good}$ smaller than $\mu_{sl.low}$, a small σ_{fl}, and a small $max_{steps.loop}$. Standard errors were smaller as more data were used to parameterize the model and therefore it improved the parameter precisions. Mean step length in good habitat quality was estimated to be smaller than in low habitat quality when using VHF and GPS data to fit the model, consistent with the literature (Johnson *et al.* 2002; Morales *et al.* 2004). The opposite was found by Bauduin *et al.* (Chapter 1) when the model was fit only with the VHF data. Longer steps in low quality habitats may have been undetected due to the bias of the VHF data which surveyed caribou over the main population range, altering therefore the estimate for the mean step length in low quality habitats. It seemed (visually) that the fidelity of the individuals to their mating area was stronger in the GPS data which reinforced the attraction of the site during the mating season for this model parameterization. The maximum number of steps in the outgoing portion of the foray loop was a trade-off with the mean step length in low quality habitat as the loop is

done in low quality habitats. Under the new model, more steps were necessary for the simulated individuals to achieve a given distance from their starting point, because of the lower mean step length.

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Appendix 2.B: Construction of potential future landscapes for the climate change and landscape conservation scenarios.

Climate change scenarios

We evaluated four different climate change scenarios. CC0 was a scenario without climate change, while scenarios CCMin, CCMed and CCHigh represented a gradient of minimum, medium and high climate change impacts. These scenarios represented possible climate change impacts. They did not correspond to any particular climate forecasts such as those of the Intergovernmental Panel on Climate Change (IPCC) assessment reports (e.g. IPCC 2007) as it was beyond the scope of this study to do detailed simulations of the vegetation under the different IPCC scenarios. Climate impact scenarios were defined in terms of their effects on vegetation. The effects were modelled by changing the rules for vegetation succession and disturbances based on the literature. We applied these rules to the current landscape to forecast the potential state in 2080 of alpine tundra, mature fir stands (older than 50 years) and regenerating stands (younger than 30 years) for each scenario. The year 2080 was chosen because of the data availability for vegetation and disturbances, which are rarely forecast further than the time period 2070-2100 (Gray 2008; Logan 2012; Régnière, St-Amant & Duval 2012; Périé *et al.* 2014).

   a) Alpine tundra

Alpine tundra in Gaspésie is climate driven (Dumais *et al.* 2014) with wind being a major factor (Renard, McIntire & Fajardo 2015). Even though no change was observed in the treeline position between 1975 and 2008, researchers noticed a shrub densification of *Betula glandulosa* above the treeline and a development of a more erected tree from for some krummholz (*P. glauca*) (Dumais *et al.* 2014). *B. glandulosa* radial growth is positively associated with summer temperatures (Dumais *et al.* 2014) and climate models predicted an increase of these temperatures for the Gaspésie peninsula for the horizon 2090 (Logan 2012). It is therefore possible that alpine tundra may be colonized by upright vegetation (i.e., erect trees) on its rim due to climate change. The tundra was assumed constant under CC0. We shrunk the tundra polygons (as defined in Gaudry 2013) with interior buffering in the scenarios including climate change. No estimation of alpine tundra reduction was available from the literature or experts, so shrinkage amounts were chosen for simplicity and to show significant difference with the current state. For most tundra sites, we buffered by 100, 200 and 500m in CCMin, CCMed and CCHigh, respectively. The exception was the Mount Albert summit, the plateau in the center of the Gaspésie National Park (Mosnier *et al.* 2003), which gave the name to subpopulation located there (Fig. 2.1a). Mount Albert is composed of serpentine (Sirois & Grandtner 1992) which is less subject to vegetation colonization relative to the other tundra areas. We buffered this area by 50 m, 100 m and 250 m for CCMin, CCMed and CCHigh, respectively.

   b) Mature fir stands and regenerating stands

The abundance and distribution of mature fir stands and regenerating stands are driven by both climate and disturbances.

   i) Impact of climate change

Due to climate change, the potential habitat of balsam fir is likely to decrease across Québec (Périé *et al.* 2014). Predictions of these changes to 2080 have been mapped over eastern North America on a grid cell of 20 x 20 km (source: Ministère des Forêts, de la Faune et des Parcs du Québec, MFFP). Potential habitat for balsam fir is predicted to be either lost, lower in quality compared to the present, or else mostly unchanged. Potential habitat is predicted to increase in quality in some locations, but not in our study area. Using a GIS, we determined the predicted habitat change at the centroid of each fir stand polygon in our study area. We applied a mortality probability which changed the fir stand into "other" when balsam fir potential habitat was predicted to be either lost or to decline in quality. No mortality probability values were available from the literature or experts so we chose values which provided a reasonable range of consequences among our scenarios. No mortality was applied on fir stands for CC0. Mortality probabilities for fir stands where potential habitat conditions were predicted to be lost in 2080 were set at 0.01, 0.10 and 0.50 in CCMin, CCMed and CCHigh respectively. Mortality probabilities in stands where habitat quality decreases were predicted were set at 0.01 and 0.10 in CCMed and CCHigh.

ii) Impact of disturbances inside protected areas

We used the current protected areas and the biodiversity reserves planned by the Québec government (source: Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques du Québec, MDDELCC) to represent protected areas in our scenarios. Forest harvesting is excluded from these areas so only rules about natural disturbances were applied to forest stands inside these areas. Forest stands already accounted for the climate change impacts on fir stands.

The dominant natural disturbances in Gaspésie are spruce budworm outbreaks (Saucier *et al.* 2003) and, to a lesser extent, windthrow. Spruce budworm outbreaks have a mean interval frequency of about 40 years in eastern Québec and this frequency has not changed much since the mid-16th century (Boulanger & Arseneault 2004). Our scenarios were evaluated at 2080 so we defined 2000 as the reference year for spruce budworm impacts in the outbreak cycle, corresponding to two outbreak intervals. Analysis of the maps from the 3rd and 4th forest inventories (source: MFFP), spanning more than two decades, indicated that the impact of windthrow, fire and other disturbances were small compared to that of spruce budworm in our study area. We assumed the magnitude and effects of natural disturbances, other than spruce budworm outbreaks, to be constant over the simulation interval. Therefore we used 2000 as the reference year for all natural disturbances.

For scenario CC0, we assumed that the forest is in a dynamic equilibrium, and so the forest stand ages in 2000 inside the protected areas resulting from natural disturbances were used to represent those of 2080. Using the ecoforestry maps, we selected all forest polygons inside the protected areas which were undisturbed by human activities prior to 2000. The age of these stands in 2000 was kept to represent their age in 2080. The few stands inside protected areas affected by human disturbances before 2000 were classed as mature in 2080.

