UNIVERSITÉ DU QUÉBEC À RIMOUSKI

EFFET DE L'HÉTÉROGÉNÉITÉ DU PAYSAGE ET DES PERTURBATIONS ANTHROPIQUES SUR L'ÉCOLOGIE DU CARIBOU DE LA GASPÉSIE

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DÉDICACE

À mes enfants, actuel et futur.
À eux qui vivront cet enjeu mondial qu'est l'érosion de la biodiversité.
Je leur souhaite de pouvoir toujours contempler ces derniers caribous.

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RÉSUMÉ

Les espèces animales ont majoritairement évolué dans un milieu hétérogène où les ressources varient en qualité et en quantité dans le temps et l'espace. L'activité humaine a toutefois altéré les habitats de plusieurs espèces, forçant celles-ci à s'ajuster ou disparaître. En modifiant inégalement la répartition des espèces et des ressources, nous influençons indirectement les relations trophiques et les différents compromis entre les besoins et les contraintes, ce qui peut affecter à la fois le comportement, la distribution et la survie des espèces animales. L'objectif principal de cette thèse était de mieux comprendre l'influence de l'hétérogénéité du paysage, qu'elle soit due à des phénomènes naturels ou anthropiques, sur différentes facettes de l'écologie d'une espèce sensible aux modifications du paysage, le caribou (*Rangifer tarandus caribou*), et plus spécifiquement sur la population de la Gaspésie-Atlantique.

Certaines proies ont développé une stratégie anti-prédatrice consistant à se réfugier dans les zones fortement utilisées par l'homme et où les prédateurs s'aventurent rarement. Dans le premier chapitre, l'objectif était donc de déterminer comment le caribou réagissait face au risque induit par la présence de randonneurs. Nous avons émis l'hypothèse que la perception du risque allait différer en fonction du statut reproducteur de la femelle en lien avec la vulnérabilité à la prédation du faon. Nos résultats appuient partiellement notre hypothèse. Les femelles suitées ont diminué leur niveau d'alerte près des sentiers en présence de randonneurs alors que les femelles seules ont presque doublé le temps passé en vigilance en présence d'un nombre élevé de randonneurs sur les sentiers. Toutefois, les deux catégories de femelles se sont éloignées des sentiers lorsque ceux-ci étaient accessibles aux randonneurs et que des randonneurs y étaient présents.

Dans un contexte de conservation, il est primordial de connaitre, non seulement l'impact des modifications des habitats, mais également de la présence humaine sur les espèces à statut précaire. Dans le deuxième chapitre, mon objectif était de relier la réponse du caribou, en termes de déplacements et de patrons d'utilisation de l'espace, face à des variations d'intensité d'un dérangement de faible ampleur, dans ce cas le ski hors-piste. Nous avons émis l'hypothèse que les caribous adaptent leurs réponses comportementales en fonction de l'intensité du stimulus. Nos résultats ont appuyé cette hypothèse, l'évitement du domaine skiable étant modulé par le nombre de skieurs. Les déplacements de fuite des caribous vers de basses altitudes étaient également exacerbés par l’augmentation du nombre de skieurs. Nos résultats ont révélé une réponse comportementale relativement forte face à cette perturbation ainsi qu’une perte fonctionnelle d’habitat non négligeable.

Les espèces sociales peuvent combiner leurs propres connaissances du territoire à celles d’autres individus dans leur prise de décisions. Toutefois, plus le paysage est hétérogène, plus les sources de conflits au sein d’un groupe sont nombreuses. Nous voulions donc tester l’importance relative du bagage d’informations détenues par un groupe et de la présence potentielle de conflits d’intérêt en fonction des caractéristiques du paysage. Notre hypothèse principale était que les individus seraient plus enclins à quitter le groupe dans les endroits qu’ils connaissent bien, alors qu’ils seraient moins enclins à se séparer d’un groupe dans les milieux qui leurs sont moins familiers. Nous avons effectivement montré que la probabilité de fission augmentait avec la connaissance du paysage. Toutefois, la présence d’habitats préférentiels et l’existence de liens sociaux avec les membres du groupe modulaient à la baisse cette augmentation de la probabilité de fission.

Au sein d’une population, on peut retrouver différentes stratégies comportementales qui ne résultent pas nécessairement en des impacts équivalents sur le taux de survie. Nous avons donc voulu tester l’effet de la marginalité du comportement d’utilisation de l’espace des caribous sur la survie individuelle. L’hypothèse principale étant qu’en absence de forte compétition intraspécifique (c.-à-d. la principale force favorisant la persistance de comportements marginaux), les comportements les plus conformistes devraient assurer une plus forte probabilité de survie. Conformément à cette hypothèse, les individus qui affichaient un comportement marginal avaient un plus haut risque de mortalité que les individus plus conformistes, sauf dans le cœur de leur domaine respectif, où les conformistes et les marginaux faisaient face à un risque similaire. Ainsi, être prévisible dans l’espace pourrait accroître la capacité des prédateurs à trouver et capturer une proie.

En conclusion, l’hétérogénéité du paysage et des perturbations ont influencé les comportements des caribous, ce qui se répercutait également sur leur distribution et leur survie. Cette thèse souligne l’importance de s’attarder à la fois aux ajustements comportementaux à l’échelle individuelle, mais également aux effets de ces ajustements sur la distribution et la survie individuelle.

ABSTRACT

Most animals live in patchy environments, where resources are not homogeneously distributed in time or space. Human activities can increase landscape heterogeneity with implications for the distribution of resources and interspecific interactions. These changes can affect the behaviour, distribution and survival of a species. The objective of my research was to assess the influence of landscape heterogeneity, caused by natural or anthopogenic processes, on the spatial ecology and survival of the endangered Atlantic-Gaspésie population of woodland caribou (*Rangifer tarandus caribou*). Throughout their North American distribution, woodland caribou are vulnerable to human disturbance and habitat modification.

Some prey have developed an anti-predator strategy that involves taking refuge in areas highly used by humans, where predators are relatively absent. In this first chapter of the dissertation, my objective was to quantify and evaluate the spatial and behavioural response of caribou to the presence of hikers. We[1] hypothesized that the response of female caribou would differ according to maternal status, due to the predation vulnerability of the calf. Our results partially supported the hypothesis. Females with a calf decreased their vigilance near trails used by hikers, while females without a calf doubled their time spent in vigilance. However, all female caribou tended to move away from trails in the presence of hikers.

Landscape modification can combine with human-caused disturbance to increase the energetic costs associated with space-use and reduce the overall quality or availability of habitat for caribou. In the second chapter, I related the movement and distribution of GPS collared caribou to the presence of backcountry skiers. We hypothesized that caribou would vary their disturbance response in relation the number and distance of skiers. Our results supported the hypothesis; the displacement of caribou was correlated with the number of skiers. Our results revealed a relatively strong behavioural response with a measurable loss of functional habitat.

For social species such as caribou, individuals will engage in cooperative decision making to acquire resources and lower their risk of predation. However, a highly heterogeneous landscape can reduce the benefit of group cohesion. We tested the

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[1] I used the plural pronouns “we” and “our” to recognize co-authorship of manuscripts that resulted from this research.

relative importance of landscape knowledge, social bond and habitat characteristics in dictating the fission dynamics of monitored caribou. We hypothesized that individuals would be more prone to leave a group when in a familiar environment. We found that fission probability increased with landscape knowledge, however, this increase was lower in preferred habitat or when individuals shared strong social bonds.

Variation in behaviour has implications for individual fitness. We assessed the relationship between survival and marginality, a measure of interanimal variation in behaviour and space use. The Gaspésie caribou occur at a low density with relatively little intraspecific competition. Density dependence is one of the main drivers promoting the persistence of marginal behaviour. Thus, we hypothesised that conformist behaviour would be dominant and that such individuals would have a greater probability of survival. In accordance with our hypothesis, individuals with marginal behaviour had greater mortality risk, except in the core area of their respective home range, where both behavioural types faced similar risk. Being predictable in space could increase the ability of predators to find and kill prey.

In conclusion, landscape heterogeneity and human-caused disturbance influenced the behaviour, distribution, and survival of the Gaspésie caribou. More broadly, results of this research suggest that the responses of caribou, in particular historically low-density populations, is the product of a range of ecological and biological factors. Thus, when considering behaviour and space use one should test the effects of habitat heterogeneity, social dynamics, learned behaviour and human-caused disturbance and habitat change.

Key words: behaviour, caribou, human activities, landscape heterogeneity

INTRODUCTION GÉNÉRALE

Les espèces animales ont majoritairement évolué dans un milieu hétérogène où les ressources varient en qualité et en quantité avec le temps et l'espace. Conceptuellement, chaque espèce perçoit différemment le paysage, dépendamment de sa mobilité, de sa taille, de ses contraintes et de ses besoins (Kotliar et Wiens, 1990; Levin, 1992). Pour une espèce donnée, un paysage hétérogène peut être défini comme la perception de discontinuités des différentes ressources (Wiens, 1976) qui évoluent naturellement, tant spatialement que temporellement, par le biais de la succession végétale ou de variations climatiques ou encore plus récemment par le biais des modifications anthropiques. Selon la théorie des niches, une espèce ne peut persister dans un milieu donné que si les caractéristiques environnementales permettent une croissance de la population sans émigration (Grinnell, 1917; Giller, 1984). Ces caractéristiques peuvent être classées en deux grandes catégories : (i) les besoins biotiques et abiotiques de l'espèce et (ii) l'environnement biotique composé des compétiteurs, prédateurs et pathogènes et toutes les interrelations entres ces éléments (Guisan et Thuiller, 2005; Soberón, 2007). Les deux catégories sont étroitement liées; une espèce adaptant sa recherche alimentaire (Stephens et Krebs, 1986; Turchin, 1991; Katz *et al.*, 2013), sa stratégie antiprédatrice (Mitchell, 2009; Laundré *et al.*, 2010) et ses interactions sociales (Fortin *et al.*, 2009; Sueur *et al.*, 2011; Merkle *et al.*, 2015) à la configuration spatiotemporelle des différentes ressources essentielles à l'espèce dans le paysage.

En étudiant à la fois le comportement, la distribution des individus ainsi que les différences de survie qui en résultent, nous pouvons comprendre et expliquer les effets des facteurs environnementaux et populationnels (Figure 1.1). J'aborderai principalement dans cette thèse comment l'hétérogénéité dans les facteurs environnementaux peut influencer les espèces animales, de leur comportement à leur survie. L'accent sera mis sur les facteurs environnementaux suivants : l'acquisition des ressources, le risque de prédation et les impacts des perturbations anthropiques. J'aborderai également les effets importants des facteurs populationnels, plus spécifiquement la variabilité intra- et interindividuelle et la socialité. Finalement, je discuterai de l'importance des échelles spatiotemporelles, biologiques et d'intensité des perturbations.

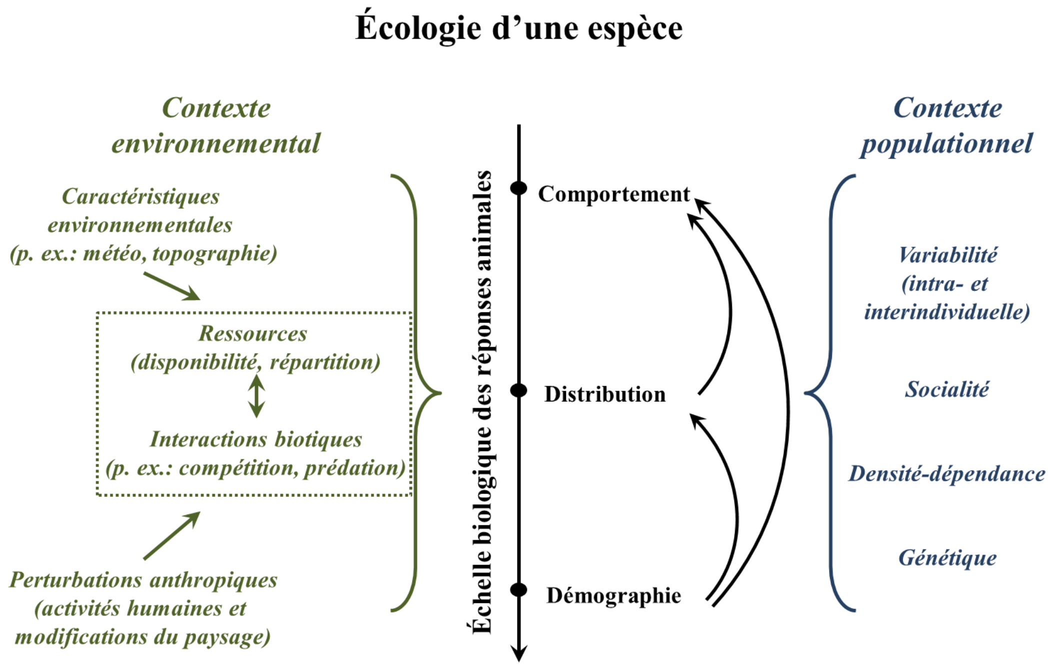

Figure 1.1. Schématisation non exhaustive des facteurs environnementaux et populationnels pouvant influencer différentes facettes de l'écologie d'une espèce.

Compromis acquisition des ressources – risque de prédation

La théorie de la quête alimentaire optimale (lib. de « optimal foraging » *sensu* MacArthur et Pianka, 1966; Stephens et Krebs, 1986), malgré ses nombreuses critiques au sujet de ses prémisses et ses applications (Pyke, 1984; Sih et Christensen, 2001), fourni un cadre théorique utile pour s'intéresser à la quête alimentaire d'un individu dans un milieu hétérogène. Cette théorie stipule que le comportement d'alimentation d'un individu, sujet à des contraintes, est adaptatif et a évolué pour maximiser sa valeur adaptative. Pour un herbivore par exemple, les contraintes peuvent inclure les processus digestifs et le choix de ressources alimentaires (Spalinger et Hobbs, 1992), la disponibilité de ces ressources de même que le risque de prédation (Hernández et Laundré, 2005). La différence de valeur adaptative entre les conséquences d'être tué par un prédateur et celles résultant du gain d'énergie potentiel devrait expliquer, du moins partiellement, l'évolution et l'adaptation des comportements d'alimentation (Brown, 1988, 1992; Abramsky *et al.*, 2002). Ce compromis entre l'acquisition des ressources alimentaires et la sécurité est dépendante des contraintes de disponibilité des ressources et de la variation du risque de prédation dans le paysage (Lima *et al.*, 1985; Werner et Hall, 1988; Verdolin, 2006). Généralement, dans les endroits relativement sécuritaires, les ressources deviennent limitées dans le temps, forçant les proies à quitter de tels refuges et faire face à un risque de prédation plus élevé (Hugie et Dill, 1994). Ce compromis qui est à la base de nombreux choix des proies, tant dans leur budget d'activité (Ruckstuhl, 1998; Lesmerises *et al.*, 2017) que leur utilisation de l'espace (Cowlishaw, 1997; Winnie et Creel, 2007), influence ultimement leur survie.

Relations prédateur – proie

La peur d'être tué par un prédateur est un facteur clé orientant plusieurs facettes du comportement animal (Hernandez et Laundré, 2005; Laundré, 2010; Rösner *et al.*, 2014). L'évitement de secteurs risqués, l'augmentation de la vigilance et, en dernier recours, la fuite en sont quelques exemples qui témoignent de l'influence de la peur sur les choix d'un animal (Welp *et al.*, 2004; Katz *et al.*, 2013). Comme les proies connaissent rarement la position exacte des prédateurs, elles doivent maintenir un certain niveau de vigilance. Toutefois, ce niveau de vigilance est lui aussi soumis à des compromis entre l'acquisition des ressources et le risque de prédation. En effet, un animal en vigilance ne peut généralement pas satisfaire, du moins efficacement, ses autres demandes simultanément (Blanchard et Fritz, 2007; Pays *et al.*, 2011). Les proies vont donc diminuer leur niveau de vigilance avec le temps suite au dernier stimulus ayant entrainé une vigilance accrue et ce, au profit d'autres activités essentielles (Mitchell, 2009). Un prédateur, à son tour, ne va pas insister dans sa chasse si une proie est déjà avertie de sa présence et que cela se traduit par une baisse des probabilités de réussite (Brown, 1999). Autant les prédateurs que les proies vont donc ajuster leurs déplacements, leur patrons d'utilisation de l'espace et leur budget d'activité dans le but d'augmenter ou de diminuer le taux de rencontre et le succès de la chasse (Mitchell, 2009).

Un prédateur peut s'appuyer sur plusieurs techniques pour repérer sa proie : traquer les ressources de la proie (Flaxman et Lou, 2009; Williams et Flaxman, 2012), traquer les fortes abondances de proies (Flaxman et Lou, 2009), ou encore traquer les caractéristiques qui augmentent son succès de chasse (Quinn et Cresswell, 2004; Laundré, 2010). En réponse, la proie tente de minimiser les rencontres en se déplaçant dans son domaine vital afin de minimiser sa prédictibilité (Mitchell et Lima, 2002; Mitchell, 2009), et/ou en choisissant des habitats présentant un risque de prédation plus faible (Hernandez et Laundré, 2005; Laundré *et al.*, 2010). Toutefois, les paramètres servant à l'estimation du risque de prédation par la proie restent difficiles à tester, bien que la présence de signes de prédateurs (p. ex. : odeur et détection visuelle) et les expériences passées soient susceptibles d'y jouer un rôle. L'évaluation du risque de prédation à grande échelle par les proies est potentiellement plus difficile pour elles, d'autant plus qu'elles peuvent faire l'objet d'une prédation par plusieurs espèces de prédateurs, chacun ayant son propre comportement de chasse et de traque. Du point de vue de la proie, il peut devenir difficile d'ajuster ses patrons de sélection des ressources et d'utilisation de l'espace dans le but d'éviter toutes les espèces de prédateurs en même temps. L'exemple de la population de caribou forestier (*Rangifer tarandus caribou*) de

Charlevoix est un cas très concret où les femelles évitant efficacement le loup (*Canis lupus*) se retrouvent dans des habitats où le risque de rencontre avec l'ours noir (*Ursus americanus*) est plus important, ayant comme résultat une mortalité des faons majoritairement due à la prédation par l'ours (Leblond *et al.*, 2016). Des modifications majeures du système avec lesquelles la proie n'a pas évolué peuvent aussi mener à des comportements antiprédateurs mal adaptifs (Byers, 1997).

Utilisation de l'espace et sélection des ressources

Caractériser la distribution animale et l'importance relative de chacun des facteurs écologiques sur les décisions comportementales s'opère souvent à l'aide de deux différentes familles de méthodes trop souvent confondues, à savoir l'utilisation de l'espace et la sélection des ressources. L'utilisation de l'espace réfère à la proportion de temps qu'un individu passe dans chaque catégorie d'habitat et comment l'animal se déplace dans le paysage (Hall *et al.*, 1997). La sélection des ressources considère quant à elle la disponibilité des différentes ressources (Johnson, 1980; Manly *et al.*, 2002). La sélection des ressources reflète le compromis entre les besoins et les contraintes d'une espèce (ressources et conditions environnementales). D'ailleurs la distribution animale a souvent été reliée au concept de niche écologique qui réfère également aux caractéristiques biotiques et paysagères nécessaires pour assurer le maintien d'une espèce indéfiniment (Grinnell, 1917; Hutchinson, 1978). Le concept de niche écologique peut être séparé en deux types distincts, la niche fondamentale et la niche réalisée. Cette dernière intègre les interactions (c.-à-d., la compétition et la prédation) entre les individus et les espèces (Hutchinson, 1957). Conceptuellement, la sélection des ressources peut être interprétée comme la niche écologique réalisée, alors que les différentes ressources présentes dans le paysage représentent la niche fondamentale (Soberon, 2007; Basille *et al.*, 2008). Rettie et Messier (2000) ont montré que la sélection des ressources par une espèce donnée est dépendante de l'échelle étudiée et est fortement liée aux facteurs limitant la croissance de la population. Les facteurs limitant davantage la population seront considérés à large échelle spatiale par les individus de cette espèce, alors que les autres facteurs seront pris en considération à de plus fines échelles. Ainsi, étudier le comportement de sélection des ressources sans considérer le contexte peut mener à des conclusions erronées.

Perturbations anthropiques

La population humaine a une énorme influence sur le comportement animal (Beale et Monaghan, 2004; Constantine *et al.*, 2004; Stankowitch, 2008). La présence humaine est reconnue pour induire chez les animaux une réaction comportementale similaire à celle des prédateurs, en initiant la peur et la fuite (Frid et Dill, 2002). Cette peur vient interférer avec le risque naturel de prédation, ce qui peut se traduire par un effet encore plus important que les prédateurs seuls, au point de reconnaître l'humain comme une hyper-espèce clé de voûte (lib. « hyperkeystone species », *sensu* Worm et Paine, 2016). Cette appellation provient de l'effet important de l'humain sur plusieurs espèces clés (c.-à-d., une espèce qui surpasse nettement l'importance attendue selon sa biomasse) que ce qui ajoute un niveau supérieur à ce qui est retrouvé dans la nature.

Activités humaines

La présence humaine peut modifier les budgets d'activité (Lord *et al.*, 1997; Duchesne *et al.*, 2000; Ciuti *et al.*, 2012; Lesmerises *et al.*, 2017), les comportements sociaux (Manor et Saltz, 2003, Rutledge *et al.*, 2010; Ansmann *et al.*, 2012) et de reproduction (Giese, 1996; Ellenberg *et al.*, 2007; Slabbekoorn et Ripmeester, 2008) chez plusieurs espèces. Les changements de comportement induits par des perturbations anthropiques, souvent considérés a priori négatifs, peuvent parfois avantager certaines espèces ou individus à l'intérieur d'une population. Ceux-ci vont généralement augmenter leur tolérance envers les humains au point de ne plus déclencher aussi rapidement leurs comportements anti-prédateurs (Papouchis *et al.*, 2001) et leurs réponses physiologiques (Walker *et al.*, 2006) et pouvoir les côtoyer tout en se comportant relativement normalement. Cette augmentation de la tolérance va permettre à des proies de diminuer leur niveau de vigilance au profit, entre autres, de comportement d'alimentation en présence d'humain en se servant de leur présence comme protection contre les prédateurs afin de maximiser leur gain énergétique (Shannon *et al.*, 2014). Les humains vont également rendre disponible, volontairement ou non, une quantité non négligeable de nourriture variée, ce qui peut se traduire par des changements dans les comportements de quête alimentaire chez certaines espèces (Belant *et al.*, 1998; Morey *et al.*, 2007; Yirga *et al.*, 2012).

Modifications du paysage

Les modifications du paysage engendrées par les activités humaines, telles que la voirie, l'urbanisation et les industries forestières, minières et pétrolières ont contribué à la fragmentation et à la perte d'habitats favorables à de nombres espèces (Debinski et Holt, 2000; Brooks *et al.*, 2002; Schmiegelow et Monkkonen, 2002; Ryall et Fahrig, 2006; Polfus *et al.* 2011). En altérant ainsi la qualité de l'habitat, les perturbations anthropiques peuvent avoir des impacts importants sur la distribution des espèces dans le paysage (Trzcinski *et al.*, 1999; Vors *et al.*, 2007) et potentiellement déséquilibrer les relations prédateurs – proies (Schneider, 2001; Courbin *et al.*, 2009) et le compromis alimentation – risque de prédation (Shannon *et al.*, 2014). Par exemple, les grands carnivores sont généralement moins prompts à tolérer la présence humaine. Ils vont plutôt ajuster leurs déplacements aux patrons spatiotemporels des principales activités humaines, évitant les structures anthropiques en présence d'humains (Theuerkauf *et al.*, 2003; Hebblewhite et Merrill, 2008, Valeix *et al.*, 2012). Dans de tels cas, les proies peuvent diminuer leur risque de prédation en exploitant ces espaces libres de prédateur (c.-à-d., des refuges) créés par l'activité humaine et ainsi augmenter leur valeur adaptative (Berger, 2007; Shannon *et al.*, 2014; Steyaert *et al.*, 2016). À l'inverse, les structures linéaires peuvent bouleverser la relation prédateur – proie à l’avantage du prédateur (Morris et Gilroy, 2008; McKenzie *et al.*, 2012). Ces structures facilitent leurs déplacements à travers leur territoire (Barding et Nelson, 2008; Dickie *et al.*, 2017) et peuvent également augmenter leur succès de chasse par un taux de rencontre plus élevé avec la proie (McKenzie *et al.*, 2012). Finalement, la présence et l’abondance de nourriture d’origine anthropique peut influencer, non seulement le comportement de quête alimentaire tel que discuté plus haut, mais également la distribution des espèces, autant chez les herbivores (Vercautaren et Hygnstrom, 1998), les omnivores (Prange *et al.*, 2004) que chez les carnivores (Yirga *et al.*, 2012; Newsome *et al.*, 2015).

Dans le cas d’espèces sensibles au dérangement, l’altération de l’habitat et le stress associé à la présence humaine peuvent mener à une contraction marquée de leur aire de répartition et ultimement de leur abondance (Brooks *et al.*, 2002; Krauss *et al.*, 2010). La plupart des pays se sont dotés d’un réseau d’aires protégées qui ne sont malheureusement pas toujours suffisantes à assurer le maintien à long terme des populations à risque (St-Laurent *et al.*, 2009). En effet, même à l’intérieur de ces aires protégées, plusieurs espèces doivent faire face à une variété et une abondance de perturbations anthropique non négligeables (p. ex. : les routes, les hôtels, les chalets et les sentiers de randonnée) (Brown *et al.*, 2012; Richard et Côté, 2015; Lesmerises *et al.*, 2017, 2018a). L’accumulation de perturbations dans le paysage peut compromettre la persistance de ces espèces plus sensibles au dérangement (Johnson *et al.*, 2015; Rudolph *et al.*, 2017). La quantité et l’importance des perturbations anthropiques viennent donc moduler l’intensité de la réponse chez les espèces fauniques.

Variabilités intra et interindividuelle

Même si les décisions individuelles font partie intégrante de la réponse populationnelle, les écologistes ont, depuis quelques années, reconnus l’importance de s’attarder à la variabilité comportementale à différent stimuli (Sih *et al.*, 2004; Lopez *et al.*, 2005;

Gillingham et Parker, 2008; Hebblewhite et Merrill, 2008). Le sexe, le statut reproducteur et l’âge sont souvent identifiés parmi les facteurs intrinsèques influençant le plus les différences entre les individus d’une même population, ci-après nommée variabilité interindividuelle (Ferrari *et al.*, 1998; Leblond *et al.*, 2010; Ciuti *et al.*, 2012; Lesmerises et St-Laurent, 2017), mais la génétique (Oldroy et Thompson, 2006; Dochterman *et al.*, 2015), les soins maternels (Taylor *et al.*, 2012) et la condition physique des individus (Ciuti *et al.*, 2012) sont autant d’autres facteurs expliquant cette variabilité. Selon l’hypothèse de la variation de la niche (lib. « niche variation hypothesis »), la magnitude de la variabilité interindividuelle est corrélée à la largeur de la niche comportementale de la population (Bolnick *et al.*, 2007) (Figure 1.2). Il est d’ailleurs reconnu qu’à l’intérieur même d’une population d’une espèce dite « généraliste », les individus ont généralement tendance à afficher un comportement dit « spécialiste », réduisant ainsi le chevauchement des niches comportementales (Bolnick *et al.*, 2007). La plage de la variabilité de comportements possibles étant plus large, les individus vont adopter un comportement susceptible de faire diminuer l’intensité de la compétition intraspécifique tout en maintenant leur valeur adaptative (Maret et Collins, 1997; Swanson *et al.*, 2003) (Figure 1.2).

La présence de variabilité interindividuelle chez la plupart des populations étudiées démontre qu’il existe plus d’une stratégie favorable à la survie et permettant un succès reproducteur suffisant pour assurer la pérennité de cette variabilité au sein d’une même population (Dall *et al.*, 2004; Fortin *et al.*, 2008; Smith et Blumstein, 2008). Ces différents comportements affichés par les différents individus peuvent être efficaces dans les mêmes conditions (Svanback *et al.*, 2008) ou encore varier temporellement en efficacité, selon les conditions environnementales, tant que ces conditions aient une certaine cyclicité permettant aux différents comportements de se maintenir (Dingemanse *et al.*, 2004; Fortin *et al.*, 2008). La persistance d’une large plage de variabilité comportementale, et donc de nombreux comportements différents, s’explique écologiquement par une forte pression de la compétition intraspécifique

(Clutton-Brock et Albon, 1982; Svanbäck et Bolnick, 2007). Les individus marginaux, soit ceux situés aux extrémités de cette plage, font face à moins de compétition, mais utilisent une stratégie différente de celle utilisée par la majorité de la population qui peut, elle, s'avérer suboptimale, que ce soit dans l'acquisition de nourriture ou dans les tactiques anti-prédatrices. En résumé, dans cette dynamique, les deux forces évolutives en question sont la sélection naturelle pour les stratégies comportementales les mieux adaptées au milieu et la compétition intraspécifique qui limite le nombre d'individus pouvant afficher ce type de comportement (Svanbäck et Bolnick, 2007). Une relaxation à long terme d'une force ou l'autre devrait donc permettre un réajustement de cette plage de variabilité, soit en supprimant les comportements marginaux, soit en les favorisant. Ce pan de l'écologie comportementale reste toutefois à être mieux compris.

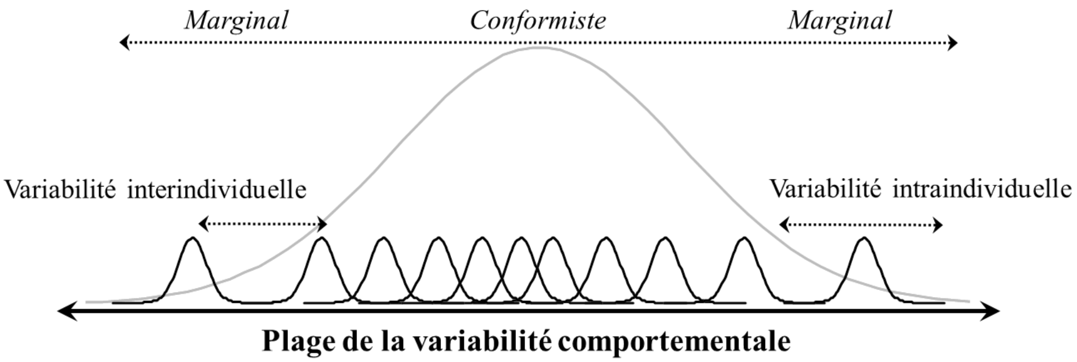

Figure 1.2. Schématisation de la variabilité comportementale au sein d'une population. Les courbes noires représentent la distribution des comportements des différents individus composant la population, tandis que la courbe grise représente la distribution des comportements observés dans l'ensemble de la population. Les individus à chaque extrémité de la plage de variabilité étant considéré marginaux par rapport à la majorité des individus composant la population.

La largeur des niches comportementales individuelles représente conceptuellement la variabilité intraindividuelle, aussi appelée variabilité individuelle (Figure 1.2). Ce type de variabilité peut s'avérer très important dans un contexte de changements environnementaux, tant spatialement que temporellement (Dingemanse *et al.*, 2010). Cette capacité, pouvant être variable d'un individu à l'autre, à ajuster sa morphologie, son état physiologique et son comportement en fonction des différentes conditions environnementales auxquelles il fait face se nomme la plasticité phénotypique (West-Eberhart, 1989). Dans le cas d'ajustements strictement comportementaux, les écologistes utilisent davantage le terme plasticité comportementale (Komers, 1997; Dingemanse et Wolf, 2013). Un individu qui est davantage plastique va pouvoir ajuster son comportement en fonction des differents stimuli, augmentant par le fait même sa variabilité individuelle. L'ajustement de son comportement a généralement des coûts et les individus peuvent afficher une constance, ou répétabilité, dans un type de comportement donné, mais également entre les différents comportements (Dall *et al.*, 2004; Sih *et al.*, 2004; Bell *et al.*, 2009). Ce phénomène est particulièrement étudié dans le domaine de la personnalité animale, où les traits de personnalité et leurs comportements associés peuvent être corrélés entre eux (« behavioural syndrome » *sensu* Sih *et al.*, 2004). La variabilité intrainviduelle a toutefois été moins étudiée dans le domaine de l'écologie spatiale, en étant plus souvent « contrôlée » que mise de l'avant (p. ex. : Gillies *et al.*, 2006; Leblond *et al.*, 2016). Néanmoins, la fidélité à certains sites particuliers dans le domaine vital d'un individu est une sorte de répétabilité comportementale qui a été étudié chez plusieurs taxons (cervidés : Schaefer *et al.*, 2000, Lafontaine *et al.*, 2017; chauve-souris : Russo *et al.*, 2005, Hillen *et al.*, 2009; oiseaux : Warnock et Takekawa, 1996, Lindberg *et al.*, 1998).

