UNIVERSITÉ DU QUÉBEC À RIMOUSKI

SÉLECTION DES SITES DE MISE BAS ET SURVIE DES FAONS CHEZ LE CARIBOU FORESTIER : IMPACTS DE DIFFÉRENTES STRATÉGIES COMPORTEMENTALES SUR LA PERFORMANCE INDIVIDUELLE

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Composition du jury :

Joël Bêty, président du jury, UQAR

Martin-Hugues St-Laurent, directeur de recherche, UQAR

Christian Dussault, codirecteur de recherche, MDDEFP

Chris Johnson, examinateur externe, UNBC

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RÉSUMÉ

La majorité des populations de caribous forestiers (*Rangifer tarandus caribou*) sont en déclin et la prédation, dont les effets semblent exacerbés par l'aménagement forestier, est considérée comme le principal facteur limitant proximal. De plus, la survie des faons caribous est hautement variable entre les années, ayant comme résultante une forte influence sur le taux de croissance des populations. Les objectifs de cette recherche étaient de déterminer 1) l'effet de l'aménagement forestier sur la sélection des sites de mise bas chez le caribou forestier, 2) le taux de survie des faons et 3) les patrons de sélection d'habitat qui augmentent le risque de prédation des faons. Pour atteindre ces objectifs, nous avons utilisé les données télémétriques de femelles et faons caribous évoluant en forêt boréale aménagée que nous avons analysées à l'aide de fonctions de sélection des ressources pour répondre aux objectifs 1 et 3 et d'un modèle de Cox pour répondre à l'objectif 2. Nos résultats indiquent que les femelles sélectionnaient leur site de mise bas de manière à réduire le risque de prédation et ce, aux trois échelles spatiales étudiées. Le taux de survie des faons caribous a été estimé à 43% après 90 jours de vie. Les femelles qui ont perdu leur faon par prédation ont démontré un évitement moins important des routes et une sélection moins forte des peuplements mixtes et décidus matures. De plus, les femelles qui ont perdu leur faon par prédation et qui avaient une proportion élevée de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement abondantes. Cette étude a permis de caractériser les sites de mise bas, un habitat critique du caribou, en plus de démontrer les impacts de l'aménagement forestier et du territoire sur le comportement et la survie du caribou. Ces résultats permettront de guider les stratégies d'aménagement en plus d'affiner notre compréhension des impacts cumulés sur la survie du caribou forestier.

Mots clés : aménagement forestier, caribou forestier, fonction de sélection des ressources, prédation, *Rangifer tarandus caribou*, réponse fonctionnelle, sélection d'habitat, site de mise bas, succès reproducteur, survie des faons.

ABSTRACT

Most woodland caribou (*Rangifer tarandus caribou*) populations are declining and predation, which is exacerbated by forestry activities, is considered the most important proximal limiting factor. Moreover, caribou calf survival is highly variable between years and might play a dominant role on population growth rate. The objectives of this study were to determine 1) the effect of forest management on calving site selection in woodland caribou, 2) calf survival rate, and 3) habitat selection patterns that increase predation risk for calves. To achieve these objectives, we used GPS locations of collared females and VHF locations of collared calves that evolved within a highly managed forested landscape and analysed these data with resource selection functions (for objectives 1 and 3) and a Cox model (objective 2). Our results demonstrated that female caribou selected calving sites to reduce predation risk at the three spatial scales studied. Caribou calf survival was estimated as 43% after 90 days of life. Females that did not lost their calf displayed a stronger avoidance towards high road density areas and a stronger selection towards mixed and deciduous stands than females that lost their calf from predation. Further, females that lost their calf from predation and that had a low proportion of <5 years-old cutovers within their calving home range were mostly observed in areas where <5 years-old cutovers were locally absent. Also, females that lost their calf from predation and that had a high proportion of <5 years-old cutovers within their calving home range were mostly observed in areas with a high local density of <5 years-old cutovers. In this study, we characterized calving sites, a critical habitat for caribou, and we provided a robust demonstration of the impacts of human-induced disturbances on woodland caribou behavior and survival. These results will guide forest management strategies, in addition to refining our understanding of the cumulative impacts on woodland caribou survival.

Keywords: calf survival, calving site, forest management, functional response, habitat selection, predation, *Rangifer tarandus caribou*, reproductive success, resource selection function, woodland caribou.

TABLE DES MATIÈRES

INTRODUCTION GÉNÉRALE

Comme la majorité des processus comportementaux, la sélection d'habitat est un processus adaptatif (Rettie & Messier 2001; Morris 2003) qui est soumis aux pressions de la sélection naturelle (Darwin 1859) et de la sélection sexuelle (Darwin 1871). Ces forces évolutives ont participé, au fil des générations, à l'adaptation des individus à leur environnement. Ainsi, la sélection d'habitat exercée par un individu devrait refléter la stratégie d'utilisation de l'espace qui maximise sa valeur adaptative individuelle (Rettie & Messier 2001). Cependant, depuis le dernier siècle, l'homme a grandement modifié les divers habitats de la planète (Sanderson et al. 2002), remaniant par le fait même les forces évolutives. De plus, ces modifications d'habitats s'opèrent à grande vitesse. Ainsi, la sélection d'habitat exercée par certaines espèces pourrait être mal adaptée à leur nouvel environnement qui se modifie rapidement dû à l'anthropisation (Faille et al. 2010; St-Laurent & Dussault 2012).

ANTHROPISATION DE LA FORÊT BORÉALE

L'anthropisation et l'empreinte humaine sont présentes dans tous les biomes incluant celui de la forêt boréale (Sanderson et al. 2002). Avant l'avènement de la mécanisation et de l'industrialisation de l'aménagement forestier, la forêt boréale était principalement perturbée par des événements naturels tels les feux de forêt, les chablis et les épidémies d'insectes (Brokaw & Rent 1999; Spies & Turner 1999). De nos jours, les opérations de récolte forestière sont reconnues comme étant la perturbation majeure à l'intérieur de la forêt boréale (McRae et al. 2001). Ce changement dans le régime de perturbations modifie également la composition et la structure de la forêt. En effet, la récolte forestière simplifie la structure et standardise l'âge des peuplements en plus de globalement rajeunir la matrice forestière (Axelsson & Östlund 2001; Bergeron et al. 2002). Suite à cette récolte, l'empreinte humaine reste importante en forêt boréale puisque l'aménagement forestier se traduit également par la construction d'un dense réseau routier (Forman & Alexander 1998). Une fois mis en place, ce réseau routier favorise l'implantation de structures anthropiques pérennes tels les chalets, les pourvoiries et les autres établissements de villégiature, supportant une plus grande présence humaine en forêt boréale.