Under climate change, spruce budworm outbreaks in Gaspésie are predicted to be 10-14 years longer and 26-75% less severe over 2080-2100 than at present (Gray 2008). Spruce budworm population growth rates are predicted to decline during 2041-2070, under

expected condition of climate and forest cover (Régnière, St-Amant & Duval 2012). Accordingly, we assumed that spruce budworm impacts on forest stands would be less than they currently are in our climate change scenarios. We simulated this by decreasing the proportion of regenerating stands, and therefore increasing the one of mature stands as a consequence, in the projected landscapes to reflect a reduction of the mortality due to spruce budworm outbreaks. From the landscape created for CC0, we selected the regenerating stands inside protected areas for which spruce budworm outbreak was the recorded disturbance. We randomly sampled some of these forest stands and turned them as mature in 2080. Based on Gray (2008), the proportions of stands sampled were 0.25, 0.50 and 0.75 for scenarios CCMin, CCMed and CCHigh, respectively.

iii) Impact of disturbances outside protected areas

Outside protected areas, the majority of the landscape is managed for timber production (source: Bureau du forestier en chef, BFEC). Efforts are made to prevent or combat spruce budworm outbreaks (Bureau du forestier en chef 2013). Damaged wood is salvaged, and plantations may be established in affected areas. Losses to budworm defoliation are accounted for in periodic calculations of annual allowable cut (AAC; Bureau du forestier en chef 2013). Windthrow is similarly managed for (Bureau du forestier en chef 2013). Therefore, outside protected areas, modifications on forest stands could be regarded as mainly due to forest management. We used the forecasts made by the BFEC to represent the forest composition outside protected areas in 2080 and we did not simulate any extra natural disturbances on these stands.

In Québec, public forest lands are spatially stratified into management units. The BFEC develops management plans and calculates AAC for each unit. There are five management units in Gaspésie, covering 72% of the forest outside protected areas. We assigned the small areas of private forests to these management units, based on the stand proximity within each unit. We applied the BFEC plans to these slightly modified units.

Due to ecosystem management practices in Québec, BFEC plans are expected to increase the amount of old forest, and slightly decrease the proportion of regenerating forest relative to the present day. Plans also entail a decreased proportion of fir stands in our study area (source: BFEC). We used the per-unit harvest rates and AACs under all scenarios; climate change impact on fir stands was accounted for beforehand. In each unit, we calculated the proportional decrease in the areas of fir and regenerating stands and increases in old forests from 2008 to 2083. These years were the closest matched to the dates of the ecoforestry maps (2005) and the simulation endpoint (2080). Within each unit, we randomly selected fir and regenerating stands up to the indicated proportional area, and reclassified them as follows. Fir stands were reclassified as type "other" for their forest type. Regenerating stands were reclassified as "other" for their age category. The BFEC defined regenerating forest stands as those less than 10 years old (Bureau du forestier en chef 2013). We assumed the indicated proportional reductions applied also to our broader definition of regenerating stands, as those younger than 30 years (Gaudry 2013). The BFEC defined old forest as those older than 80 years (Bureau du forestier en chef 2013), whereas we needed to forecast the abundance of mature forest older than 50 years (Gaudry 2013). In each unit, the projected increase in the abundance of old forest exceeded the remaining area of age between 30 and 50 years or undetermined. Accordingly, in simulated landscapes of 2080, all forest stands not explicitly classed as regenerating were classed at mature. This

approximation will not affect scenario outputs as the proportion of forests between 30 and 50 years old are expected to be small compared to the other age categories, especially given ecosystem management practices intended to increase the amount of mature forests (source: BFEC).

Landscape conservation scenarios

We defined two protected areas scenarios (PA0 and PA+) and three road restoration (Road0, Road50 and Road100) scenarios in a factorial design, leading to six different landscape conservation scenarios.

a) Protected areas

Protected areas in PA0 represented the current existing protected areas where no forestry activities were allowed inside (Fig. 2.1a) and the above rules on vegetation were applied according to these areas. In the scenario PA+, we increased land protection by adding the reserves of biodiversity defined by the MDDELCC (Fig. 2.1a). The impacts of natural disturbances and forest management as previously defined were applied according to this new larger set of protected areas.

b) Road restoration

Our simulated landscape restoration scenarios removed roads and therefore decreased movement barriers in the landscapes (Dyer *et al.* 2002; Fortin *et al.* 2013; Beauchesne, Jaeger & St-Laurent 2013). The habitat quality layer used in the caribou movement model recognized three road types (Gaudry 2013; Bauduin *et al.* Chapter 1). Of these, restoration is most likely to happen on the secondary/gravel road type (Fig. 2.1b). In scenario Road0, we did not simulate any restoration. In Road50, we reduced the density of secondary roads by half inside the protected areas (defined according to the land protection scenario PA0 or PA+). The locations of particular road segments to be restored into natural habitats might further impact the movement of the caribou. Optimizing the sites for road restoration is a topic for future research. Here, we focused only on decreasing road densities estimated per cell in the gridded landscape, therefore simulating a random selection of the segment to be restored. In Road100, we completely removed all secondary roads inside the protected areas. Secondary roads were defined in the RSF models as the density of roads within 1 km buffers so we did not have to choose which road segments to remove in Road50 scenarios. We simply reduced the density values by half. Existing paved roads and trails were not modified in any scenario.

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Chapter 3: Maximizing ecological representativeness and functional connectivity over time when designing protected area networks

Résumé

La modification du paysage et les changements climatiques sont reconnus comme des moteurs du déclin de la biodiversité. Les aires protégées sécurisent le paysage contre de nouvelles modifications et aident les espèces à faire face aux changements climatiques. Pour être efficaces, les aires protégées doivent couvrir une part représentative de la biodiversité régionale et être connectées entre elles pour faciliter le mouvement des individus. Nous avons défini un réseau d'aires protégées pour la Gaspésie avec ces critères. Nous avons créé plusieurs scénarios de réseau d'aires protégées. Nous avons évalué leur représentativité écologique et calculé deux mesures de connectivité fonctionnelle sur le long terme pour le caribou de la Gaspésie-Atlantique. Nous avons sélectionné le scénario avec le meilleur compromis entre ces caractéristiques. Le réseau proposé protège une part représentative de la biodiversité régionale et maximise au cours du temps le mouvement du caribou entre et à l'intérieur des aires protégées.

Abstract

Habitat change and climate change are recognized as two main drivers of the current biodiversity decline. Protected areas can secure landscapes from additional modifications and may also help species cope with the impacts of climate change. To be effective, protected areas need to cover a representative sample of the regional biodiversity, as well as being functionally connected so as to facilitate individual movements. We defined an effective protected area network for the Gaspésie region using these criteria. We created multiple alternate scenarios of protected area networks. We evaluated the ecological representativeness and calculated two measures of long-term functional connectivity for the Atlantic-Gaspésie caribou population for each network. We selected the network showing the best trade-off between the three features. The proposed network ensured that a representative sample of the regional biodiversity was covered by the protected areas and that caribou movement between and inside the protected areas was maximized over time.

Introduction

Habitat change is recognized as the main driver of the current decline of terrestrial species (Secretariat of the Convention on Biological Diversity 2006). Securing parts of the landscape with new protected area implementations is part of the solution to counter the current biodiversity loss we are facing (Coetzee, Gaston & Chown 2014). However, the effectiveness of protected areas on species conservation is not guaranteed (Ervin 2003; Geldmann *et al.* 2013). Many factors could limit their effectiveness (Gaston *et al.* 2008), some of which can be overcome by a better design of protected areas. For example, poor ecological representativeness within protected areas (Rodrigues *et al.* 2004), or the lack of connectivity between them (Andrello *et al.* 2014), are two weaknesses of protected area networks that can be improved to increase their effectiveness.