Interactions sociales

La dynamique des groupes sociaux chez les animaux est un phénomène bien étudié (p. ex., Fortin *et al.*, 2009; Sueur *et al.*, 2011; Merkle *et al.*, 2015). En écologie, un groupe est généralement défini comme une association d'individus dans le temps et l'espace appartenant à une même population (Krause et Ruxton, 2002). La fusion de quelques individus en un groupe social rend la prise de décision plus complexe puisque les membres doivent atteindre un certain niveau de consensus dans leurs patrons de mouvements afin de garder le groupe intact (Couzin *et al.*, 2005; Leonard *et al.*, 2012). Il arrive que les conflits d'intérêts entre les membres du groupe soient assez importants pour résulter en la fission du groupe, c'est-à-dire le départ d'un ou plusieurs individus (Sueur *et al.*, 2011). Dans un tel cas, la fission résulte en une perte des avantages d'être en groupe, tels que la diminution du risque de prédation (Roberts, 1996), l'augmentation de l'efficacité dans la recherche alimentaire (Creel et Creel, 1995) et dans la recherche de partenaires (Krause et Ruxton, 2002). À l'inverse, vivre en groupe accroit, entre autres, la transmission de maladie et de parasites (Côté et Poulinb, 1995, mais voir Mooring et Hart, 1992), la compétition pour les ressources (Molvar et Bowyer, 1994; Lian *et al.*, 2007) et les conflits d'intérêt dans la prise de décision collective (Couzin *et al.*, 2005; Conradt, 2011, Sueur *et al.*, 2011). Ces coûts incluent la dépense d'énergie lié aux comportements agonistiques (Krause et Ruxton, 2002; Fortin *et al.*, 2004) ou encore les aggressions qui mènent à la morbidité, voire directement à la mortalité (Beauchamp, 2014; Ward et Webster, 2016).

Il a été suggéré que l'hétérogénéité du paysage pouvait influencer la dynamique de fission-fusion; les bénéfices d'être associé à des individus possédant des informations au sujet des ressources (p. ex. : nourriture, site de repos, refuge et partenaire) peuvent être surpassés par les conflits d'intérêt lorsque la variabilité spatiotemporelle du paysage atteint un certain seuil (Sueur *et al.*, 2011). Dans ces milieux fortement hétérogènes, les groupes sociaux importants vont se subdiviser en sous-groupes d'après les différents besoins en ressources (Conradt et Roper, 2000). À des niveaux intermédiaires d'hétérogénéité, les groupes vont démontrer une forte dynamique de fission-fusion liée aux coûts parfois trop élevés associés au fait de demeurer avec un groupe en particulier (Conradt, 1998; Sueur *et al.*, 2011). D'autres caractéristiques du paysage peuvent également influencer la dynamique de fission-fusion et la taille des groupes (Pays *et al.*, 2007; Fortin *et al.*, 2009). En effet, les proies vont généralement former de plus gros groupes cohésifs en milieux ouverts afin de maximiser l’effet de dilution, étant donné les fortes probabilités de détection par les prédateurs dans de tels milieux (Jarman, 1974; Pays *et al.*, 2007; Fortin *et al.*, 2009).

Dans des milieux hétérogènes, le type, la quantité et la qualité des ressources varient constamment dans le temps et l’espace et les individus doivent connaitre suffisamment leur environnement pour bien ajuster leurs mouvements. La présence de congénères peut faciliter cette prise de décision, puisque chaque individu possède un bagage différent de connaissances, dicté par leurs déplacements antérieurs (Reebs, 2000; Conradt et Roper, 2003). Ces différences sont d’autant plus marquées pour les populations affichant une forte dynamique de fission-fusion, puisque leurs expériences passées devraient différer davantage. Chez les bisons (*Bison bison*), une espèce montrant une forte dynamique de fission-fusion, les individus vont se fier aux connaissances des autres pour repérer les parcelles de bonne qualité lorsque leurs connaissances personnelles sont insuffisantes (Merkle *et al.* 2015). Conceptuellement, cette propension à utiliser l’information publique devrait également varier avec l’hétérogénéité du paysage; un milieu homogène ne changeant pas, les individus n’ont pas à mettre à jour continuellement leurs connaissances de leur domaine vital alors qu’en milieu hétérogène, le type, la quantité et la qualité des ressources varient dans l’espace et dans le temps, nécessitant une mémoire spatiale et des informations à jour dans le choix des parcelles.

Notions d’échelles

Comme la perception des différentes ressources dans le paysage et les besoins sont spécifiques à l’espèce étudiée, nous devons adapter nos analyses en conséquence (Hall *et al.*, 1997). Ceci mène donc à une question fondamentale en écologie spatiale que plusieurs auteurs ont déjà posée (Wiens, 1989; Levin, 1992; Fauchald et Tveraa, 2006; DeCesare *et al.*, 2012) : de quelle façon devons-nous identifier l’échelle la plus appropriée pour étudier le processus en question? Wiens (1989) a suggéré qu'un phénomène écologique particulier est constant tout le long d'un domaine, mais changeant entre les domaines (Figure 1.3). Cette transition pouvant ne pas être représentatif du phénomène en question, choisir arbitrairement une échelle spatiotemporelle peut conduire à des conclusions incomplètes, voire erronées (Wiens, 1989, Wheatley et Johnson, 2009). De plus, l'inclusion de plusieurs échelles d'analyses, particulièrement dans le cas de la sélection des ressources, a montré une réponse plus globale du phénomène étudié (Mayor *et al.*, 2009; DeCesare *et al.*, 2012).

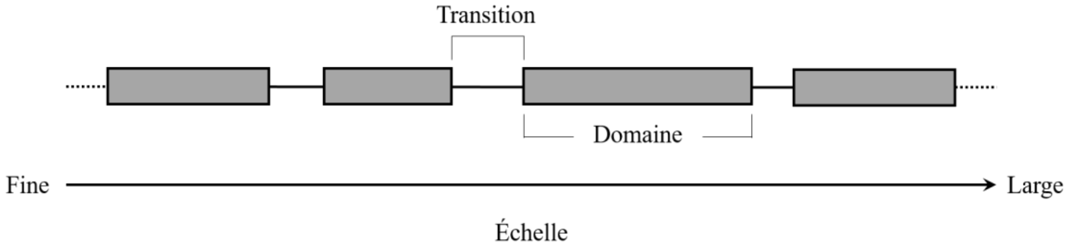

Figure 1.3. Le domaine représente une portion du spectre de l'échelle à l'intérieur duquel les mécanismes d'un phénomène écologique sont constants. Les domaines adjacents sont séparés par des zones de transition relativement chaotiques dans les relations processus-patrons (adapté de Wiens, 1989).

Des liens sont également possibles entre les échelles spatiotemporelle et biologique, surtout dans le domaine de l'écologie des perturbations (*sensu* Johnson et St-Laurent, 2011). Selon ce modèle, une perturbation de courte durée et de faible ampleur n'engendrera pas les mêmes conséquences sur les individus qu'une perturbation majeure présente à long terme. Ainsi, les animaux vont moduler leurs réactions face à une perturbation en fonction de son intensité, allant d'un stress physiologique et d'un changement comportemental momentané (Lord *et al.*, 1997; Duchesne *et al.*, 2000; Ciuti *et al.*, 2012) à des répercussions sur la survie des individus (Ruhlen *et al.*, 2003; Schwartz *et al.*, 2010), voire à la persistance de la population (Kerr et Currie, 1995; Johnson *et al.*, 2015; Rudolph *et al.*, 2017), lorsque les réponses comportementales perdurent temporellement et qu'elles impliquent une baisse de la survie individuelle et/ou de la reproduction des individus.

L'étude de plusieurs facettes de l'écologie d'une espèce permet donc de quantifier l'importance d'une perturbation donnée et d'en obtenir une vision intégratrice. De nombreuses études ont démontré un évitement des perturbations anthropiques chez les populations animales, sans toutefois pouvoir relier ces changements comportementaux à la survie des individus (p. ex. : Polfus *et al.*, 2011; Wasser *et al.*, 2011; Ciuti *et al.*, 2012; Rogala *et al.*, 2012; Lesmerises *et al.*, 2013). La réponse comportementale, bien qu'intéressante d'un point de vue de gestion ou de compréhension des relations prédateur-proie, n'est pas suffisante pour savoir si les individus réussissent à se soustraire aux effets physiologiques néfastes associés à la perturbation. Étudier la survie individuelle en fonction de la présence de perturbations permet d'avoir une image plus complète des impacts anthropiques sur les populations. Pourtant, les études montrant des impacts sur la survie individuelle sont plus rares (p. ex. : Ruhlen *et al.*, 2003; Leblond *et al.*, 2016), même s'il est ainsi plus facile de mettre en évidence les mécanismes sous-jacents au déclin des différentes populations. Des études ont démontré qu'une proportion trop importante de zones perturbées peut limiter l'efficacité de la réponse comportementale et compromettre la persistance d'une population dans ce milieu (Winfree *et al.*, 2009; Michalski et Peres, 2007; Johnson *et al.*, 2015; Rudolph *et al.*, 2017). L'absence de milieu naturel, ou l'effet néfaste des secteurs perturbés bordant les secteurs encore vierges, ne permettent pas à la population de maintenir un taux de croissance positif.

La notion d'échelle biologique pourrait également être vue sous un autre angle; un individu pourrait être considéré comme une unité qui compose les sous-populations, qui elles-mêmes composent les métapopulations et ainsi de suite (DeCesare *et al.*, 2012). Mysterud et Ims (1998) ont été parmi les premiers à considérer les différences entre les individus de différentes unités (p. ex. : famille, groupe social, harde, meute et sous-population) dans les modèles analytiques. Le comportement des individus pouvant changer selon leur appartenance à un groupe et selon les caractéristiques de ce groupe (Fortin *et al.*, 2009; Lesmerises & St-Laurent 2017), il devient donc important de considérer cette notion de variabilité entre les niveaux de cette échelle biologique.

Modèle biologique: caribou de la Gaspésie

Le caribou des bois est reconnu pour être sensible aux changements environnementaux, ce qui en fait un excellent modèle biologique pour s'intéresser aux réponses comportementales face à l'hétérogénéité du paysage et aux perturbations anthropiques (Apps et McLellan, 2006; Courbin *et al.*, 2009; Leblond *et al.*, 2013; Dussault *et al.*, 2012). En tant que proie, le caribou interagit avec plusieurs prédateurs dans son aire de répartition et démontre conséquemment des patrons d'utilisation de l'espace assez variés, et ce à plusieurs échelles spatiotemporelles (Bergerud *et al.*, 1984; Terry *et al.*, 2000; Mosnier *et al.*, 2003; Courbin *et al.*, 2009). Sa stratégie antiprédatrice visant à se distancer des autres pour mettre bas (Bergerud et Page, 1987), ainsi que sa propension à se rassembler en petits groupes pour l'élevage des jeunes ou pour la reproduction, induisent des variations dans la dynamique de fission-fusion (Barrette et Vandal, 1986; Holand *et al.*, 2004). Cette distribution et les différences comportementales couplées à une génétique et une morphologie variable ont entraîné une sous-classification de cette espèce en trois écotypes (montagnard, forestier, et toundrique; Banfield, 1961). Même si la notion d'écotype est parfois débattue (Yannic *et al.*, 2016), les caribous montagnards (c.-à-d., vivant en haute altitude et réalisant des courtes migrations altitudinales) constituent un modèle biologique particulièrement intéressant pour étudier la réponse comportementale face aux changements paysagers puisqu'ils vivent souvent dans des milieux très hétérogènes créés distribués le long d'un gradient altitudinal (Ouellet *et al.*, 1996; Apps *et al.*, 2001; Mosnier *et al.*, 2003). En effet, cette configuration montagnarde crée des îlots de toundra alpine ceinturés par une matrice de forêt subalpine et par une bande de forêt montagnarde, cette dernière fragmentée par l'industrie forestière et l'urbanisation (Johnson *et al.*, 2015; Boudreau, 2017). Les caribous montagnards utilisent généralement ce gradient altitudinal pour échapper à la prédation, particulièrement durant la période de mise bas (Bergerud *et al.*, 1984; Mosnier *et al.*, 2003). La prédation est d'ailleurs reconnue comme étant le principal facteur limitant de plusieurs populations de caribou à travers le Canada (Seip, 1992; Rettie et Messier, 2000; Wittmer *et al.*, 2005; Festa-Bianchet *et al.*, 2011).

La population de caribou Gaspésie-Atlantique (nommée ci-après caribou de la Gaspésie) est un vestige de l'aire de répartition qu'occupait jadis la population de caribou au sud du fleuve St-Laurent, qui s'étendait de la Nouvelle-Angleterre à la Nouvelle-Écosse ainsi que toute la portion sud du Québec (Bergerud et Mercer, 1989). Appartenant à l'écotype montagnard (COSEPAC, 2011), cette harde est génétiquement distincte des populations de caribou forestier habitant la forêt boréale au nord du Saguenay-Lac-Saint-Jean (Courtois *et al.*, 2003, Yannic *et al.*, 2014, 2016). Cette population était abondante en Gaspésie au début du 20e siècle, mais a rapidement décliner à 500-1000 en 1953 (Moisan, 1956), pour aujourd'hui n'atteindre que moins de 100 individus (Morin, 2017). À cause de ce déclin rapide, la harde a été identifiée comme en voie de disparition en 2000 (COSEPAC, 2002). Le caribou de la Gaspésie est maintenant étroitement associé au parc de la Gaspésie et est divisée en trois sous-groupes associés aux trois massifs principaux, nommément (d'ouest en est) le Logan, le Albert et les McGerrigles (Ouellet *et al.*, 1996; Mosnier *et al.*, 2003). Contrairement aux autres populations de caribous au Québec, peu de travaux de recherche ont été effectués directement sur la population de la Gaspésie (mais voir Dumont, 1993; Crête et Desrosiers, 1995; Ouellet *et al.*, 1996; Mosnier *et al.*, 2003), particulièrement au cours des deux dernières décennies.

Malgré la disparition du loup en Gaspésie à la fin du 19e siècle et la création du parc de conservation de la Gaspésie en 1937, cette population souffre toujours d'une forte prédation exercée sur les faons par le coyote (*Canis latrans*) et l'ours noir (Crête et

Desrosiers, 1995). Cette pression de prédation est le fruit de la compétition apparente (Holt, 1977) entre le caribou et principalement l'orignal (*Alces americanus*), mais également dans une moindre mesure avec le cerf de Virginie (*Odocoileus virginianus*). En effet, la présence de réserves fauniques au pourtour du parc combinée à un régime de coupes forestières soutenues dans les dernières décennies (Boudreau 2017) ont fait augmenter les populations d'orignaux et de cerfs dans la région (Dorais et Lavergne, 2010; Lamoureux *et al.*, 2012). Les prédateurs ont également augmenté en abondance (Lesmerises, 2012 Frenette, 2017), supportés par une densité de proies plus élevée, un habitat plus favorable en termes de ressources alimentaires végétales et de structures linéaires facilitant la prédation (Frenette, 2017). Le caribou étant une espèce moins productive (Whitten *et al.*, 1992; Pinard *et al.*, 2012) et plus vulnérable à la prédation que les autres cervidés avec lesquels il cohabite (Seip, 1992), la plus forte prédation auquel il fait face, par le biais de la compétition apparente, a eu un fort impact sur le taux de croissance de la population. L'augmentation du nombre de coyotes et d'ours noirs à l'échelle de la Gaspésie est d'ailleurs corrélée à la baisse du recrutement, malgré la présence de deux périodes de contrôle des prédateurs au cours des dernières décennies (Frenette, 2017; Lesmerises et St-Laurent, 2018).

La présence de coupes forestières a aussi plusieurs effets directs sur le caribou, par une baisse de la quantité de lichens disponibles pendant plusieurs décennies (Stone *et al.*, 2008; Boudreault *et al.*, 2013) et une diminution d'habitats de bonne qualité (Nadeau-Fortin *et al.*, 2016), les caribous étant reconnus pour éviter les coupes et les chemins forestiers (Courbin *et al.*, 2009`; Polfus *et al.*, 2011; Leblond *et al.*, 2013) et pour sélectionner les forêts matures (Hins *et al.*, 2009). À l'échelle nationale, la persistance même d'une population de caribou est généralement compromise au-delà d'environ 35 – 45 % d'habitats perturbés (Environnement Canada, 2011; Rudolph *et al.*, 2017), alors qu'en Gaspésie le pourcentage d'habitats perturbés dépasse 60 % depuis plusieurs années (Nadeau-Fortin, 2015, Lesmerises et St-Laurent, 2018).

À ces changements paysagers à grande échelle s'ajoute également une pression supplémentaire associée à la pratique de plus en plus populaire d'activités de récréotourisme (p. ex. : randonnée, vélo de montagne et ski hors-piste). En effet, les gestionnaires du parc national de la Gaspésie reçoivent de plus en plus de demandes pour développer ou autoriser diverses activités, tant en hiver qu'en été (P. Lévesque, directeur, comm. pers.). La plupart des études réalisées sur le caribou/renne (*R.t. tarandus*) montrant un évitement des perturbations humaines, s'attardaient davantage à des perturbations majeures (mines : Dyer *et al.*, 2001; Boulanger *et al.*, 2012, routes : Vistnes et Nellemann, 2001; Leblond *et al.*, 2013, foresterie : Courbin *et al.*, 2011; Polfus *et al.*, 2011, hôtel : Nellemann *et al.*, 2000; Reimers et Colman, 2009). Certaines études sur l'impact des randonneurs sur le budget d'activité des caribous ont déjà été réalisées et montraient une hausse du temps passé en vigilance et un évitement des habitats préférentiels en présence d'humains, laissant croire à une modification comportementale non négligeable (Dumont, 1993; Duchesne *et al.*, 2000; Reimers *et al.*, 2003; Reimers et Colman, 2009).

Ainsi, étudier l'influence de l'hétérogénéité du paysage et des perturbations anthropiques sur le comportement, la distribution et la survie est hautement pertinent. Bien que les questions écologiques et comportementales soient les composantes centrales de ma thèse, l'acquisition de ces connaissances est grandement utile afin d'améliorer les mesures de conservation actuellement préconisées et diminuer les probabilités d'extinction de la population de caribou de la Gaspésie.

Objectifs généraux

L'objectif principal de ma thèse était de mieux comprendre l'influence de l'hétérogénéité du paysage sur différentes facettes de l'écologie d'une proie, en l'occurrence le caribou de la Gaspésie. Plus précisément, j'ai lié l'hétérogénéité spatiotemporelle (naturelle ou anthropique) du paysage au budget d'activité (chapitre

1), aux déplacements (chapitre 2), à l'utilisation de l'espace (chapitre 2), à la dynamique des groupes sociaux (chapitre 3) et à la survie individuelle (chapitre 4) des caribous de la Gaspésie. Le deuxième objectif visait à comprendre et documenter les impacts directs et indirects de l'homme sur la conservation du caribou; cet objectif transversal s'insère indirectement dans tous mes chapitres et découle directement du statut précaire de la population.

Chapitre 1.

L'homme est parfois reconnu comme une espèce hyper clé de voûte (Worm et Paine, 2016) considérant son importance dans la transformation des écosystèmes mondiaux et le fait qu'il est généralement perçu comme un risque de prédation et ce, autant par les grands prédateurs que par les proies (Frid et Dill, 2002). La faune réagit donc en évitant la présence et l'activité humaine à différentes échelles selon les espèces étudiées. Ainsi, en modifiant inégalement la répartition des espèces, nous influençons indirectement les relations trophiques. Par exemple, certaines proies ont développé une stratégie anti-prédatrice consistant à se réfugier dans les zones fortement utilisées par l'homme et où les prédateurs s'aventurent très rarement (Berger, 2007, Steyaert *et al.*, 2017). Notre objectif était donc de déterminer comment le caribou, une espèce relativement sensible au dérangement humain, mais également à la prédation, réagissait face au risque induit par la présence de randonneurs sur les sentiers du parc de la Gaspésie. Nous avons émis l'hypothèse que la perception du risque allait différer en fonction du statut reproducteur de la femelle à cause de la vulnérabilité à la prédation du faon. Nous avons donc analysé deux comportements importants du budget d'activité estival des caribous pouvant expliquer leur gestion du risque que représentent les humains et les prédateurs, soit la vigilance et l'alimentation. Nous avons prédit que les femelles avec faon allaient davantage utiliser les humains comme écran à la prédation (hypothèse du refuge à la prédation) en abaissant leur temps en vigilance et augmentant leur temps passé en alimentation, alors que les femelles sans faon allaient davantage percevoir les humains comme un stress (hypothèse du risque de prédation) et démontrant un patron opposé dans leur budget d’activité.

Chapitre 2.

Pour plusieurs espèces fauniques, bon nombre d’études ont mis en évidence un changement direct de comportement d’individus suivis suite à un dérangement par l’homme (Beale et Monaghan, 2004; Constantine *et al.*, 2004; Stankowitch, 2008), entre autres dans leurs déplacements et leurs patrons d’utilisation de l’espace (Trzcinski *et al.*, 1999; Rogala *et al.*, 2012; Leblond *et al.*, 2013). Depuis quelques années, les demandes visant à élargir l’offre des activités récréotouristiques dans l’est de l’Amérique du Nord, en particulier le ski hors-piste, sont en forte croissance. Dans un contexte de conservation, il est primordial de connaitre l’impact d’un tel dérangement sur les espèces à statut précaire qui fréquentent les sites envisagés pour le développement d’activités récréotouristiques. Dans ce deuxième chapitre, mon objectif était de relier la réponse du caribou, en termes de déplacements et d’utilisation de l’espace, à l’intensité d’une perturbation, dans ce cas le ski hors-piste. Nous émettions l’hypothèse que les caribous vont adapter leurs réponses comportementales en fonction de l’intensité du stimulus. Nous avons donc prédit une augmentation de l’évitement du domaine skiable et des vitesses de déplacement en direction opposée à la source de dérangement, avec une augmentation de l’intensité de la perturbation, ici représentée par le nombre de skieurs.

Chapitre 3.

La connaissance du territoire est vraiment importante lors de la prise de décision dans la direction et la destination des mouvements dans un paysage hétérogène où les ressources varient spatialement et temporellement (Schmidt *et al.*, 2010; Fagan *et al.*, 2013). Les espèces sociales ont la possibilité de pouvoir combiner leurs propres connaissances du territoire à celles d’autres individus, particulièrement lorsque leur connaissance du paysage où elles se trouvent est limitée (Reebs, 2000; Conradt et Roper, 2003; Couzin *et al.*, 2005; Merkle *et al.*, 2015). La configuration des parcelles de qualité dans l’habitat d’une espèce peut également influencer la dynamique des groupes sociaux. En effet, afin de maintenir la cohésion entre les membres d’un groupe, les individus doivent faire des compromis entre leurs besoins individuels et les besoins collectifs (Couzin *et al.*, 2005). Plus le paysage est hétérogène, plus les sources de conflits entre les membres d’un groupe sont nombreuses, augmentant la fission-fusion des groupes, afin de subvenir aux besoins individuels (Sueur *et al.*, 2011). Au-delà d’un certain seuil d’hétérogénéité, les désavantages associés au fait de demeurer groupés deviennent suffisant pour dissoudre la plupart des groupes. Nous voulions donc tester l’importance relative du bagage d’informations détenues par un groupe d’individus et de la présence potentielle de conflits d’intérêt en fonction du degré d’hétérogénéité du paysage. Notre hypothèse principale était que les individus seraient plus enclins à quitter le groupe dans les endroits qu’ils ont fréquemment visités et qu’ils connaissent bien, alors qu’ils seraient moins enclins à se séparer d’un groupe dans les milieux qui leurs sont moins familiers. Cette hypothèse assume qu’un individu qui quitte son groupe se fie davantage à ses propres connaissances du territoire pour orienter ses mouvements et ses choix subséquents de parcelles d’habitat.

Chapitre 4.

La variabilité interindividuelle dans le comportement animal a été intensément étudiée (Sih *et al.*, 2004; Lopez *et al.*, 2005; Gillingham et Parker, 2008; Hebblewhite et Merrill, 2008). Pour une proie, le choix des parcelles qu’elle utilise va déterminer le risque de prédation auquel elle fera face (Hernandez et Laundré, 2005; Laundré *et al.*, 2010; Rösner *et al.*, 2014). Toutefois, d’autres facteurs importants peuvent également venir influencer la prise de décision d’un individu quant à ses patrons d’utilisation de l’espace (p. ex. la compétition intra- et interspécifique, la quantité et la qualité de nourriture). L’ensemble de ces choix affectent sa capacité à survivre dans le milieu. Au sein d’une même population, on peut retrouver différentes stratégies dans leur utilisation de l’espace (Leblond *et al.*, 2016), et ses stratégies ne résultent pas nécessairement en des taux de survie équivalents. Selon la théorie de la sélection naturelle, la meilleure stratégie devrait être la plus couramment utilisée. Toutefois, dans un contexte de changement globaux et de perturbation de l’habitat, les stratégies dites marginales pourraient être plus efficace à assurer la survie des individus. Nous avons donc voulu tester l’effet de la marginalité du comportement d’utilisation de l’espace des caribous de la Gaspésie sur la survie individuelle. L’hypothèse principale étant qu’en absence de forte compétition intraspécifique, principale force favorisant la persistance de comportements marginaux, les comportements les plus conformistes, donc affichés par la majorité de la population, devraient assurer une plus forte probabilité de survie. Toutefois, le paysage à l’étude a fortement changé au cours des dernières années, en plus d’accueillir un nouveau prédateur opportuniste (le coyote), ce qui pourrait favoriser l’apparition de comportements plus marginaux (hypothèse alternative).

CHAPITRE I

REFUGE OU RISQUE DE PRÉDATION? PERCEPTIONS DIFFÉRENTES DES RANDONNEURS PAR LES FEMELLES CARIBOU BASÉES SUR LEUR STATUT REPRODUCTEUR

REFUGE OR PREDATION RISK? ALTERNATE WAYS TO PERCEIVE HIKER DISTURBANCE BASED ON MATERNAL STATE OF FEMALE CARIBOU

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1.1 Résumé

La présence humaine dans l'environnement est souvent une source de stress perçu autant par les ongulés que par les prédateurs eux-mêmes comme une augmentation du risque de prédation. Ainsi, lorsque les prédateurs sont davantage affectés par les activités humaines, la présence de randonneurs peut créer un espace relativement libre de prédateurs qui peut servir de refuge aux proies. Nous avons mesuré la réponse comportementale de femelles caribous en présence de randonneurs durant l'été dans le parc national de la Gaspésie. Nous avons utilisé ces données afin de déterminer si les caribous répondaient négativement à la présence humaine (c.-à-d., l'hypothèse du risque de prédation) ou si l'activité humaine résultait plutôt en une diminution du risque perçu (c.-à-d., l'hypothèse du refuge contre la prédation). Les femelles caribou suitées ont passé près de la moitié moins de temps à s'alimenter par rapport aux femelles seules. Elles ont aussi diminué leur niveau d'alerte près des sentiers en présence de randonneurs alors que les femelles seules ont plutôt augmenté, voire presque doublé, leur vigilance avec un nombre élevé de randonneurs sur les sentiers. Toutefois, les deux catégories de femelles se sont éloignées des sentiers lorsque les sentiers étaient ouverts aux randonneurs et encore davantage lorsque des randonneurs étaient présents.

1.2 Abstract

Human presence in natural environments is often a source of stress that is perceived by large ungulates as an increased risk of predation. Alternatively, disturbance induced by hikers creates a relatively predator-free space that may serve as a refuge. We measured the behavioural responses of female caribou to disturbance associated with the presence of hikers during summer in the Gaspésie National Park. We used those data to determine if caribou responded negatively to human activity (i.e., the *predation risk hypothesis*) or if human activity resulted in a decrease in the magnitude of perceived risk (i.e., the *refuge hypothesis*). Female caribou with a calf spent nearly half of their time feeding, regardless of the presence of a trail or the number of hikers. They also decreased their vigilance near trails when the number of hikers increased. Conversely, lone females fed less frequently and almost doubled the time invested in vigilance under the same circumstances. However, both groups of females moved away from trails during the day, especially in presence of hikers. We demonstrated that risk avoidance was specific to the maternal state of the individual. Lactating females accommodated the presence of hikers to increase time spent foraging and nutritional intake, providing support for the refuge hypothesis. Alternatively, lone females with lower energetic requirements and no maternal investment in a vulnerable calf appeared

less tolerant to risk, consistent with the predation risk hypothesis. Hikers influenced the vigilance – feeding trade-off in caribou, underlining the importance of appropriate management of linear structures and human activities, especially across the critical habitat of endangered species. Even if some individuals seemed to benefit from human presence, this behavioural adaptation was not sufficient to reduce annual calf mortality associated with predation.

1.3 Introduction

Human disturbance can be an important driver of animal behaviour (Ciuti *et al.*, 2012; McLeod *et al.,* 2013). Humans and their activities may be perceived as predation risk (i.e., *predation risk* hypothesis) (Frid and Dill, 2002) leading to a landscape of fear and the altered distribution or behaviour of wildlife species (Hernandez and Laundré, 2005; Laundré *et al.*, 2010; Rösner *et al.,* 2014) with the potential for fitness costs (Dussault *et al.,* 2012; Strasser and Heath, 2013). In some instances, habitat alteration and the stress associated with human presence have led to dramatic decreases in population distribution and abundance (Brooks *et al.,* 2002; Krauss *et al.,* 2010). Even within protected areas, where often there are conservation measures designed to maintain natural and undisturbed habitats for wildlife, most animals must cope with a variety of anthropogenic disturbances (e.g., roads, resorts, cabins, and hiking trails) (Brown *et al.,* 2012; Richard and Côté, 2015).

Across many landscapes, humans often play the role of the apex predator and shape prey and predator distributions (Basille *et al.,* 2009; Valeix *et al.,* 2012). Unlike predators, however, humans may be more spatiotemporally predictable, especially in parks, where hunting is often prohibited and visitation most often occurs during daytime and on roads and hiking trails. In such an environment, habituation to human-caused threat is a possibility (Bremset-Hansen and Aanes, 2015). Alternatively, outside parks where hunting is allowed, humans may act as the dominant natural predator and an important driver of ungulate behaviour (Ciuti *et al.*, 2012). In many cases, large carnivores are much less adaptable to human presence. They may adjust their movement to the spatiotemporal pattern of human activity, avoiding anthropogenic features when humans are present (Theuerkauf *et al.*, 2003; Hebblewhite and Merrill 2008; Ordiz *et al.*, 2011; Valeix *et al.*, 2012). This may occur even in parks where human activities are highly regulated (Whittington *et al.*, 2005). In such cases, prey can modulate predation risk by exploiting the enemy-free spaces created when the presence of humans and associated infrastructure displaces predators (i.e., the *refuge hypothesis*) (Berger, 2007; Shannon *et al.*, 2014; Steyaert *et al.*, 2016). Predation risk varies in space and time, thus, antipredator strategies should be adaptable to variation in risk. In protected areas, prey should adjust their space use to match the diurnal pattern of human activity (Gaynor *et al.*, 2018), such as hikers on marked trails during the day.