Cette perturbation anthropique qu'est l'aménagement forestier peut également avoir plusieurs impacts sur la faune. Comme suggéré par Johnson et St-Laurent (2011), les perturbations anthropiques, selon leur magnitude et l'échelle spatio-temporelle à laquelle elles modifient l'environnement, peuvent avoir des impacts sur la physiologie (Creel et al. 2002; Wikelski & Cooke 2006; Renaud 2012), le comportement (Blumstein et al. 2005; Stankowich 2008; Leclerc et al. 2012) et le budget énergétique (Bélanger & Bédard 1990; Williams et al. 2006) des animaux ainsi que sur la démographie des populations (Carney & Sydeman 1999; Phillips & Alldredge 2000) et sur la structure des communautés animales (Addessi 1994; Peres 2000; Winfree et al. 2007). Alors que certaines espèces tirent profit de l'aménagement forestier, d'autres s'en trouvent défavorisées, soulignant du même coup que la réponse de la faune face aux perturbations anthropiques demeure complexe (Johnson & St-Laurent 2011). À titre d'exemple, de 5 à 10 ans suite à l'exploitation forestière, il est commun d'observer une augmentation de la densité d'orignaux (*Alces alces*) qui s'explique par une hausse de la nourriture disponible et du couvert de protection (Peek et al. 1976; Potvin et al. 2005). À l'opposé, l'exploitation forestière semble être pour le caribou (*Rangifer tarandus*) le facteur clé qui entraîne une cascade d'effets négatifs (Smith et al. 2000; Fisher & Wilkinson 2005; Schaefer & Mahoney 2007).

IMPACT DE L'ANTHROPISATION DE LA FORÊT BORÉALE SUR LE CARIBOU FORESTIER

La tendance générale des populations de caribous est au déclin (Courtois 2003; Vors & Boyce 2009) et l'écotype forestier de la sous-espèce du caribou des bois (*Rangifer tarandus caribou*) n'y fait pas exception. En effet, la limite sud de son aire de répartition ne cesse de régresser vers le nord depuis le début du 19^{e} siècle (Bergerud 1974; Courtois 2003; McLoughlin et al. 2003), ce qui a conduit à sa désignation comme espèce menacée au

Canada (COSEPAC 2002) et vulnérable au Québec (MRNF 2005). Plus récemment, le COSEPAC (2011) a attribué au caribou forestier associé à la forêt boréale le statut d'unité désignable boréale (DU6), soulignant son caractère distinct stipulant qu'il s'agit d'un élément irremplaçable de la biodiversité nationale. Les causes du déclin du caribou forestier sont multiples et synergiques et semblent exacerbées par l'aménagement forestier. Les impacts induits par les coupes forestières et le développement du réseau routier impliquent une augmentation de la chasse et du braconnage (Bergerud 1971, 1974), la perte, la fragmentation et l'altération d'habitats (Nellemann & Cameron 1996; Vors et al. 2007) ainsi qu'une augmentation de la prédation (Seip 1991; Wittmer et al. 2005; Gustine et al. 2006).

Les coupes forestières, en plus de réduire la proportion de vieilles forêts matures (*i.e.* l'habitat préférentiel du caribou; Mahoney & Virgl 2003; Bowman et al. 2010), augmentent la proportion de jeunes peuplements forestiers dans le paysage qui sont davantage composés d'essences décidues et de sapin baumier (*Abies balsamea*). Ces essences sont des ressources alimentaires pour l'orignal qui augmente en densité (Peek et al. 1976; Potvin et al. 2005), ce qui déclenche une réponse numérique du loup gris (*Canis lupus*), le prédateur principal des caribous adultes (Seip 1991). Ces mêmes jeunes peuplements forestiers sont également riches en petits fruits, baies et plantes herbacées, des sources de nourriture importantes pour l'ours noir (*Ursus americanus*; Beeman & Pelton 1977; Landers et al. 1979; Brodeur et al. 2008). Ce dernier est également reconnu comme un prédateur du caribou s'attaquant particulièrement aux faons âgés de moins de 6 semaines (Adams et al. 1995; Pinard et al. 2012). Les coupes forestières augmentent donc la pression de prédation sur le caribou forestier par l'augmentation des densités de loup gris et d'ours noir et ce, tant à l'échelle locale que régionale (Landers et al. 1979; Seip 1991; Potvin et al. 2005).

Le développement du réseau routier favorise les prélèvements par la chasse, qu'elle soit légale ou non, en facilitant l'accès au territoire (Johnson 1985). De plus, les routes constituent des corridors linéaires qui sont utilisés par les loups pour faciliter leurs déplacements dans le paysage (James & Stuart-Smith 2000; Whittington et al. 2005). Ainsi, la probabilité de rencontre avec un prédateur (Whittington et al. 2011), de même que le risque de prédation est supérieur près des routes (James & Stuart-Smith 2000). Suite à la construction du réseau routier, on assiste à l'implantation de structures anthropiques pérennes, à l'augmentation des activités récréotouristiques et de l'achalandage humain qui y est associé, des sources supplémentaires de dérangement pour le caribou (Duchesne et al. 2000; Dyer et al. 2001; Leblond et al. 2013). Cependant, bien que tous ces facteurs aient une influence sur la persistance du caribou dans le paysage, l'élément proximal reliant les modifications du paysage au déclin des populations semble être la prédation (McLoughlin et al. 2003; Festa-Bianchet et al. 2011).

LA PRÉDATION CHEZ LE CARIBOU FORESTIER

La prédation joue un rôle important dans la dynamique des populations de plusieurs espèces d'ongulés (Skogland 1991; Linnell et al. 1995; Hebblewhite et al. 2002). Chez le caribou, quoiqu'elle ne soit pas à l'origine de toutes les mortalités (les autres sources étant par exemple l'abandon maternel, la malnutrition, la noyade et les maladies; Adams et al. 1995; Linnell et al. 1995), il est suggéré que la prédation puisse agir comme principal facteur limitant (Bergerud & Elliot 1986; Rettie & Messier 1998; Wittmer et al. 2005). La prédation peut affecter tant les adultes (Rettie & Messier 1998; McLoughlin et al. 2003) que les faons (Gustine et al. 2006; Pinard et al. 2012). Bien que la survie des femelles adultes soit un facteur important qui influence la dynamique des populations, la survie des faons caribous est hautement variable (Seip & Cichowski 1996; Gustine et al. 2006; Pinard et al. 2012) et pourrait jouer un rôle dominant sur le taux de croissance de la population (Gaillard et al. 1998, 2000; Raithel et al. 2007). Les principaux prédateurs des faons caribous forestiers incluent le loup gris, l'ours noir, le grizzly (*Ursus arctos*), le carcajou (*Gulo gulo*), le lynx (*Lynx sp.*) et l'aigle royal (*Aquila chrysaetos*; Bergerud 1971; Adams et al. 1995; Gustine et al. 2006; Pinard et al. 2012). Une des stratégies utilisées par le caribou afin de réduire le risque de prédation est de s'isoler spatialement de ses prédateurs et des proies alternatives en sélectionnant des habitats différents de ces derniers (Bergerud et al. 1984; Bergerud et al. 1990; James et al. 2004).