Achieving ecological representativeness in a protected area network means that all the various habitats within some focal region are also found inside the protected areas, in proportion to their regional abundance (Beaver & Llewellyn 2009; Secretariat of the Convention on Biological Diversity 2009). Aiming for a good ecological representativeness in biodiversity conservation is related to the coarse filter of the ecosystem management strategy (Noss 1987; Hunter 1991), which states that the protection of the majority of the regional habitats should protect the majority of the regional biodiversity. However, protected area networks should aim to represent the landscape in its pre-industrial form and not protect habitat types resulting from human disturbances. Ecological representativeness in a network is low when protected area locations are skewed towards a certain type of habitats (Scott *et al.* 2001; Joppa & Pfaff 2009), usually because of economic or social reasons. In this case, some species may have their habitat conditions under-represented inside the protected area network (Rodrigues *et al.* 2004) and their survival is likely diminished. A poor ecological representativeness in a protected area network likely decreases its effectiveness in conserving regional biodiversity.

However, defining protected areas only through a coarse filter approach in order to achieve a high ecological representativeness may not be sufficient to protect all regional species. So-called fine filter approaches (Noss 1987; Hunter 1991) protect specific features of the environment so as to secure focal, often endangered or highly valued, species whose

needs are not automatically satisfied by representation criteria alone. Even if a fine filter is defined for one, or a few, focal species, it may also be beneficial for other species with similar needs (Breckheimer *et al.* 2014). Accounting for functional connectivity between protected areas (Minor & Urban 2008) is an example of a fine filter approach to conservation; functional connectivity being specific to a particular species or population (Baguette & Van Dyck 2007; Kadoya 2009). A protected area network with high functional connectivity facilitates the movement between different protected areas for individuals, increasing their access to resources or their escape from predators (Bennett & Mulongoy 2006). This may increase population survival (Andrello *et al.* 2014) and, as a consequence, the effectiveness of the protected area network.

Climate change is among the main drivers now modifying ecosystems. Its negative impacts on biodiversity have increased rapidly over the past century (Secretariat of the Convention on Biological Diversity 2006). Climate change disrupts environmental patterns and species' habitats globally (Loarie *et al.* 2009; Dawson *et al.* 2011). As a result, species distribution and individual movement patterns are impacted (Chen *et al.* 2011; Lawler *et al.* 2013). The effectiveness of single fixed protected areas designed for the species' current needs will likely decrease in the future as some species might not find their needed resources inside these areas under a new climate. Mobile individuals are then likely to leave the protected areas (Araújo *et al.* 2004; Vos *et al.* 2008). Maximizing functional connectivity of protected area networks is one approach to helping species cope with climate change (Vos *et al.* 2008; Nuñez *et al.* 2013). Enhancing functional connectivity between protected areas would help individuals access resources available in more distant protected areas. Because of the "cost of waiting", managers need to actively account for climate change effects when implementing new protected areas (Hannah *et al.* 2007).

In this study, we present a design strategy for effective protected area networks that optimizes both coarse and fine filter methods. We aimed to achieve high degrees of ecological representativeness and of functional connectivity in our proposed network. We illustrated this method on the Gaspésie region of Québec, Canada. First, we created a large sample of protected area network scenarios. A quantitative measure of ecological representativeness was then calculated for each network. Movement estimates from an individual-based model defined for the endangered Atlantic-Gaspésie caribou population

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(*Rangifer tarandus caribou*) was used to derive two measures of functional connectivity for each network. We calculated the proportional area of the networks reachable by caribou as well as the one where the movement potential (capacity) was estimated as high. We used movement estimates under current and projected future conditions including different climate change scenarios to test the effects of accounting for future environmental conditions when enhancing network functional connectivity. We also used time-averaged movement estimates to define functional connectivity measures robust to current and possible future conditions. To identify the most effective protected area network for our study area, we selected the scenario with the best trade-off between ecological representativeness and the two time-averaged functional connectivity measures. This study presents a methodology to design protected area network that are approximately optimal from an environmental point of view, specifically for caribou conservation in our study region. Some elements concerning the feasibility of the new protected area implementations have been included but we did not undertake a full evaluation of the social and economic constraints in Gaspésie.

Material and methods

Study area

The Gaspésie natural region (Fig. 3.1) is a physiographically defined area of approximately 25,000 km² at the eastern end of the Gaspésie peninsula in Québec, Canada (MDDELCC 2014). Excepting the coasts, it belongs to the balsam fir - white birch bioclimatic domain (Saucier *et al.* 2003). The maritime climate of the area leads to abundant precipitation and infrequent wildfire; the main natural disturbance is spruce budworm (*Choristoneura fumiferana*) outbreaks (Saucier *et al.* 2003). Approximately 90% of the Gaspésie region is covered by forests and 80% of these are on public lands (MDDELCC 2014). Forestry activities, and the large network of roads associated, represent the main human disturbance. Only 34% of the area is free from measurable human footprint (MDDELCC 2014).
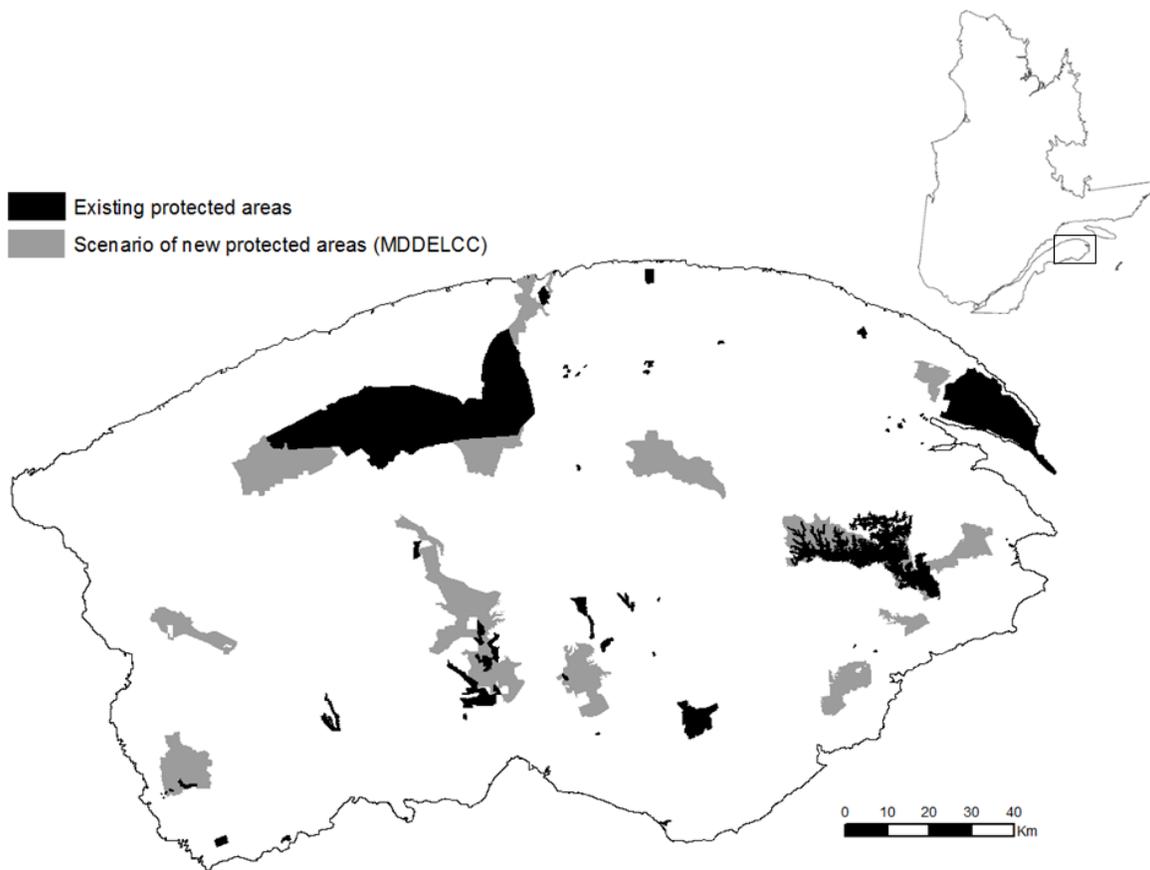
Figure 3.1: The Gaspésie natural region with existing protected areas and the additions proposed by the government of Québec (MDDELCC). Right inset: Province of Québec (Canada) with study area outlined.