Even when selecting habitat with lower predation risk, prey are rarely completely safe (Elgar, 1989; Lima and Dill, 1990). Thus, an animal's activity budget is often a trade-off between security and food intake (Fortin *et al.*, 2004), which is mainly influenced by the risk associated with the occupied habitat (Boving and Post, 1997; Gavin and Komers, 2006; Liley and Creel, 2008) and by the quality of food resources (Fortin and Fortin, 2009). Also, intrinsic factors such as age, body condition and reproductive status could interact to influence the trade-off between vigilance and foraging (Bachman, 1993; Wolff and Van Horn, 2003; Winnie and Creel, 2007).

For mammals, lactation has an extremely high energetic cost; females often adjust their behaviour, including exposure to risk, to meet those nutritional demands (White and Berger, 2001; Wolff and Van Horn, 2003; Hamel and Côté, 2008). Where nutritional intake is limited, lactating females might be more tolerant of human activities that reduce predation risk and increase foraging time (Lima and Bednekoff, 1999). According to the two main hypotheses that relate behaviour to the trade-off between nutrition and risk, lactating females should tolerate low-risk disturbances and use human presence as a refuge against predation to reduce vigilance and increase the time spent foraging (i.e., the *refuge hypothesis*). In contrast, females without a calf should be less prone to take risk, adjusting their vigilance to human presence (i.e., the *predation risk hypothesis*).

In this study, we assessed the behavioural response of Atlantic-Gaspésie caribou (*Rangifer tarandus caribou* Gmelin; hereafter referred to as Gaspésie caribou) to the presence of hikers in the Gaspésie National Park. We used those data to determine if variation in human activity triggered a vigilance response associated with risk, the predation risk hypothesis, or a decrease in the magnitude of perceived risk, the refuge hypothesis. We tested those hypotheses relative to the maternal state of individual caribou: females with and without a dependent calf.

1.4 Material and Methods

1.4.1 Study area

The study area covered the range of the Gaspésie caribou population, corresponding approximately to the limit of the Gaspésie National Park (48°50’N; 66°00’W) and surrounding habitat protected by provincial law (Fig. 2.1). The caribou range encompasses the McGerrigle Mountains, in its eastern part, which are dominated by Mount Jacques-Cartier (1268 m), and the Chic-Chocs Mountains in the western part, which include Mount Albert (1154 m) and Mount Logan (1128 m). The elevational gradient determines three ecological zones characterized by differences in vegetation type. The highest elevation zone (> 1050 m) is alpine tundra and is characterised by a mat of lichens, mosses and graminoids along bare rocks and ericaceous shrubs. The subalpine forest (900–1050 m) is essentially a transition zone where tree height decreases with elevation, forming a krummholz belt before transitioning to alpine tundra. Finally, the montane area (100–900 m) is represented by closed forest composed of balsam fir (*Abies balsamea* Mill.), white spruce (*Picea glauca* Moench), black spruce (*P. mariana* Mill.), and birch (*Betula* sp.). Most caribou are found at elevations > 700 m and are subdivided into three subpopulations, namely Albert (*n* = ~15 individuals), Jacques-Cartier (*n* = ~70 individuals), and Logan (*n* = ~15 individuals) (Ouellet, Ferron et Sirois 1996; Mosnier *et al.*, 2003).

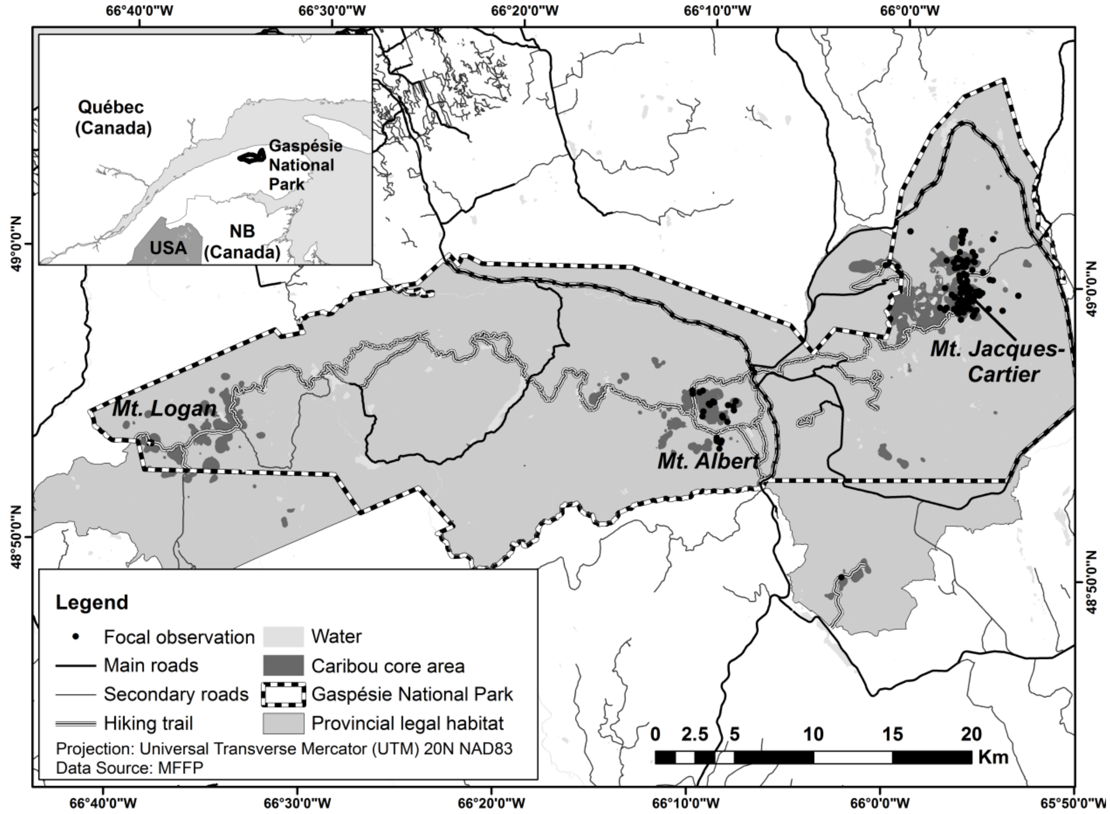

Figure 2.1. Estimated location of each focal caribou during behavioral observations in Gaspésie National Park, during the summers of 2013–2014.

Gaspésie National Park is mostly visited during summer months, especially during July and August (L. Sirois and G. Fortin, unpublished data). Some of the most popular trails pass through critical habitat for caribou (Fig. 2.1). To decrease human access during periods when caribou are vulnerable to disturbance, access to these trails is closed from

October to mid-June. Buses, available from 10:00 – 16:00, are also required to access the ‘Jacques-Cartier’ trail. Moose (*Alces americanus americanus* Gray), black bears (*Ursus americanus* Pallas), coyotes (*Canis latrans* Say) and a few white-tailed deer (*Odocoileus virginianus* Zimm.) are also found within Gaspésie National Park. Wolves (*Canis lupus* L.) were extirpated from the south shore of the St. Lawrence River in the mid-1800s.

1.4.2 Caribou locations

To test the two competing hypotheses, we used GPS collars to collect spatial locations for Gaspésie caribou. In total, 43 adult caribou (17 M; 26 F), proportionally distributed amongst the three subpopulations (i.e., McGerrigle: *n* = 28; Albert: *n* = 6; Logan: *n* = 9), were captured, fitted with GPS-Argos telemetry collars and followed for 2.5 years. Collars were programmed to acquire locations every two (model TGW-4680-3, Telonics Inc. Mesa, Arizona) or three hours (model TGW-4680, Telonics Inc. Mesa, Arizona) and to transfer relocations from the previous week via an Argos link every four days. To limit the potential negative impacts of helicopter activity, and as recommended by the Animal Welfare Committee [Université du Québec à Rimouski (UQAR) certificate #CPA-52-13-112; ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) certificate #CPA FAUNE 13-08], captures were divided into two sessions of 22 and 21 animals each, conducted in early winter 2013 and 2014, respectively. For these analyses, we only considered location data collected for females and categorized individuals according to the presence of a calf (Table 2.1). We calculated the mean proportion of locations for each 100 m distance class away from a trail for closed and open hours. Caribou were found mostly in open alpine areas resulting in a low probability of habitat-related bias in GPS fix success. Also, we did not assess any behavioural or location parameters that could be influence by fix rate. Thus, for these analyses we used all the location data, regardless of fix interval.

1.4.3 Activity budget

We conducted 30-min focal observations of collared females exclusively for the Mount Albert and McGerrigle subpopulations during the summer tourism period (May 25th – August 20th). We restricted our observations to these two subpopulations because it was difficult to access and observe caribou on Mount Logan. To find caribou, we walked along the two main hiking trails (Jacques-Cartier and Albert) watching for females. We also used VHF and GPS–collar locations to locate caribou when they were not visible from the trails. We stayed as far as possible from caribou during the focal observations. When more than one collared female were located, we randomly chose one animal and described its behaviour according to 11 activity budget categories: lying (lying on ground, regardless of the head position), feeding (standing head down, including the time biting, cropping and masticating), walking, food searching (walking head down), running, trot, vigilance (standing and being alert, ears pointing in a specific location), standing (no alert position, often ruminating), grooming, social interaction, and other (represented less than 0.5% of the observation period). We noted the individual's identification (confirmed with VHF frequency and ear tag), time of day, date, group size (calves included), and the approximate distance and the azimuth of the caribou from our observation point. We stopped the focal observation if the caribou detected our presence.

1.4.4 Estimating disturbance by hikers

We deployed 23 trail cameras (Spypoint BF-6, GG Telecom, Victoriaville) on hiking trails and monitored human presence. Most of the trails had two cameras, one at the beginning and one almost on the summit. Each trail was divided into 200-m segments and we calculated the number of hikers per hour on each segment, assuming a constant speed of hikers between each camera. We related each caribou observation to the nearest trail segment and inferred the number of hikers that occurred at that time (rounded to the nearest hour) and place.

In addition to the number of hikers, we related caribou behaviour to hourly temperature using meteorological stations installed on three summits in the National Gaspésie Park (L. Sirois and G. Fortin, unpublished data). For each focal observation, we used the air temperature at the nearest meteorological station.

1.4.5 Geomatics analyses

Using a GIS database including trails and habitat categories (derived from a 1 : 20 000 ecoforestry map, MFFP), we calculated the distance of the observed caribou to the nearest trail and the percentage of open habitat in a 200 m-radius from the caribou location. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies, bare rock). Open habitat (2-ha resolution) included alpine tundra and wetlands. In the model below, we developed a distance variable that was tested as a decay function with different constants [$\exp(-\alpha/\text{distance})$, where $\alpha = 50$, 100, 250, or 500] (Carpenter *et al.*, 2010) or as a binary variable ($0 <$ threshold >1) with different thresholds (100, 250, and 500 m). The decay or binary method providing the lowest AIC_c (Burnham and Anderson 2004) was retained and used in our subsequent statistical analyses. For time spent feeding, the most parsimonious covariate for distance to a trail was a decay distance ($\alpha = 250$) and a binary variable (0 if $\leq$ 500 m; 1 otherwise) for female without and with a calf, respectively. For time spent vigilant, the most parsimonious distance covariates were binary with thresholds of 100 m and 500 m for females without and with a calf, respectively. Although more complex, a unique decay function or distance threshold allowed us to better represent the behavioural response of each demographic group.

1.4.6 Statistical analyses

We focused the statistical analyses exclusively on the vigilance and foraging behaviours of monitored caribou. A literature review suggested that these were the most important behaviours for testing the trade-off between security and food acquisition as well as the propensity of females to use human presence as a refuge against predation (Wolff and Van Horn, 2003; Winnie and Creel, 2007). We used a negative binomial distribution to model the number of seconds spent in vigilance during the focal observation and a fractional logit regression (*sensu* Papke and Wooldridge, 1996) to assess the proportion of the activity budget spent feeding. For both analyses, we used the individual ID as a random factor to take into account interindividual variability in behaviour (Gillies *et al.*, 2006). We used AIC_c to evaluate the importance of hikers relative to the foraging and vigilance behaviour of observed caribou. We fit two statistical models for each behaviour, testing if the addition of the anthropogenic variables (i.e., distance to a trail, number of hikers, and the interaction between them) to our basic model (i.e., group size, temperature in °C as a continuous variable, hour as a continuous variable, and proportion of open habitat) resulted in a more parsimonious model. We normalized all independent variables, except time of day, for better model convergence. We used cross-validation to assess the predictive ability of the most parsimonious model. We fitted the model with 80 % of the data and then performed a Spearman correlation (r_s) between predicted and observed values for the independent data (20 %).

We used Kolmogorov-Smirnov tests to compare space use by caribou along trails. We compared the frequency distribution of caribou locations within four distance classes from the nearest trail (1000, 2000, 3000, > 4000 m) relative to opening hours (trails closed or opened) and the presence of hikers (hikers vs. no hikers). This resulted in 12 comparisons. Habitat characteristics do not change along trails according to the time of day or the presence of hikers, thus, such covariates were unnecessary for this analysis. All statistical analyses were conducted using R (The R Core Team version 2.15).

1.5 Results

We completed 351 focal observations (summer 2013: 9F for 143 focal observations; summer 2014: 15F for 208 focal observations). In 2014, calves suffered a high mortality rate, resulting in a relatively small sample size for that class (i.e., females with a dependent calf) (Table 2.1). On average, focal observations occurred for 1728 seconds (SD = 232). We retained only observations longer than 1000 seconds (n = 221). This threshold avoided bias that might be associated with dominant behaviours that occur exclusively during short observation periods. We retained 60 and 161 focal observations of females with and without a calf, respectively. On average, females with and without a calf were within 100 m of a trail 7 % and 11 % of their time, respectively, with a greater use of these areas during closed hours (17:00 to 10:00) (Fig. 2.2). Caribou were further from the trail during hours when the trails were open, especially when hikers were present (all combinations of opening hours/number of hikers for caribou distribution near trails were significantly different $p < 0.05$, except for the distance category < 1000m for females with a calf; there was no statistically significant difference between closed and open hours when hikers were not present, $p = 0.07$) (Fig. 2.2).

Table 2.1. Presence of calf during focal observation of female caribou in Gaspésie National Park, during the summer tourism period (May 25th – August 20th). We indicated the first date of each maternal state, by year, for all females followed during this study. C25 to C45 were captured in February 2014. C04 and C06 died during winter 2013-2014.

ID – Subpop.	**2013**			**2014**		
	With calf	**Without calf**	**No. of GPS locations**	**With calf**	**Without calf**	**No. of GPS locations**
C02 – M.	May 25th	July 4th	372	May 25th	July 15th	176
C04 – M.	-	May 25th	877	-	-	
C05 – M.	May 25th	-	300	-	May 25th	121
C06 – M.	May 25th	June 26th	867	-	-	
C11 – A.	May 25th	May 26th[1]	306	-	May 25th	296
C13 – M.	May 25th	-	204	-	May 25th	308
C16 – A.	May 25th	-	408	-	May 25th	324
C20 – M.	-	May 25th	659	-	May 25th	135
C23 – M.	May 25th	-	978	May 25th[2]	-	225
C25 – M.	-	-		May 25th	July 3rd	251
C27 – M.					May 25th	245
C30 – M.	-	-		-	May 25th	174
C37 – M.				-	May 25th	350
C40 – M.	-	-		-	May 25th	359
C41 – M.	-	-		May 25th	June 4th	333
C42 – M.	-	-		-	May 25th	275
C43 – M.	-	-		-	May 25th	365
C45 – M.	-	-		-	May 25th	392

[1] We did not do any focal observation before C11 lost its calf. C11 was considered as without a calf in 2013.

[2] C23 and its calf died by predation in 16 June 2014.

Females had different tolerance to human disturbance as the model selection for distance covariate showed. Caribou with a calf spent a greater amount of time feeding and displaying vigilance behaviours (Table 2.2), mainly at the expense of time spent lying, although the variability in time spent feeding and being vigilant was very high. The negative binomial and fractional logit models explained a relatively small part of the variation in observed behaviour (Spearman *r* from cross-validation varied between 0.022 and 0.258) (Table 2.3). Models that included anthropogenic variables were the most parsimonious in explaining the total time of vigilance for all females and the proportion of time spent feeding for females without a calf (Table 2.2). Interestingly, vigilance of females with and without a calf differed in their response to human presence (Table 2.3; Fig. 2.3). The interaction between 'Distance to a trail' and 'Hikers' revealed that females without a calf increased their vigilance rate near trails relative to the number of hikers, while females accompanied by their calf decreased their time being vigilant under the same circumstances. *A posteriori* analyses showed that this decrease in vigilance was generally associated with a greater proportion of time foraging (~ 20 %).

As the group size of caribou increased, the model for females with a calf predicted a decrease in time spent vigilant. This response was not apparent when considering caribou without a calf (Table 2.3). Increasing temperature influenced the feeding time of females without a calf negatively while the proportion of open habitat had a positive effect. For both groups of caribou, distance to the nearest trail had a greater influence on feeding time rather than the number of hikers or the interaction between the two terms.

Table 2.2. The influence of the presence of a calf and the distance to a trail on the four main behaviours [mean % (SD)] of female caribou in the Gaspésie National Park, during the summers of 2013-2014.

	Female with calf				Female without calf			
Behaviour	< 100 m	100-500 m	> 500 m	Total	< 100 m	100-500 m	> 500 m	Total
	(n = 9)	(n = 11)	(n = 40)	(n = 60)	(n = 45)	(n = 65)	(n = 51)	(n = 161)
Feeding	42.2 (42.1)	40.8 (42.0)	50.9 (31.2)	47.7 (34.7)	23.7 (33.2)	28.0 (32.0)	35.6 (32.8)	29.2 (32.7)
Lying	37.5 (47.2)	30.1 (40.5)	20.7 (32.4)	25.0 (36.2)	55.6 (45.2)	50.4 (42.7)	40.2 (41.2)	48.6 (43.1)
Vigilance	2.3 (3.65)	8.8 (20.2)	13.6 (15.7)	11.0 (15.8)	6.3 (11.2)	6.5 (12.1)	7.1 (8.7)	6.6 (10.8)
Walking	9.5 (21.4)	3.7 (4.1)	4.2 (7.3)	4.9 (10.1)	4.8 (8.0)	4.8 (8.1)	5.4 (9.8)	5.0 (8.6)

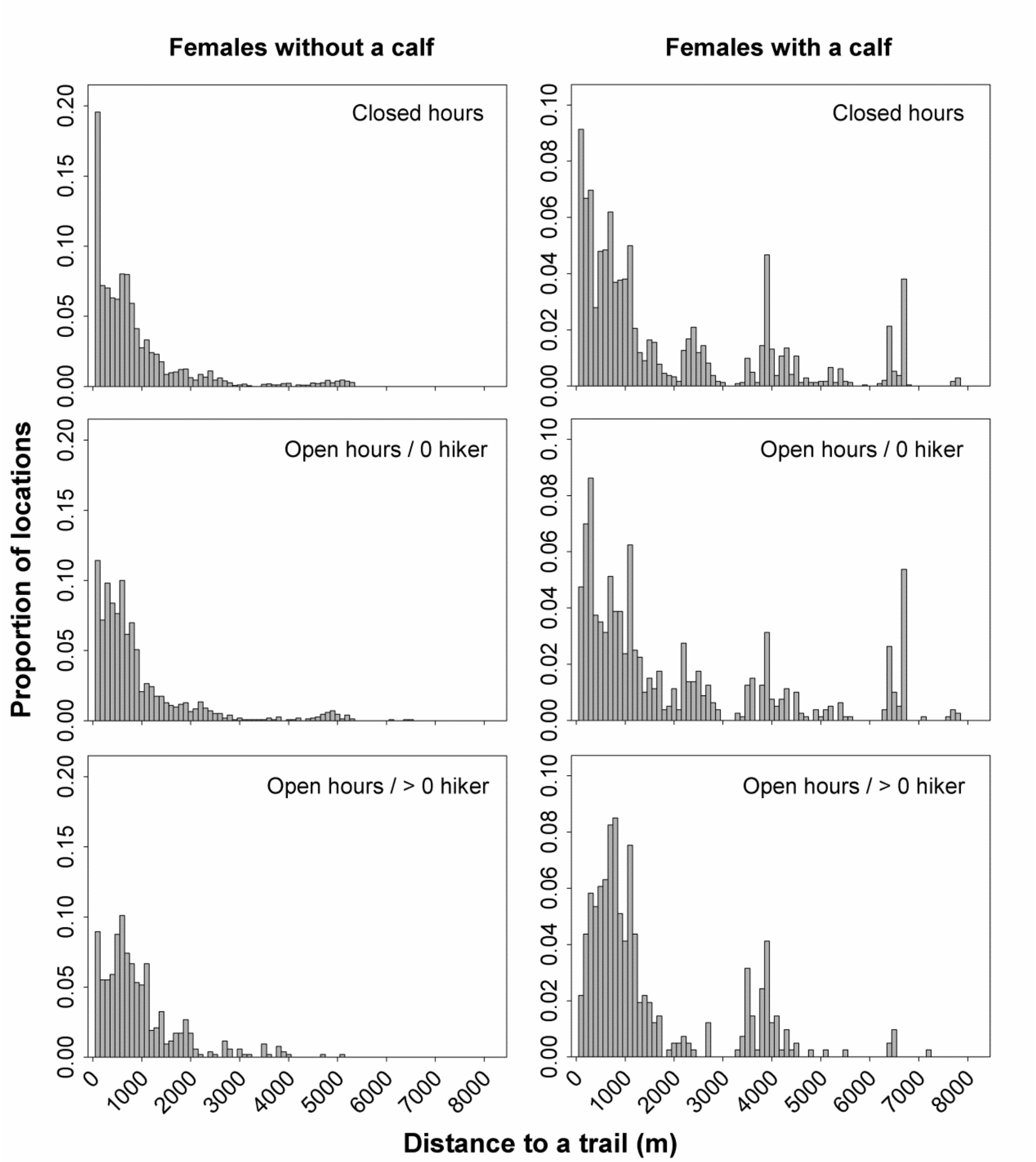

Figure 2.2. Proportion of locations of female caribou by 100-m distance classes from the nearest trail in the Gaspésie National Park, during the summers of 2013–2014.

Table 2.3. Candidate models explaining feeding and vigilance behaviours of female caribou during the summers of 2013 and 2014, Gaspésie National Park. The ranking was based on the AIC_c for each category of females (i.e. with or without a calf). Model number of parameter (K), log-likelihood (LL) and difference in AIC_c values (ΔAIC_c) are shown. Model performance was assessed using independent cross-validation (r_s).

Model		Female with calf			Female without calf		
	K[1]	ΔAIC_c	LL	r_s	ΔAIC_c	LL	r_s
Feeding							
Temp. + Grp Size + Open hab. + Hour	6	0.000	-40.2	0.022	4.978	-93.0	0.085
Model 1 + Trail + Hikers + Trail*Hikers	10	5.052	-38.7	0.103	0.000	-87.2	0.193
Vigilance							
Temp. + Grp Size + Open hab. + Hour	5	5.804	-348.5	0.108	0.093	-759.7	0.099
Model 1 + Trail + Hikers + Trail*Hikers	9	0.000	-341.4	0.241	0.000	-756.3	0.258

[1] Random factor for individual (ID) was included in all models

Table 2.4. Coefficient and 95% confidence intervals (CI) of the most parsimonious model explaining feeding and vigilance behaviour of female caribou in the Gaspésie National Park, during the summers of 2013–2014. Coefficients for which the 95% CI did not overlap zero are shown in bold.

	Feeding		Vigilance	
	Female with calf	Female without calf	Female with calf	Female without calf
Temperature	-0.224 [-0.775; 0.327]	**-0.632 [-6.367;-0.871]**	0.078 [-0.352; 0.507]	-0.063 [-0.464; 0.338]
Group size	-0.014 [-0.587; 0.559]	-0.026 [-0.531; 0.478]	**-0.768 [-1.317; -0.219]**	-0.258 [-0.662; 0.146]
Open habitat	-0.152 [-0.718; 0.414]	**0.579 [0.122; 1.036]**	-0.243 [-0.684; 0.198]	0.015 [-0.415; 0.445]
Hour	0.185 [-0.105; 0.475]	0.171 [-0.053; 0.394]	-0.075 [-0.302; 0.151]	0.091 [-0.156; 0.339]
Dist. to trail	-	**1.879 [0.437; 3.322]**		
Close /Far to trail (1/0)			**-1.784 [-2.607; -0.960]**	-0.070 [-0.888; 0.747]
Hikers	-	-0.045 [-0.875; 0.785]	0.210 [-0.393; 0.813]	-0.347 [-0.711; 0.016]
Trail*Hikers	-	-0.969 [-2.712; 0.780]	**-1.704 [-3.191; -0.217]**	**1.140 [0.162; 2.119]**

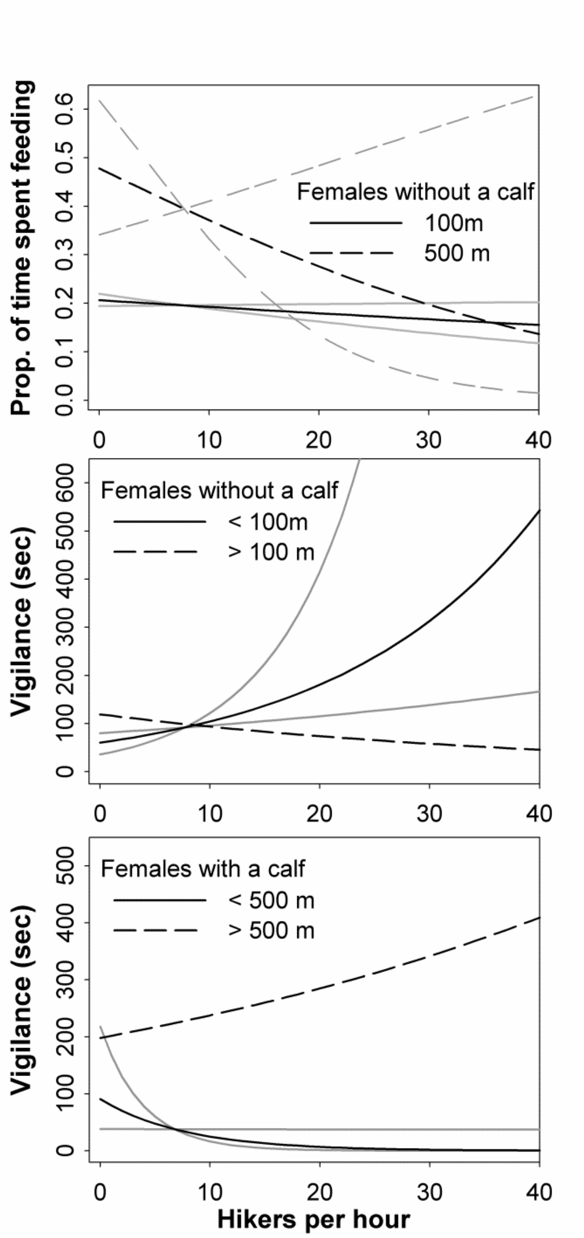

Figure 2.3. Representation of the most parsimonious models explaining caribou behavior (feeding and vigilance) in relation to their distance to a trail and the number of hikers in the Gaspésie National Park, during the summers of 2013–2014. Gray lines represent the 95% confidence interval

1.6 Discussion

Our results suggest that reproductive status and the perception of predation risk are two important factors that influence how ungulates react to low-risk disturbances, such as the presence of hikers. For woodland caribou in Gaspésie National Park, the presence of humans on hiking trails triggered a response for all females, but was expressed differently depending on the presence of a calf. Thus, the behavioural responses of caribou were too complex to be classified as one of the two concurrent hypotheses. Consistent with the refuge hypothesis, lactating females were less vigilant along trails that were frequented by hikers, but they still avoided trails during daytime, in support of the predation risk hypothesis. In contrast, females without a calf were less tolerant of human presence, being relatively more vigilant when a large number of hikers were common and moved away from trails during the daytime, as suggested by the predation hypothesis.

Even within a species, individuals do not evaluate risk similarly (Winnie and Creel, 2007). Differences in human avoidance amongst female caribou suggest that risk is context-specific. Assuming that females adapt their antipredator strategy to the vulnerability of their offspring, as suggested by Dussault et al. (2012) and Leclerc et al. (2014), we might assume that females with a calf experience a different landscape of fear than those without a calf (Leblond *et al.,* 2016). This difference is particularly noticeable in Gaspésie National Park, where the two apex predators, coyotes and black bears, are not known to be efficient predators of adult caribou (Crête and Desrosiers, 1995; Boisjoly *et al.*, 2010; Bastille-Rousseau *et al.,* 2015). Our results showed that some lactating females left areas near a trail when hikers were frequent, but those that stayed were less vigilant within the 500-m threshold distance from trails. This 500-m threshold is relatively consistent with other studies of ungulates that have reported a human-induced refuge from predators (Berger, 2007; Shannon *et al.,* 2014). Although coyotes and black bears were found to use trails and gravel roads more often than expected based on random locations in our study area (see Gaudry, 2013, a companion study conducted in the Gaspésie National Park), the automated camera traps distributed along the hiking trails showed that no coyote and only a few black bears used trails in the hour following the passage of a hiker (F. Lesmerises and M.-H. St-

Laurent, unpublished data). These data suggested that predators avoided humans; similar results were observed in other studies and regions (Ciucci *et al.*, 1997; Hebblewhite and Merrill, 2008). In total, this information supports the assertion of human-induced refuges. The hypothesis of refuge from predator is a plausible explanation for variation in time spent vigilant in relation to hikers. However, we cannot clearly test the mechanisms that might explain that response as we did not consider survival or predator activity inside/outside the refuge. To our knowledge, a similar response has not been reported for other populations of woodland caribou at the behavioural scales we assessed. Yet, many caribou populations suffer from high predation rates across landscapes with human activity (Festa-Bianchet *et al.,* 2011; Whittington *et al.,* 2011; Bradley and Neufeld, 2012), especially on calves (Gustine *et al.,* 2006; Leclerc *et al.*, 2014).

Findings from other populations of *Rangifer* also suggest that females with a calf incur a higher nutritional cost associated with gestation during the last trimester and milk production to support the dependent calf (Parker *et al.*, 2009). Facing higher energetic demands and seeking to maximise nutritional intake, lactating females were probably more prone to accommodate low-risk disturbances, such as small groups of interspersed hikers (Gustine *et al.,* 2006).

Trade-offs in predation risk relative to forage intake or quality has been observed for other species that have high nutritional requirements or are in poor condition (Lima et Dill 1990). From a behavioural perspective, this is often expressed as an altered activity budget where vigilance is decreased to the benefit of increased feeding rates (Winnie and Creel, 2007; but see Hamel and Côté, 2008). As widely observed in other taxa (coati [*Nasua narica*]: Burger and Gochfeld, 1992; birds: Lima, 1995; Przewalski's gazelle [*Procapra Przewalskii*]: Li *et al.*, 2012), females with dependent young decrease their vigilance rate with increasing group size, relying more on conspecifics to alert the group of danger. Such adjustment of antipredator tactics in accordance with foraging demands was also found in male elk (*Cervus canadensis*) in Montana (Winnie and Creel, 2007). In our study, it is unlikely that female caribou demonstrated increased foraging activity along trails because of higher forage quality or quantity. We did not specifically test for differences in nutritional quality near and distant to trails, but vegetation sampling did not reveal a systematic difference in vegetation community or greater quantity of forage adjacent to trails (F. Lesmerises and M.-H. St-Laurent, unpublished data).

The decrease in vigilance that we observed for lactating females may be a relatively new response by caribou in this population. In contrast, Dumont (1993) working in the same study area observed an increase in the time spent vigilant by females with and without a calf. This difference could potentially be explained by the fact that Dumont (1993) did not consider other covariates in his model and he did not integrate the effect of distance of individual animals to a trail. However, female caribou could also face a higher risk of predation recently as coyote populations are likely increasing in the Gaspésie region (St-Laurent *et al.,* 2009; MFFP unpublished data). Lactating females are now potentially more vulnerable to predation resulting in this use of human-induced refuge. Alternatively, caribou could have developed some level of habituation to hikers, such as has been observed for other human-caused disturbances (Stankowitch, 2008; Brown *et al.*, 2012; Johnson and Russell, 2014). Even if these tactics resulted in lower vigilance and higher foraging rates in relatively predator-free areas, these choices may carry unobserved physiological costs. Other studies have revealed different physiological stresses caused by human presence [e.g. increased cortisol level (Eggermann *et al.*, 2013), higher heart rate (Weisenberger *et al.*, 1996)] that we did not measure in this study.