LA SÉLECTION D'HABITAT DU CARIBOU FORESTIER

La sélection d'habitat est un des processus centraux en écologie puisqu'elle permet, entre autres, de comprendre comment les individus se distribuent dans le paysage, ce qui peut influencer la dynamique écologique et évolutive de l'espèce (McLoughlin et al. 2010; Morris 2011). Selon la définition de Morris (2003), la sélection d'habitat est le processus par lequel un individu occupe de manière non aléatoire une portion des habitats qui lui est disponible. De plus, la sélection d'habitat peut être considérée comme un processus hiérarchique (Johnson 1980) qui vise à atténuer l'influence des différents facteurs limitants (Rettie & Messier 2000; Dussault et al. 2005). En effet, la sélection d'habitat à plus large échelle spatiale et temporelle vise à atténuer l'effet du facteur limitant le plus important. Ce facteur limitant dirigera, si nécessaire, la sélection d'habitat à de plus fines échelles spatiales et temporelles et ce, jusqu'à ce que l'effet de ce facteur limitant soit suffisamment atténué. Par la suite, le second facteur limitant en importance dirigera la sélection d'habitat aux échelles spatiales et temporelles inférieures. Ainsi, la sélection d'habitat à une échelle spatiale donnée est contrainte par les choix faits aux échelles spatiales supérieures (Schaefer & Messier 1995). Il est donc important d'analyser plusieurs échelles spatiales afin de s'offrir une vision holistique de la sélection d'habitat et des différents facteurs limitants qui peuvent l'influencer.

La sélection d'habitat du caribou forestier est un processus qui a été largement étudié un peu partout dans l'aire de répartition de l'espèce [*e.g.* Alaska (Nellemann & Cameron 1996; Joly et al. 2010), Alberta (James et al. 2004; McLoughlin et al. 2005), Ontario (Ferguson et al. 1988; Ferguson & Elkie 2004), Québec (Courtois et al. 2007; Hins et al. 2009), Saskatchewan (Rettie & Messier 2000, 2001) et Terre-Neuve (Mahoney & Virgl 2003; Schaefer & Mahoney 2007)]. Durant la période de mise bas et d'élevage en bas âge, les femelles sélectionnent généralement les peuplements résineux matures (Mahoney & Virgl 2003), les tourbières et les landes à lichen (Hins et al. 2009). De plus, les femelles caribous sélectionnent les altitudes relatives plus élevées (Gustine et al. 2006; Pinard et al. 2012), ce qui leur permet de détecter plus efficacement les prédateurs et de s'isoler spatialement des loups qui utilisent davantage les vallées et les habitats en basse altitude lors de leurs déplacements (Bergerud et al. 1984; McPhee et al. 2012; Lesmerises et al. 2012). Les femelles caribous évitent les parterres de coupes en régénération de même que les routes qui sont associées à un risque de prédation plus élevé (James & Stuart-Smith 2000; Hins et al. 2009; Whittington et al. 2011). En fait, le caribou cherche à s'isoler spatialement de ses différents prédateurs pour diminuer la probabilité de rencontre (Tinbergen et al. 1967; Brown et al. 1986; Stuart-Smith et al. 1997). Cette stratégie d'évitement semble efficace, puisque la proportion de caribous observée dans le régime alimentaire du loup est plus faible que celle retrouvée dans le paysage (James et al. 2004).

Lorsque la sélection d'habitat à large échelle spatiale est efficace et permet de diminuer suffisamment le risque de prédation, les femelles caribous orientent leur sélection d'habitat à fine échelle au second facteur limitant en importance : la disponibilité en nourriture. En effet, les besoins énergétiques sont élevés durant les derniers stades de gestation (McEwan & Whitehead 1972) et particulièrement pendant la période de lactation (Chan-McLoed et al. 1994). La disponibilité de lichens, de plantes herbacées et de carex (Bergerud & Nolan 1970; Bergerud 1972), des sources de nourriture pour le caribou forestier, s'avère donc importante et pourrait dicter la sélection d'habitat à fine échelle (Lantin et al. 2003; Carr et al. 2007).

Le caribou forestier exprime également de la fidélité à son domaine vital saisonnier et ce, particulièrement pendant la période de mise bas (Faille et al. 2010). Exprimer de la fidélité à un site peut être favorable puisque cette stratégie permet de se familiariser avec la distribution des ressources alimentaires et des prédateurs (Greenwood 1980). Ainsi, ce comportement peut augmenter la valeur adaptative des individus qui l'exercent (Schieck & Hannon 1989; Beletsky & Orians 1991). Cependant, il a été suggéré que cette stratégie comportementale puisse s'avérer néfaste pour le caribou forestier (St-Laurent & Dussault 2012). En effet, exprimer de la fidélité à un site qui a été profondément modifié (*e.g.* coupes forestières) peut s'avérer délétère puisque le risque de prédation augmente lorsque l'habitat est composé davantage de jeunes peuplements forestiers (Seip 1991; Potvin et al.

2005; Brodeur et al. 2008). Ainsi, la sélection d'habitat exercée par un caribou pourrait être mal adaptée à son environnement si celui-ci demeure fidèle à des milieux profondément perturbés (Faille et al. 2010; St-Laurent & Dussault 2012).

Le mécanisme de réponse fonctionnelle est également important en sélection d'habitat et peut à l'occasion réunir sous une même vision des résultats divergents (Hebblewhite & Merrill 2008). La réponse fonctionnelle se définit comme un changement dans la sélection d'un habitat selon sa disponibilité ou la disponibilité d'autres habitats dans le paysage (Mysterud & Ims 1998). Ainsi, les attributs intrinsèques d'un habitat influencent sa sélection par une espèce, mais le degré de sélection est également influencé par l'environnement dans lequel évolue l'animal. De manière plus concrète, les réponses fonctionnelles nous indiquent, par exemple, une plus grande tolérance envers les structures anthropiques lorsque celles-ci se retrouvent dans des habitats de grande qualité (*e.g.* chez le loup gris, Lesmerises et al. 2012) ou que la sélection de la nourriture est plus importante lorsque celle-ci est moins abondante dans le domaine vital (*e.g.* chez l'orignal, Mabille et al. 2012). Chez le caribou, il a été démontré que la sélection des peuplements résineux matures augmentait avec la proportion de jeunes coupes forestières dans le paysage (Moreau et al. 2012). Les réponses fonctionnelles peuvent s'observer à plusieurs échelles spatiales et peuvent expliquer la plasticité comportementale exprimée par certaines espèces comme le caribou (COSEPAC 2011; Moreau et al. 2012).