The existing network of protected areas covers 5.5% (1371 km²) of the Gaspésie natural region (Fig. 3.1). Currently, these protected areas cannot achieve the ecological representativeness of 12% requested by the government of Québec (Brassard et al. 2010). A scenario proposed by the Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques du Québec (MDDELCC) defined 20 new protected areas that would increase the area protected in the Gaspésie natural region up to 12.3% (3080 km²) (MDDELCC 2014) (Fig. 3.1).

The Gaspésie National Park (802 km²) is currently the biggest protected area in the region (LeSage & Paquin 2000). This park helps conserve 42 endangered and vulnerable species of plants and animals (MDDELCC 2014), including the Atlantic-Gaspésie caribou

population. This caribou population is designated as endangered (Environment Canada 2014) and is of great concern regarding its small size and long-term, ongoing decline (Lalonde 2015). These caribou rely on alpine tundra, which is possibly threatened by climate change (Dumais *et al.* 2014; Renard, Isabel & McIntire 2015), and old fir forests during winter. The fir forests around the park are affected by the intense forestry (Mosnier *et al.* 2003), and also possibly by climate change (Périé *et al.* 2014). Threatened species in Gaspésie which are sensitive to disturbances and habitat fragmentation (e.g., Bicknell's thrush *Catharus bicknelli*) or which have the same habitat conditions as the caribou (e.g., Eastern pipistrelle *Perimyotis subflavus*) will likely benefit from the conservation measures defined for the caribou. Because of its designated status, the vulnerability of its habitat, and its potential to be an umbrella species, we chose the Atlantic-Gaspésie caribou as our focal population to define functional connectivity.

Building protected area networks

We built multiple candidate protected area networks for the Gaspésie region by combining the existing protected areas (Fig. 3.1) with new ones, using The Canadian BEACONs (Boreal Ecosystems Analysis for Conservation Networks) project tools (Saucier 2011; BEACONs 2015). First, we used the Builder tool to create new potential protected areas, called benchmarks, using hydrological catchments as spatial units or sites (Saucier 2011). To create a benchmark, the Builder algorithm first selects one catchment seed in the landscape, based on its position in the stream network and its intactness. From this seed, the algorithm traverses the stream network, adding catchments as it goes, provided they satisfy a specified intactness requirement. Catchments are added up to a specified size criterion for benchmarks, unless blocked by lack of hydrologically connected or intact unit (Saucier 2011; BEACONs 2015). The construction based on catchments and a stream network is intended to ensure hydrological connectivity for aquatic species, often forgotten in conservation measures on land.

We used a catchment unit layer (source: BEACONs project team) defined over our study area using the National Hydrological Network at resolution 1:50,000 (Version 14 NRCAN 2011-2014) and the Canada Digital Elevation Model Data at resolution 1:50,000

(NRCAN 2001-2012). The catchment's average size was 2.3 km² (SD = 1.3 km²). Headwaters were abundant in our study area (representing 33% of the catchments) and were well distributed over the landscape. We chose catchment seeds to be only headwaters (Saucier 2011) because of their hydrological importance and to reduce potential upstream river contamination inside the protected areas (Lowe & Likens 2005). We defined catchment intactness using a raster of human footprint for the Gaspésie area (MDDELCC 2014). Six different types of disturbances were defined and we gave them an equal weight. We defined intactness ranging from zero (i.e., not intact), where the six types of disturbances were present, to one (i.e., most intact) where no disturbance was present. Then, we calculated an average intactness value per catchment. We defined the intactness threshold for the Builder tool as the median catchment intactness value. To define the median, we only considered catchments outside existing protected areas and on public lands. Only catchments with intactness value above the threshold could be included in benchmarks. In order to create realistic protected areas that could be implemented in Gaspésie, we set the intactness of the catchments completely overlapping private lands (MDDELCC 2014) to zero so that they were never included into benchmarks. We used the mean size of the new protected areas proposed by the MDDELCC (Fig. 3.1; mean = 85.5 km², SD = 61.4 km²; MDDELCC, 2014) as the benchmark size to reach. It defined a plausible size of protected area for implementation in Gaspésie and also allowed comparisons with the MDDELCC scenario. We also considered in the following steps some benchmarks which did not reach the defined size due to a lack of connected intact catchments. We kept benchmarks as small as 31.2 km², as it is the size of the smallest contiguous protected area defined by the MDDELCC in their scenario (MDDELCC 2014).

Once all benchmarks were built, we used the Ranker tool (option 4, Saucier 2011) to create 500,000 different networks scenarios. This tool assembled groups of benchmarks with the existing protected areas until covering 12.3% of the study area, to match the MDDELCC scenario. As part of the Ranker tool's design, existing protected areas were defined using the limits of the catchments whose centroids were included inside as opposed to the actual boundaries of the protected areas.

Network ecological representativeness

For each network created we calculated an ecological representativeness index using the Ranker tool (Saucier 2011). We measured ecological representativeness by four environmental criteria: elevation, surficial deposit, drainage class and potential vegetation type (MDDELCC 2014). Potential vegetation was defined by the "Ministère des Forêts, de la Faune et des Parcs du Québec" (MFFP) as the vegetation present on a site or potentially present, in the case of no disturbances occurring (Brassard *et al.* 2010). These four criteria defined habitat types whose environmental characteristics were independent of human activities and were available for the whole study area at a fine enough resolution (source: MDDELCC). Surficial deposit, drainage class and potential vegetation type have been used for the gap analysis comparing the ecological representativeness of the existing protected areas in Gaspésie with the scenario proposed by the MDDELCC (MDDELCC 2014).

For each of the four criteria, the Ranker tool calculates a dissimilarity metric between the distributions of the criterion values within and outside the network. The measures were at the catchment level. For continuous criteria (e.g. elevation), the ranker uses a two-sample Kolmogorov-Smirnov statistic as the dissimilarity metric. For categorical data (e.g. surficial deposit, drainage class, and potential vegetation type), a Bray-Curtis statistic is used. Finally, a distance metric combines all dissimilarity metrics together (Saucier 2011). The Ranker tool reported the distance metric for each of the 500,000 networks created. We defined network ecological representativeness as the inverse of the distance metric so that the smaller distances or greater similarities led to higher representation scores. We calculated the same way the ecological representativeness score for the MDDELCC network. As a constraint of the Ranker tool, the MDDELCC network was defined by the limits of the catchments whose centroids were inside the protected areas and the dissimilarity metrics were calculated based on these limits.