During our focal observations, only one coyote was heard and one black bear viewed in the vicinity of caribou. Fresh indirect signs (i.e. tracks and scats) were, however, frequently observed in the morning, suggesting nocturnal movements of predators; this was corroborated by our camera traps along trails. Assuming that predators avoided humans, as suggested by the refuge hypothesis (Berger, 2007; Shannon *et al.*, 2014) and previous studies (Theuerkauf *et al.,* 2003; Hebblewhite and Merrill, 2008; Ordiz *et al.,* 2011; Valeix *et al.,* 2012), caribou should have been found near trails only during the daytime, which was contrary to our results. The location data from the GPS collars revealed that the greatest use of areas near hiking trails by caribou occurred during the night. The similarity in nocturnal distribution of caribou and predator probably increased the encounter rates near trails as reported by Whittington et al. (2011). Despite the diurnal refuge provided by trails, calf survival during the study was extremely low, being no better than survival observed during the study of Dumont (1993) (see Lalonde, 2014 for historical calf recruitment rates), when caribou did not show any use of the same trails.

1.7 Conclusion

Hikers influenced caribou behaviour, especially the vigilance–feeding trade-off. Females without a calf increased their time spent in vigilance near trails and humans, while females accompanied by a calf were more prone to accommodate such relatively low-risk disturbance. Facing higher predation risk and nutritional demands, some lactating females appeared to use the presence of hikers as a shield against predation. However, given the extremely low calf survival in this population, this adaptation did not appear to be sufficient to counterbalance the negative impact of predators that used linear structures at night. These findings highlighted the importance of the appropriate management of linear structures and human activities, especially across the critical habitat of endangered species.

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CHAPITRE II

RÉPONSES SPATIOTEMPORELLES DES CARIBOUS MONTAGNARDS À L'INTENSITÉ DU SKI HORS-PISTE.

SPATIOTEMPORAL RESPONSE OF MOUNTAIN CARIBOU TO THE INTENSITY OF BACKCOUNTRY SKIING.

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2.1 Résumé

Les activités récréotouristiques augmentent les risques de rencontres entre l'humain et la faune, lesquelles peuvent être perçues comme un risque de prédation. Ce patron d'évitement de l'humain est bien connu, bien que souvent relié à des perturbations anthropiques majeures. La réponse de la faune à des activités humaines moins intensives et/ou éphémères, telles que le ski hors-piste et la randonnée, est moins bien documentée. Pourtant, ces activités sont parfois réalisées dans des aires protégées, où les gestionnaires tentent de conserver des espèces à statut précaire. C’est le cas de la population montagnarde du caribou de la Gaspésie−Atlantique dans le parc national de la Gaspésie. Afin d’évaluer les impacts du ski hors-piste, nous avons utilisé les données télémétriques GPS provenant de 20 caribous fréquentant un secteur de ski partiellement inclus dans le parc national de la Gaspésie. Plus de 12% des localisations de caribou étaient à l’intérieur du secteur de ski lorsque ce dernier était inutilisé par les skieurs. L’utilisation de ce secteur par le caribou diminuait toutefois à 6% en présence de skieurs. Les coefficients de la fonction de sélection des ressources suggéraient que les caribous évitaient la zone de ski et que la réponse à la perturbation était modulée par le nombre de skieurs. Les caribous n’étaient pas significativement déplacés dans les premières six heures suite à l’exposition aux skieurs, mais se déplaçaient par la suite sur une période allant jusqu’à 48 heures après l’exposition, vers des habitats à de plus faibles altitudes où le risque de prédation par le coyote était potentiellement plus élevé. Nos résultats ont révélé une réponse comportementale relativement forte face à cette perturbation et une perte fonctionnelle d’habitat notable. Les gestionnaires de parcs de conservation devraient considérer même de petits nombres d’écotouristes compte de l’impact relativement important qu’ils peuvent avoir sur le comportement et la distribution d’espèce menacée.

2.2 Abstract

Nature-based activities promote human-fauna encounters, which may be perceived as a type of predation risk. This pattern of human avoidance is well-known, but is often related to major anthropogenic disturbances. The response of animals to less intensive or ephemeral human activities, such as backcountry skiing and hiking is not well studied. Yet, these activities occur in many protected areas, where managers are trying to conserve some of the most threatened species. This is the case for the Endangered Atlantic-Gaspésie mountain caribou in the Gaspésie National Park. To assess the impact of backcountry skiing, we used GPS telemetry to monitor 20 caribou frequenting a ski area partially included in the Park. More than 12% of caribou locations were within the ski area when skiers were absent. Use of that area by caribou decreased to 6 % when there were skiers. Coefficients from a resource selection function suggested that caribou avoided the ski area, and the disturbance response was modulated by the number of skiers. Caribou were not significantly displaced within the first 6 hours of exposure to skiers, but thereafter moved away from the ski area for ~48 hours to lower elevation habitats where predation from coyotes was potentially greater. Our results revealed a relatively strong disturbance response and corresponding functional loss of a possible noticeable portion of habitat as a result of backcountry skiing. Park managers should consider even small numbers of recreationists as they could have an important impact on animal distribution.

2.3 Introduction

Human activities are increasing in intensity across previously undisturbed landscapes. Even within protected areas, many endangered species must cope with human-caused disturbance and habitat change (Ashley and Robinson, 1996; Ramp *et al.*, 2006; Brown *et al.,* 2012). Nature-based activities require roads, trails and other infrastructure that can have a negative impact on the ecology of protected areas (Ashley and Robinson, 1996). This infrastructure promotes human-fauna encounters with variable consequences on animal behaviour, physiology and demography (Bateman and Fleming, 2017). In some cases, human-fauna encounters could be detrimental to wildlife (e.g. Thompson 2015; Lesmerises *et al.,* 2017) as human presence may be perceived as predation risk (Frid and Dill, 2002), resulting in a landscape of fear that structures the distribution or behaviour of many species (Hernandez and Laundré, 2005; Laundré *et al.,* 2010; Rösner *et al.,*, 2014). In some cases, however, there is a differential perception of risk potentially providing human-caused refugia for prey species (Hebblewhite *et al.,* 2005; Berger, 2007; Steyaert *et al.,* 2016). Moreover, nature-based activities often trigger the avoidance of the habitats and linear features that are most intensively used by people (Klein *et al.*, 1995; Seip *et al.*, 2007; Polfus *et al.*, 2011; Thompson, 2015). Following such a response, animals may be displaced to suboptimal habitat (Nellemann *et al.*, 2000) or they may occur at a higher density in optimal habitat (Fortin *et al.*, 2013; Lesmerises *et al.*, 2013; Thompson, 2015) with potential fitness costs (Dussault *et al.*, 2012; Strasser and Heath, 2013).

An increase in the popularity of nature-based activities, including backcountry skiing, has led to a greater number of people using natural areas (Cordell *et al.*, 2008). Wildlife must now share its habitat with skiers and hikers, even in protected areas. Numerous studies suggest that many species will avoid trails or ski areas when humans are present frequently or in high densities (caribou and reindeer *Rangifer tarandus*: Duchesne *et al.*, 2000; Nellemann *et al.*, 2000, elk *Cervus canadensis*: Ferguson and Keith, 1982; Rogala *et al.*, 2011, mountain goat *Oreamnos americanus*: Richard and Côté, 2015, and wolf *Canis lupus*: Rogala *et al.*, 2011). However, when humans occur infrequently, the response of wildlife is more variable ranging from selection of habitat near hiking trails (elk: Rogala *et al.*, 2011) to no impact of nordic skiers on space use (elk and moose *Alces americanus*: Ferguson and Keith 1982), to avoidance of hiking trails (wolf: Rogala *et al.*, 2011). Furthermore, the unpredictability of backcountry activities can potentially amplify the negative response of wildlife. As an example, Miller et al. (2001) reported that the flight distance and distance moved of three species of birds (*Pooecetes gramineus*, *Sturnella neglecta*, and *Turdus migratorius*) and mule deer (*Odocoileus hemionus*) was greater when disturbed by pedestrians that were off trail relative to those found on the trail.

Caribou and reindeer are declining worldwide (Vors and Boyce, 2009) and woodland caribou (*R. t. caribou*) are known to be highly sensitive to human disturbances (Duchesne *et al.*, 2000; Nellemann *et al.*, 2000; Seip *et al.*, 2007; Vors *et al.*, 2007; Lesmerises *et al.*, 2017). From a conservation perspective, the mountain ecotype of woodland caribou is of particular concern (Johnson *et al.*, 2015; Ray *et al.*, 2015;

Wittmer *et al.,* 2007), as many populations are now found in heavily disturbed landscapes (Boudreau, 2017; Rudolph *et al.,* 2017), and are declining rapidly (Vors and Boyce 2009; Johnson *et al.*, 2015). In eastern Canada, the designatable unit Atlantic-Gaspésie caribou represents the last remnant population of mountain caribou, a relict herd found on the south shore of the St-Lawrence River (COSEWIC, 2011; St-Laurent *et al.,* 2009). This herd, designated as Endangered, has declined by 63% over the past 30 years and was estimated at ~70 individuals in 2016 (COSEWIC, 2014; Morin, 2017). In addition to the legacy of forestry and mining, restrictive hunting regulations have promoted an increase in the abundance of moose across the Gaspésie Peninsula (Landry and Lavergne, 2007), followed by an increase in predator populations, namely black bears (*Ursus americanus*) and coyotes (*Canis latrans*) (Ministère des Forêts, de la Faune et des Parcs du Québec, hereafter MFFP, unpublished data). Apparent competition (Holt, 1977) with moose and deer has greatly reduced the survival and recruitment of caribou (Frenette, 2017). Backcountry skiers may interact with and displace mountain caribou as both caribou and skiers seek high-elevation, open alpine terrain (Mosnier *et al.,* 2003). A recent study demonstrated the impacts of summer recreation on the activity budget of female caribou in Gaspésie (Lesmerises *et al.*, 2017), suggesting the potential for similar impacts during the winter.

Parks and protected areas are under considerable pressure to increase recreation opportunities and visitorship even when such activities might conflict with conservation of biodiversity including threatened or endangered species (Arlettaz *et al.,* 2013; Coleman *et al.,* 2013; Richard and Côté 2015). The precariousness of most of mountain caribou populations combined with the pressure to increase human activities in their distribution suggests that we require a more complete understanding of the response of caribou to such disturbance. Thus, our main objective was to assess the influence of backcountry skiers (disturbance intensity) on the distribution and movement of mountain caribou during winter. We hypothesized that because human presence is often perceived as a stress, or even predation risk, by wildlife, the intensity of disturbance by skiers would influence the magnitude of displacement of caribou from the ski area.

2.4 Methods

2.4.1 Study area

The study area covers a portion of the range of the Gaspésie caribou population, corresponding to the northwest part of the McGerrigle Mountains (48°50’N; 66°00’W) (Fig. 3.1). In total, the caribou range encompasses the McGerrigle Mountains in the east, which are dominated by Mount Jacques-Cartier (1268 m), and the Chic-Chocs Mountains in the western part, which includes Mount Albert (1154 m) and Mount Logan (1128 m). The altitudinal gradient determines three ecological zones characterized by differences in vegetation type. The highest elevation zone (> 1050 m) is composed of alpine tundra, a mat of lichens, mosses and graminoids along with bare rocks and ericaceous shrubs. The subalpine forest (900–1050 m) is essentially a transition zone where tree height decreases with altitude, forming a krummholtz belt before transitioning to alpine tundra. Finally, the montane area (100–900 m) is represented by closed forest composed of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and birch (*Betula* sp.).

Most caribou are found at elevations > 700 m and are subdivided into three groups (Ouellet *et al.*, 1996; Mosnier *et al.*, 2003), namely Albert (n= ~20 ind.), McGerrigle (n=~27 ind.), and Logan (n=~23 ind.) (Morin, 2017). Moose, black, coyotes and a few white-tailed deer (*Odocoileus virginianus*) are also found within the Gaspésie National Park. Coyotes, and to a lesser extent bears, are responsible for the majority of predation events on caribou calves (Crête and Desrosiers, 1995). We also have some evidence suggesting that coyotes hunt adult caribou in our study area, as observed in

Newfoundland (Bastille-Rousseau *et al.*, 2015). Wolves were extirpated from the south shore of the St. Lawrence River in the mid-1800s.

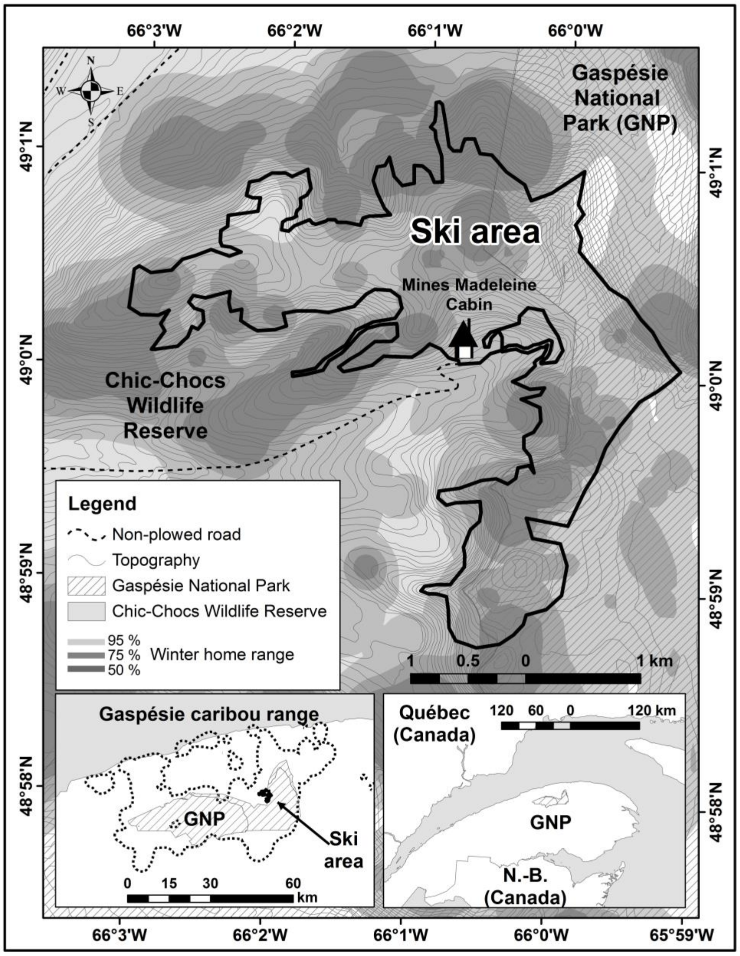

Figure 3.1. Study area and location of the ski area in the Chic-Choc Wildlife Reserve and the Gaspésie National Park, Québec, Canada. Individual home ranges were calculated, for each winter, using the biased random bridge method (Benhamou 2011).

2.4.2 Ski area and activity

In the Gaspésie National Park and its immediate surrounding (i.e. critical habitat legally protected), backcountry skiing is restricted to specific areas that are accessible between

December and late April. We conducted our study in one area that was ≥12 km from the nearest accessible road. We assumed that most of the skiers or hikers rented the only available cabin in the immediate area. Thus, we used the rental logbook to assess the number of skiers present in this sector, called ‘mines Madeleine’. That skier count was probably underestimated and served as an index of human disturbance.

The mines Madeleine ski area covers 687 ha (Fig. 3.1). We considered the area as ‘Active’ (i.e., with presence of skiers or hikers) for a 24h-period when the cabin was rented by one or more people. For example, if skiers rented the cabin for January 2nd, the sector was categorized as ‘Active’ between 12h00 January 2nd and 12h00 January 3rd. There were insufficient data to provide a more precise measure of the activity of skiers.

2.4.3 Habitat characteristics

We used ecoforest maps to assess five different habitat categories (‘mature conifer’, ‘immature conifer, ‘open conifer’, ‘alpine barren ground’, and ‘others’). The minimum polygon size was 4 ha for forested stands and 2 ha for non-forested areas (e.g., lakes, alpine barren, open conifer, etc.). We used a digital elevation model (25x25-m cell) to calculate slope in degrees. We calculated the distance of caribou to the ski area. We suspected a non-linear response, thus, we used a decay function [exp(-α/distance)] to transform the distance measure. We tested a range of α values (50, 100, 250, 500, 1000, 2000) (Carpenter *et al.,* 2010) and used Akaike’s Information Criterion (AIC_c) to select the α value that provided the most parsimonious model, after including factors for natural and anthropogenic disturbance (see *Statistical analyses* below).

2.4.4 Caribou locations

We used GPS locations collected from 43 adult caribou (17 M, 26 F; corresponding to ~ 52% of the population in 2013) proportionally distributed amongst the three groups (i.e., McGerrigle n = 28, Albert n = 6, Logan n = 9), to assess the impact of skiers on the distribution of monitored caribou. Caribou were captured using a net-gun fired from a helicopter, fitted with GPS-Argos telemetry collars and followed for 2.5 years; collars were programmed to acquire locations every 2 (model TGW-4680-3, Telonics Inc. Mesa, Arizona) or 3 hours (model TGW-4680, Telonics Inc. Mesa, Arizona). Only physical contention was used during our manipulations. To limit potential negative impacts of disturbances from helicopter activity and associated collaring, animal captures occurred during two sessions of 22 and 21 animals in mid February 2013 and in early March 2014, respectively [Université du Québec à Rimouski (UQAR) certificate # CPA-52-13-112; MFFP certificate # CPA FAUNE 13-08]. We removed the first 5 days of GPS locations following an animal capture in a 2-km radius surrounding the ski area in order to limit the influence of collaring activities and helicopter flights on the observed movements of caribou.

We used caribou locations collected during the skiing period 2013 to 2015 (i.e., between December 1st and April 30th) only. We used the minimum convex polygon (100% MCP; to increase the contrast between use and availability, Leclerc *et al.*, 2012) to delineate the seasonal home range of each animal and retained only individuals with home ranges that overlapped the ski area. The number of random points equaled the number of caribou locations within each individual's seasonal range. For each caribou and random location, we extracted the habitat category, elevation, calculated the minimum Euclidian distance to the ski area using ArcGIS 10.0 (Redlands, CA, 2010), and the number of skiers present (using the cabin rental logbook). We used a decay function (Carpenter *et al.*, 2010) to transform the Euclidian distance to the ski area as the response of caribou to disturbance is often nonlinear, decreasing with an increasing distance from the source of the disturbance (e.g., Johnson *et al.*, 2015).

2.4.5 Statistical analyses

2.4.5.1 Caribou space use

We first assessed the space use by caribou within the ski area and in zones around the ski area (i.e., 0-250, 250-500, 500-750, 750-1000, 1000-1500, 1500-2000, and >2000 metres) according to the categorical number of skiers (i.e., 0, 1-4, 5-8, and 9-12). To do so, we summed the number of caribou locations within each zone, and we divided the sum by the total number of locations acquired for that individual caribou for that number of skiers. We then averaged those percentages of use for each caribou and calculated the standard error. Secondly, we used resource selection functions (RSF; Johnson *et al.*, 2006) to relate the distribution of monitored caribou to the presence of skiers. The RSF was constructed using a mixed effects logistic regression where individual ID and year were considered random factors (Gillies *et al.*, 2006). We used AIC_c to identify the most parsimonious of three candidate models: 1) the first included only habitat and topography variables, 2) the second included also the distance to the ski area, and 3) the third included also the number of skiers and the interaction term between the number of skiers and the distance to the ski area, as we hypothesised that disturbance intensity would influence the displacement of caribou from the ski area (Table 3.1). There was a low level of multicolinearity in our dataset (VIF < 1.69). We used a *k*-fold cross-validation (Boyce *et al.*, 2002) to assess the predictive accuracy of the best model. We used the location data from 75% of the individuals to generate the RSF model and the remaining 25% for validation. We conducted 10 replicates of the *k*-fold process and then used a Spearman rank statistic to test for a significant correlation and reported the mean r_s value and its standard deviation.

Table 3.1. Ranking of candidate models used to assess the resource selection patterns of caribou interacting with skiers in Gaspésie (Canada) from 2013 to 2015 (December 1st to April 30th). The number of parameters (k), log-likelihood (LL) and difference in AIC_c values with the most parsimonious model (ΔAIC_c) are shown. Model performance was assessed using a *k*-fold cross-validation (mean Spearman $r_s \pm \text{SD}$).

Model	k	ΔAIC_c	LL	r_s
1) Habitat[1] + Elevation	6	436.29	-24,852.14	0.75 ± 0.25
2) Model 1 + Decay distance to ski area ($\alpha = 2000$)[2]	7	127.61	-24,696.80	0.77 ± 0.16
3) Model 2+ Number of skiers + Decay distance X Number of skiers	9	0.00	-24,630.99	0.81 ± 0.16

[1] Mature conifer stands were used as the reference category in all the RSF models

[2] Alpha value used in the decaying function to transform Euclidean distance (see Section 2.3).

2.4.5.2 Caribou movement

We used the successive GPS locations to interpolate the movement paths of monitored caribou. We removed all paths that had a time between two successive locations (Δt) longer than the fix rate needed to acquire locations. We only kept path segments starting in the ski area. We calculated the path length and the distance of the starting and ending points of those path segments to the boundary of the ski area. Then, we subtracted the value of the starting point from the ending point in order to assess if the individual was moving toward or away from the ski area. We also calculated the difference in elevation between the ending and starting point of each path. We related the elevational shift and the net displacement of caribou from the ski area to a range of path durations (2 or 3h, 6h, 12h, 18h, […] 120h). This allowed us to evaluate the duration of the potential impact of skiers on caribou movement. Path duration was a function of 6-h increments as collars were scheduled to record a location every 2nd or 3rd hour.

In order to evaluate the impact of skiers on the localised movements of caribou, we used mixed effects linear regression. We developed three models to test the hypothesis that the intensity of the response of caribou was correlated with the magnitude of recreation activity, as indexed by the number of skiers. We used 1) the net displacement from the ski area (m), 2) caribou path length (m), and 3) the difference in elevation (m) of paths following skier activity as dependent variables in those models. Path length and net displacement were log-transformed to meet the assumption of normality.

For each model, the variable of interest was the number of skiers that potentially interacted with caribou, as measured at the beginning of the movement path; we included other covariates to control for confounding effects. This included quadratic terms for ski day (starting December 1st each year), as we expected potential non-linear responses due to snow depth and daylight duration, as well as time of day, as caribou moved more during day light. We added path length (m) in the displacement and elevation analyses to control for longer paths that had a greater probability to induce a larger difference in displacement and elevation. We also included ski year and individual ID to control for interindividual variability while taking into account the different time step between two successive locations (Δt) generated by the 2 and 3-h fix rate. Preliminary analyses also showed similar patterns for both fix rates, suggesting no effect of using two different Δt in the same analysis. We scaled and standardized covariates because of convergence issues resulting from large differences in measurement units.

We computed the coefficients of all three models for each path duration (2h to 120h, see section 2.4). Increasing the duration of the path in fixed increments allowed us to identify the temporal extent or any lag in the displacement of caribou following an encounter with skiers. We then focused on the magnitude of the coefficient of the number of skiers to describe the caribou response. We used the pseudo-R^2 developed by Nakagawa and Schielzeth (2013) to evaluate the predictive ability of the models (r.squaredGLMM from the MuMIn package). There was a low level of multicolinearity among variables in the movement models (VIF < 1.32). All statistical analyses were performed using R 3.3.3 (The R core Team, 2017).

2.5 Results

2.5.1 Human use

Few skiers were present during the first 40 days of the ski period (starting December 1st) in 2013 and 2014, but overall, skiers used the ski area during 83.9% of our study period (Fig. 3.2). The highest rate of use occurred between the 50th and 100th days of each ski period (mid-February to mid-March). On average, 7.04 ± 3.83 (SD) skiers were found each day in the ski area.

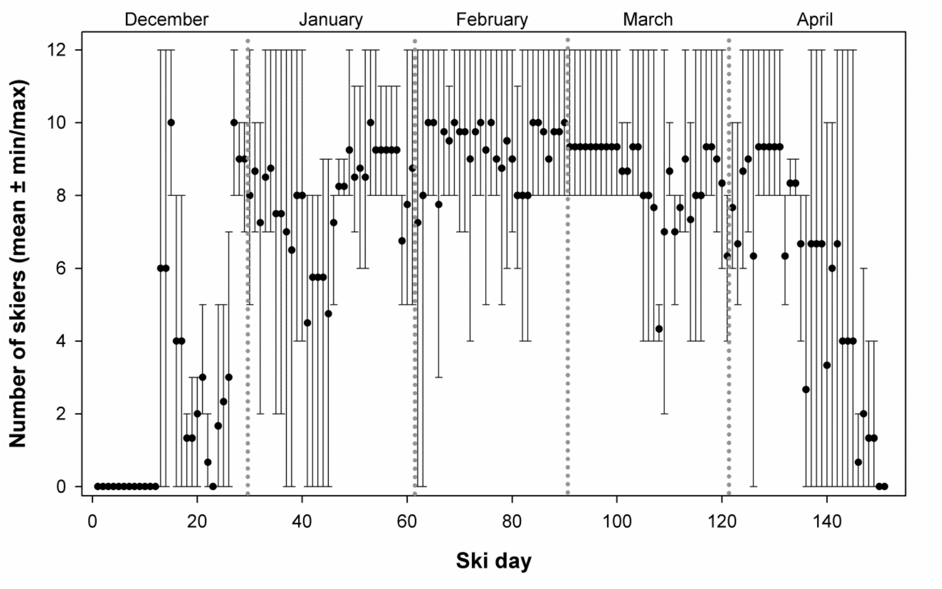

Figure 3.2. Average number of skiers in the ski area from 2013 to 2015 (December 1st to April 30th), as a function of ski day (day 1 corresponds to December 1st).

2.5.2 Impact of skiers on space use by caribou

Twenty different caribou (7M and 13F), some monitored for >1 year, included at least a part of the ski area in their seasonal home ranges. Caribou all belonged to the McGerrigle subpopulation. These individuals used the ski area more intensively (~12.5% of caribou locations) when skiers were absent. In comparison, < 6.2% of the caribou locations occurred in the ski area when skiers were present (Fig. 3.3). The best model explaining resource selection by caribou included the interaction term between distance to the ski area and the number of skiers (Table 3.1). Model coefficients suggested that caribou avoided the ski area, but the disturbance response was modulated by the presence and the number of skiers (Fig. 3.4, Table 3.2). However, even at low numbers, skiers negatively influenced the probability of occurrence of caribou. Our models were relatively robust, with r_S ranging from 0.69 to 0.78.

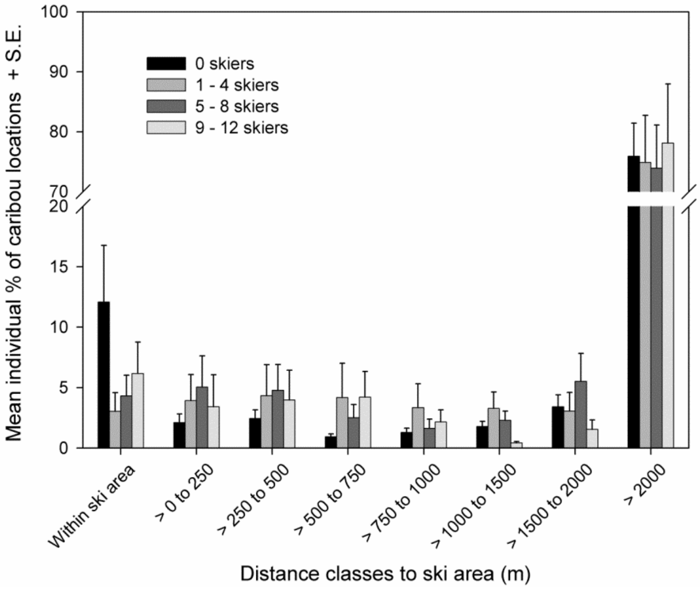

Figure 3. Mean use and standard error of the ski area and different buffer zones (0-250, 250-500, 500-750, 750-1000, 1000-1500, 1500-2000, and >2000 m) by caribou, from 2013 to 2015 (December 1st to April 30th) as a function of the number of skiers (0, 1-4, 5-8, and 9-12).

Table 3.2. Coefficients (β) and 95% confidence interval (95%CI) of the most parsimonious model describing habitat selection patterns of caribou interacting with skiers in Gaspésie (Canada) from 2013 to 2015 (December 1st to April 30th). Coefficients for which the 95% CI did not overlap zero are shown in bold.

Variable[1]	B	[lower:upper 95%CI]
Immature conifer	**0.444**	**[0.364: 0.525]**
Open conifer	**-0.613**	**[-0.694: -0.532]**
Other habitat	**-0.512**	**[-0.570: -0.455]**
Alpine tundra	**1.124**	**[1.057: 1.191]**
Elevation (km)	**-2.546**	**[-2.710: -2.381]**
Decay distance to ski area (α=2000)	0.172	[0.021: 0.323]
Number of skiers	**-0.066**	**[-0.077: -0.055]**
Number of skiers X Decay distance to ski area	**0.097**	**[0.079: 0.115]**

[1] Mature conifer stands were used as the reference category in all the RSF models

2.5.3 Impact of skiers on caribou movement

Although skiers were present across the study area throughout a large portion of the winter, monitored caribou demonstrated a differential response to the number of skiers. Also, there was a lag between the occurrence of skiers and the corresponding movement of caribou as we observed no clear displacement until 12 hours after disturbance (Fig. 3.5a). Our results showed that caribou were pushed to lower elevation habitats which tended to result in faster movement rates over a relatively long time period (~ 3 days) (Fig. 3.5b and 3.5c). According to the change in magnitude of the coefficients, caribou moved away from the ski area for approximately 42 hours after the initial disturbance (Fig. 3.5a and 3.5b). Ski day and path length had a significant relationship with the three measures of caribou movement (net displacement from the ski area, path length, difference in elevation) throughout the time span studied (0 to 120h), while there was no significant relationship with time of day (see Suppl. Mat. 1 for coefficients of all covariates for movement analyses). The mean (± SD) marginal pseudo-R^2 (excluding the contribution of random factors) of the series of models was 0.12 ± 0.05 (max = 0.22), 0.24 ± 0.09 (max = 0.37), and 0.09 ±0.02 (max = 0.12) for the net displacement, path length, and difference in elevation models respectively. The mean of conditional pseudo-R^2 (0.49, 0.61, and 0.24, respectively) were relatively higher showing the importance of adding random factors.

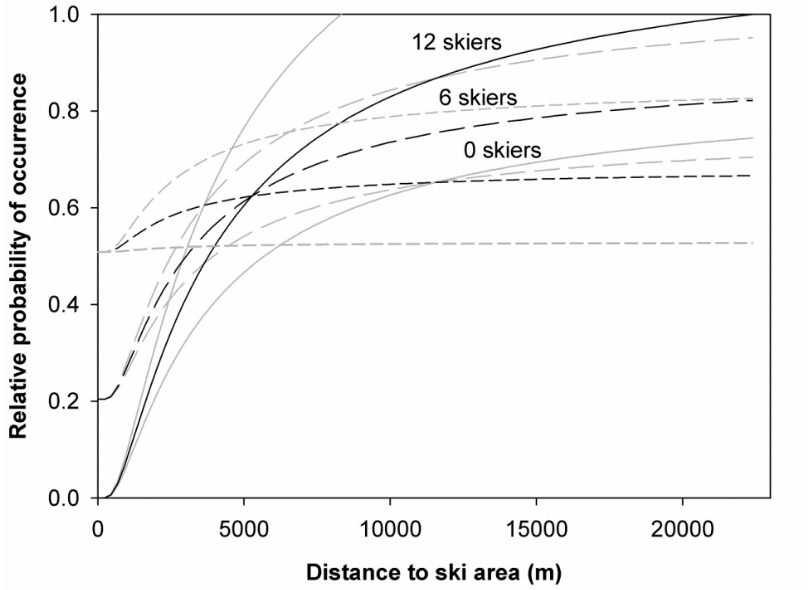

Figure 3.4. Relative probability of occurrence of caribou in relation to the distance to the ski area and the number of skiers as modelled from the most parsimonious resource selection function, Gaspésie (Canada), 2013 to 2015 (December 1st to April 30th). Gray lines represent the 95% confidence intervals of the interaction. We used the 95% confidence interval of the coefficient 'distance to the ski area' for the "zero skier" curve as there was no effect of the number of skiers.