Tandis que plusieurs études ont caractérisé la sélection d'habitat des caribous, peu ont établi de liens proximaux entre la sélection d'habitat et la valeur adaptative des individus. À ma connaissance, quatre études du genre ont été réalisées, utilisant la survie des femelles adultes (McLoughlin et al. 2005; Courtois et al. 2007; Wittmer et al. 2007) ou la survie des faons (Dussault et al. 2012) comme indice de la valeur adaptative. De manière générale, ces études démontrent que la probabilité de survie d'un individu est réduite lorsque celui-ci fréquente davantage d'habitats perturbés ou de jeunes peuplements en régénération (Courtois et al. 2007; Wittmer et al. 2007; Dussault et al. 2012). Cependant, il apert que des résultats divergents soient parfois obtenus; en effet, Wittmer et al. (2007) ont démontré un impact positif des vieilles forêts sur la survie des femelles caribous en Colombie-Britannique, tandis que McLoughlin et al. (2005) ont observé le contraire en Alberta. Une partie de l'explication de cette différence pourrait résider dans l'existence d'une réponse fonctionnelle, soulignant l'importance d'intégrer ce principe dans notre compréhension de la sélection d'habitat et de son influence sur la survie.

OBJECTIFS, HYPOTHÈSES ET RÉSULTATS

L'objectif principal de cette étude était de caractériser et comprendre les impacts de l'aménagement forestier sur la sélection des sites de mise bas ainsi que sur les liens entre la sélection d'habitat et la survie des faons, *i.e.* un indicateur de la valeur adaptative des femelles caribous forestiers. De manière plus précise, cette étude visait à 1) caractériser les sites de mise bas du caribou forestier en tenant compte du risque de prédation et de la disponibilité de nourriture et ce, à trois échelles spatiales; 2) estimer le taux de survie des faons caribous forestiers de la naissance jusqu'à 90 jours de vie; 3) déterminer les patrons de sélection d'habitat qui augmentent le risque de prédation des faons, le tout dans l'aire de distribution continue de l'espèce au Québec.

Dans le cadre du premier objectif, nous avons émis deux hypothèses qui découlent de la prémisse voulant que la sélection d'habitat soit un processus hiérarchique (Johnson 1980) et que l'influence d'un facteur limitant sur la sélection d'habitat soit reliée à son importance pour l'espèce étudiée (Rettie & Messier 2000). Ainsi, notre première hypothèse stipule qu'à large échelle spatiale, les sites de mise bas seraient sélectionnés de manière à réduire le risque de prédation, ce dernier étant le principal facteur limitant chez le caribou (McLoughlin et al. 2003; Festa-Bianchet et al. 2011). Notre seconde hypothèse stipule qu'à fine échelle spatiale, une fois le risque de prédation atténué par une sélection d'habitat efficace aux échelles spatiales supérieures, le caribou sélectionnerait des sites de mise bas où la disponibilité en nourriture, le second facteur limitant en importance, serait plus élevée (McEwan & Whitehead 1972; Chan-McLoed et al. 1994). Nous n'avons émis aucune hypothèse en lien avec le deuxième objectif, car celui-ci est davantage descriptif. Sachant que la prédation est la principale cause de mortalité chez les faons caribous (Pinard et al.

2012) et que le risque de prédation est associé aux perturbations anthropiques (Courtois et al. 2007; James & Stuart-Smith 2000; Whittington et al. 2011), notre hypothèse pour le troisième objectif stipule que les femelles qui fréquentent davantage les milieux perturbés auraient une probabilité plus élevée de perdre leur faon par prédation que le femelles qui fréquentent des milieux moins perturbés.

Cette étude a démontré que la sélection du site de mise bas était dirigée de manière à réduire le risque de prédation et ce, aux trois échelles spatiales étudiées (Chapitre 1). Nos résultats indiquent que, à large échelle spatiale, les femelles sélectionnaient l'altitude et les peuplements résineux et évitaient les coupes forestières et les endroits où la densité de routes était élevée pour donner naissance à leur faon. À fine échelle spatiale, les femelles caribous ont mis bas loin des routes et des coupes forestières, tout en évitant les peuplements où la disponibilité de nourriture et la densité d'arbres matures étaient élevées (Chapitre 1). Pour le deuxième objectif, le taux de survie des faons caribous a été estimé à 53 % et 43 % après 30 et 90 jours de vie, respectivement (Chapitre 2). La principale cause de mortalité a été attribuée à la prédation (71 % des mortalités) et l'ours noir a été identifié comme étant le principal prédateur des faons (83 % des cas de prédation; Chapitre 2). En regard du 3^{e} objectif, nos résultats indiquent que la probabilité qu'une femelle perde son faon par prédation n'était pas influencée par la composition de son domaine vital annuel, mais diminuait avec l'augmentation de la proportion de dénudé sec à l'intérieur de son domaine vital de mise bas. À fine échelle spatiale, les femelles qui ont perdu leur faon par prédation ont démontré un évitement plus faible des routes ainsi qu'une sélection moins forte envers les peuplements mixtes et décidus matures que les femelles dont le faon a survécu (Chapitre 2). De plus, les femelles qui ont perdu leur faon par prédation et qui avaient une faible proportion de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement absentes (Chapitre 2). Qui plus est, les femelles qui ont perdu leur faon par prédation et qui avaient une proportion élevée de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement abondantes.

De manière générale, nos résultats indiquent que la sélection des sites de mise bas est exercée de façon à réduire le risque de prédation par le loup. Malgré cette sélection, la prédation demeure la principale cause de mortalité des faons puisque l'ours noir constitue leur principale menace. De plus, ce risque de prédation ne se distribue pas de manière aléatoire dans le paysage. Ainsi, les différents patrons de sélection d'habitat exprimés par les femelles résultent en des différents gains de valeur adaptative.

CHAPITRE 1
ÉVALUATION MULTI-ÉCHELLE DE L'IMPACT DES ROUTES ET DES COUPES FORESTIÈRES SUR LA SÉLECTION DES SITES DE MISE BAS CHEZ LE CARIBOU DES BOIS

Cet article a été publié dans la revue internationale révisée par les pairs
Forest Ecology and Management (Volume 286, pages 59-65).