Network functional connectivity

We defined network functional connectivity using movement estimates for the Atlantic-Gaspésie caribou population. Bauduin *et al.* (Chapter 2) estimated caribou movement

potential as the difference between the predicted movements under a spatially explicit individual-based model (Bauduin *et al.* Chapter 1) and under a null model. Movement potential was estimated for the present landscape, and forecast for 2080 under four different climate change scenarios. These scenarios represented a gradient of potential climate change impacts on vegetation succession and the rates of natural disturbances. The current landscape was defined from the ecoforestry maps from Québec's 4th decennial forest inventory program (source: MFFP). We derived functional connectivity measures using movement potential estimates for the current time period and at 2080 under each climate scenario, as well as time-averaged estimates. For the time-averaged estimates, we averaged the movement potential estimates for the current time period with the averaged values for the future. The derived time-averaged functional connectivity estimates are then robust to current and possible future conditions.

We defined two functional connectivity measures for each of the six movement potential estimates (i.e., for the current time, for each of the four climate scenarios, and the time-averaged estimates). Firstly, we converted the movement potential estimates into binary maps to define the areas that were reached by simulated caribou. Areas where no caribou movement was simulated represented areas where the Atlantic-Gaspésie caribou was unlikely to go. We calculated for each created network and for the MDDELCC scenario, the proportional area reached by caribou. We interpreted higher proportions as indicative of increased accessibility of the protected areas for caribou and thus of greater functional connectivity for the network. Secondly, we estimated the proportional network area with movement potential estimates above 0.01 km², which was the cutoff to represent areas used more than random as defined by Bauduin *et al.* (Chapter 2). These areas were preferred due to habitat quality, absence of movement barriers, mating fidelity or proximity to caribou range (Bauduin *et al.* Chapter 2). A large value for this high movement potential proportional area meant that the protected areas were simultaneously reachable (i.e., connected functionally) and that, internally, they had few barriers to movement.

Network selection

We identified the network scenario with the best trade-off between ecological representativeness and each of the functional connectivity measures. To do so, we incrementally decreased a quantile value Q, from 1 to 0, until at least one network was identified as having both its ecological representativeness and functional connectivity measure above the Qth quantile values. We also modelled, for descriptive purposes, the relationship between the network ecological representativeness and each time-averaged functional connectivity measures by linear regression. Finally, we selected as our best network, with the same quantile method, the scenario with the best trade-off between ecological representativeness and the two functional connectivity measures calculated using the time-averaged movement potential.

Results

Protected area networks

The Builder tool constructed 690 different benchmarks. The mean size of the benchmarks was 86.8 km² (SD = 4.0 km²). On average, the Ranker tool added 25 benchmarks (SD = 2.2) to the 62 existing protected areas to create the networks. The mean size of the created networks was 3138.5 km² (SD = 24.6 km²). Their ecological representativeness score ranged from 2.76 to 7.63 (mean = 4.71, SD = 0.64) (Fig. 3.2). The score for the MDDELCC network was 4.65 (Fig. 3.2). Using the time-averaged movement potential estimates, the proportions of protected areas reachable by caribou for the created networks ranged from 0.256 to 0.715 (mean = 0.466, SD = 0.052) (Fig. 3.2a). The proportions of protected areas in which caribou movement potential was above 0.01 km² ranged from 0.096 to 0.216 (mean = 0.136, SD = 0.013) (Fig. 3.2b). For the MDDELCC network, these values were 0.448 (Fig. 3.2a) and 0.168 (Fig. 3.2b), respectively.

a)

b)