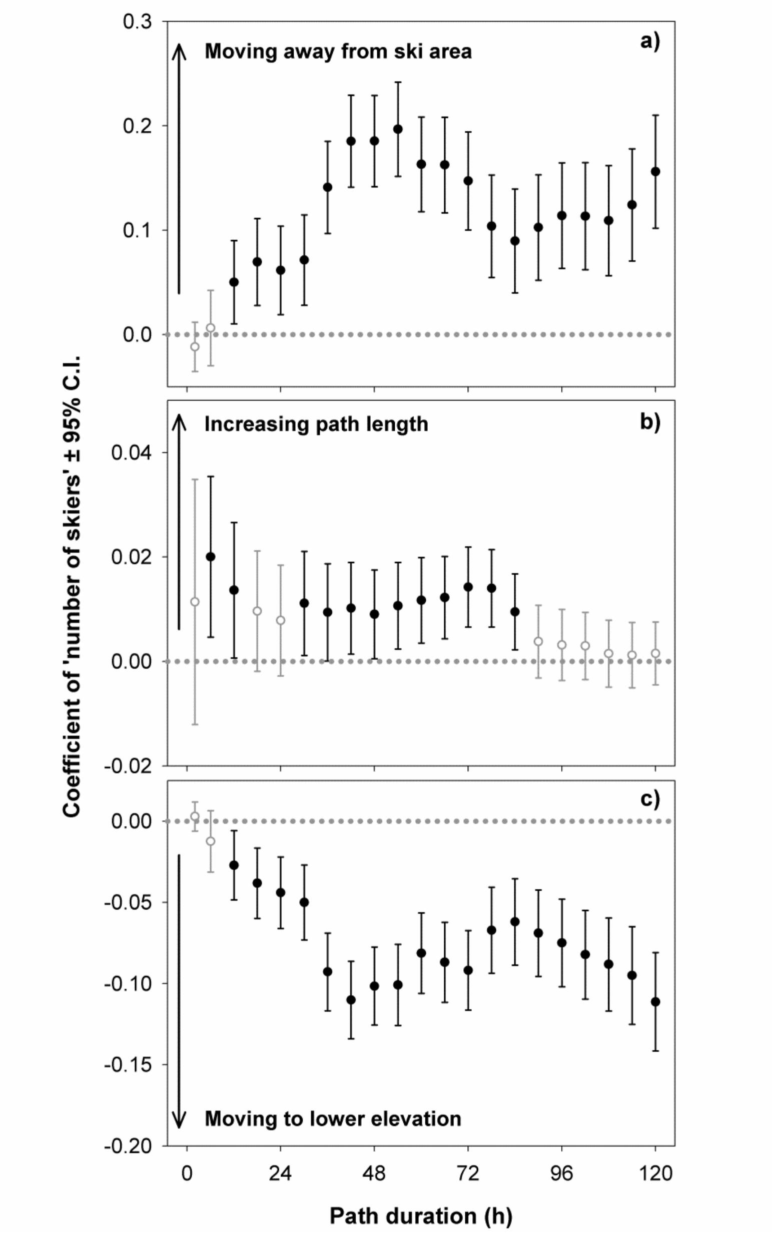

Figure 3.5. Coefficient estimates and 95% confidence interval of the variable ‘number of skiers’ from the three linear mixed effects models explaining a) net displacement from the ski area, b) path length, and c) difference in elevation, of caribou paths of varying duration, Gaspésie (Canada) from 2013 to 2015 (December 1st to April 30th). Gray lines indicate that the 95% confidence intervals included zero.

2.6 Discussion

Our study provided clear evidence that caribou were displaced by backcountry skiers and that monitored animals adjusted their response relative to the intensity of disturbance. As we hypothesized, caribou may have perceived human presence as a stress with the disturbance stimulus being of sufficient intensity to influence movement and displace caribou to habitat at lower elevations. Caribou in Gaspésie National Park are frequently in contact with humans throughout the year. This population is not naive to human activities and may have developed some familiarity or even habituation to backcountry recreationists. This suggests that the observed disturbance-response would be of an even greater magnitude for other populations of mountain caribou that are found in areas with less human presence.

In Gaspésie, caribou used high elevation alpine areas to avoid coyotes (the only predator in winter) that are mostly found in the valleys (Mosnier *et al.*, 2008; Gaudry, 2013). Similarly, humans used the ski area almost every day during the peak of winter, resulting in a high risk of encounter with caribou. Our results suggest that this cohabitation could be problematic for caribou because they were displaced for at least a few days to lower elevations, where coyotes are more common (Gaudry, 2013). However, the important difference between our conditional and marginal pseudo-R^2 suggested a high variance in caribou response toward skiers. One plausible hypothesis is that some caribou could have developed a certain level of tolerance toward human presence as skiing and hiking are strictly regulated inside the park and human encounter are frequent throughout the year.

At a coarse spatial scale, we observed displacement from the ski area suggesting a functional loss of suitable habitat (see Polfus *et al.*, 2011 for indirect habitat loss, and Gaudry 2013 for caribou response to hiking trails and roads). This response is similar to the avoidance of major disturbances like highways (Leblond *et al.*, 2013), tourist resorts (Nellemann *et al.*, 2000), mines (Boulanger *et al.*, 2012), and other industrial infrastructure (Johnson and Russell, 2014), except that these disturbances are permanent whereas skiers are only present during winter days. However, caribou in Gaspésie did not appear to respond immediately to the disturbance. We observed a statistically significant movement away from the study area ~12 hours after exposure to skiers (Fig. 3.5). This could be explained by a delay associated with the departure of skiers or the relatively slow movement of caribou related to deep, alpine snow conditions. The duration of this displacement (~42 hours) is also an important finding as other studies have not demonstrated such a lasting response for mobile animals like *Rangifer* (e.g. Reimers *et al.*, 2003).

The unpredictability of backcountry skiers could increase the negative response of caribou. As an example, Miller et al. (2001) recorded a greater impact of pedestrians when they occurred beyond a hiking trail. Similarly, Seip et al. (2007) found that caribou abandoned large blocks of high-quality habitat when confronted with backcountry snowmobiles that were inconsistent in their number and timing. The avoidance observed in our study persisted for at least 5 days, as shown by a significant displacement, and we observed a displacement trend even after 120 hours. However, caribou did return to the ski area and they were not always displaced, especially when there were few skiers. Thus, our data provide evidence that in some circumstances wildlife can accommodate low-intensity disturbance associated with recreational activities (Bateman and Fleming, 2017). The findings from other researchers suggest that tolerance and habituation of disturbance is complex, varying considerably among species and populations. For example, Richard and Côté (2015) reported a year-round avoidance of a large ski area by mountain goats in Jasper National Park.

The avoidance of skiers caused caribou to redistribute themselves, potentially increasing the density and perhaps competition within patches of habitat. This ‘refuge effect’ is well-known in conservation ecology (Berryman and Hawkins, 2006) and has been observed for caribou displaced by roads (Fortin *et al.*, 2013) and forest clearcuts (Lesmerises *et al.*, 2013). The higher density could potentially lead to greater predation risk as predators are known to select areas with higher prey abundance (Tremblay-Gendron, 2012). Higher densities could also lead to food depletion in the refuge habitat, especially for food-limited populations (Reimers *et al.*, 2003).

We used the count of the number of skiers who rented the cabin as an estimate of the number of skiers that may have interacted with caribou. That skier count was probably underestimated and served only as a coarse index of human disturbance. For example, some rare skiers could have used the study area without being resident at the cabin. We are confident, however, that this index represented daily variation in skier activity and numbers, and that the statistical relationship represents the actual avoidance responses of caribou. These results are consistent with other studies that showed an increase in the response by caribou following an increase in the intensity of the disturbance stimulus (Dyer *et al.*, 2001; Vistnes and Nelleman 2001; Johnson and Russell, 2014; Lesmerises *et al.*, 2017). Schaefer and Mahoney (2007) found a greater impact of forest harvesting on caribou avoidance behaviour for females than for males. Similar differences could be possible for skier disturbances. However, we did not test for sex-biased difference in response to skiers due to our small sample size. Further research is needed to disentangle potential differences between sexes, as most other studies on the behavioural responses of *Rangifer* to anthropogenic disturbances focused on females only or on undifferentiated individuals.

2.7 Conservation implications

Our results highlighted the importance of understanding the influence of relatively subtle human activities, when compared to large resorts, highways or industrial development, on the behaviour and distribution of terrestrial wildlife. In this case, a relatively small number of backcountry skiers consistently displaced an endangered and declining population of mountain caribou. Although we did not assess variation in habitat quality among areas or the energetic costs of moving away from skiers (e.g., Fancy and White, 1987; Johnson *et al.*, 2002), that displacement likely resulted in a greater risk of predation for those displaced caribou. Predation and resulting low survival is the primary mechanism for the decline in the Gaspésie caribou herd (Frenette, 2017).

These results strongly suggest that park managers should take into account even small numbers of recreationists when making development decisions and considering visitor management. Instead of avoiding a small area adjacent to a hiking trail or a road, we showed that animals facing disturbance avoided a large block of habitat used by skiers. These endangered caribou are located almost exclusively in a relatively small National Park that is surrounded by intensively managed forests. Thus, the loss of suitable habitat could be significant at the scale of the population, even more so considering that caribou moved to riskier low-elevation habitat where encounter probabilities with coyotes was higher. The next step in understanding the population consequences of disturbance is an accounting of the cumulative impact of ecotourism on caribou survival and recruitment. This is likely a function of changes in habitat use, including lower quality or less abundant forage (Nellemann *et al.*, 2000), greater vigilance resulting in altered activity budgets (Lesmerises *et al.*, 2017; Murphy and Curatolo, 1987; Skogland and Grovan, 1988), and the energetic implications of displacement-related movements through deep-snow environments (Reimers *et al.*, 2003).

2.8 Acknowledgments

We are grateful to C. Isabel and P. Lévesque for providing logistical support in the Gaspésie National Park and access to the cabin rental data. Collaring caribou would have been impossible without the presence of excellent technicians and biologists on our team: B. Baillargeon, D. Grenier, J. Mainguy, and G. Tremblay. We thank K.

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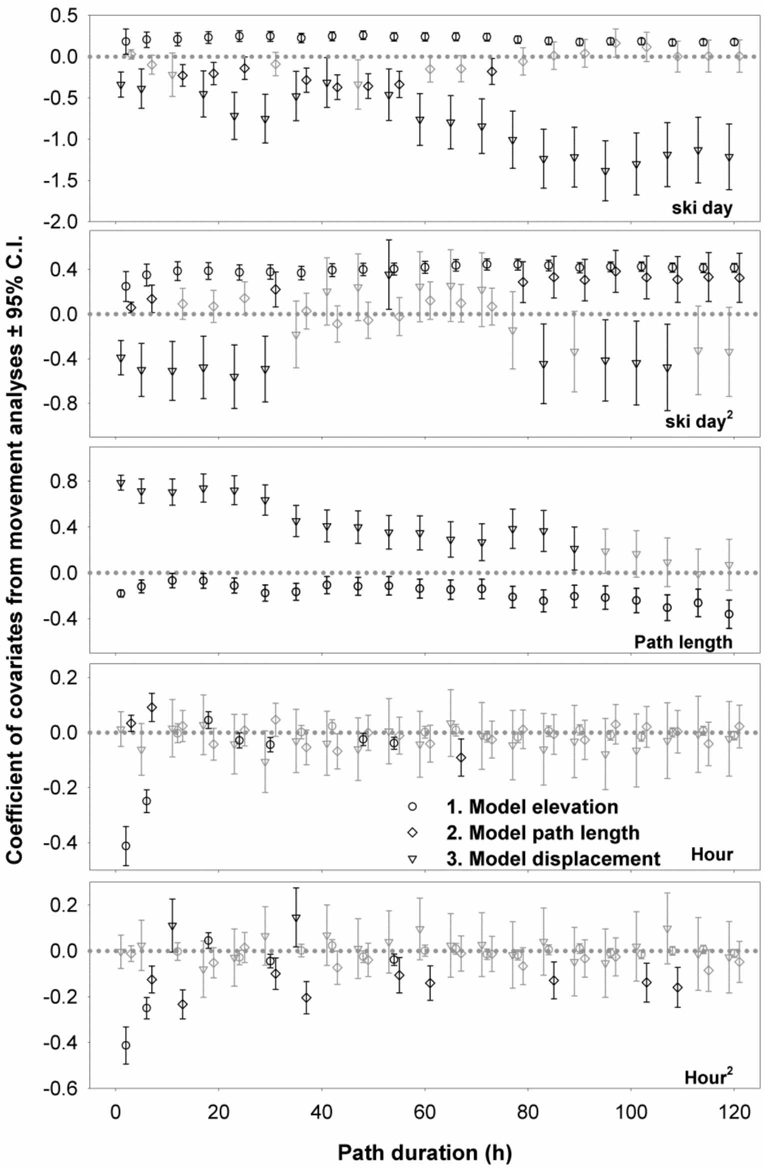

Suppl. Mat. 1 Coefficient estimates of each covariate (except 'number of skiers', already shown in Fig. 3.5) in the three linear mixed effects models explaining the difference in 1) elevation (circle), 2) path length (diamond), and 3) net displacement from the ski area (triangle) for caribou paths of varying duration (hours). These paths all started in the ski area in Gaspésie (Canada) between 2013 and 2015 (December 1st to April 30th). Gray symbols indicate that the 95 % confidence intervals included zero.

CHAPITRE III

LA CONNAISSANCE DU PAYSAGE EST UN IMPORTAT FACTEUR DE LA DYNAMIQUE DE FISSION CHEZ UN ONGULÉ ALPIN.

LANDSCAPE KNOWLEDGE IS AN IMPORTANT DRIVER OF THE FISSION DYNAMICS OF AN ALPINE UNGULATE.

Frédéric Lesmerises, Chris J. Johnson, Martin-Hugues St-Laurent

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3.1 Résumé

Les décisions de mouvements collectifs sont souvent basées sur les connaissances du groupe et les connaissances personnelles. Chez les sociétés animales affichant une dynamique de fission-fusion, les individus ont rarement le même bagage de connaissances au sujet de l'environnement, puisque la connaissance est le reflet des décisions passées de l'individu qu'il ait été seul ou en groupe. La connaissance de l'environnement est particulièrement essentielle dans les paysages hétérogènes où les ressources varient dans le temps et l'espace. En effet, l'hétérogénéité du paysage, un produit de la quantité et de la configuration des ressources, aussi bien que des prédateurs et des compétiteurs, est à la base des décisions individuelles et collectives inhérant au mouvement. Nous avons évalué les décisions de mouvement d'un ongulé alpin en fonction de la connaissance de l'environnement et de l'hétérogénéité du paysage. Nous avons émis l'hypothèse que les individus baseraient leurs décisions sur les informations passées dans les endroits qu'ils connaissent bien, particulièrement dans les secteurs fortement hétérogènes. Ces décisions individuelles auraient des conséquences sur les décisions de mouvement des groupes. Afin de tester cette hypothèse, nous avons utilisé les données télémétriques GPS pour suivre les mouvements d'environ 45% des individus (n=28) d'une petite population de caribou des bois, *Rangifer tarandus caribou*, entre 2013 et 2016. Nous avons évalué la probabilité de fission des dyades (c.-à-d. un groupe composé de deux individus) de caribou (n=3681, provenant de 172 combinaisons de dyades différentes) en relation avec la connaissance du paysage, l'hétérogénéité du paysage et les liens sociaux entre les membres des dyades. La probabilité de fission était influencée par l'interaction entre les variables décrivant la connaissance du paysage et les liens sociaux entre les membres de la dyade. La probabilité de fission et l'influence de l'habitat ou des liens sociaux augmentaient avec la connaissance du paysage. Dans les endroits familiers, les individus étaient plus susceptibles de rester avec l'autre membre de la dyade s'ils partageaient un fort lien social ou s'ils étaient dans un habitat préférentiel. De tels ajustements fins dans le mouvement et les décisions sociales démontrent l'importance de l'information tenue par des conspécifiques lorsqu'ils se déplacent dans un environnement moins familier. En restant avec le groupe, les individus peuvent accéder à des ressources de haute qualité sans les les coûts de recherche de telles ressources.

3.2 Abstract

Collective movement decisions are often based on personal and conspecific knowledge. In fission–fusion animal societies, individuals rarely have the same level of information about their environment, with knowledge being a reflection of past individual and collective decisions. Knowledge of the environment is particularly essential in heterogeneous landscapes, where resources may vary in space and time. Indeed, landscape heterogeneity, a product of the quantity and configuration of resources as well as predators and competitors, is the basis of both individual and collective movement decisions. We assessed individual movement decisions of an alpine ungulate as a function of landscape knowledge and landscape heterogeneity. We hypothesized that individuals would base their decisions on previous information in areas they know well, especially in highly heterogeneous landscapes. These individual decisions would have consequences for the collective movement decisions of groups. To test this hypothesis, we used GPS collars to monitor the movements of ~45% of the individuals (n=28) of a small population of woodland caribou, *Rangifer tarandus caribou*, between 2013 and 2016. We assessed the fission probability of caribou dyads (i.e., groups composed of two individuals) (n=3681, from 172 dyad combinations) in relation to landscape knowledge, landscape heterogeneity and social bonds between dyad members. The probability of group fission was influenced by the interaction between the variables describing landscape knowledge of dyadic members and social bonds. The probability of group fission and the influence of habitat or social bonds on fission probability increased with landscape knowledge. In familiar landscapes, individuals were more likely to stay with conspecifics if they shared a strong social bond or if they were in preferential habitat. Such fine adjustments in movement and social decisions demonstrated the importance of the information held by conspecifics when occupying unfamiliar areas. By staying with conspecifics, individuals could gain access to high-quality resources without the energetic cost of locating such resources.

3.3 Introduction

Living in a group can confer advantages, as communication among conspecifics lowers predation risk (Roberts, 1996) and increases the efficiency of resource detection and acquisition (Creel and Creel, 1995). However, group living also incurs costs to the individual animal, such as transmission of diseases and parasites (Côté and Poulinb, 1995; but see Mooring and Hart, 1992), reduced reproductive opportunities and increased competition for resources (Lian *et al.*, 2007; Molvar and Bowyer, 1994). These costs include aggression that leads to reduced fitness, morbidity or mortality (Beauchamp, 2014; Krause and Ruxton, 2002; Ward and Webster, 2016). The advantages and disadvantages of group living can also be dynamic. Grouping with conspecifics may benefit the individual only during certain seasons or under specific environmental conditions or interspecific challenges, such as the presence of predators or when searching for resources across highly heterogeneous landscapes (Creel and Winnie, 2005; Fortin *et al.*, 2009).

The ecological variability in the benefits and costs of staying in a group drives fission–fusion dynamics (Kerth *et al.*, 2006; Merkle *et al.*, 2015). Each individual builds its own decision-making rules based on its intrinsic characteristics (e.g. landscape knowledge, habitat preference, nutritional state and reproductive demand), often creating groups of similar individuals (e.g. age class, sex and family bond) (Conradt, 1998; Ruckstuhl, 1998, 1999; Sueur *et al.*, 2011). Consequently, similar individuals have stronger social bonds (Bercovitch and Berry, 2013; Carter *et al.*, 2013; Djakovic *et al.*, 2012) and are more likely to maintain group structure (Carter *et al.*, 2013; Merkle *et al.*, 2015).

Groups composed of familiar individuals are more stable, with group behaviour offering numerous advantages: cooperative antipredator behaviour (Chivers *et al.*, 1995), reduction in competition (Utne-Palm and Hart, 2000) and greater reproductive opportunity (Höjesjö *et al.*, 1998). Familiar individuals also learn more easily from each other (Figueroa *et al.*, 2013; Valsecchi *et al.*, 1996). In domestic pigs, *Sus domestica*, for example, individuals show less neophobia towards a new food item if a familiar individual recently experienced the same item (Figueroa *et al.*, 2013). This social learning from familiar individuals could be advantageous in heterogeneous landscapes.

Landscape heterogeneity is closely linked to the distribution of resources and predators and is known to have direct and indirect effects on the decision making of species exhibiting fission–fusion dynamics (Fortin *et al.*, 2009; Kelley *et al.*, 2011; Smith *et al.*, 2008). In a relatively homogeneous landscape, there are fewer reasons for interindividual variation in decision making. Thus, Sueur et al. (2011) hypothesized that groups should be more cohesive in such landscapes. Alternatively, in a very heterogeneous landscape, interindividual variation in decision making should be common (Sueur *et al.*, 2011).

When minimizing predation risk and maximizing nutritional gain, animals will often base their decisions on past experiences (Merkle *et al.*, 2014; Valeix *et al.*, 2009). Beyond leadership and dominance level, individual and conspecific information are both known to have important impacts on collective decisions (Couzin *et al.*, 2011; Merkle *et al.*, 2015). For group dynamics of bison, *Bison bison*, Merkle *et al.* (2015) found that landscape knowledge, whether or not the area was visited by the individual in the last year, had great influence on the decision to follow the group or not. Greater knowledge of the landscape induced a higher probability of leaving the group. Uninformed individuals tend to increase group stability by reaching a consensus more easily (Couzin *et al.*, 2011). Individuals, however, are rarely completely informed or uninformed of location, quantity and quality of resources available locally. It is currently unclear how group dynamics change from very unfamiliar places to frequently used patches, especially in heterogeneous landscapes.

Our objective was to assess how familiarity among conspecifics, landscape heterogeneity and landscape knowledge of woodland caribou, *Rangifer tarandus caribou*, as measured by the intensity of use of an area by an individual in the past, influenced the fission rate of groups of animals. In our study, group fission was defined as the splitting of dyads composed of two collared caribou. We hypothesized that individuals transiting areas they know well should find high-quality resource patches without relying on conspecific information. This knowledge of local resources should allow individuals to make their own choices in regards to habitat and group membership. As the availability of conspecific information is closely linked to the number of individuals in a group, the importance of landscape knowledge could also be influenced by group size. Increasing landscape heterogeneity should increase the fission rate, at least at a low or medium level of heterogeneity, as conflicts of interests between dyadic members is positively correlated to landscape heterogeneity. We also hypothesized that fission probability was influenced by familiarity among conspecifics, with groups of familiar individuals having a lower fission probability.

We used the Atlantic-Gaspésie caribou population as a biological model to test our hypothesis. *Rangifer* are social animals that are known to demonstrate fission–fusion group dynamics (Body *et al.*, 2015). This population is small, allowing for the monitoring of a high proportion of the individuals with GPS telemetry devices (Lesmerises *et al.*, 2017). Furthermore, this population is found across a relatively heterogeneous landscape composed of forest and alpine ecosystems.

3.4 Methods

3.4.1 Study Area

The study area covered the eastern part of the range of the Gaspésie caribou population, corresponding approximately to the limit of the Gaspésie National Park (48°50’N, 66°00’W). Much of the distribution of caribou is across high-elevation alpine habitats, which are dominated by Mount Jacques-Cartier (1268 m). Three ecological zones span the elevational gradient of the study area. The highest elevation zone (>1050 m) is composed of alpine tundra, a mat of lichens, mosses and graminoids along bare rocks and ericaceous shrubs. The subalpine forest (900–1050 m) is a transition zone where tree height decreases with elevation, forming a krummholtz belt before becoming alpine tundra. Finally, at the lowest elevations, the montane zone consists of closed forest composed of balsam fir, *Abies balsamea*, white spruce, *Picea glauca*, black spruce, *P. mariana*, and birch, *Betula* sp.

Caribou are found between 200 and 1260 m, but typically occur above 700 m (Mosnier, Ouellet, Sirois, and Fournier, 2003; Ouellet, Ferron, and Sirois, 1996). Gaspésie caribou are subdivided into three subpopulations, namely Albert (n = ~20 individuals), McGerrigle (n = ~40 individuals) and Logan (n = ~15 individuals) (Morin, 2017). Moose, *Alces americanus,* black bears, *Ursus americanus,* coyotes, *Canis latrans,* and a few white-tailed deer, *Odocoileus virginianus,* are also found within Gaspésie National Park. Wolf, *Canis lupus,* was extirpated from the south shore of the St Lawrence River in the mid-1800s.

3.4.2 Caribou locations

We used GPS locations of Gaspésie caribou collected via a telemetry monitoring programme that took place between 2013 and 2016. In total, 43 adult caribou (n = 17 males, 26 females), proportionally distributed among the three subpopulations (i.e. n = 28 in the McGerrigle, n = 6 in the Albert, n = 9 in the Logan subpopulations), were captured, fitted with GPS-Argos collars and followed for 2.5 years (see Lesmerises *et al.*, 2017, for more details). For the subsequent analyses, we kept only location data from the 28 individuals (19F; 9M) from the McGerrigle subpopulation as the number of individuals monitored in the two other subpopulations was insufficient to assess group dynamics.

Collars were programmed to acquire locations every 2 h (model TGW-4680-3, Telonics Inc., Mesa, AZ, U.S.A.) or every 3 h (model TGW-4680, Telonics Inc.) and to transfer relocations from the previous week via an Argos link every 4 days. To limit the potential negative impacts of helicopter activity, and as recommended by the Animal Welfare Committee (Université du Québec à Rimouski (UQAR) certificate no. CPA-52-13-112; Ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) certificate no. CPA FAUNE 13-08), captures were divided into two sessions of 22 and 21 animals each, conducted in early winter 2013 and 2014, respectively. Each collar had a drop-off mechanism (CR-2A, Telonics Inc.) programmed to release the collar on 1 June or 15 June 2016.

3.4.3 Biological periods

Social interactions are sensitive to biological period (Body *et al.*, 2015). For instance, calving female caribou tend to disperse and isolate themselves from other individuals (Bergerud and Page, 1987). In contrast, during the rutting period, groups are more cohesive (Body *et al.,* 2015). To accommodate these differences, we represented the social dynamics of caribou across five biological periods (Courtois, 2003): spring (15 April – 20 May), calving (21 May – 20 June), summer (21 June – 15 September), rut (16 September – 31 October) and winter (1 November – 14 April).

3.4.4 Dyad formation and fission

We considered two adult individuals being together (i.e. a dyad) if they were <50 m apart during a minimum of two successive locations. This distance threshold was determined using the group definition proposed by Whitehead (2008): members of a group will be closer to one another when compared to lone individuals or other groups.

Using an iterative process, we calculated the number of dyads according to a distance threshold varying between 1 m and 150 m. After a rapid increase in dyad number, we found a threshold at ~50 m above which the number of new dyads decreased for each increment of distance (see Appendix, Fig. A1). This threshold was consistent with field observations of caribou groups made in a companion study focused on the impact of hikers on the behaviour of Gaspésie caribou (Lesmerises *et al.*, 2017). Only dyads for which members had the same fix rate (2 or 3 h) were kept for subsequent analyses. As our dyad formation – or group fusion – was dependent on the precision of GPS locations, we removed all locations having a position dilution of precision (PDOP) value >10 (Cargnelutti *et al.*, 2007; Coulon *et al.*, 2008). To minimize the number of false fission events resulting from infrequent erroneous locations, we considered a dyad valid at time t_{+2} if the two individuals were together at t_0 and t_{+2}, even if members were more than 50 m apart at t_{+1} (Fig. 4.1). For location sequences with one missing GPS location, we considered the group valid if before and after the missing location each member was <50 m from each other. If two or more successive locations were missing, the dyad was dismissed.

Fusion and fission events were calculated according to the centroid of locations of two associated individuals (Fig. 4.1). A centroid, the averaged geographical locations of both individuals at time t, represented the dyad location at this given time. For example, the fusion of individuals i and j resulted in a dyad ij, for which we calculated the centroid of locations i and j at each time step and drew a straight-line segment linking two successive centroids, representing the dyad step. A fission event Fi_{ij} was characterized by two or more successive steps during which animals of a dyad were >50 m apart from each other. From fission event Fi_{ij}, the dyad path was divided in two different steps F_i and F_j, indicating the end of the dyad ij (Fig. 4.1). Consequently, two caribou could generate several distinct dyads together, and each caribou could be part of dyads with different individuals.

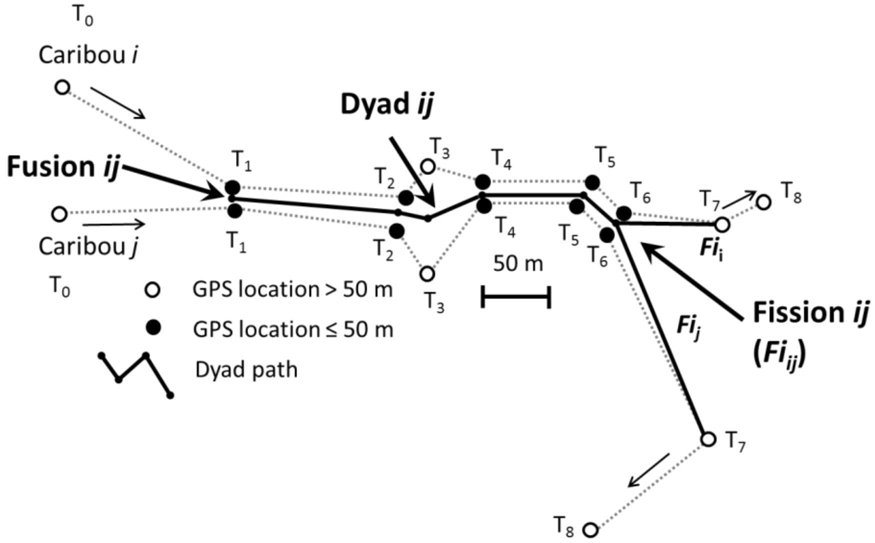

Figure 4.1. Schematic representation of a dyad path formed by individuals *i* and *j*. Dotted lines represent individual paths.

3.4.5 Statistical analyses

We combined explanatory variables (see Table 4.1 and the section below for a description) into candidate statistical models (Table 4.2) to assess how familiarity among conspecifics, landscape heterogeneity and landscape knowledge of caribou influenced the fission rate of groups of animals. We used time-dependent Cox proportional hazards models, where the time to fission served as the dependent variable, to test the influence of landscape knowledge on the decision of GPS-collared caribou to stay with another collared individual in a dyad (coxme package, R 3.2.1, R Foundation for Statistical Computing, Vienna, Austria). Each step was considered as a time interval in the Cox models. All variables except familiarity and landscape knowledge (calculated seasonally) were calculated for each time interval. Dyadic members did not die after a fission event, as would be applied to a survival-based Cox proportional hazards model; thus, two individuals could have formed dyads at multiple times throughout the study. We added dyadID (i.e. the identities of both members –

“ID1-ID2”), sex combination (M-M, M-F, F-F) and year as random factors in our analysis to control for this potential pseudoreplication. We used a quadratic term for Julian days (as fixed variables) and biological period (as random factor) to model temporal variations in social behaviour.

The Cox proportional hazards model allowed us to calculate the instantaneous hazard or likelihood of dyad fission. We used AIC_c (Akaike’s information criterion corrected for small sample size; Burnham and Anderson, 2004) to rank the candidate models. We used the variance inflation factor (VIF) to test for excessive multicollinearity among the independent variables.

3.4.6 Explanatory variables

We used a set of variables (Table 4.1) that coincided with our main hypothesis that local knowledge (i.e. the intensity of use of an area by an individual in the past) allowed caribou to make an independent decision without relying on conspecific information. Cox proportional hazards models included measures of familiarity with the dyad member, landscape heterogeneity, and staying or not staying in a habitat patch. We developed other variables known to influence interindividual decision making and sociality in terrestrial mammals: predation risk (Banks, 2001; Beauchamp, 2014), habitat (Fortin *et al.*, 2009; Pays *et al.*, 2012) and individual and social characteristics (Lusseau, 2007; Carter *et al.*, 2013).