1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Les populations de caribous des bois (*Rangifer tarandus* caribou) sont en déclin et la prédation est considérée comme le facteur limitant le plus important en Amérique du Nord. Le caribou est reconnu pour réduire le risque de prédation en s'isolant spatialement des prédateurs et des proies alternatives. Cette stratégie est maintenant compromise par les activités forestières qui réduisent la quantité d'habitat préférentiel du caribou en plus de déclencher une augmentation de la densité de proies alternatives et des différents prédateurs. Notre objectif était d'étudier l'influence du risque de prédation et de la disponibilité en nourriture sur la sélection des sites de mise bas chez le caribou des bois à trois échelles spatiales (de la plus large à la plus fine : à l'échelle du domaine vital annuel, domaine vital de mise bas et à l'échelle du peuplement forestier) en forêt boréale au Québec, Canada. En utilisant la télémétrie GPS, nous avons identifié les sites de mise bas et nous les avons caractérisés en utilisant des fonctions de sélection des ressources. Nous avons déterminé les caractéristiques de l'habitat en utilisant les cartes écoforestières et les cartes topographiques à l'échelle du domaine vital annuel et du domaine vital de mise bas et avec des inventaires de végétation à l'échelle du peuplement forestier. À l'échelle du domaine vital annuel et du domaine vital de mise bas, les femelles caribous ont sélectionné des sites de mise bas situés à une altitude relative plus élevée et où la densité de route était faible. À l'échelle du domaine vital annuel, elles ont également sélectionné des sites de mise bas où la proportion de jeunes et de vieilles coupes était moindre. À l'échelle du peuplement forestier, les femelles ont mis bas loin des routes et des jeunes coupes, en utilisant des peuplements où la surface terrière d'épinette noire et de sapin baumier était faible. À cette fine échelle, les femelles sélectionnaient toujours des sites de mise bas à une altitude relative plus élevée et où la disponibilité des ressources alimentaires était plus faible comparée à des sites de mise bas aléatoires dans le même type de peuplement forestier. La sélection d'un site de mise bas a été dirigée par le risque de prédation de la plus large échelle spatiale à la plus fine. Par conséquent, nos résultats suggèrent que les femelles ne semblent pas être en mesure de diminuer le risque de prédation aux échelles spatiales plus larges, malgré un évitement généralisé des routes et des coupes. Nous recommandons l'agglomération des activités forestières à l'intérieur de zones de gestion intensive, afin d'isoler spatialement de larges massifs forestiers exempts de perturbations anthropiques. Si ce n'est pas possible, nous recommandons de concentrer les activités forestières dans des zones de basse altitude puisque le caribou sélectionne systématiquement les altitudes plus élevées et ce, à toutes les échelles spatiales.

Cet article, intitulé « *Multiscale assessment of the impacts of roads and cutovers on calving site selection in woodland caribou* », a été publié dans la revue internationale révisée par les pairs *Forest Ecology and Management* (Volume 286, pages 59-65). Les résultats ont également été divulgués lors d'une présentation orale au *14th North American Caribou Workshop*, à Fort St. John (Colombie-Britannique, Canada) en septembre 2012. En tant que premier auteur, j'ai réalisé la totalité des analyses géomatiques et statistiques et j'ai contribué à l'écriture du manuscrit. Les autres auteurs, soit Martin-Hugues St-Laurent et Christian Dussault, ont participé à toutes les étapes du cheminement de ce manuscrit, incluant un apport non négligeable à l'élaboration de l'idée originale, des objectifs et des hypothèses de recherche, à l'écriture du manuscrit en plus de rassembler l'important financement nécessaire pour mener à terme cette recherche.

1.2 MULTISCALE ASSESSMENT OF THE IMPACTS OF ROADS AND CUTOVERS ON CALVING SITE SELECTION IN WOODLAND CARIBOU

ABSTRACT

Woodland caribou (*Rangifer tarandus caribou*) populations are declining worldwide, and predation is considered their most important limiting factor in North America. Caribou are known to reduce predation risk by spacing themselves away from predators and alternative prey. This strategy is now compromised by forestry activities that reduce the amount of suitable caribou habitat and trigger an increase in densities of alternative prey and predators. Our objective was to investigate the influence of predation risk and food availability on selection of a calving location by woodland caribou at three spatial scales (from coarse to fine: annual home range, calving home range, and forest stand scales) in the boreal forest of Québec, Canada. Using GPS telemetry, we identified calving locations and assessed those using Resource Selection Functions. We determined habitat characteristics using digital ecoforest and topographic maps at the annual and calving home range scales, and with vegetation surveys at the forest stand scale. Caribou selected calving locations located at relatively high elevation and where road density was low, both at the annual and calving home range scales. Within the annual home range scale, they also selected calving locations where the proportion of young and old cutovers was lower than in random areas of similar size. At the forest stand scale, females calved away from roads and young cutovers, using stands where the basal area of black spruce and balsam fir trees was low. At this fine scale, females still selected calving locations located at a relatively high elevation and where the availability of food resources was lower than in random areas located within the same habitat type. The selection of a calving location was driven by predation risk from the largest to the finest spatial scale. Therefore, our results suggest that females may not be able to lower predation risk at larger scales, despite general avoidance of roads and cutovers. We recommend amalgamating all forestry activities within intensive management zones in order to spatially isolate large patches of suitable calving habitat from anthropogenic disturbances. If not possible, we recommend concentrating forestry activities

in low-lying areas since caribou consistently selected for relatively high elevations at all scales.

Keywords: calving, cutovers, hierarchical habitat selection, Québec, woodland caribou.

1. Introduction

Caribou (*Rangifer tarandus*) populations are declining worldwide (Vors and Boyce, 2009; Festa-Bianchet et al., 2011) and the southern limit of their range has regressed northwards since the 19th century (McLoughlin et al., 2003; Vors et al., 2007). Causes of this decline include hunting and poaching (Bergerud, 1971), habitat alteration and loss (Nellemann and Cameron, 1996; Vors et al., 2007), cumulative impacts of anthropogenic activities (Johnson et al., 2005), and predation (Seip, 1991; Gustine et al., 2006). Predation is usually considered to be the most important proximal factor limiting caribou populations (McLoughlin et al., 2003; Festa-Bianchet et al., 2011) and its effects appear exacerbated by habitat alteration (Wittmer et al., 2007; Courbin et al., 2009).

Forest management that involves logging and the development of a dense forest road network intensifies predation pressure on caribou (James and Stuart-Smith, 2000; Vors et al., 2007). In addition to reducing the availability of preferred caribou winter habitat, i.e., old-growth coniferous forest (Mahoney and Virgl, 2003; Bowman et al., 2010), logging increases the proportion of early successional stands which are favourable to moose (*Alces alces;* Potvin et al., 2005) and thus triggers a numerical response in wolf (*Canis lupus*), the main predator of adult caribou (Seip, 1991). Early successional stands are also favourable by black bear (*Ursus americanus*; Brodeur et al., 2008) which is recognized as an important predator of caribou calves (Mahoney and Virgl, 2003; Pinard et al., 2012). Caribou appear able to reduce predation risk by wolves, the predator with which it co-evolved, through spatial segregation (James et al., 2004) but their calves suffer from black bear predation in regions where there is a significant human footprint (Mahoney and Virgl, 2003; Pinard et al., 2012). Some authors have also suggested that wolf-avoidance strategies displayed by caribou could result in an increased exposure to predation risk by bear (Faille et al., 2010; Pinard et al., 2012; St-Laurent and Dussault, 2012). If true, the wolf avoidance strategy used by caribou is potentially maladaptive due to recent increases in bear density across caribou range.

Habitat selection is a hierarchical process (Johnson, 1980) through which an animal aims to reduce the influence of limiting factors depending on their relative importance, and the most important limiting factors likely drive selection patterns at larger spatial scales (Rettie and Messier, 2000; Dussault et al., 2005). During the calving period, female caribou select habitats that minimize predation risk, such as old-growth coniferous forests (Lantin et al., 2003; Mahoney and Virgl, 2003), open lichen woodlands and peatlands (McLoughlin et al., 2005; Hins et al., 2009), and areas located at high elevation or in rugged terrain (Nellemann and Cameron, 1996; Pinard et al., 2012). Females avoid cutovers and other regenerating areas (Hins et al., 2009), as well as cabins and roads (Vistnes and Nellemann, 2001; Carr et al., 2011; Pinard et al., 2012). Such anthropogenic features are known to be associated with higher predator occurrences (Whittington et al., 2011), which results in higher predation risk (James and Stuart-Smith, 2000).