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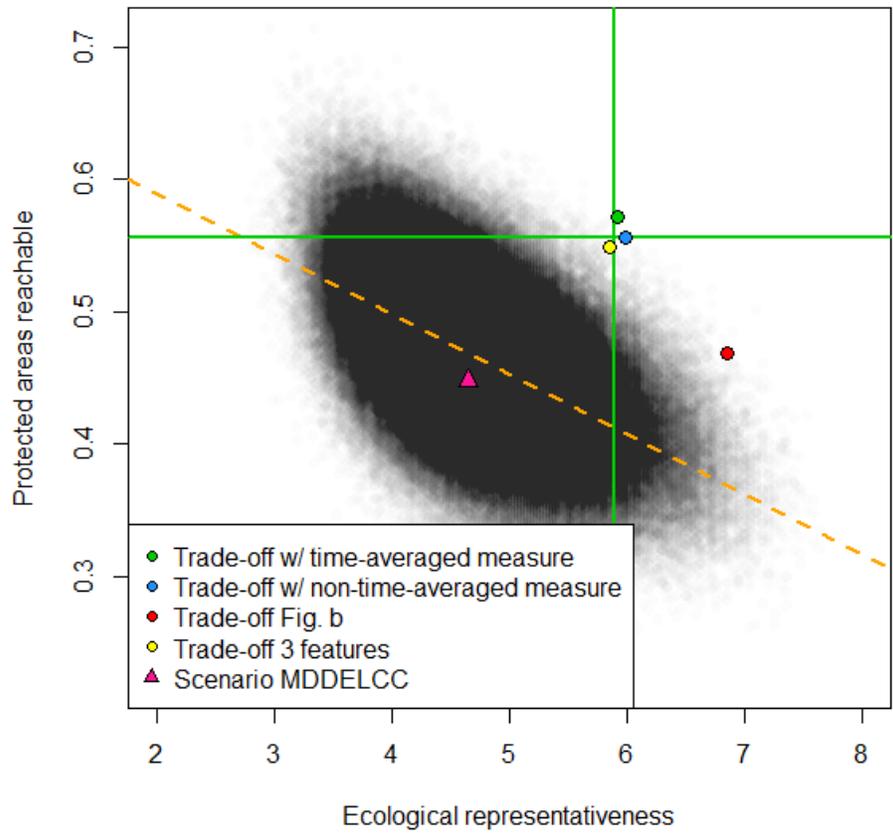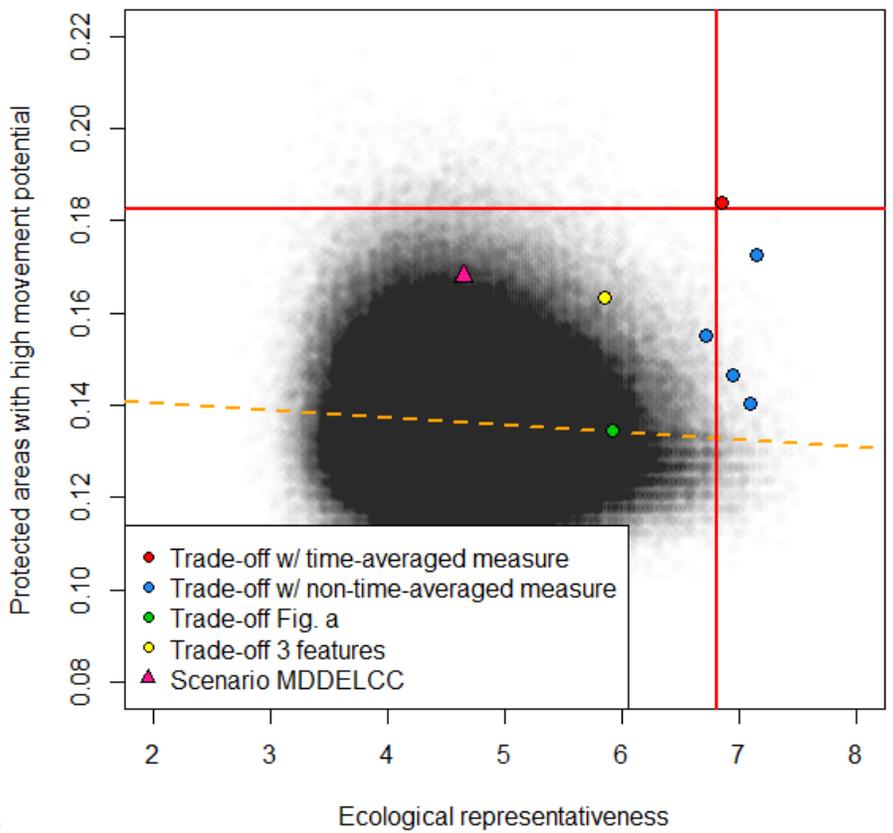
Figure 3.2: Scatter plots of network time-averaged functional connectivity against ecological representativeness. a) The time-averaged functional connectivity index represents the proportion of protected areas reachable by the caribou. b) The time-averaged functional connectivity index represents the proportion of protected areas in which the caribou movement potential was above 0.01 km². The orange dashed lines represent fitted linear regression models of the functional connectivity features against ecological representativeness. The solid lines represent the feature values at quantile Q (Q = 0.956 in Fig. a and Q = 0.998 in Fig. b) to identify the scenario (dot of the same color as the solid lines) with the best trade-off between the two features plotted. The blue dots represent the networks selected as the best trade-off using each non-time-averaged movement potential estimates to calculate the functional connectivity measure presented. The five blue dots in each figure are not all visible due to some overlaps. The yellow dot identifies the network with the best trade-off between ecological representativeness and the 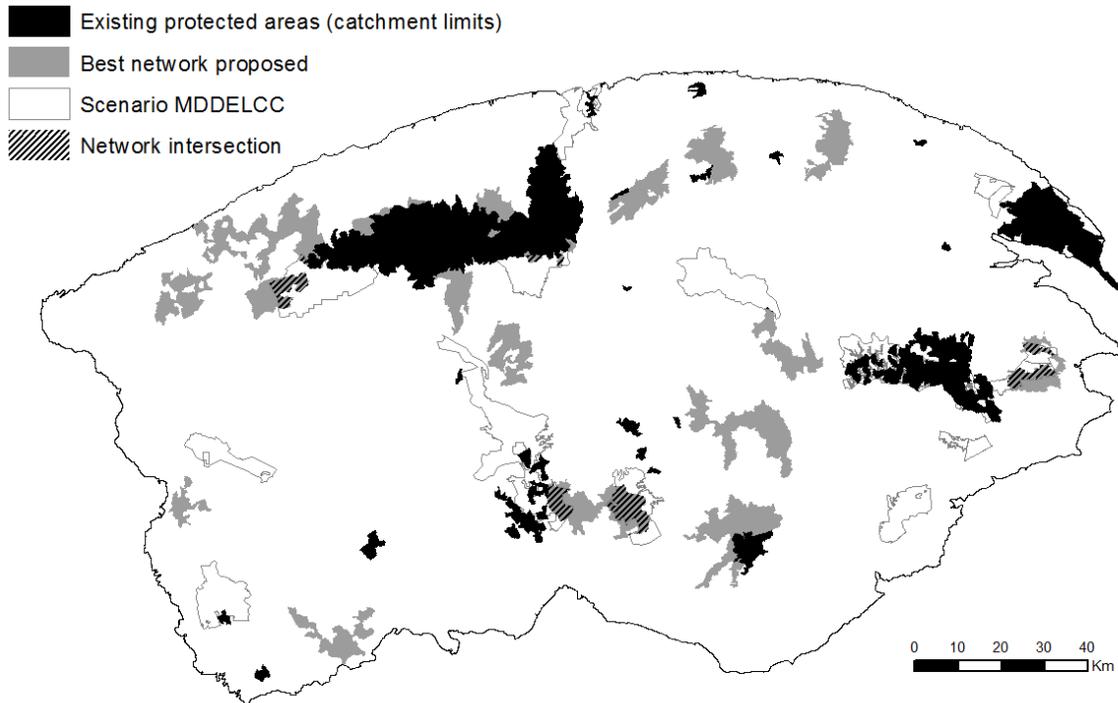two time-averaged functional connectivity measures. This network scenario is the one mapped in Figure 3.3. The pink triangle represents the network scenario proposed by the government of Québec (MDDELCC). a) The red dot represents the scenario with the best trade-off between the two features plotted in Fig. b. b) The green dot represents the scenario with the best trade-off between the two features plotted in Fig. a.

Network ecological representativeness and functional connectivity trade-off

As the best trade-off between ecological representativeness and the proportional network area reachable by caribou, we identified different network scenarios if we used the time-averaged measure (green dot, Fig. 3.2a) or the measures derived from the movement potential estimates for the current time period and the different climate change scenario independently (blue dot(s), Fig. 3.2a). All the non-time-averaged measures gave the same network scenario for the best trade-off, and it has very similar feature values as the one identified with the time-averaged measure. There was a strong and statistically significant negative relationship between the two network features (slope = -0.045, t(499998) = -469.2, p < 0.001; calculated with the time-averaged measure) (orange dashed line, Fig. 3.2a).

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As the best trade-off between network ecological representativeness and the proportional area of high movement potential, different network scenarios were also identified depending on the movement potential estimates used to calculate the functional connectivity measure. The network scenario identified using the time-averaged measure (red dot, Fig. 3.2b) had a similar ecological representativeness score as those for the networks identified using the non-time-averaged measures (blue dots, Fig. 3.2b). All these scenarios differed more in their proportional areas of high movement potential. There was a lesser, but significant, negative relationship between the two network features (slope = -0.002, $t(499998) = -57.5$, $p < 0.001$; calculated with the time-averaged measure) (orange dashed line, Fig. 3.2b).

Figure 3.3 shows the network scenario selected by the best trade-off between ecological representativeness and the two time-averaged functional connectivity measures. This network was very similar, in terms of feature values, to the one identified using the trade-off between ecological representativeness and proportional area reachable (yellow and green dots, Fig. 3.2a). It performed a bit less, both for the ecological representativeness and the proportional area of high movement, than the scenario with the best trade-off with these two features only (yellow and red dots, Fig. 3.2b). The network resulting from the best trade-off of all three features performed better than the MDDELCC scenario in terms of ecological representativeness and proportional area reachable (yellow dot and pink triangle, Fig. 3.2a). It performs slightly less for the proportional area with high movement potential (yellow dot and pink triangle, Fig. 3.2b). The new protected areas from our proposed network scenario overlapped only slightly with the areas proposed by the MDDELCC (Fig. 3.3).

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Figure 3.3: Protected area network scenario with the best trade-off between ecological representativeness and the two measures of time-averaged functional connectivity. The existing protected areas are represented by their catchment limits as used in the analysis by the BEACONs tools. The outlines of the new protected areas proposed by the government of Québec (MDDELCC) are overlaid with their intersections (dashed areas) with our proposed scenario.

Discussion

We used one coarse and two fine filters to evaluate a large sample of potential protected area networks in Gaspésie, to identify the one that might most effectively protect regional biodiversity through time. We maximized the trade-off between ecological representativeness and two measures of functional connectivity robust to the current and possible future environmental conditions to select the best network. The design, if implemented, would protect a more diverse set of habitat types, thus increasing the protection of the local biodiversity, while facilitating the movements across the landscape

for our focal species and potentially other threatened species, for the current time period and for the future.