We derived contrasted habitat categories of cover type as well as food availability and quality (Table 4.1) from 1:20 000 ecoforestry maps published and updated by the MFFP. Minimum mapping unit was 4 ha for forested polygons and 2 ha for nonforested areas (e.g. water bodies). For each dyad step, we calculated the proportion of open habitat (including all alpine tundra types and wetlands) and considered this category as preferential habitat as Gaspésie caribou select these cover types most strongly (Ouellet *et al.*, 1996; Mosnier *et al.*, 2003). Also, we calculated the crossing rate of a habitat edge (i.e. edges between each habitat category) as the number of edges intersected by the dyad step divided by the step length. The crossing rate represented the number of choices each dyad member had to make during their association with each habitat crossing. Thus, dyadic members had to make a decision about staying in the currently occupied habitat or going into a new habitat patch according to assumed changes in habitat quality and inherent nutritional needs.

Table 4.1. Description of explanatory variables, including habitat categories, used to explain the relative probability of dyad fission in woodland caribou, Gaspésie (Canada), between 2013 and 2016.

Explanatory variable	Description
Habitat	
Alder stand	Alder stands >2 ha
Agricultural field	Agricultural fields, including uncultivated fields
Partial cut	Partial cuts <20 years old
Recent cut	Cutblocks ≤5 years old
Old cut	Cutblocks 6–20 years old
Krummholz	Noncommercial dwarf tree stand
Young deciduous stand	Deciduous trees >75% of basal area; <60 years old
Old deciduous stand	Deciduous trees >25% of basal area; >60 years old
Human	Area with human footprint other than by forestry and power lines
Power lines	Right-of-way of power lines
Young mixed stand	Coniferous trees >25% and <75% of basal area; <60 years old
Old mixed stand	Coniferous trees >25% and <75% of basal area; >60 years old
Nonregenerated stand	Nonregenerated forest stands >20 years originating from cutblocks or natural disturbances
Natural disturbance	Burned areas, windfall and insect outbreak stands <20 years old
Young coniferous stand	Coniferous trees >75% of basal area; <60 years old
Old coniferous stand	Coniferous trees >75% of basal area; >60 years old
Open coniferous stand	Open coniferous woodland (tree canopy closure <25%)
Open stand	Alpine tundra and wetlands
Variable	
Julian day	Julian day
Julian day^2	Quadratic term of Julian day
Movement rate	Movement rate (m/s)
Open habitat	Proportion of open habitat under dyad step
Difference in elevation	Difference in elevation between ending and starting points of dyad step
Group size	Group size at the beginning of the dyad step
Decay distance to caribou (α=250)	Distance to the nearest caribou at the starting point of the dyad step transformed by a decay function
Dyad familiarity	Half-weight index (see equation 1)
Landscape knowledge	Mean kernel volume of dyad members at the starting point (0 = minimum, 100 = maximum)
Edge density (km/km^2) (radius=500 m)	Habitat edge in a 500 m radius buffer around the starting point of the dyad step
Edge density^2	Quadratic term of edge density
Edge crossing	Number of edges crossed by a dyad step divided by its step length

We also calculated the edge density of habitat in different buffer zones (500, 1000, 1500 and 2000 m) around the starting point of a step (see Beauchesne *et al.*, 2013). This metric allowed us to test the influence of the spatial heterogeneity of habitat on the decision of an individual caribou to maintain association with a group. The buffer size with the lowest AIC_c (Burnham and Anderson, 2004) was retained and used in subsequent candidate models. Woodland caribou that occupy mountainous terrain are known to select relatively high-elevation habitats to avoid predation (Mosnier *et al.*, 2003; Johnson *et al.*, 2004); thus, we generated a variable that characterized the relative difference in elevation between the starting and ending points of each step. Consequently, steps moving downhill had a negative value, while uphill steps had a positive value.

In addition to indices of landscape heterogeneity, we calculated the movement rate by dividing the path length (m) by the duration of the path(s). Also, we calculated the distance to the nearest caribou (i.e. the distance between the starting point of the dyad path and the nearest collared caribou, other than dyadic members) to represent the possibility of joining another group. If another group is close, individuals have a greater opportunity to leave their group to join another. Conversely, if there is no immediately adjacent group, individuals could hesitate to leave a group and lose the advantages conferred by group membership. We expected a nonlinear effect as immediately proximal conspecifics are likely more important than further individuals, with that relationship decaying exponentially with distance. Thus, we used a decay function, exp(-α/distance), to represent the exponential decrease in the influence of that distance variable (Carpenter *et al.*, 2010). We used an information-theoretic approach to test a range of α values for the decay function, where α = 250, 500, 1000, 2000 or 3000 (Lesmerises *et al.*, 2017). The α with the lowest AIC_c (Burnham and Anderson, 2004) was retained and used in our subsequent Cox models. In social species, individuals do not interact randomly (Lusseau, 2007; Vander Wal *et al.*, 2014); hence we calculated a half-weight index. This was represented as the proportion of time two individuals were together during a given period (Ginsberg and Young, 1992; Whitehead, 2008):

$$\frac{x}{x+y\text{ab}+0.5(y\text{a}+y\text{b})} \qquad (1)$$

where *x* represents the number of observations that two individuals, a and b, are seen together, *y*a is the number of observation during which only individual a is seen, *y*b is the number of observation during which only individual b is seen, and *y*ab is the number of observations during which individual a and b are seen in different groups. This ratio controlled for missing GPS locations as it removed the observations where only one individual was observed. We also estimated the group size using the caribou locations and the same threshold for dyad (i.e. 50 m). We considered two caribou to belong to the same group even if they were >50 m apart only if another group member was found at <50 m from both caribou. As we monitored a large proportion of the McGerrigle population, we assumed that group size estimated with the collared caribou was correlated with the real group size.

To test the importance of knowledge in decision making, we created an index of landscape knowledge for each dyad member, which we summed to represent the total dyad knowledge. We tested three periods of landscape knowledge: 3 months, 6 months, and all GPS locations available for each individual. We covered a wide time span as we knew that caribou could exhibit long-term spatial fidelity (Faille *et al.*, 2010; Lafontaine *et al.*, 2017). Using GPS locations for these thresholds, we estimated a bivariate normal kernel density (kernelUD in adehabitatHR) with the ad hoc method to calculate the smoothing factor. This measure served as a proxy of landscape knowledge, assuming that an animal's knowledge is correlated with the intensity of use of some portion of the landscape. For each dyad member, we then subtracted the kernel value (ranging from 0 for the most used area to 100, the limit of the home range) at the starting point of the dyad step from 100. Following this calculation, the maximum value for landscape knowledge was 100 and the minimum was 0 for each dyad member. We summed the landscape knowledge of both dyad members. Each independent variable was centred (values subtracted by the mean) and standardized (divided by standard deviation), except decay distance, to ensure model convergence.

3.5 Results

In total, GPS locations revealed 3681 dyads from 172 dyadIDs. Fission events occurred at different rates throughout the year, with three peaks in frequency: early spring to calving, July, and during the rutting period (Fig. 4.2). The highest fission rate was observed in July and the lowest during winter (between February and April). Caribou associations tended to be shorter during summer, especially in August, just before the rut. In contrast, some caribou dyads were very cohesive during winter, lasting in one case for 26.5 days.

The most parsimonious model (model 6.3) revealed the importance of landscape knowledge and landscape configuration for dyad dynamics (Table 4.2). There was no indication of excessive multicollinearity (VIF <5). The effect of edge density (as a proxy of landscape heterogeneity) on the relative probability of fission was nonlinear, with higher fission probability at low and high fragmentation levels (Fig. 4.3).

The proxy of landscape knowledge (kernel density) calculated using all individual GPS locations provided a better explanation than shorter time periods (3 or 6 months) (Table 4.2). Landscape knowledge increased the risk of dyad fission, but also influenced the individual effect of other variables as shown by significant interactions (Table 4.3, Fig.

4.4). In very unfamiliar landscapes, habitat or social bond did not influence fission probability.

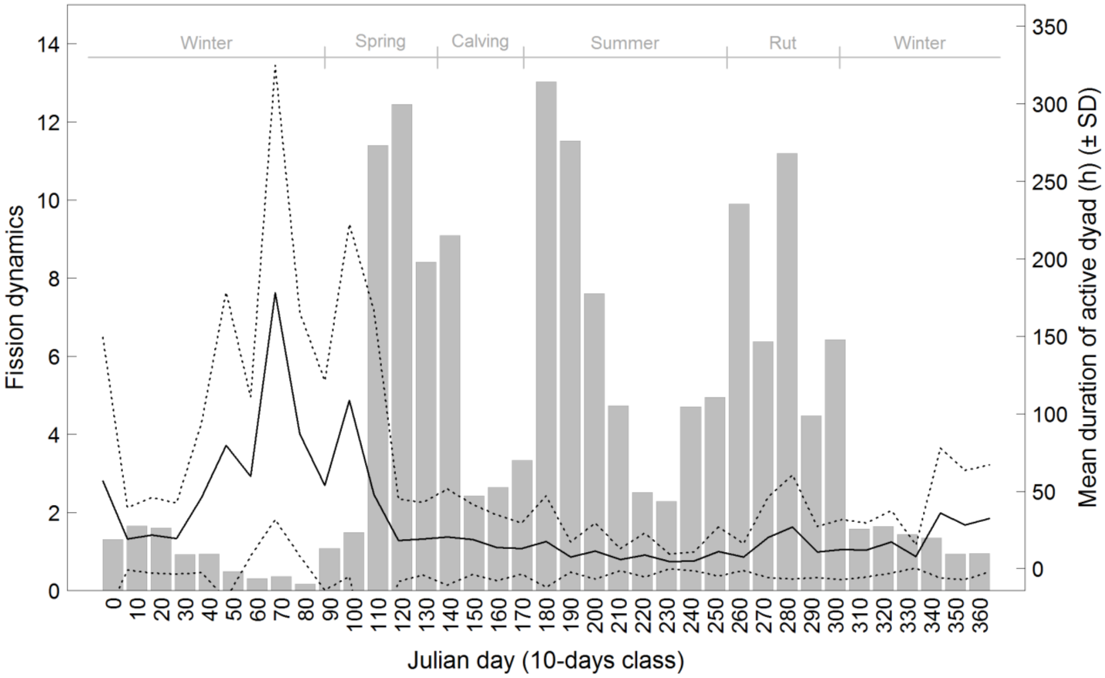

Figure 4.2. Annual variation in fission dynamics calculated as the number of fission events divided by the number of collared individuals by 10-day classes (bars) and mean duration (solid line) ± standard deviation (dotted line) of active dyads for the Gaspésie caribou population (Gaspésie, Canada) between 2013 and 2016.

The probability of group fission was lower for dyads formed by two individuals with strong social bonds and for dyads moving in open areas when experience in an area, and presumably knowledge of that landscape, increased (Fig. 4.4a–b). When crossing numerous edges along their path (i.e. high edge crossing rates), suggesting increased habitat heterogeneity and resource decision making, dyads had a higher probability of fission, especially in frequently used areas (Fig. 4.4c). Individuals belonging to larger groups had a greater probability of leaving their dyadic member when both had little information about the landscape (Fig. 4.4d).

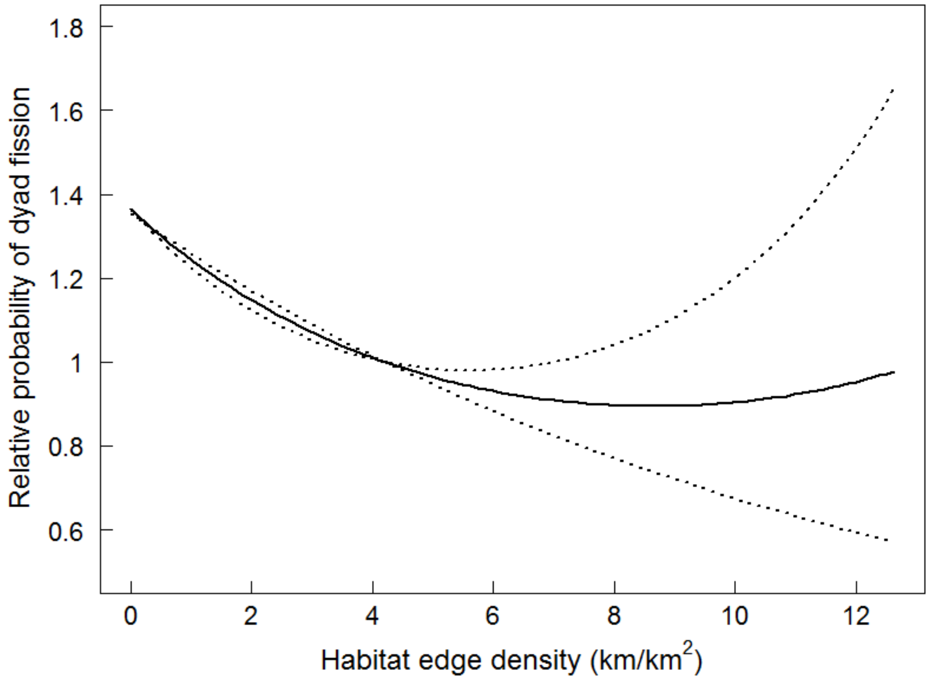

Figure 4.3. Nonlinear effect of edge density (in a 500 m radius around the starting point of the dyad path) on the relative probability of dyad fission for Gaspésie caribou (Gaspésie, Canada), between 2013 and 2016. Dotted lines represent the 95% confidence interval.

Table 4.2. Candidate Cox proportional hazards models explaining fission risk of caribou dyads for the Gaspésie caribou population, between 2013 and 2016.

No.	Model	LL	ΔAIC_c
0	Null model	-26292.590	1107.120
1	Movement rate + Julian day + Julian day^2 + Diff. in elevation	-26031.361	596.393
2.1	Model 1 + Group size + Dist to nearest caribou + Dyad familiarity + Landscape knowledge.3months	-25986.273	472.824
2.2	Model 1 + Group size + Dist to nearest caribou + Dyad familiarity + Landscape knowledge.6months	-25986.815	474.732
2.3	Model 1 + Group size + Dist to nearest caribou + Dyad familiarity + Landscape knowledge.Life	-25986.784	475.229
3	Model 1 + Open habitat + Edge density + Edge density^2+ Edge crossing	-25805.576	158.339
4.1	Model 3 + Group size + Dist to nearest caribou + Dyad familiarity + Landscape knowledge.3months	-25758.675	31.979
4.2	Model 3 + Group size + Dist to nearest caribou + Dyad familiarity + Landscape knowledge.6months	-25759.063	33.118
4.3	Model 3 + Group size + Dist to nearest caribou + Dyad familiarity + Landscape knowledge.Life	-25758.837	33.457
5.1	Model 2.1 + Dist. caribou*Dyad familiarity + Dyad familiarity*Landscape knowledge.3months + Group size*Land. knowledge.3months	-25975.211	460.141
5.2	Model 2.2 + Dist. caribou*Dyad familiarity + Dyad familiarity*Landscape knowledge.6months + Group size*Land. knowledge.6months	-25979.365	468.787
5.3	Model 2.3 + Dist. caribou*Dyad familiarity + Dyad familiarity*Landscape knowledge.Life + Group size*Land. knowledge.Life	-25972.460	457.866
6.1	Model 5.1 + Open hab.*Land. knowledge.3months + Edge density^2*Land. knowledge.3months + Edge crossing*Land. knowledge.3months + Group size*Land. knowledge.3months	-25740.268	9.250
6.2	Model 5.2 + Open hab.*Land. knowledge.6months + Edge density^2*Land. knowledge.6months + Edge crossing*Land. knowledge.6months + Group size*Land. knowledge.6months	-25747.443	23.585
6.3	**Model 5.3 + Open hab.*Land. knowledge.Life + Edge density^2*Land. knowledge.Life + Edge crossing*Land. knowledge.Life + Group Size*Land. knowledge.Life**	-25733.544	0.000

The ranking was based on the AIC_c. Log likelihood (LL) and difference in AIC_c values (ΔAIC_c). The most parsimonious model is shown in bold.

Table 4.3. Coefficient (β) and 95% confidence intervals of the most parsimonious Cox proportional hazards model explaining the likelihood of fission for dyads (*N* = 3681) of individuals of the Gaspésie caribou population, between 2013 and 2016

Variable	B	95 % CI (lower, upper)
Julian day	0.005	(-0.053, 0.064)
Julian day^2	**0.147**	**(0.072, 0.222)**
Movement rate	**0.174**	**(0.156, 0.192)**
Open habitat	**-0.138**	**(-0.185, -0.092)**
Difference in elevation	**-0.131**	**(-0.155, -0.107)**
Group size	0.033	(-0.049, 0.116)
Decay distance to caribou (α=250)	**-0.561**	**(-0.864, -0.259)**
Dyad familiarity	**-0.819**	**(--1.006, -0.633)**
Landscape knowledge	**0.238**	**(0.104, 0.372)**
Edge density (radius=500 m)	**-0.108**	**(-0.153, -0.064)**
Edge density^2	**0.026**	**(0.002, 0.050)**
Edge crossing	**0.211**	**(0.195, 0.228)**
Land. knowledge*Edge crossing	**0.031**	**(0.013, 0.049)**
Land. knowledge*Edge density^2	0.003	(-0.020, 0.026)
Land. knowledge*Open habitat	**-0.053**	**(-0.093, -0.012)**
Land. knowledge*Dyad familiarity	**-0.140**	**(-0.269, -0.011)**
Dyad familiarity*Dist to caribou	0.162	(-0.238, 0.127)
Land. knowledge*Group size	**-0.137**	**(-0.212, -0.062)**

Coefficients for which the 95% CI did not overlap zero are shown in bold.

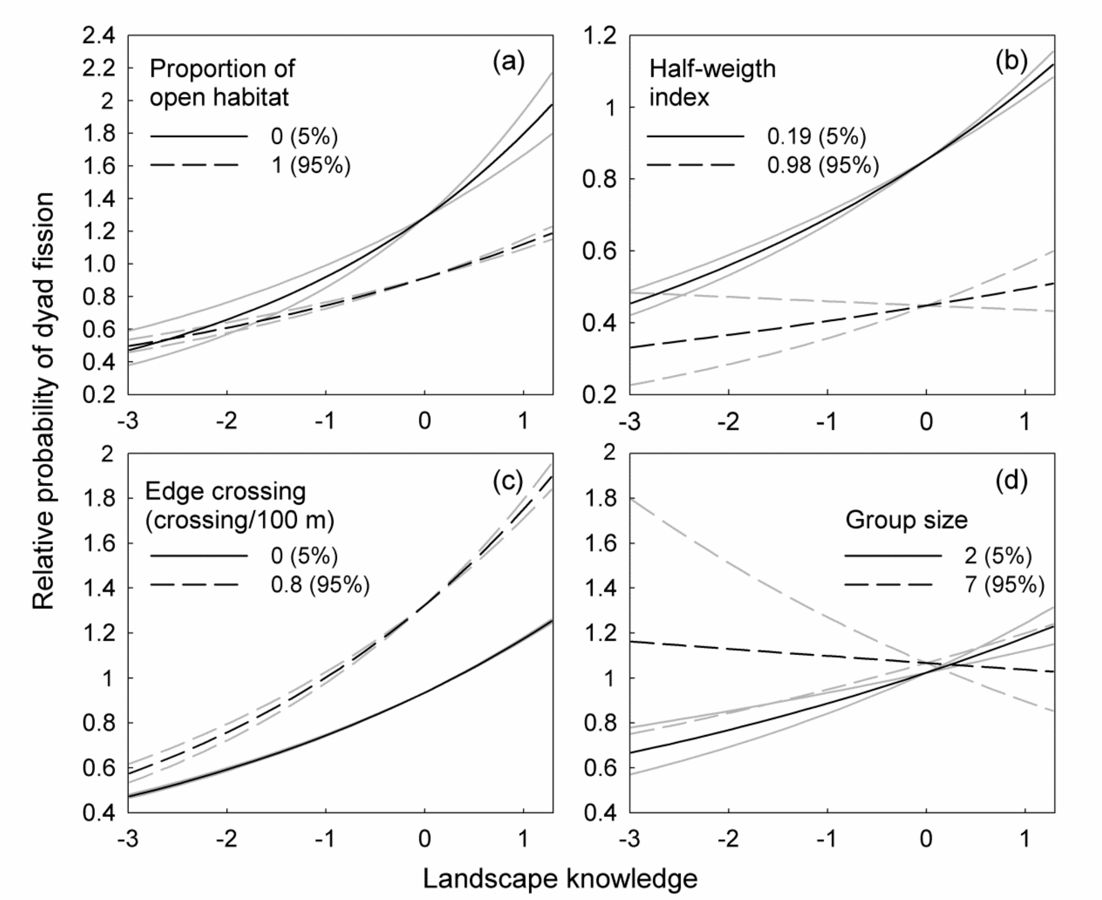

Figure 4.4. Interaction representing the effect of landscape knowledge with (a) proportion of open habitat, (b) the social bond between individuals, (c) edge crossing rate and (d) group size on the relative probability of dyad fission for Gaspésie caribou (Gaspésie, Canada), between 2013 and 2016. Only the 5% and 95% percentiles of the four variables are represented. Grey lines represent the 95% confidence interval.

3.6 Discussion

Our results highlight the importance of landscape knowledge for individual caribou in collective movement decisions, especially in a heterogeneous landscape. We found that animals responded differently to the landscape depending on previous experience and their social context. We empirically demonstrated that individuals moving in frequently used areas made decisions that were consistent with their preferences (i.e. habitat and dyadic member) even if those decisions caused the dyad to split.

Our findings reveal that landscape knowledge caused individuals to make fine adjustments in their social dynamics, thus supporting our hypothesis. Caribou transiting frequently used areas clearly showed a preference to stay with individuals with whom they had stronger bonds. With less previous knowledge of the landscape, caribou did not exhibit such behaviour; there was a low probability of leaving a dyad regardless of the bonds linking the dyad members. By choosing to stay with the group in unfamiliar areas, individuals have a greater opportunity to learn from other more informed caribou (Lamprecht, 1992; Beauchamp, 2000; Couzin *et al.*, 2005). Such behaviour is well known for semidomesticated reindeer *R. tarandus* (Paine, 1988) and for migratory caribou during the migration to calving grounds (Miller *et al.*, 1972; Torney *et al.,* 2018). However, staying with dissimilar individuals could lead to important conflicts in the timing of activities (e.g. feeding versus drinking behaviour) or the achievement of some movement destination resulting in fitness costs for dimorphic ungulate species (*Cervus elaphus*: Conradt, 1998; *Ovis canadensis*: Ruckstuhl, 1998, 1999). In altered landscapes, learning from other individuals also can be costly if the leaders make maladaptive choices (Sigaud *et al.*, 2017). For our data, there was a low probability of group fission for dyads composed of two strongly bonded and well-informed individuals. Similar individuals (e.g. sex, body condition and reproductive status) often share similar needs and stronger social bonds, possibly explaining that result (Djakovic *et al.*, 2012; Bercovitch and Berry, 2013; Carter *et al.*, 2013).

We found that landscape heterogeneity had complex effects on group dynamics. The highest fission probabilities occurred when dyads were in areas with a low or high edge density (i.e. our proxy of landscape heterogeneity). As theoretically reported by Sueur et al. (2011), the high fission probability in very heterogeneous landscapes could be explained by resource diversity and the conflict of interest that may arise between individuals. The high fission probabilities in homogeneous landscape could hypothetically be explained by the absence of a variety of resources locally that lead to fission in case of asynchronous needs. Indeed, if dyadic members had asynchronous needs in a homogeneous landscape, individuals could not access the resources locally or through short excursions away from the group, so they would have to leave the group and move to another patch where the necessary resource could be found. Also, in a homogeneous landscape, information sharing is less valuable as there are fewer opportunities to choose among patches of different quality and individuals can learn more rapidly. For a dyad found at intermediate levels of landscape heterogeneity, resources are more diverse and can longer support dyads formed by individuals with different needs. These animals could have acquired needed resources without leaving their groups, or they could have made only short excursions out of the group that were not detected by our sampling method (with 2 h or 3 h fix intervals). Finally, for landscapes with a heterogeneous patch structure, conflict between individuals could increase rapidly, as Sueur et al. (2011) predicted. A highly heterogeneous landscape contains numerous smaller patches with greater spatial variation in resources. This would promote group fission if the location of those patches was unknown or the acquisition of resources in those patches was limited by intraspecific competition. In support of this hypothesis, we found a positive relationship between edge crossing and fission probability.

Beyond heterogeneity, habitat characteristics, and more specifically the proportion of open habitat, also influenced the fusion–fission dynamics of dyads. Our results revealed that, when in open habitats, caribou remained in groups regardless of their familiarity with the patch. In our study area, caribou selected and used mostly open alpine habitats (Ouellet *et al.*, 1996; Mosnier *et al.*, 2003). This is a strategy that provides spatial segregation from the main predators, coyotes and black bear, as they use lower-elevation and more forested habitats (Mosnier *et al.*, 2003; Mosnier *et al*., 2008). Reduced predation risk associated with open habitat probably increased the duration of a dyad, even if individuals were not in a well-known patch. In the case of social species, such as caribou, grouping could be a part of an antipredator strategy (Banks, 2001; Kelley *et al.*, 2011). Cooperative defence is easier in open habitat where groups of individuals can detect the presence of predators and synchronize antipredator behaviour, including movement. In frequently used portions of the range, the fission rate was greater in closed rather than open habitat. Fortin et al. (2009) made similar observations for a bison population, showing that the crossing of edges between open to closed habitats increased the fission rate. In our case, however, we found that individuals were reluctant to leave a group in closed habitat if they were in an unfamiliar landscape. In a risky environment, the advantages of conspecific information and the potential ‘dilution effect’ could be greater than the cost of staying with the group in habitat not well suited for cooperative defence.

We only focused on fission events, not fusion, because leaving a group implies numerous consequences for predation risk, intraspecific competition and sharing information. Also, we suspected a high level of correlation between factors that explained fusion and fission events (i.e. fusion being the inverse of fission). With only 45% of the population monitored, all network analyses were also impossible as those analyses necessitate a larger proportion of the population identified at each observation (Whitehead, 2008). However, a more complete study including network components and fusion events would increase our understanding of group dynamics.

3.7 Conclusion

Our results highlight the importance of landscape knowledge in movement decisions for a species showing fission–fusion dynamics. In unfamiliar landscapes, caribou tended to remain together while they were more prone to make their own decision in frequently used areas or heterogeneous habitats with a high edge density even if it led to group break-up. As we did not collar all caribou in our study, individuals that decided to leave a dyad could potentially have followed other caribou. In such circumstances, the decision for the future destination could be a group rather than an individual choice. Such changes in movement and social decisions could have important consequences for species like caribou facing rapidly changing landscapes due to human land use and climate change (Hinzman *et al.*, 2005; Post and Forchhammer, 2008). This may be especially apparent when considering the risk of predation, an important limiting factor for many populations of woodland caribou (Wittmer *et al.*, 2005), including the Gaspésie population (Frenette, 2017). However, we do not have a complete understanding of how social interactions reduce predation risk, and how such behaviours may vary across season. More research is needed to disentangle the relative importance of individual and conspecific knowledge for social species, such as caribou, that now must navigate landscapes that are changing in the composition and configuration of habitats as well as altered predator–prey dynamics (Johnson *et al.*, 2015; Wittmer *et al.*, 2010).

3.8 Acknowledgments

We are grateful to C. Isabel and P. Lévesque for providing logistical support in the Gaspésie National Park, and to two anonymous referees for constructive comments on a previous version of this manuscript. Collaring caribou would have been impossible without the presence of excellent technicians and biologists on our team: B. Baillargeon, D. Grenier, J. Mainguy and G. Tremblay. This work was supported by the Fonds de Recherche du Québec – Nature et Technologies (FRQNT), the Ministère des Forêts, de la Faune et des Parcs du Québec, the Canada Foundation for Innovation (John R. Evans Leaders Fund Grant no. 26442 to M.-H. St-Laurent), the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grants 386661-2010 and 2016-05196 to M.-H. St-Laurent), the Société des Établissements de Plein Air du Québec, the Fondation de la Faune du Québec, the Consortium en foresterie Gaspésie-Les-Îles and the Université du Québec à Rimouski (Fonds Institutionnel de Recherche). F. Lesmerises was supported by a FRQNT scholarship and Fondation de l'UQAR grants.

Appendix

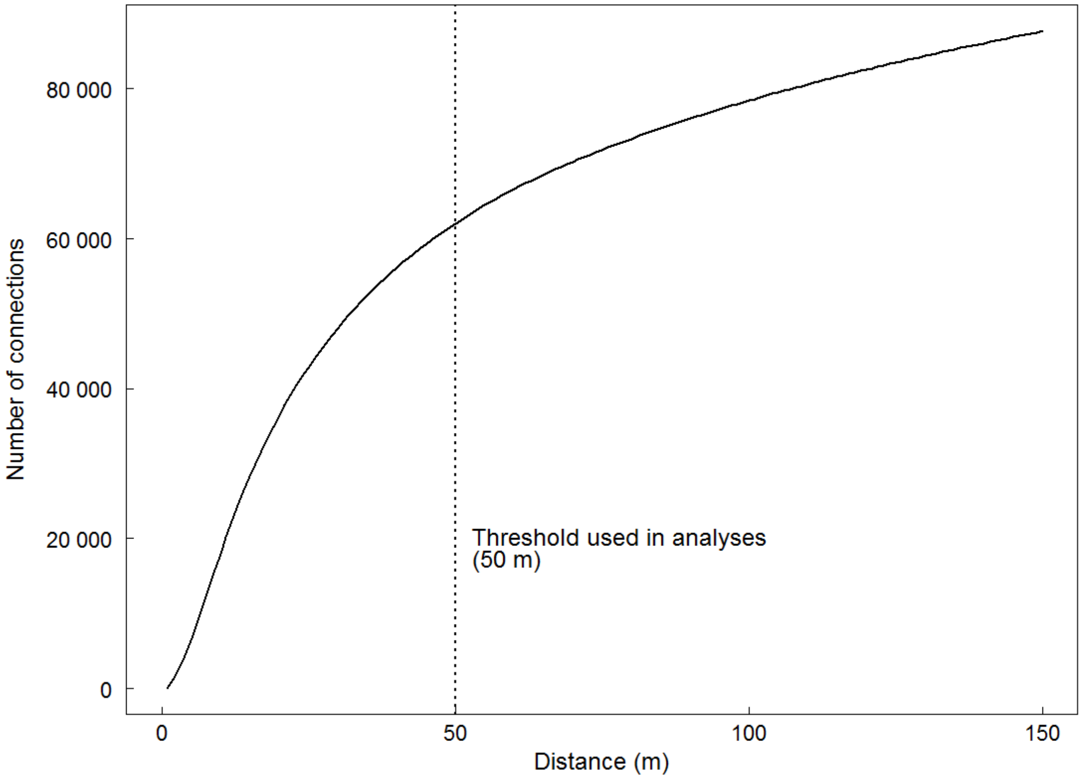

Figure A1. Number of connections (dyads) for individual woodland caribou in relation to the Euclidean distance for individual animals measured with GPS locations, in Gaspésie National Park, Canada, between 2013 and 2016.