There have been few descriptions of calving site selection at a fine spatial scale, and available studies yielded variable conclusions. For example, Carr et al. (2007) found that female caribou were seeking a high density of mature trees, as well as thick vegetation ground cover; Pinard et al. (2012) did not find any selection of concealment cover, but showed avoidance of black spruce stands with a high basal area. Nevertheless, both studies found that female caribou were selecting calving sites located at a high elevation relative to surrounding areas. Both wolves and moose are known to use low elevations and slopes as travel routes (Bergerud et al., 1984; Seip, 1991; Dussault et al., 2007; Leblond et al., 2010; Tremblay-Gendron, 2012; Lesmerises et al., 2012). Thus, high elevation can be used as a suitable strategy to maintain separation from wolves and moose as well as to detect an oncoming predator and escape more efficiently (Chekchak et al., 1998; Carr et al., 2007). It is possible that the selection of high elevations at larger spatial scales decreases predation risk sufficiently so that caribou may switch selection pattern toward the second most important limiting factor at a finer scale, food. Food can also be a limiting factor guiding the selection of calving sites because energy requirements are high during the last stages of gestation (McEwan and Whitehead, 1972) and during lactation (Chan-McLoed et al., 1994). The abundance of terrestrial lichens, forbs, and grasses, sources of food for lactating females (Bergerud and Nolan, 1970; Bergerud, 1972), was shown to be important for calving site selection (Lantin et al., 2003; Carr et al., 2007). We believe that a tradeoff between caribou food acquisition and predation risk could explain regional differences in calving site selection at a fine spatial scale (Gustine et al., 2006; Panzacchi et al., 2010).

Our objective was to assess calving site selection of woodland caribou (*R. t. caribou*; hereafter referred as caribou) at multiple spatial scales. We investigated the joint influence of elevation and forestry activities on calving site selection by caribou, two variables frequently reported to reduce and increase predation risk, respectively (Landers et al., 1979; Bergerud et al., 1984). Assuming that predation by wolves is likely perceived by caribou as their main limiting factor, we hypothesized that female caribou will select, at larger spatial scales, calving sites located at high elevation and away from roads, where predation risk by wolves have been shown to be lower (Bergerud et al., 1984; James and Stuart-Smith, 2000; McPhee et al., 2012). We also predicted that, at finer spatial scale, female caribou will select habitat types allowing them to find suitable food resources, the second most important limiting factor. Because caribou diet in spring is diversified (Bergerud and Nolan, 1970; Bergerud, 1972) and that energy requirements are high during the last stages of gestation (McEwan and Whitehead, 1972) and during lactation (Chan-McLoed et al., 1994), we expected calving sites to support relatively high availabilities of forbs, grasses, and lichens. Further, we examined the potential trade-off between predation risk and food availability by parturient caribou (Barten et al., 2001; Gustine et al., 2006). Considering that caribou are known to reduce predation risk (Rettie and Messier, 2001), we expected them to seek food resources away from cutovers, especially at lower altitude were predators were shown to thrive in our study area (Tremblay-Gendron, 2012; Lesmerises et al., 2012).

2. Study area

The study area (27,168 km^2) was located 125 km north of Saguenay (Québec, Canada; 48°28'-50°59' N, 69°59'-72°15' W). The northern part of the study area is characteristic of the black spruce (*Picea mariana*) – moss (*Bryophyta*) domain, while the southern part is transitional between the black spruce – moss and the balsam fir (*Abies balsamea*) – white birch (*Betula paperifera*) domains (Robitaille and Saucier, 1998). The understory of the black spruce – moss domain is mainly composed of mosses, ericaceous shrubs, and forbs (mostly *Cornus canadensis*, *Clintonia borealis*, and *Maianthemum canadense*). The most common tree species are black spruce, balsam fir, jack pine (*Pinus banksiana*), white birch, and trembling aspen (*Populus tremuloides*). Within the balsam fir – white birch domain, the most abundant tree species are balsam fir, white birch, white spruce (*Picea glauca*), and black spruce as well as trembling aspen. Topography is characterized by low rolling relief ranging between 250 and 900 m (Robitaille and Saucier, 1998). Mean annual temperature varied between -2^{o}C and 0^{o}C, and mean annual precipitation ranged between 1,000 mm and 1,300 mm, 30% to 35% of which fell as snow, while mean daily temperature during the calving period (21st May – 20th June) varied between 10°C and 16°C (Robitaille and Saucier, 1998).

3. Methods

3.1. Capture and determination of calving site

Between 2004 and 2011, we captured a total of 38 female caribou using a net-gun fired from a helicopter (Potvin and Breton, 1988), and equipped them with GPS collars (Lotek 2200L or 3300L, Telonics TGW-3600). We programmed the GPS collars to attempt location fixes every 4 hours. Capture and handling procedures were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate no. CPA-30-08-67). Following Pinard et al. (2012), we examined the movement pattern of each female during the calving period (21st May – 20th June) to assess the location of its calving site. Typically, females increase movement rates (from one to ten times) a few days prior to calving (Bergerud et al., 1990), and then suddenly become sedentary for approximately 3 days post-calving (Ferguson and Elkie, 2004) because of the restricted mobility of the new-born calf (Pinard et al., 2012). The movement rate of females then slowly increases (Ferguson and Elkie, 2004) as their calves become more mobile. When we observed this movement pattern for a female during a given calving season, we estimated the calving site location as the centroid of all GPS locations recorded during the period of restricted mobility (~ 3 days). Because our method did not allow us to find the placenta or other evidence of the parturition site, we use the term "calving location" to account for the fact that we could not accurately determine the true calving site.

3.2. Data analysis

As habitat selection is a hierarchical process and scale of selection may reveal the influence of different limiting factors (Rettie and Messier, 2000), we assessed calving location selection by female caribou at three different spatial scales: the annual home range scale, the calving home range scale, and the forest stand scale. At the annual home range and calving home range scales, we used 1:20,000 digital ecoforest maps, published by the Ministère des Ressources naturelle et de la Faune du Québec, to describe caribou habitat. We updated these maps annually to include habitat modifications resulting from forestry practices and natural disturbances. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies, bogs). Based on previous studies (Hins et al., 2009; Leblond et al., 2011), we combined polygons available on ecoforest maps into 8 habitat types (Table 1) known to be important for caribou. We also created a digital elevation model using topographic maps.