A poor ecological representativeness of the landscape in protected area networks may decrease the network's effectiveness for conservation. Managers need to work towards achieving a better representation of the regional biodiversity when implementing new protected areas. Gap analyses are a common tool to estimate the ecological representativeness of protected area networks (e.g., Rodrigues et al. 2004; Wiersma and Nudds 2009). Our methodology used a distribution matching methodology that in effect minimizes gaps with respect to a chosen set of environmental covariates, and gave us one distance metric per network scenario. These single metric values allowed us to easily compare a large sample of different networks and select the one best suited to our goal. Many studies have evaluated protected areas connectivity and have used cost distances (Sundblad, Bergström & Sandström 2011) or graph and circuit theory techniques (Baldwin *et al.* 2010; Rayfield, Fortin & Fall 2011). We defined functional connectivity using movement estimates from individual-based models (Bauduin *et al.* Chapter 1 and 2) which included constraints from known characteristics of the focal caribou population. This also allowed us to account for complex movement behaviors (e.g., seasonal site fidelity) which cannot be easily replicated in models that are more static.

There was a trade-off between network ecological representativeness and the two functional connectivity measures we defined. We identified a strong negative relationship between network ecological representativeness and the proportion of protected areas reachable by caribou. There is only one caribou population in Gaspésie so the networks that were more connected for caribou were the ones with protected areas clustered around the Gaspésie National Park where the population lives (Mosnier *et al.* 2003; Lalonde 2015). In order to achieve a high ecological representativeness, protected areas needed to be scattered over the region to capture the diversity of the landscape; this explains the negative relationship between representation and reachability (Almany *et al.* 2009). The lesser negative relationship between network ecological representativeness and the proportional area of high movement potential for caribou was dependent of the study region. Habitats of good quality reachable for caribou are mostly located close to the Gaspésie National Park (Gaudry 2013), inducing the same trade-off as for the accessibility metric. However, the

relationship was weaker because areas with high movement potential were already protected inside the Gaspésie National Park (Bauduin *et al.* Chapter 2). Therefore, there were few opportunities for new protected areas to increase that functional connectivity measure in this respect, hence giving a weaker relationship.

We used functional connectivity measures calculated using predicted future movement potential estimates as a network design criterion. It is more efficient to take future climate change impacts into account now instead of waiting for the changes to occur and then reacting (Hannah *et al.* 2007). Therefore, averaging movement estimates for the current time period and different scenarios of climate change, as we have done here, was a simple option to address this need. However, there were differences in the network abilities to protect areas of high movement potential for caribou depending on the movement potential estimates used. In this case, averaging the movement estimates to select the best network scenario would select a network that was sub-optimal for any particular scenario but that might perform reasonable well under a large range of possible future environmental conditions. The differences in movement estimates for the different scenarios resulted from the different assumptions made about the future environmental conditions. This part could be improved by a robust climate change model coupled with the animal movement model to obtain reliable movement predictions over time instead of relying on different landscape scenarios. Until such models are available, we felt that averaging results from different scenarios was a good compromise to create a robust estimate over time that would be best under a wide variety of conditions.

The network expansion proposed by the Québec government to achieve the 12% coverage target was quite different than the one produced by our analysis. The MDDELCC network surprisingly achieved a lower ecological representativeness than our proposed network and had roughly the mean score of our sample. However, a gap analysis showed strong positive results and improvements for this network compared to the current network of existing protected areas (MDDELCC 2014). The ministry had to respect design criteria and constraints, like socio-economic issues or the inclusion of rare ecosystems (Boisjoly 2015, personal communications), that we did not consider. In particular, the ministry excluded, as potential areas to be protected, all territories dedicated to maple farming, mining activities, blueberry farming, wind farming, gas and oil exploration, as well as some

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forestry activities. This could explain the sub-optimal ecological representativeness achieved by their network. Regarding functional connectivity, their scenario provided less access for the Atlantic-Gaspésie caribou to the protected areas than the network we proposed. However, their network covered a slightly larger area of high movement potential for caribou than our network. The process used by the government of Québec to define new protected areas did not specifically include functional connectivity for the Atlantic-Gaspésie caribou. The performance of their network was quite good for these features, especially considering that they were not explicitly part of the design. The differences with our proposed network could also arise from the method which selects only near-intact hydrological catchments as units. Some areas, such as the area south-east of the Gaspésie National Park included in the MDDELCC scenario, were too highly disturbed for any protected areas to be built, and therefore could not be represented in any network.

Our study provided a methodology to define an effective protected area network based on the trade-off between ecological representativeness and functional connectivity over time, including climate change potential impacts. Our methodology yields network designs that may be close to ideal from an environmental or conservation point of view, but which does not fully respect all constraints of the use of public lands. The Gaspésie region is highly disturbed by human activities. Taking into account all the social and economic constraints would have reduced too much the area for potential new protected area implementations, giving little space for designing different network scenarios or exploring the limits of what is possible. However, this methodology could easily include more features in the choice of the best network scenario, and the selected scenario would then be represented as the best trade-off between all selected features. It would be easy, given the data availability, to add constraints in the choice of the network with, for examples, the ecological representativeness of the future landscape under climate change, the functional connectivity of several species important for the ecosystem (Minor & Urban 2008), the economic cost of excluding human activities from the proposed areas, the potential benefit with tourism if protected areas act as parks (Mayer 2014), or any of the constraints included by the MDDELCC in their scenario. Target features and constraints can be defined by local managers to help meet local biodiversity goals. They could easily be implemented in the presented method to propose a better suited network for the region. Moreover, we selected

the one network with the best trade-off between our chosen features but it would be possible to select a subset of best scenarios and look at the protected areas most often used in these networks (Saucier 2011). We could then recommend protected areas with a gradient of importance to fulfill the regional needs instead of a single scenario.

Acknowledgements

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General conclusion

In the first chapter of this thesis, I built a spatially explicit individual-based model (IBM) to explain and simulate the movement of the Atlantic-Gaspésie caribou population (*Rangifer tarandus caribou*). I parameterized the model from a sparse VHF telemetry dataset using a pattern-oriented modeling strategy. Then, I used the model to simulate caribou movements to estimate the population landscape use. My main finding is that extensive, high-resolution telemetry data is not required to select and parameterize a robust daily movement model. These tasks can be accomplished by using IBMs in a pattern-oriented modeling strategy. For my specific case study, I obtained a good understanding of movement characteristics of the Atlantic-Gaspésie caribou and of the variables controlling it. For example, the inter-patch movement of the caribou as a foray loop movement is novel. This looping pattern and the importance of the mating site fidelity confirmed the use of the memory by the caribou when moving through its landscape. Using the fitted IBM, I was able to map the population's current landscape use.

In my second chapter, I tested how movement potential of the Atlantic-Gaspésie caribou may be impacted by climate change and evaluated the potential for conservation activities to mitigate such impacts. I simulated caribou movements and estimated the population movement potential in alternate landscapes resulting from different climate change and conservation scenarios. Climate change acted to decrease caribou movement potential through the impacts on the vegetation cover. Reducing the movement barriers by restoration of secondary roads inside the protected areas had a greater mitigation potential than a mere increase in the area protected. However, even with low climate change impacts, the proportion of roads that needed to be restored to mitigate the loss of movement potential due to climate change was too important. This highlights the necessity of multiple combined conservation actions are needed to protect species movement.