CHAPITRE IV

EFFET DE LA MARGINALITÉ COMPORTEMENTALE SUR LA SURVIE DU CARIBOU

EFFECT OF BEHAVIOURAL MARGINALITY ON CARIBOU SURVIVAL

Frédéric Lesmerises, Chris J. Johnson, Martin-Hugues St-Laurent, soumis à *Ecosphere.*

4.1 Résumé

La variabilité comportementale interindividuelle a été étudiée pour un large éventail d'espèces. Cependant, peu de chercheurs ont considéré la marginalité, ou le degré auquel un choix fait par un individu est situé à une extrémité de la distribution de tous les choix possibles pouvant être fait par les individus composant la population animale en question, sur la valeur adaptative. Nous avons exploré l'effet de la marginalité comportementale sur la probabilité de survie des caribous des bois (*Rangifer tarandus caribou*). Pour ce faire, nous avons utilisé des colliers télémétriques GPS pour enregistrer les déplacements et la survie de 43 individus et distribuer leur comportement d’utilisation de l’espace le long de deux axes d’un cadrage multidimensionnel. Nous avons utilisé des modèles des risques proportionnels de Cox avec des variables temporelles en utilisant la formulation de Anderson et Gill, afin d’évaluer si la marginalité et la prédictabilité avaient un effet sur le risque de mortalité. La prédation était la principale cause de mortalité. Nous avons trouvé que les individus qui affichaient un comportement marginal avaient un plus fort risque de mortalité que les individus plus comformistes, excepté dans le cœur de leur domaine vital respectif, où les conformistes et les marginaux faisaient face à un risque similaire. Comme le caribou est une espèce sociale, partager une utilisation de l’espace commune est susceptible d’être une adaptation afin de minimiser les risques de prédation. Alternativement, être prévisible dans l’espace pourrait accroître la capacité des prédateurs à trouver et capturer une telle proie, expliquant l’augmentation des risques de mortalité dans le cœur des domaines vitaux des individus conformistes.

4.2 Abstract

Interindividual variability in behaviour has been studied extensively for a wide-range of species. However, few researchers have considered the fitness consequences of marginality, or the degree to which a choice made by an individual is located at one of the extremities of the distribution of all other choices made in a given animal population. We explored the effect of marginal behaviours on the probability of survival of woodland caribou (*Rangifer tarandus caribou*). To do so, we used GPS collars to record the movement and fate of 43 caribou and distributed their space use behaviour along two axes of a multidimensional scaling of environmental variables. We used Cox proportional-hazard models, with time-dependent variables incorporated using the counting formulation of Andersen and Gill, to evaluate if marginality and predictability had an effect on mortality risk. Predation was the primary cause of mortality. We found that individuals that exhibited marginal behaviour had higher mortality risk than more conformist individuals, except in the core area of their

respective home range, where conformist and marginal individuals faced similar risk. As caribou is a social species, sharing a common space use strategy is likely an adaptation for minimising the risk of predation. Alternatively, being predictable in space could increase the ability of predators to locate and capture such prey, explaining the increase of mortality risk in the core area of a conformist home range.

4.3 Introduction

Variability in behaviour is well documented in animal populations (Bolnick *et al.,* 2007; Calsbeek, 2008; Thurfjell *et al.,* 2017). For resource-limited populations or territorial species, intraspecific competition can lead to an increase in the diversity of resources that are used by individuals (Clutton-Brock *et al.*, 1982; Svanbäck and Bolnick, 2007) resulting in density-dependent natural selection and ultimately the evolution of ecological traits (Bolnick, 2004; Calsbeek, 2008). In other populations or species, variability in behaviour can be caused by intrinsic factors such as age (Thurfjell *et al.,* 2017), sex (Winnie and Creel, 2007; Body *et al.,* 2014; Patrick and Weimerskirch, 2014), and reproductive status (Steyaert *et al.,* 2016; Lesmerises and St-Laurent, 2017). According to the niche variation hypothesis, the magnitude of the inter-individual variability, defined as behavioural variation among individuals, is correlated with the width of the behavioural niche of the population (Bolnick *et al.,* 2007).

We define behavioural marginality as the degree to which a choice made by an individual is located at one of the extremities of the distribution of all other choices made by other individuals in that population. Marginal individuals, who exhibit rare behavioural phenotypes in a given population, may have access to alternative resources not used by more conformist individuals, therefore decreasing their competition with conspecifics (Maret and Collins, 1997; Swanson *et al.,* 2003).

Individuals can also adjust their behaviour according to the environmental and intrinsic conditions, especially in uncertain or changing environments (Woo *et al.*, 2008). In mountain goats (*Oreamnos americanus*), for example, the mating tactics and mate choices of males varied in relation with their age (Mainguy *et al.*, 2008). Some females from different species are also known to adjust temporarily their space use and activity budget to the proximity of human presence during the rearing period, in order to improve the survival of vulnerable juveniles (*Ursus arctos*: Steyaert *et al.*, 2016; *Rangifer tarandus*: Lesmerises *et al.*, 2017; *Alces americanus*: Berger, 2007). This capacity to temporarily adjust behaviour in response to changing environmental or intrinsic conditions is, however, highly variable among individuals, with some individuals showing more repeatability in their behaviours than others (Bell *et al.*, 2009; Stamps *et al.*, 2012). From a prey perspective, being predictable due to low intra- and inter-individual variability in space use and anti-predator tactics could increase the encounter risk with predators having good spatial memory, but could also increase collaborative defences for social prey species. For a conformist individual who adopts a consistent or the dominant space use strategy, synergic effects could arise between predictability in habitat choices and the intensity of use of a given area.

Through natural selection, species have evolved to adopt fitness-rewarding behaviour (Nilsen *et al.*, 2004). In a changing landscape, however, the behavioural strategies of individuals in a population may not maximise survival and fitness, at least in the short term. Maladaptive behaviours may occur when individuals are facing biotic and abiotic conditions that differ with those in which the species have evolved (Byers 1997; Aldridge and Boyce, 2007; Dussault *et al.*, 2012).

Space use integrates complex behavioural decisions based on intra- and inter-specific competition (Davis *et al.*, 2017), antipredator strategy (Thaker *et al.*, 2011; Palmer *et al.*, 2017), quality, quantity and configuration of resources (Lurz *et al.*, 2000; Marzluff *et al.*, 2004), and social structure (Fortin *et al.*, 2009; Lesmerises *et al.*, 2018a).

Consequently, space use can have important impacts on individual survival or recruitment (Brinkman *et al.,* 2004; Lafontaine *et al.,* 2017). A considerable number of studies have investigated the space use (Ouellet *et al.,* 1996; Schaefer *et al.,* 2000) and habitat selection (Apps *et al.*, 2001; Mosnier *et al.,* 2003) of woodland caribou (*Rangifer tarandus caribou*) and revealed high inter-individual behavioural variability. However, only a few studies have directly investigated the link between space use and individual fitness (e.g. Losier *et al.*, 2015; Lafontaine *et al.*, 2017) or between habitat selection and individual fitness (e.g. Dussault *et al.,* 2012; Leblond *et al.,* 2013, 2016).

Here, we investigated the relationship between intraspecific variation in space use and the probability of survival of adult woodland caribou. In particular, we explored that relationship relative to an individual's location on the marginal–conformist axis. The marginal–conformist axis represents the range of behavioural possibilities for an individual, ranging from the most unusual to the most common behaviours found in a population. As woodland caribou are a medium-sized herbivore with low reproductive productivity and relatively high vulnerability to predators, we hypothesize that natural selection results in the evolution of space use strategies that optimize adult survival and reproduction. The most common and conformist anti-predator strategy present in the population should result in the lowest mortality risk, even if alternative strategies could exist and yield similar survival rates. As an alternate hypothesis, in a changing landscape marginal behaviours could be a better strategy for adjusting to new environmental conditions. We predict that individuals that adopt such a marginal strategy should have a higher probability of survival.

4.4 Methods

4.4.1 Study area

The study area covered the range of the Gaspésie caribou population (48°50’N; 66°00’W) (Fig. 5.1). In total, the caribou range encompasses the McGerrigle Mountains in the east, which are dominated by Mount Jacques-Cartier (1268 m), and the Chic-Chocs Mountains in the west, which includes Mount Albert (1154 m) and Mount Logan (1128 m). The altitudinal gradient determines three ecological zones characterized by differences in vegetation type. The highest elevation zone (> 1050 m) is composed of alpine tundra, a mat of lichens, mosses and graminoids along with bare rocks and ericaceous shrubs. The subalpine forest (900–1050 m) is essentially a transition zone where tree height decreases with elevation, forming a krummholtz belt before transitioning to alpine tundra. Finally, the montane area (100–900 m) is represented by closed forest composed of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and birch (*Betula* sp.). In the past decades, intensive forestry practices around the Gaspésie National Park had largely reduced the proportion of mature conifer forests in favour of young mixed or conifer stands (Boudreau 2017).

Most caribou are found at elevations > 700 m and are subdivided into three groups (Ouellet *et al.*, 1996; Mosnier *et al.*, 2003), namely Albert (n = ~20 ind.), McGerrigle (n = ~27 ind.), and Logan (n = ~23 ind.) (Morin 2017). Moose, black bears (*Ursus americanus*), coyotes (*Canis latrans*) and a few white-tailed deer (*Odocoileus virginianus*) are also found in Gaspésie National Park. Coyotes, and to a lesser extent bears, are responsible for the majority of the predation events on caribou calves (Crête and Desrosiers 1995). Some evidence also suggests that coyotes could prey on adult caribou, as observed in Newfoundland (Bastille-Rousseau *et al.*, 2015). Wolves (*Canis lupus*) were extirpated from the south shore of the St. Lawrence River in the mid-1800s.

4.4.2 Caribou monitoring program

We used location data from GPS collars to quantify marginality and intra-individual variability in space use (i.e., variation in space use for a given individual throughout the study). Those data were collected from 2013 to 2016 during a GPS monitoring program that included 43 adult caribou (17 M, 26 F; corresponding to ~ 52% of the population in 2013) proportionally distributed amongst the three groups (i.e., Jacques-Cartier n = 28, Albert n = 6, Logan n = 9). Caribou were captured, fitted with GPS-Argos telemetry collars and followed for 2.5 or 3.5 years; collars were programmed to acquire locations every 2 (model TGW-4680-3, Telonics Inc., Mesa, Arizona) or 3 hours (model TGW-4680, Telonics Inc., Mesa, Arizona). To limit potential disturbances from helicopter activity and associated collaring activities, caribou capture occurred during two sessions of 22 and 21 animals in mid February 2013 and in early March 2014, respectively. We programmed the GPS collars to trigger a mortality signal after 6 hours of inactivity. We used transmitted GPS locations to identify the time of death and the locations of dead caribou. The delay between mortality and collar retrieval ranged from 2 days to ~2 months, but was usually ~ 1 or 2 weeks. The capture and collaring protocol was approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate # CPA-52-13-112) and of the Québec Ministry of Forests, Wildlife and Parks (certificate # CPA FAUNE 13-08).

4.4.3 Biological periods

The space use and mortality rates of caribou can vary seasonally (Rettie and Messier 2000; Briand *et al.*, 2009; Bastille-Rousseau *et al.*, 2016a). To accommodate these differences, we evaluated space use and marginality according to five biological periods (following Courtois, 2003): spring (April 15th to May 20th), calving (May 21st to June 20th), summer (June 21st to September 15th), rut (September 16th to October 31st), and winter (November 1st to April 14th).

4.4.4 Habitat characteristics

We used ecoforest maps to identify 13 landcover categories (Table 5.1). The minimum polygon size was 4 ha for forested stands and 2 ha for non-forested areas (e.g., lakes, bare rock, open conifer, etc.). We extracted the landcover category under each caribou location. Elevation is known to strongly influence the space use of Gaspésie caribou (Mosnier *et al.,* 2003); thus, we used a digital elevation model (20m x 20m cell) to identify the elevation of each caribou location. Due to the small sample of mortalities, we limited the number of covariates in our survival models (but used all landcover categories for assessing marginality, see next section), and only included the 'mature conifer' and 'alpine barren ground' (i.e. bare rock, shrublands and alpine wetlands) landcover types.

We calculated the minimum distance from the end of each caribou step to natural (river and stream) and anthropogenic (forestry road and trail) linear features. Due to the relatively low density of trails and roads in the Gaspésie National Park, we suspected a non-linear response to anthropogenic structures. We used a decay function [$\exp(-\alpha/\text{distance})$] to transform the measured distances (Lesmerises *et al.*, 2018b). We tested a range of α values (50, 100, 250, 500, 1000, 2000) and used Akaike's Information Criterion (AIC_c) (Burnham and Anderson, 2004) to select the α value that provided the most parsimonious model, after including factors for natural and anthropogenic disturbance (Lesmerises *et al.*, 2018b).

Table 5.1. Description of landcover categories used to explain the space use behaviour of woodland caribou, Gaspésie (Canada), between 2013 and 2016.

Habitat / Variable	**Description**
Alder stand	Alder stand > 2ha
Anthropogenic	Area with human footprint other than by forestry
Bare rocks	Alpine tundra and bare rocks
Forest cut	Cutblocks 0–20 years old
Krummholz	Non-commercial dwarf tree stand
Natural disturbance	Burned areas, windfall and insect outbreak stand < 20 years old
Old coniferous stand	Coniferous trees > 75% of basal area; > 60 years old
Old deciduous and mixed stand	Coniferous trees < 75% of basal area; >60 years old
Open coniferous stand	Open coniferous woodland (tree canopy closure < 25%)
Shrubland	Alpine shrubland
Wetlands	Wetlands
Young coniferous stand	Coniferous trees > 75% of basal area; < 60 years old
Young deciduous and mixed stand	Coniferous trees < 75% of basal area; < 60 years old

4.4.5 Behavioural marginality and intra-individual variability

We connected successive GPS locations with linear segments; each segment represented a movement ‘step’. We used those steps to represent the exposure of individual caribou to factors that were hypothesized to influence mortality. To assess the influence of behavioural marginality on the survival of caribou, we first calculated, for each biological period and each year, the individual percentage of GPS location in each of the 13 landcover categories. We then used a nonparametric multidimensional scaling (MDS) (vegan package) routine to spatially distribute the seasonal space use strategies of individual caribou into two dimensions (Fig. 5.1). Each object in the MDS represents an individual-year. Individual-years with similar space use are closer than individual-years with different space use. We used the individual-year locations and a kernel density estimator (kernelUD library adehabitatHR) and the “href” calculation of the smoothing factor, for each subpopulation and period to calculate the ecological distribution of the monitored caribou (values ranging from 0 to 100). We then extracted the kernel value for each individual-year (Fig. 5.1). For a given year, an individual showing ecological space use strategy adopted by many other individuals had a value near 100, while an individual showing a strategy completely different had a value close to 0. In order to estimate the behavioural marginality, we subtracted the kernel value from 100. Therefore, a marginal individual had a higher value of behavioural marginality, while a conformist caribou had a smaller value. We also calculated the standard deviation of marginality values for each animal to assess the intra-individual variability in their ecological space use strategy among biological period and year. We removed individuals from the analysis if they were monitored for less than 3 biological periods; this provided a more robust measure of the variability in behavioural marginality among biological periods.

4.4.6 Spatial predictability

Knowing that canids have an excellent spatial memory (Fujita *et al.*, 2012; Broadway *et al.*, 2017), we evaluated the spatial predictability of caribou and included this variable in our survival analyses. We assumed a relationship between the intensity of use of a given area by caribou and the predictability of space use for a predator. We used the kernel method (kernelUD in 'adehabitatHR' package, Calenge 2015) to estimate the home range of each caribou and extracted the mean kernel value under each caribou step. We used that measure as an index of the intensity of use.

4.4.7 Survival analyses

We used Cox proportional-hazard models, with time-dependent variables incorporated using the counting formulation of Andersen and Gill, to evaluate if marginality and predictability had an effect on mortality risk (Johnson *et al.*, 2004). Intra-individual variability in behavioural marginality as well as spatial predictability were calculated for the life of the individual; marginality was calculated for each biological period, while distances to linear structures and habitat proportions were calculated for each time step. We added the subpopulation, the biological period and the year as random factors. We built different candidate models in accordance with our hypotheses and ranked them with AIC_c (Table 5.2). In each model, we included the sex as covariate because mortality rates are usually higher for male in *Rangifer* (Frenette, 2017). We used the '*coxme*' package (Therneau, 2015) for the Cox proportional-hazard model and the R 3.3.3 statistical software (The R core Team 2017) for all statistical and spatial analyses.

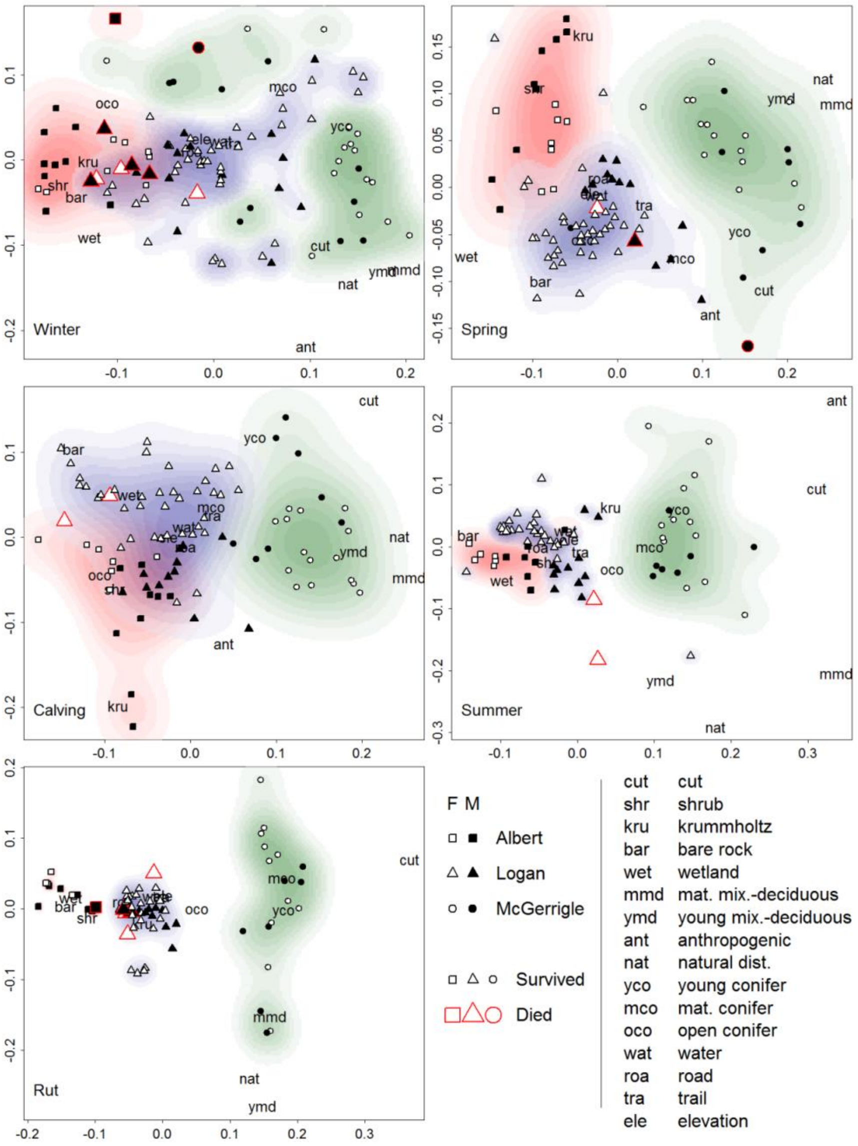

Figure 5.1. Two-dimensional distribution, using MDS, of the space use strategies adopted by the Gaspésie caribou during the five biological periods, between 2013 and 2016. Each symbol represents an individual-year. Kernel densities were generated for each subpopulation (Albert: red, Logan: green, McGerrigle: blue). Symbols with a red border indicated that an individual died during this biological period. The different habitat attributes associated with space use were shown using abbreviations listed in the legend.

Table 5.2. Candidate Cox proportional hazards models explaining mortality risk of caribou from the Gaspésie caribou population, between 2013 and 2016. The ranking was based on the AIC_c. Log-likelihood (LL) and difference in AIC_c values (ΔAIC_c) are presented. The most parsimonious model is noted with bold font.

	Model	LL	Δ AIC_c
1	Sex + Dist. to water + Dist. to road/trail	-41.889	8.908
2	Model 1. + Open habitat + Mature conifer	-40.730	9.997
3	Model 1. + Marginality + Intensity of use	-37.987	2.555
4	Model 1. + Intra-individual variability+ Intensity of use	-38.923	6.404
5	Model 3. + Intra-individual variability	-36.783	2.797
6	**Model 2 + Marginality + Intensity of use + Marginality * Intensity of use**	-36.523	**0.000**
7	Model 1 + Intra-individual variability + Intensity of use + Intra-individual variability * Intensity of use	-38.169	6.091

4.5 Result

Of the 43 monitored caribou, 22 (11 F; 11 M) died during the study, and mortality events occurred mostly in winter (3 F; 6 M) and rut (3 F; 3 M). Three mortalities (2 F; 1 M) were removed from the analysis as those individuals survived less than the three biological periods necessary to calculate intra-individual variability in behavioural marginality.

The three subpopulations showed different ecological space use patterns, and these patterns changed according to biological period (Fig. 5.1). Conformist individuals from the McGerrigle subpopulation used high elevation and open habitat (bare rock and open conifer) more than those from the Logan subpopulation who were found more in forested landscape. Conformist individuals from the Albert subpopulation used landcover categories in a similar way as those from the McGerrigle with the exception of using shrublands and wetlands more frequently.

Table 5.3. Coefficient (β) and 95% confidence intervals of the most parsimonious Cox proportional hazards model explaining the mortality risk of the Gaspésie caribou, between 2013 and 2016. Coefficients for which the 95% CI did not overlap zero are shown in bold.

Variables	Coefficient	95% C.I.
Sex – Male	0.3100	[-0.7533, 1.3732]
Dist. to water (m)[1]	**-0.0062**	**[-0.0101, -0.0023]**
Dist. to road/trail[1,2]	2.4993	[-0.1937, 5.1922]
Marginality	**0.0811**	**[0.0210, 0.1412]**
Intensity of use	**0.0805**	**[0.0246, 0.1364]**
Marginality*Intensity of use	**-0.0009**	**[-0.0018, -0.0001]**

[1] A positive coefficient means a mortality risk lower near the linear structure

[2] Distance transformed using a decay function (α = 500)

The most parsimonious model explaining mortality risk included linear features and the interaction between marginality and intensity of space use (Table 5.2). This model was more parsimonious than the second best model that included a covariate representing intra-individual variation. According to our best model, marginal individuals had a higher mortality risk than conformists, but this relationship was modulated by the location of the individual in its home range (Table 5.3). Conformists had a lower risk of mortality in parts of their home range they used less while their mortality risk was not significantly different from marginal individuals in the core area of their home range (Figure 5.2). For a given level of marginality, individuals were at higher risk in the core of their home range than in the area less frequently used. We also found that mortality was more likely (one-tailed *t*-test; $t_{1.163}$ p = 0.06) for individuals with a more marginal behaviour (i.e. greater intra-individual variability) even if there was a high variance between individuals (Figure 5.3). Indeed, 12 individuals showed a higher marginality value during the period they died than their average marginality, while 9 individuals showed the opposite pattern. Contrary to our expectations, caribou had a greater risk of dying near lakes and rivers while being safer near roads and hiking trails (Table 5.3).

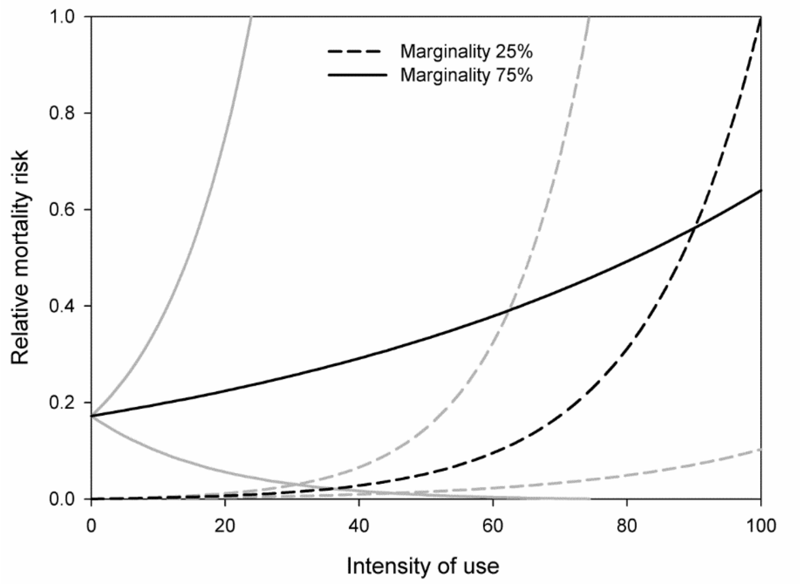

Figure 5.2. Interaction between marginality and intensity of use explaining mortality risk according to the most parsimonious Cox proportional hazards model for Gaspésie caribou, between 2013 and 2016. Gray lines represent the 95% confidence interval of the interaction.

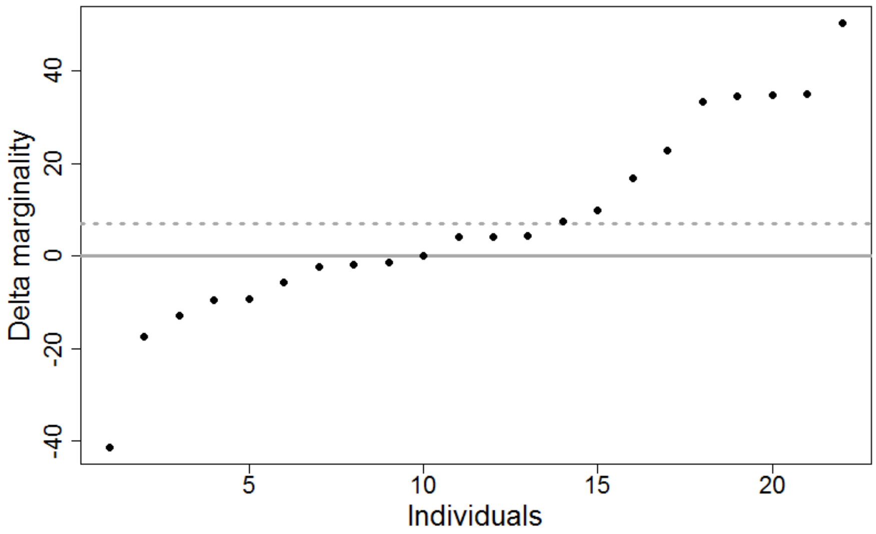

Figure 5.3. Difference between marginality values when Gaspésie caribou died and their mean marginality during the study (2013-2016). Individuals are sorted from the lowest to the highest values of the difference (delta) in marginality Dotted line represents the average of the delta in marginality.

4.6 Discussion

Our results highlighted the influence of behavioural marginality on ungulate survival. We found that even in a landscape altered by forestry, conformist caribou tended to have, on average, a lower mortality risk than marginal individuals (Fig 5.3.). However, the intra-individual variability (i.e. width of individual marginality) did not appear to significantly modulate the mortality risk in our study (Table 5.2). These results provide little support for our hypothesis that rapid environmental change favours ecological strategies that differ from the most common or conformist behaviour.

From an evolutionary perspective, our findings support the conclusions of other studies that suggest that intraspecific competition is an important driver of the persistence of marginal behaviour in a population (Clutton-Brock *et al.*, 1982; Svanbäck and Bolnick, 2007). Historically, the Gaspésie caribou occurred at a low density suggesting relatively little competition for nutritional resources (Ouellet *et al.,* 1996). Intraspecific competition was probably even lower during our study due to the decline of the population since 1996 (from 125 to 80 individuals, with a peak at ~150 in 2007, Morin 2017). Theory suggests that a continuing reduction in intraspecific competition would favour conformist not marginal behaviours.

In our study, conformist caribou had greater survival than marginal individuals. Although space use choices and landscape characteristics differed between subpopulations and biological periods, the results strongly suggest that choosing a space use strategy commonly adopted by other individuals will result in better survival. This result also suggests that density-dependence is an important mechanism influencing survival over generational periods, assuming that caribou exhibiting similar use of the various landcover types are also spatially close to each other. This assumption is nevertheless plausible considering the high sociality of Gaspésie caribou (Lesmerises *et al.*, 2008b) and the relatively low availability of suitable montane habitat in the population range. Wittmer et al. (2005) found an increase in the growth rate of caribou populations with their population size and density, suggesting a potential Allee effect. In this study, we found a similar relationship at the scale of the individual animal. Caribou that adopted the space use patterns of the majority were more likely to survive when compared to individuals that adopted marginal behaviours. We did not explore the mechanisms that explained this pattern, but perhaps caribou are more effective in avoiding or defending against predators following some minimum population density or group size. The lower survival probability for individuals showing marginal behaviour could also be an indirect outcome of their personality, as marginality may be correlated with individual traits, such as boldness, known to influence prey vulnerability (Santos *et al.,* 2015).

Our results did not suggest that intra-individual variability in behavioural marginality had a strong influence on survival. The second best Cox regression model included intra-individual variability as a covariate, but there was relatively little effect on mortality risk. The environment, in particular weather, varied within and among years and harsh winter conditions were known to influence the survival of mountain caribou (Hegel *et al.,* 2010). Thus, intra-individual variability in behaviour might be an adaptive response to short-term changes in weather. The lack of an effect suggests that such variability was accommodated uniformly by caribou or weather had relatively little influence on the fitness of individuals in this system.

Caribou had a greater probability of dying in the core of their home range, where they are more predictable for coyotes and bears, the main predators for this population (Crête and Desrosiers, 1995). This relationship was stronger for conformist individuals that were more predictable in habitat choices and potentially occurred at a higher density since caribou is a social species. These results are consistent with the known distribution and hunting behaviour of predators found across the range of the Gaspésie caribou (Messier *et al.,* 1986; Crête and Desrosiers, 1995; Murray and St-Clair, 2017).

More generally, predators increase the likelihood of encounter with a potential prey, by first selecting large range-size areas with a relatively high density of prey (Kunkel and Pletscher, 2001; Sims *et al.,* 2006; McPhee *et al.,* 2012). At a finer scale, predators select habitat types or topographic features where their prey are more vulnerable (Hopcraft *et al.,* 2005; Balme *et al.,* 2007; Whittington *et al.,* 2011). A prey that demonstrates fidelity in space and time increases its knowledge of the distribution of resources and risks, which could have some benefits for fitness (Schmidt, 2004; Forrester *et al.,* 2015), but that strategy may also result in greater predictability and reduced search times for predators. Similarly, Lafontaine et al., (2017) argued that female caribou with a high fidelity to their wintering ranges in the boreal forest were more predictable to wolves. In this case, predictability in space (i.e., in the core of their home range), resulted in a higher risk of mortality.

Our results suggested that linear features influence mortality risk. Unlike past studies, however, natural, not anthropogenic, linear features were the main driver of risk (DeMars and Boutin, 2018; Dickie *et al.*, 2017). For the Gaspésie population, anthropogenic linear features tended to increase, not decrease, adult survival, a finding opposite to other reported results (Whittington *et al.*, 2011; DeMars and Boutin, 2018). Our results could support the human-shield-against-predation hypothesis, as reported for other species (Berger, 2007; Steyaert *et al.*, 2016). Human activities along trails and roads in the National Park could have created a refuge for caribou. A companion study showed that females with calves decreased their vigilance time when hikers were present (Lesmerises *et al.*, 2017). Furthermore, our study was conducted in a National Park with very few anthropogenic features. In such cases, predators could take advantage of natural linear features, such as creeks and streams, as they are more uniformly distributed and less likely to have human presence.

4.7 Conclusion

We used an innovative approach to explore the influence of intraindividual and intraspecific behavioural choices on survival. Our results suggested that not all space use behaviours of caribou were equal in terms of mortality risk. We found that conformist individuals had greater survival relative to individuals that demonstrated atypical space use. Caribou is a social species; thus we anticipate some level of conformist behaviour. Such a strategy may assist with acquiring forage and avoiding or evading predators (Lesmerises *et al.*, 2018b). However, being predictable in space may provide some advantage to the predators, explaining the increase in mortality risk when caribou were located in the core area of the conformist home range. Further studies are necessary to understand how such marginal behaviours persist for populations such as the Gaspésie caribou where intraspecific competition is unlikely to be a driver of individuality and marginal behaviours. This includes an investigation of plausible mechanisms, including heritable or learned maternal behaviours, body condition, parasitism, and the dynamic nature of predation.