We contrasted habitat use and availability by comparing the calving location with 10 locations randomly distributed within each individual annual home range (for the annual home range scale) or calving (21st May – 20th June) home range (for the calving home range scale) based on simulations obtained using the Pitman efficiency of the Mantel-Haenszel test for stratified data (Mandrekar and Mandrekar, 2004). We defined home ranges using 100% MCP (Mohr, 1947), because kernel estimation provides biased estimates when animals exhibit site fidelity behaviour (Hemson et al., 2005) such as caribou in our study area (Faille et al., 2010). MCPs are known to overestimate home range size by including unused habitats (Grueter et al., 2009). However, our objective was not to assess home range size but habitat selection, and MCPs were more likely to provide the desired contrast between used and available habitat types to highlight habitat selection. To consider the influence of the surrounding environment on habitat selection and match the accuracy of calving location, we calculated the elevation, proportions of coniferous stands, open lichen woodlands, peatlands, young (≤ 5 years-old) and old (6 – 40 years-old) cutovers as well as road density, within 829 m radius circular buffers centered on each calving and random location. We used an 829 m buffer size as it represented the median daily distance traveled by females during the calving period. We conducted all spatial analyses using ArcGIS 10.0 (ESRI Inc., Redlands, California, USA).

For the forest stand scale, we conducted vegetation surveys in the field that allowed us to investigate fine scale habitat characteristics that cannot be assessed on ecoforest maps but that might be crucial for the calving location selection. We contrasted habitat use and availability by comparing vegetation characteristics found at the calving location with three random locations distributed within the same habitat type (see Table 1) in the calving home range of each female. We measured visual obstruction provided by vegetation (i.e., lateral cover) below 1 m above ground level in the four cardinal directions, shrub density in three 4 m^2 plots spaced 15 m apart along a north – south axis, basal tree area using a factor 2 prism, and percent ground cover of forbs, grasses, and terrestrial lichens in three 1–m^2 plots spaced 15 m apart along a north – south axis. We conducted vegetation surveys during the calving period in 2010 and 2011 to measure environmental conditions experienced by females at that time of the year. Specifically for the forest stand scale, we overlaid calving locations on ecoforest maps and removed calving events from our analysis when a major disturbance occurred after a calving event but before field surveys were conducted (2010 and 2011).

3.3. Statistical analysis

We used Resource Selection Functions (RSF; Manly et al., 2002) to assess the selection of calving location at each spatial scale. We conducted conditional logistic regressions using the library *Survival* in R 2.13.0 (R Development Core Team, 2011) to compare the calving location (use) to random locations (availability), and used a combination of female – year to define the conditional stratum. Prior to statistical analyses, we assessed multicolinearity between independent variables using the variance inflation factor, and confirmed that multicolinearity was absent from our dataset (VIF<10; Graham, 2003). We performed model selection (Burnham and Anderson, 2001) and evaluated different candidate models (see below) using the Quasi-likelihood under Independence Criterion (QIC; Pan, 2001), since conditional logistic regression provides pseudo-likelihood estimates (Pan, 2001). We used model averaging for models with a Δ QIC < 2.

We considered five hierarchically-structured candidate models for the annual and calving home range scales as well for the forest stand scale (each containing different variables). The ELEVATION, NATURAL, ROAD, CUTOVER, and COMPLETE models (see Table 2 for model description) allowed us to assess the joint influence of cutovers and elevation on calving location selection. As we expected that caribou might experience trade-off between predation risk and food availability (Barten et al., 2001; Gustine et al., 2006), we added elevation × % young cutovers + elevation × % old cutovers interactions in more complex models.

We determined the fit of the best supported model at each spatial scale by using a k-fold cross-validation (Boyce et al., 2002). We calculated parameter estimates using 80% of the strata (i.e., female – year combination), and applied the resulting equation to calculate the logit values of the remaining 20%. We then ranked logit values in each stratum and summed the number of real calving locations (used) in each rank. We calculated a Spearman correlation between the rank and the number of real calving locations (used) in each rank (Leblond et al., 2011), and repeated this procedure 1000 times.

4. Results

We identified and analyzed 51, 55, and 48 different calving locations at the annual home range, calving home range and forest stand scales, respectively. The number of calving locations differ among scales since we discarded calving locations where a major disturbance occurred between the calving event and field surveys (forest stand scale), and we were not able to define annual home ranges when a female died during a calving year. At the larger spatial scales, i.e., the annual and calving home range scales, the most parsimonious model was the ROAD model (Table 3). However, we conducted model averaging at the annual home range scale because the CUTOVER model was equivalent to the ROAD model (Δ QIC < 2, Table 3). At both scales, females selected calving locations at high elevations with a low road density (Table 4). Moreover, females selected coniferous stands while avoiding young and old cutovers at the annual home range scale, and peatlands at both the annual and calving home range scales (Table 4). The validation procedure indicated that the most parsimonious models were robust to cross-validation (r_s ± SD; annual home range scale = 0.76 ± 0.11 and calving home range scale = 0.70 ± 0.14).

At the forest stand scale, 43 of the 48 calving locations were in coniferous stands, 3 in old cutovers, and 2 in peatlands. The best supported model from the candidate set was the COMPLETE model (Table 3). At this fine scale, females still selected calving locations away from roads and we found a tendency toward selection of higher elevations (Table 4). Caribou response to young cutovers changed with elevation (Table 4). At a relatively low elevation, the distance to young cutover did not have a strong influence on calving location selection, while females selected calving location farther from young cutovers more frequently than randomly expected at higher elevations (Figure 1). Females also avoided calving in areas where lateral cover was dense and basal area of mature trees, especially balsam fir, was high (Table 4). Finally, females selected calving locations where the abundance of forbs, terrestrial lichens, and grasses was lower than their availability at random sites (Table 4). The most parsimonious model at the forest stand scale was also robust to cross-validation (r_s ± SD = 0.74 ± 0.24).

5. Discussion

Our objective was to investigate calving location selection by caribou at three spatial scales. Our results were consistent with the hypothesis that predation was the primary limiting factor guiding calving location selection at large spatial scales. Further, our results indicated that food availability did not influence calving location selection at a finer spatial scale, providing limited support to the hypothesis that caribou could limit predation risk at large scale and select for food availability at fine scale (Rettie and Messier, 2000).

At the annual home range scale, calving females selected coniferous stands and avoided young and old cutovers. Previous studies have suggested that female caribou avoid calving in areas supporting a high vegetation biomass, such as cutovers, as they perceive those habitats as more risky (Gustine et al., 2006). Conifer stands, on the other hand, are recognized as suitable caribou habitat (Mahoney and Virgl, 2003; Hins et al., 2009) that may favor spatial segregation between caribou and their predators and alternative prey (James et al., 2004; Bowman et al., 2010). Roads and elevation, two variables associated with predation risk, were also the two most important variables driving selection of calving location at large spatial scales (Bergerud et al., 1984; Pinard et al., 2012). Although we did not directly assess wolf predation risk, roads and other linear corridors are known to facilitate wolf's movements across the landscape (James and Stuart-Smith, 2000; Whittington et al., 2005), and caribou were shown to have a higher probability of crossing a wolf's path along roads (Whittington et al., 2011), resulting in increased predation risk (James and Stuart-Smith, 2000). Higher elevation could help caribou to detect oncoming predator and escape more efficiently (Chekchak et al., 1998; Carr et al., 2007) in addition to segregate from wolves (Bergerud et al., 1984; Seip, 1991). Although variation in elevation in Québec is not as important as in other parts of the caribou range (e.g. British Columbia or Alberta), studies conducted in the same study area or close to our study area demonstrated that wolves (Tremblay-Gendron, 2012; Lesmerises et al., 2012) and moose (Dussault et al., 2007; Leblond et al., 2010) strongly react to elevation or differences in elevation, preferring to use lower elevation and gentle slope, respectively, to move through the landscape. These findings, in addition to calving females not showing strong selection toward food-rich habitat types, support the hypothesis that predation is the main limiting factor influencing calving site selection at large spatial scales (Gustine et al., 2006; Pinard et al., 2012).