In the third chapter, I developed a method to design protected area networks in the Gaspésie region that may effectively conserve biodiversity over time. I created a large number of alternate protected area networks which I evaluated and ranked based on ecological representativeness and two measures of functional connectivity for the Atlantic-

Gaspésie caribou. Functional connectivity was defined using caribou movement potential estimates for the current time period and for the future in a context of climate change. There were negative correlations among the network features such that no network could maximize each one simultaneously. But because there was a considerable variability in the relationships, it was possible to identify networks that performed well for all features. We selected, as our best scenario, the network with the best trade-off.

The presented methodology could be applied to another case study when there is the will to complete the regional protected area network by compromising conservation goals defined by a coarse filter, as well as specific species needs. By preference, the focal populations used for the fine filter must be of great importance for the species conservation itself (e.g., unique population) and also for the benefit of the whole ecosystem (e.g., an umbrella or keystone species).

The power of individual-based models

This thesis relied mostly on IBMs and they proved to be effective and flexible enough to provide useful answers to my questions. I succeeded to parameterize a model and differentiate alternate behavioral hypotheses to reproduce caribou movement with an average of less than 50 locations per individual. These locations were also spread out irregularly in time. The validation of my model demonstrated that IBMs, coupled with a pattern-oriented modeling strategy, do not require huge dataset in order to be robust models. The collection of temporally dense, high precision locations with technologies such as GPS tracking is a very recent development and remains very expensive (Hebblewhite & Haydon 2010; Latham *et al.* 2015). VHF data remain in use, and are the only data available in many areas for the fairly recent past. The use of IBMs with a pattern-oriented modeling strategy seems a relevant methodology to study movement for those species with only sparse data available.

IBMs can be highly mechanistic and rely on causal mechanisms instead of correlative patterns. Therefore one can more reliably test the impact of different input data on the fitted model outputs, for example through simulation experiments. In my second

chapter, I explored the consequences of hypothetical changes of the Gaspésie land cover on the Atlantic-Gaspésie caribou movement. The mechanistic property of the IBMs allowed me to predict how climate change and conservation activities in the landscape could affect the caribou movement potential. Results showed that both climate change and roads impacted caribou movements and that different landscape management strategies have different consequences on restoring caribou movement potential.

Importance of incorporating functional connectivity and climate change

Enhancing functional connectivity is beneficial for species conservation and therefore protected areas connected into a network are more effective than single disconnected areas (Bennett & Mulongoy 2006; Rudnick *et al.* 2012; Andrello *et al.* 2014). I included the Atlantic-Gaspésie caribou movement estimates for the current time period into the selection of the best protected area network scenario. By that, I ensured that the new protected areas I proposed to implement in Gaspésie would be beneficial today to protect this population by enhancing its movement under the current environmental conditions.

Climate change is impacting species and disrupting ecosystems globally (Loarie *et al.* 2009; Chen *et al.* 2011). On a local scale, it is more difficult to define a common trend for the impacts on species. Some species may benefit from the new environmental conditions, others may not (e.g., Périé *et al.* 2014). In my case, I discovered that climate change, as defined in my scenarios, had a negative impact on the Atlantic-Gaspésie movement potential. Therefore, climate change is likely to negatively impact landscape functional connectivity for caribou. Conversely, enhancing connectivity in a landscape helps species cope with climate change (Vos *et al.* 2008; Nuñez *et al.* 2013). Therefore, it seems imperative to protect the areas which would secure the most functional connectivity in the future for the species to be protected regionally. This management planning needs to be done now, rather than waiting for the climate change impacts to occur before taking concrete measures in the landscape (Hannah *et al.* 2007). That is why I included predictions of future caribou movements in my protected areas network design, so that network functional connectivity and therefore effectiveness would be maintained through time. I used an average of the predictions from four different climate change scenarios,

representing a gradient of the potential impacts of climate change in Gaspésie to account for different possible future conditions.

Multi-model integration

My thesis included some model integration in that the protected area network design used results from caribou movement models. However, there is room for more integration and interaction of models to achieve greater understanding of the ecosystem dynamics and to improve management decision-making in Gaspésie and elsewhere.

In the IBM that I developed, the individual entities represented caribou and there was no interaction between them. If needed, the model could be made more complex by adding sex and age structures to the individuals and interactions between them to represent herding, mating, or family behavior (e.g., Merkle, Sigaud & Fortin 2015). A demographic model could complete the movement model to simulate the abundance of the herd and the outputs of the movement model could then be density dependent (e.g., Marucco & McIntire 2010). This model could also include fitness measure as a balance between energy gain from forage ability and energy consumption (e.g., through walking, calving, etc.) (Semeniuk *et al.* 2012). I could then forecast long term population dynamic and estimate the potential for colonization and new establishment in areas distant from the caribou current range, using a stepping stone process for example. This would of course require more data on caribou interactions and demography to parameterize these additional features.

The caribou model could also be complemented by one or several IBMs for the other animal species interacting with it. The current main proximate threat for the Atlantic-Gaspésie caribou is predation by coyotes (*Canis latrans*) and black bears (*Ursus americanus*) (Crête & Desrosiers 1995). The coyote population in Gaspésie is mostly sustained by the high abundance of moose (*Alces americanus*) (Boisjoly, Ouellet & Courtois 2010). The habitat preferences of these species have been studied (Mosnier *et al.* 2008; Boisjoly, Ouellet & Courtois 2010). One could build IBMs to recreate the movement of coyotes, bears, or moose and integrate them in interaction with the caribou movement

model. The caribou individual would then not only respond to its habitat but also to the other species moving around (Latombe 2013; Latombe, Fortin & Parrott 2014; Fortin *et al.* 2015). An extension of this multi-species IBM could be the integration of demographic models for each species, with spatial dependent demographic parameters such as the prey mortality accounting for a spatially constrained predation risk (Whittington *et al.* 2011). The predicted caribou movement resulting would then be constrained by the other species movements and abundances. Predicted movement would likely be more precise. The estimated movement potential and then functional connectivity for protected area network could then be used as in my third chapter. The protected area network design could be expanded to include features representing the other species, but still targeting the caribou population. For example, the best network scenario could try to minimize the functional connectivity between the protected areas for the predators and the alternate prey, to space them out from the caribou. Coyotes, black bears and moose are not endangered in Gaspésie; the protected area network does not need to enhance their movement potential.

Apart from other animal species, the caribou movement model could be completed with a model predicting landscape conditions. In my second chapter, I included the effect of climate change as multiple scenarios. No vegetation model robust enough was available for the Gaspésie region to forecast the future state of the habitat types I was interesting in. I created four different scenarios of the future climate on the Gaspésie landscape but I could not estimate if one scenario was more likely than another. A dynamic vegetation model could be coupled with the multi-animal-species model so that the moving individuals would respond to the changes in vegetation as these would occur. Then, I could have a continuous estimate of the caribou movement on a long term instead of simulated snapshots at specific times. The protected area planning could incorporate this continuous estimate for caribou movement and then maximize functional connectivity over the entire time period.

The integration of several models implies that they interact with one another and that the outputs from one serve as inputs for another. It seems one solution to include the multiple feedbacks occurring in an ecosystem between the climate and all the species coexisting, plants and animals alike. The computer power and software are already well developed to achieve such multi-model integration (e.g., Thain, Tannenbaum & Livny 2005; Chubaty and McIntire 2015). This type of model would give a better understanding

of the whole ecosystem as a unit and help obtain more reliable predictions regarding the future. This modeling strategy would help managers make more informed decisions about the landscape and the conservation measures to apply to increase biodiversity protection regionally and help counter the global biodiversity decline.

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