4.8 Acknowledgments

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CONCLUSION GÉNÉRALE

L'objectif principal de cette thèse était de mieux comprendre l'influence de l'hétérogénéité du paysage, qu'elle soit due à des phénomènes naturels ou anthropiques, sur différentes facettes de l'écologie du caribou de la Gaspésie (voir Figure 1.1). Grâce à l'utilisation des données télémétriques provenant de près de la moitié de la population, j'ai été en mesure d'obtenir une réponse très représentative de la population étudiée. L'ajout de données comportementales issues de l'observation des caribous de deux des trois sous-groupes géographiquement distincts a permis une meilleure compréhension des réponses du caribou face aux différents stresseurs opérant dans son aire de répartition. Nous avons également utilisé avantageusement les données de caméras automatisées installées le long des différents sentiers du parc national de la Gaspésie afin d'obtenir une résolution extrêmement fine de la distribution spatiotemporelle des randonneurs, une des principales perturbations anthropiques ayant cours dans le cœur de l'aire de répartition du caribou de la Gaspésie. Ainsi, en combinant l'ensemble de ces données, dont certaines ont été recueillies pendant presque quatre années, nous avons pu répondre adéquatement à nos objectifs initiaux, soit de lier l'hétérogénéité spatiotemporelle (naturelle ou anthropique) du paysage au budget d'activité (chapitre 1), aux déplacements (chapitre 2), à l'utilisation de l'espace (chapitre 2), à la dynamique des groupes sociaux (chapitre 3) et à la survie individuelle (chapitre 4) des caribous de la Gaspésie. Nos résultats ont permis d'approfondir les connaissances disponibles quant aux réponses du caribou face aux différents éléments du paysage, de précieuses informations pour les responsables de la conservation d'espèces sensibles au dérangement et à la modification rapide du paysage. Le portrait des réponses comportementales, sociales et populationnelles que nous avons dressé est d'ailleurs le plus complet à ce jour pour cette population.

Retour sur les principaux thèmes abordés dans la thèse

Compromis acquisition des ressources alimentaires – risque de prédation

Les compromis à faire entre les opportunités alimentaires et le risque de prédation sont à la base de nombreuses décisions faites par des espèces proies, tant dans leur budget d'activité (Ruckstuhl, 1998; Lesmerises *et al.*, 2017) que leur utilisation de l'espace (Cowlishaw, 1997; Winnie et Creel, 2007). La différence de valeur adaptative entre les conséquences d'être tuée par un prédateur et celles résultant du gain d'énergie potentiel devrait expliquer, du moins partiellement, l'évolution et l'adaptation de ces comportements (Brown, 1988, 1992; Abramsky *et al.* 2002). En Gaspésie, les caribous subissent une pression de prédation très élevée, particulièrement les faons, ce qui rendrait peu probable la persistance de la population à long terme (Lesmerises, 2012; Frenette, 2017). Malgré une survie adulte variant de « moyenne » à « satisfaisante » lorsque comparée à d'autres populations de caribous au Canada (Wittmer *et al.*, 2005), le recrutement s'avère trop variable et trop faible pour assurer l'apport d'un nombre suffisant d'individus sur une base annuelle (Lesmerises, 2012; Frenette, 2017). Nous avons décelé différentes stratégies comportementales au sein de la population qui semblent déplôyées pour tenter d'atténuer cette pression de prédation. Toutefois, nos résultats ont suggéré que l'ajustement comportemental ne semble pas fait au détriment de l'apport énergétique, particulièrement pour les femelles suitées qui ont des dépenses énergétiques extrêmement importantes durant la lactation (Parker *et al.*, 2009). Celles-ci diminuaient leur vigilance en présence de randonneurs à proximité, au profit de comportements de quête alimentaire. Bien que nous n'ayons pas testé les mécanismes sous-jacents à ce résultat, l'hypothèse du bouclier humain contre les prédateurs (lib. de

« Human shield » Berger, 2007; Steyaert *et al.*, 2016) permettant cette diminution de la vigilance au sein du refuge s'avère plausible. À l'inverse, les femelles n'ayant pas mis bas ou qui avaient perdu leur faon en cours de saison, augmentaient leur taux de vigilance à proximité de randonneurs. Leurs besoins alimentaires et le risque de prédation auxquels elles font face étant plus faibles, ces femelles pouvaient accorder davantage d'énergie à l'atténuation du stress pouvant être occasionné par les randonneurs, tel qu'observé dans d'autres études (Frid et Dill, 2002; Thiel *et al.*, 2008; Rehnus *et al.*, 2013).

Variabilité intra- et interindividuelle

Nous avons mis en évidence l'importance de la variabilité intra- et interindividuelle dans le comportement du caribou, un hervivore parfois considéré spécialiste par certains auteurs, en ce qui a trait à l'utilisation des habitats et des ressources alimentaires (Thomas *et al.*, 1996; Polfus *et al.*, 2011). Ces différences pouvaient s'expliquer par la présence de faon (Chapitre 1), par le degré de connaissance du milieu (Chapitre 3), mais aussi par des choix personnels faits par chaque individu dans les patrons d'utilisation de l'espace (Chapitre 4). Nous avons démontré que les individus déviant le plus des comportements adoptés par la majorité (c.-à-d., les individus marginaux) couraient davantage de risques de mourir. L'approche novatrice utilisée a mis en évidence l'aspect important – quoique rarement étudié – de la position de la niche comportementale de l'individu par rapport à la plage comportementale de la population. Au-delà de contraster des différences comportementales entre les individus, nous avons directement lié ces différences à la survie individuelle, un des aspects les plus importants pouvant expliquer, avec le succès reproducteur, la persistance d'une espèce ou d'une population.

Notions d'échelles

Nos différents résultats appuient l'hypothèse voulant que la réponse comportementale exprimée par une espèce puisse différer selon l'échelle étudiée (DeCesare *et al.*, 2012). Tel que discuté en introduction, la notion d'échelle, bien que souvent utilisée pour des phénomènes spatiaux et/ou temporels, peut être également applicable aux réponses biologiques d'une espèce face à différentes modifications du territoire (Johnson et St-Laurent, 2011). Par exemple, les ajustements du budget d'activité des différentes femelles n'étaient pas corrélés aux patrons d'utilisation de l'espace. En effet, avoir ou non un faon n'a pas influencé, du moins de façon importante, la diminution du temps passé près des sentiers en présence de randonneurs chez les femelles étudiées. Plusieurs études ont également rapporté que la présence de randonneurs induisait généralement une réaction de déplacement des femelles vers des secteurs moins perturbés tant chez le caribou que le renne (Nellemann *et al.*, 2000; Reimers et Colman, 2009; Leblond *et al.*, 2013). Ainsi, l'utilisation des 100 premiers mètres le long des sentiers diminuait d'environ 60% entre les périodes où les sentiers étaient fermés aux randonneurs et celles où les sentiers étaient ouverts aux randonneurs et durant lesquelles des randonneurs se trouvaient à proximité des caribous. Ces deux résultats supportent la nécessité de s'attarder à différents éléments le long de l'échelle biologique des réponses aux perturbations afin de mieux documenter la réponse complète d'une population. Certes, les femelles avec faons semblaient profiter de la présence de randonneurs pour s'alimenter davantage, mais la perturbation était assez majeure pour induire un évitement du sentier. Leur niveau de tolérance envers les humains ne semblait pas suffisant pour demeurer à long terme à proximité de randonneurs. Les individus quittaient donc rapidement après leur phase d'alimentation.

Globalement, la proximité de sentiers (ski et randonnée pédestre) et de chemins forestiers dans leurs déplacements quotidiens ne semblait toutefois pas être un frein à la survie des individus (Chapitre 4). Contrairement à ce qui est observé chez d'autres populations de caribous (Whittington *et al.*, 2011; DeMars *et al.*, 2018), les rares structures linéaires présentes dans le parc de la Gaspésie semblaient plutôt avoir un effet positif, bien que marginal, sur la probabilité de survie des individus (Chapitre 4). Probablement trop rares et trop fréquentées par les skieurs et randonneurs, les structures anthropiques n'ont pas été utilisées par les prédateurs, du moins efficacement, pour traquer le caribou, alors que le contraire était observé avec les cours d'eau. En effet, les caribous avaient une plus grande probabilité de mourir près des cours d'eau. Newton et al. (2017) ont d'ailleurs démontré, chez le loup, cette relation positive entre la densité de structures linéaires anthropiques et leur utilisation, au détriment de l'utilisation des cours d'eau. Dans notre étude, près de 85% des mortalités sont survenues à moins de 150 m d'un cours d'eau et plus de la moitié étaient à moins de 50 m. À titre comparatif, la médiane de distance minimale des mortalités à une structure linéaire anthropique étaient de près de 2 km, dont une seule mortalité située à moins de 500 m. L'analyse des risques proportionnels de Cox a l'importance des cours d'eau comme facteur explicatif du risque de mortalité des individus suivis (Chapitre 4). À la lumière de ces différents résultats (c.-à-d., baisse de la vigilance chez les femelles avec faon, augmentation de la survie adulte à proximité des sentiers combiné à la forte diminution de la survie à proximité de structures linéaires naturelles), la présence de randonneurs et de skieurs le long des sentiers semblait effectivement offrir un refuge partiel contre la prédation, comme il a été observé chez d'autres espèces (orignal : Berger, 2007, ours brun : Steyaert *et al.*, 2016). Ce refuge n'a toutefois pas semblé suffisant à contrer les faibles survies adultes et juvéniles observées durant la même période de temps et corrélées à l'abondance régionale de coyotes (Frenette, 2017; Lesmerises et St-Laurent, 2018).

Nous nous sommes également intéressés à différentes échelles spatiotemporelles afin d'avoir une réponse plus globale du phénomène étudié (Mayor *et al.*, 2009; DeCesare *et al.*, 2012). Nous avons analysé les déplacements des caribous à proximité de perturbations (fine échelle spatiale) en considérant différentes phases du jour (fine échelle temporelle) (Chapitre 1 et 2), tout comme l'évitement à l'échelle du domaine vital (large échelle spatiale) sur plusieurs mois (large échelle temporelle) (Chapitre 2). Les résultats démontrent un ajustement fin des caribous, tant au niveau du budget d'activité que dans leurs déplacements, face aux variations des différents stresseurs environnementaux, mais témoignent également d'un évitement global des secteurs davantage perturbés à l'échelle saisonnière. À l'échelle de la vie de chaque individu, l'utilisation des différentes ressources à l'intérieur de leur domaine vital a influencé le risque de mortalité, soulignant l'importance des décisions comportementales réalisées (Chapitre 4).

Nos résultats ont aussi montré l'importance de s'intéresser à l'intensité des perturbations pour bien comprendre l'intensité de la réponse exprimée par une espèce animale. Par exemple, une distance moindre à un sentier et un nombre plus important de randonneurs engendraient une augmentation de la vigilance des femelles sans faons (Chapitre 1). De plus, une augmentation du nombre de skieurs hors-piste modulait à la hausse l'évitement du domaine skiable, ce qui entraînait un déplacement des caribous du domaine skiable vers des altitudes plus faibles (Chapitre 2). Cette fuite était d'autant plus rapide et importante que le nombre de skieurs était grand. Bien que cette modulation de la réponse animale à l'intensité d'une perturbation soit connue (p. ex. : Leblond *et al.*, 2013; Lesmerises *et al.*, 2013), une augmentation aussi marquée face à une perturbation d'aussi faible intensité que la simple présence de quelques skieurs hors-piste dans une zone de plusieurs hectares, est relativement nouvelle.

Contributions appliquées

En se basant sur le comportement, la distribution et la survie d'une population en danger d'extinction, notre étude a contribué à faire avancer les connaissances nécessaires à la conservation de cette population, mais également à la conservation d'autres populations de caribous au Canada, voire même d'autres espèces sensibles au dérangement humain. En effet, dans notre aire d'étude, seule quelques études comportementales basées sur l'observation directe (Moisan, 1956; Dumont, 1993) ainsi que quelques campagnes de suivis télémétriques VHF, technologie peu précise pour estimer les déplacements des caribous, avaient été réalisées dans les années 1990 (Ouellet *et al.*, 1996; Mosnier *et al.*, 2003). Ailleurs au Canada, les chercheurs travaillant à la conservation du caribou se sont davantage penchés sur des perturbations majeures, telles que les routes (Dyer *et al.*, 2002; Whittington *et al.*, 2011; Leblond *et al.*, 2013), la foresterie (Terry *et al.*, 2000; Schaefer et Mahoney, 2007; Hins *et al.*, 2009), l'exploitation des ressources minières et pétrolières (Dyer *et al.*, 2001; Boulanger *et al.*, 2012) ou encore à leurs effets cumulés (Sorensen *et al.*, 2008; Polfus *et al.*, 2011). Seulement quelques études se sont attardées aux impacts des activités récréotouristiques, pourtant omniprésentes dans les aires de répartition des différents populations de caribous (p. ex. : Duchesne *et al.*, 2000; Seip *et al.*, 2007). Nos résultats ont permis de mieux distinguer l'effet des randonneurs et des skieurs sur le comportement des caribous. Ainsi, nous avons montré que même un petit nombre de skieurs pouvait engendrer une perte fonctionnelle non négligeable d'habitat autour du domaine skiable. Notre étude montre que les caribous s'ajustaient relativement rapidement à l'arrêt des activités humaines, ce qui contraste avec les patrons d'évitement tout au long de l'année observés entre autres chez la chèvre de montagne (Richard et Côté, 2015). Ces differences suggèrent que l'habituation ou la tolérance à une perturbation est complexe et peut varier entre les populations et les espèces.

En Gaspésie, l'évitement de la présence humaine pourrait induire un risque de prédation plus élevé sur les caribous, puisque ces derniers se réfugiaient en plus basse altitude, là ou la probabilité d'occurrence du coyote est plus importante (Mosnier *et al.*, 2008; Gaudry, 2013). La présence potentielle de refuges contre les prédateurs qui semble liée à la présence humaine le long des sentiers n'a pas semblé être suffisante pour assurer une survie adulte et juvénile suffisante à maintenir une croissance de la population (Frenette, 2017; Lesmerises et St-Laurent, 2018). Même si nos résultats ne semblent pas avoir démontré d'effet négatif (voire même un effet bénéfique marginal) de la présence de sentiers et de chemins sur la survie, nous sommes convaincus que l'ouverture du territoire à un plus grand nombre de sentiers offrirait un avantage aux prédateurs, tel qu'observé dans d'autres systèmes d'étude (DeMars *et al.*, 2018; Newton *et al.*, 2017). L'absence d'effet significatif des sentiers et des chemins forestiers sur la survie des caribous est probablement liée à leur faible densité dans le parc, ce qui rend difficile la traque du caribou. En ce sens, nos résultats sont relativement nouveaux et laissent envisager que la diminution de la densité de structures anthropiques dans les aires de répartitions d'autres populations de caribou pourrait avoir un effet bénéfique. Finalement, nos travaux ont résulté en une cartographie bimensuelle des différents secteurs fortement utilisés par le caribou tout au long de l'année (résultats connexes non inclus dans cette thèse). De tels outils ont été offerts aux gestionnaires du parc national de la Gaspésie afin d'ajuster l'offre d'activités récréotouristiques à la distribution spatiotemporelle du caribou. À ce titre, les résultats issus de ce travail doctoral ont d'ailleurs été salués par les gestionnaires du Parc national de la Gaspésie, de la Société des Établissements de Plein-Air du Québec et du Ministère des Forêts, de la Faune et des Parcs du Québec; nous avons bon espoir qu'ils seront considérés dans l'élaboration de différentes mesures de conservation dans un prochain futur.

Contributions théoriques

Au-delà de leur portée en écologie de la conservation, les résultats issus de cette thèse apportent différentes contributions davantage théoriques. La science étant avant tout une accumulation de diverses petites contributions, cette thèse n'y fait pas exception. Une des principales contributions de ma thèse – liée au premier objectif de celle-ci – est d'avoir pu relier les impacts au niveau du paysage aux différentes facettes de l'écologie d'une même population afin d'avoir une réponse plus complète du caribou (*sensu* Johnson et St-Laurent, 2011). Largement discutés tout au long du présent document, nous avons mis en évidence des changements importants dans les réponses du caribou tout au long des échelles biologiques et spatiotemporelles étudiées et d'un gradient d'intensité des perturbations anthropiques, tout en ciblant les conséquences des comportements adoptés par les caribous à l'étude.

Ajustements et délais dans la réponse comportementale

Dans ma thèse, j'ai exploré de nouveaux horizons ou utilisé des méthodes novatrices pour explorer des concepts connus. Dans les chapitres 1 et 2, davantage appliqués, j'ai également fait quelques avancées en écologie animale. Par exemple, nos résultats montrent un certain ajustement des caribous femelles à la présence humaine. En effet, les femelles suitées semblaient utiliser la présence de randonneurs à proximité pour optimiser leur acquisition de ressources alimentaires. Ces résultats suggèrent que même une espèce sensible au dérangement humain qui évite normalement la présence de randonneurs ou de skieurs (Reimers *et al*,. 2003), peut ajuster son comportement selon d'autres contraintes, comme par exemple la demande énergétique et la prédation. L'analyse temporelle des réponses comportementales du caribou a aussi montré que l'évitement des activités humaines pouvait se répercuter de quelques heures à quelques jours. Cette modulation de l'évitement des skieurs et randonneurs à court et moyen terme par le caribou soulignent, encore une fois, sa capacité à s’ajuster relativement rapidement aux différents stimuli présents dans son milieu. La réponse animale n’est donc pas statique sur de longues périodes ou encore binaire (évitement ou non) comme trop souvent rapportée (Vistnes et Nellemann, 2001; Dahle *et al.*, 2008), mais plutôt changeante dans le temps selon l’intensité et la durée de la perturbation. La notion de délai dans le retour à la normale après un stimulus est aussi importante. Ce délai a déjà été soulevé dans la réponse des proies à la présence de prédateurs (Mitchell, 2009), mais est relativement nouvelle dans le domaine de l’écologie de la conservation.

Intégration du paysage dans l’étude des interactions sociales

Une vaste majorité des études sur les comportements sociaux sont le résultat d’observations directes (p. ex. : Lusseau et Newman, 2004; Sundaresan *et al.*, 2007; Carter *et al.*, 2013). Or, de nombreuses espèces ne permettent pas ce genre d’approche entre autres en lien avec leur camouflage, leur préférence envers les habitats fermés ou encore leur crainte des humains. L’utilisation de données de déplacement provenant de colliers télémétriques permet un suivi des individus marqués tout au long d’un cycle circadien et permet de s’affranchir des différents biais induits par les observateurs (Marsh et Hanlon, 2007; Tuyttens *et al.*, 2014). J’ai développé une méthode simple qui permet d’établir une distance seuil entre les individus, servant à déterminer l’appartenance des individus à des groupes sociaux, pour chaque pas de temps. Cette méthode itérative s’appuie sur la prémisse que la distance entre deux individus est moindre à l’intérieur même d’un groupe qu’entre des individus de groupes différents (Frid 1994; Carter *et al.*, 2013). Ainsi, le nombre de connexions par itération devrait rapidement plafonner une fois que la distance moyenne entre les individus d’un même groupe est atteinte. Dans le chapitre 3, nous avons identifié une distance seuil de ~50 mètres au-delà de laquelle l’augmentation du nombre de connexions diminuait rapidement. Cette approche, simple et efficace, permet d’analyser les interactions sociales à partir de données télémétriques GPS, ce qui ouvre la voie à une intégration plus facile de l'écologie spatiale dans les interactions sociales (p. ex. : Fortin *et al.*, 2009; Merkle *et al.*, 2015).

Le chapitre 3 a également montré l'importance de la connaissance du paysage des individus qui sont membres d'un groupe pour leur prise de décision lors des déplacements. En étudiant le bison (*Bison bison*), Merkle et al. (2015) avaient déjà montré qu'un individu possédant davantage de connaissances se basait sur sa propre expérience dans le choix des parcelles d'habitat utilisées, même si cela mène à délaisser le groupe, plutôt que sur le choix du groupe. Nous avons affiné cette avancée en démontrant que les liens sociaux et la qualité de l'habitat interagissaient également avec la connaissance du paysage de l'individu dans le choix de suivre ou non le groupe. Ainsi, un individu évoluant dans un milieu familier reste davantage en groupe avec les individus avec lesquels il partage un fort lien social et s'avère plus enclin à demeurer avec le groupe si ce milieu est constitué d'habitats préférentiels. Ces résultats complémentent les connaissances actuellement restreintes quant aux effets de la structure du paysage sur les interactions sociales chez les animaux. Nos résultats viennent également appuyer empiriquement l'hypothèse théorique de Sueur et al. (2011) qui stipulait que l'hétérogénéité du paysage jouait un rôle dans la dynamique de fission-fusion, par le biais de la distribution inégale des ressources et des conflits d'intérêt entre les membres du groupe.

Concept de marginalité

La variabilité interindividuelle est un sujet fortement étudiée et sa popularité ne cesse de croître (Sih *et al.*, 2004; Lopez *et al.*, 2005; Gillingham et Parker, 2008; Hebblewhite et Merrill, 2008). Pourtant, pas ou peu d'études se sont attardées au concept de marginalité. Certaines populations animales ayant des différences comportementales interindividuelles importantes, il est possible de s'intéresser à l'effet du positionnement de la niche comportementale individuelle par rapport à la plage comportementale disponible. Nos résultats ont d'ailleurs démontré une influence de la marginalité sur le risque de mortalité chez le caribou de la Gaspésie. Selon l'hypothèse de la variation de la niche (Bolnick *et al.*, 2007), le maintien de comportements marginaux serait le fruit d'une compétition intraspécifique importante pour les différentes ressources. Or la compétition intraspécifique pourrait ne plus être un facteur prépondérant guidant les choix comportementaux des caribous de la Gaspésie, en raison de leur fort déclin opéré au cours du dernier siècle. Ces résultats suggèrent la présence d'autres mécanismes (p. ex. : génétique, soins maternels, condition corporelle, parasitisme et dynamique de la prédation) susceptibles de maintenir ces comportements sous-optimaux en termes de survie.

Limites de l'étude

Une des principales faiblesses de l'étude est ironiquement fortement liée à une de ses principales forces. La faible taille de la population, divisée en trois sous-groupes géographiquement distincts, a limité la taille d'échantillon dans plusieurs analyses. Toutefois, cela m'a permis à la fois de suivre environ la moitié des individus, augmentant du coup le pouvoir d'inférence des résultats obtenus à l'ensemble de la population étudiée. La « faible » taille d'échantillon a parfois limité la capacité à tester les différences comportementales entre des groupes d'individus (p. ex. : selon le sexe ou le statut reproducteur) ou d'ajouter des variables explicatives dans certains modèles. Le statut précaire de la population a aussi limité la quantité d'information que j'ai pu récolter sur les individus au cours des captures. En effet, voulant limiter au maximum le temps de contention des caribous et en accord avec les lignes directrices des permis de bons soins aux animaux, l'équipe de capture a délaissé la prise du poids et certaines mesures morphométriques. Sans ces variables, il a été impossible d'intégrer la condition corporelle dans mes différentes analyses, ce qui pourrait masquer certaines réponses ou induire certains biais si une majorité d'individus étaient en mauvaise condition physique pendant le suivi télémétrique (donc post-capture). En effet, plusieurs études ont démontré l'importance de ce facteur, tant dans le budget d'activité (Angelier *et al.*, 2007; Evers *et al.*, 2008), dans le compromis alimentation – risque de prédation (Bachman, 1993; Winnie et Creel, 2007), dans les déplacements (Lowe *et al.*, 2006; Matthews et Rodewald, 2010; Cohen *et al.*, 2012) que dans la survie globale des individus (Burton *et al.*, 2006; Cook *et al.*, 2000).

Les différences comportementales entre les trois sous-groupes, liées entre autres aux conditions environnementales et aux différents niveaux de perturbation, ont également limité l'inclusion de tous les individus dans les mêmes modèles. Il aurait été intéressant d'utiliser des pentes aléatoires pour corriger ces différences individuelles, mais la faible taille d'échantillon pour deux sous-groupes (Albert et Logan) a grandement contraints cette initiative. Seul le chapitre 4 incluait les trois sous-groupes, car la méthode permettait une différence comportementale entre les groupes et l'objectif visait essentiellement les variations intra-groupe et intra-individuelle. Les autres chapitres incluaient soit seulement le sous-groupe des McGerrigle (Chapitre 2 et 3), soit également le sous-groupe du Albert qui a des réponses relativement similaires à celui des McGerrigle (Chapitre 1).

Le manque d'informations relatives à l'appartenance à un groupe et l'absence de données comportementales confirmant les interactions entre les individus représentent les principales faiblesses de l'utilisation des données télémétriques dans l'analyse des interactions sociales. Afin de pallier à ces limites, nous nous sommes appuyés à la fois sur une prémisse largement utilisée qui stipule que tous les individus faisant partie d'un groupe interagissent avec les membres du groupe (« *the gambit of the group* » *sensu* Whitehead et Dufault, 1999) ainsi que sur la prémisse voulant que la distance entre deux individus soit moindre à l'intérieur même d'un groupe qu'entre des individus de groupes différents (Frid 1994; Carter *et al.*, 2013).

Propositions de recherche

Ma thèse portait à la fois sur des enjeux très appliqués et des concepts davantage théoriques. Je suggérerai donc ci-après des thèmes et questions de recherche permettant de poursuivre l'acquisition de connaissances dans la foulée des résultats obtenus. Ces propositions viseront à identifier des thèmes qui auraient été difficiles à aborder avec mes données ou simplement des questions pertinentes auxquelles je n'ai pas eu le temps de répondre.

Propositions en écologie de la conservation

La survie des adultes ainsi que le recrutement, par l'intermédiaire de la reproduction et de la survie juvénile, sont les paramètres les plus importants pour assurer le maintien d'une population en danger. Pour la population de caribous de la Gaspésie, beaucoup d'efforts ont été investis afin d'identifier une des principales causes de la diminution du recrutement (c.-à-d., la prédation des faons : Crête et Desrosiers, 1995), mais nous possédons très peu de données quant à la condition physique des individus et aux liens avec leur survie (mais voir Turgeon *et al.*, 2018) et leur potentiel reproducteur. Le peu de données disponibles relativement aux taux de gestation suggère une certaine variabilité et des valeurs parfois faibles (par ex. : 60% en 2014). Cette variabilité peut être, entre autres, induite par des facteurs nutritionnels en lien avec la mère (Parker *et al.*, 2009) ou encore à la fertilité du père, sachant que des facteurs environnementaux peuvent affecter, via l'épigénétique, la capacité spermatogénique (Anway *et al.*, 2005). La survie des adultes a également été très variable au cours des dernières années, avec des valeurs s'étalant de 100 % à moins de 60 % annuellement (Frenette, 2017).

L'analyse plus poussées des facteurs pouvant affecter la condition des individus, tels que le taux de parasitisme (Irvine *et al.*, 2006; Turner *et al.*, 2012), le stress associé aux perturbations humaines (Creel *et al.*, 2002; Rangel-Negrin *et al.*, 2009; Renaud 2012) ou encore les métaux traces (Rodríguez-Estival *et al.*, 2011; Defo *et al.*, 2014) serait souhaitable, et ce sur la base des fortes densités d'orignaux (pouvant servir de réservoir pour les parasites), de randonneurs et de skieurs (pouvant induire un stress important) ainsi que de résidus miniers en plein cœur de l'aire de répartition du caribou. Les prochaines priorités de recherche devraient ainsi s'attarder à l'étude de la survie et de la condition physique des adultes et tenir compte des effets reportés du dérangement humain, puisque la présence de randonneurs peut affecter le temps passé en alimentation (Chapitre 1; Duchesne *et al.*, 2000; Ciuti *et al.*, 2012) et que l'apport énergétique obtenu durant l'été et l'automne est déterminant dans la survie des jeunes ongulés durant l'hiver (Cook *et al.*, 2010).

Plus globalement, l'écologie de la conservation se limite très souvent à la description des réponses comportementales et démographiques des populations en danger (p. ex. : Gonzalez *et al.*, 2006; Struhsaker, 2010; Leblond *et al.,* 2013;). Les prochaines étapes seraient de s'attarder aux mécanismes responsables de ces différentes réponses. L'augmentation de la pression de prédation via la modification du paysage est très souvent citée comme mécanisme responsable des déclins des populations (Gasaway *et al.*, 1992; Wittmer *et al.*, 2005; DeCesare *et al.*, 2010), mais plus rarement d'autres pistes un peu moins directes, ont été testées pour expliquer les réponses animales. Il est primordial de tester l'impact des effets cumulés des activités humaines sur l'acquisition des ressources alimentaires et la valeur adaptative des individus, considérant l'importance de la nutrition sur la condition physique des individus (Denryter *et al.*, 2017) et de ses capacités reproductrices (Parker *et al.*, 2009). Une proie en moins bonne condition physique est plus susceptible à la prédation (Winnie et Creel, 2002). Ce mécanisme pourrait potentiellement expliquer de concert avec la modification du paysage à l'avantage des prédateurs, les forts taux de prédation observés chez plusieurs populations en déclin. L'importance de la nutrition est d'ailleurs de plus en plus considérée et étudiée par les écologistes responsables de la conservation du caribou (Parker *et al.*, 2009; Denryter *et al.*, 2017)

Propositions en écologie théorique

Rarement des notions d'écologie spatiale ont été intégrées dans les analyses d'interactions sociales (mais voir VanderWaal *et al.*, 2014; Merkle *et al.*, 2015). Afin de pousser plus loin les résultats obtenus dans les chapitres 3 et 4, qui suggèrent une influence des liens sociaux sur la dynamique des groupes et une variabilité comportementale interindividuelle, il serait intéressant d'analyser les composantes du réseau social chez le caribou de la Gaspésie. Un tel projet permettrait de vérifier s'il existe un lien entre la position d'un individu dans le réseau social et sa stratégie d'utilisation de l'espace, voire même avec la marginalité de cette stratégie. Chez la girafe (*Giraffa camelopardalis*), la structure sociale était fortement influencée par la degré de chevauchement des domaines vitaux (VanderWaal *et al.*, 2014). Puisqu'une majorité d'individus conformistes semblent afficher les mêmes patrons d'utilisation de l'espace (chapitre 4), il est probable que les liens sociaux entre ces individus soient également davantage marqués. En mettant en relation la structure du réseau social chez le caribou de la Gaspésie et l'utilisation de l'espace, nous pourrions également faire un lien entre la survie et la position dans le réseau social. Les individus marginaux, en ayant une utilisation différente du territoire, pourraient afficher des charges parasitaires plus importantes en faisant le lien entre les différents sous-groupes de caribous, voire même en utilisant des habitats davatange utilsés par l'orignal (*Alces americanus*). Il a d'ailleurs déjà été démontré que la position dans un réseau social pouvait avoir des répercussions sur la transmission de maladies et de parasites (Rimbach *et al.*, 2015; VanderWaal *et al.*, 2016; Sih *et al.*, 2018). Le mécanisme inverse pourrait également être plausible, une charge parasitaire plus importante induisant des changements comportementaux (Hugues, 2013; Knight, 2013; Libersat et Gal, 2013, Vyas, 2015) eux-mêmes susceptibles d'affecter les relations sociales et l'utilisation de l'espace. Les changements comportementaux des hôtes opérés par les parasites ont été fortement étudié chez les insectes et petits rongeurs (Hugues, 2013; Knight, 2013; Libersat et Gal, 2013), mais plus rarement chez les grands mammifères.

Ouverture

Aujourd'hui, l'écologie se veut une science encore plus intégratice que jamais. Les propositions avancées dans cette thèse ne sont que quelques unes des possibilités visant à établir des liens entre les domaines trop souvent étudiés séparément, nommément l'écologie spatiale, les relations sociales, la parasitologie, l'écophysiologie et l'étude des paramètres démographiques. Bénéficiant déjà de nombreuses connaissances relatives aux populations d'espèces en déclin, dont notamment le caribou de la Gaspésie, il reste à affiner notre compréhension des mécanismes sous-jacents aux différentes réponses mises en évidence dans cette thèse et dans les autres études en conservation, afin de mieux orienter les futures avenues de recherches en écologie des perturbations et basculer concrètement vers l'écologie de la restauration.

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