The influence of elevation and roads on calving site selection was also present at the smallest spatial scale investigated (Carr et al., 2007; Pinard et al., 2012), suggesting that caribou could not sufficiently attenuate predation risk through habitat selection at larger scales. In addition, females selected calving locations supporting a low basal area of black spruce (Pinard et al., 2012) and balsam fir at the finest spatial scale. In agreement with Pinard et al. (2012) but contrary to Carr et al. (2007), they also selected calving locations with a low percentage of lateral cover. We hypothesize that the enhanced visibility in these stands could help caribou detect predators more rapidly (Poole et al., 2007).

Caribou selected calving locations away from cutovers regardless of the elevation and, contrary to our prediction, displayed stronger avoidance towards cutovers at high elevations. We hypothesize that the capacity of caribou to avoid cutovers may be fully expressed at high elevations, where cutovers are less ubiquitous, and that caribou are forced to use areas with more abundant cutovers at lower elevations. A *post-hoc* analysis demonstrated that the proportion of cutovers in the landscape is lower at higher elevations (35.4% at < 650 m and 28.7% at > 650 m), but that suitable coniferous stands are more common (42.5% at < 650 m and 52.7% at > 650 m). Females were also found to select calving locations where the abundance of food resources (i.e., terrestrial lichens, grasses, and forbs) was lower compared to random areas located in similar habitat types. Food resources were clearly not an important variable in the selection of a calving location, and predation risk remained the most important limiting factor at fine spatial scale.

Females avoided peatlands at the calving home range scale, which is surprising because this habitat type was previously reported to be selected (Rettie and Messier, 2000; Mahoney and Virgl, 2003), presumably because peatlands favor spatial segregation from predators (James et al., 2004; McLoughlin et al., 2005). In our case, we argue that peatlands were avoided because females selected areas located at higher relative elevations to calve while peatlands are found on flat terrain at lower elevations relative to the surrounding environment. Moreover, peatlands in our study area were a relatively rare habitat type (2.1%) and were much smaller in size (average 6 ha) than the bog – fen complexes found elsewhere in the caribou range (e.g., Newfoundland, Alberta). Given the low abundance and size of peatlands in our study area, we believe that this may have limited the capacity of caribou to use this habitat type to segregate from predators and alternative prey.

We benefited from previous studies conducted in the same study area to develop a more comprehensive understanding of caribou selection of a calving location. Faille et al. (2010) found that female caribou display range fidelity, especially during the calving period. Nevertheless, fidelity to a calving location could be detrimental to calf survival in cases where females continue to select a formerly suitable calving habitat that has changed following major disturbances. If habitat selection is constrained by range fidelity or is not sufficient to mitigate the influence of a dominant limiting factor, we could expect responses to take place at other biological scales (*sensu* Johnson and St-Laurent, 2011), such as the physiological scale or the energetic balance. A companion study recently demonstrated that caribou suffer physiological stress in response to anthropogenic disturbances associated with forestry activities (Renaud, 2012). In addition to demonstrating the negative influence of roads at all spatial scales, these studies suggest that females could not completely escape road and cutover influence at any scale, and are likely being forced to calve in suboptimal environments.

5. Management implications

Caribou selected particular habitat features to calve (Table 4). Our findings add further support to earlier research which reported that woodland caribou are trying to avoid predation at the coarsest spatial scale (Bergerud et al., 1990; Rettie and Messier, 2000), especially during the calving period (Hins et al., 2009; Pinard et al., 2012). We demonstrated that anthropogenic disturbances originating from forestry activities, namely roads and cutovers, are avoided at large spatial scales by females when seeking a calving location. These anthropogenic features are decreasing the quality of caribou calving habitat, as the distribution of roads and cutovers is known to shape predation risk across the landscape by increasing black bear and wolf density both locally and regionally (Landers et al., 1979; Seip, 1991; Potvin et al., 2005). Avoidance of roads and cutovers was still detectable at the finest spatial scale investigated, suggesting that females were not able to mitigate the negative influence of such disturbances at larger scales. In order to reduce the negative impacts of roads and cutovers during this critical phase of the caribou life cycle, we recommend conserving large tracts of mature forest exempt from anthropogenic disturbances, where caribou may find suitable and safe calving locations (Courtois et al., 2007, 2008; Lesmerises, 2011). In regions where such large, undisturbed areas are no longer available, we suggest concentrating logging activities in low-lying sectors to facilitate spatial segregation between caribou and predators (Bergerud et al., 1984; Pinard et al., 2012). We believe that such strategies would limit overlap between suitable calving locations and anthropogenic features originating from forestry activity, helping to maintain sustainable woodland caribou populations within highly managed landscapes.

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Table 1. Description of the habitat types used to assess calving location selection by woodland caribou in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2011.

Habitat type	Description	Availability within the study area (%)
Forested habitat types		
Coniferous	Coniferous stands with dominant tree strata ≥50-yr-old	45.3
Mixed and deciduous	Mixed and deciduous stands with dominant tree strata ≥50-yr-old	4.1
Open lichen woodland	Coniferous forest with low tree density and usually terrestrial lichens	0.7
Peatlands	Poorly drained open areas (bogs and fens)	2.1
Disturbed habitat types		
Young cutover	Cutovers aged ≤5-yr-old	7.8
Old cutover	Cutovers aged 6 to 40-yr-old	28.5
Non-forested habitat types		
Water bodies	Lakes and rivers	9.3
Others	Others non-forested areas	2.1

Table 2. Description of the candidate models at the annual home-range scale, calving home-range scale, and forest – stand scale used to assess the effect of elevation and anthropogenic disturbances on calving location selection by caribou in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011.

Model	**Variables**
Annual and calving home-range scales	
ELEVATION	Elevation
NATURAL	ELEVATION + % coniferous + % open lichen woodland + % peatlands
ROAD	NATURAL + road density
CUTOVER	ROAD + % young cutovers + % old cutovers
COMPLETE	CUTOVER + Elevation × % young cutovers + Elevation × % old cutovers
Forest stand scale	
ELEVATION	Elevation
NATURAL	ELEVATION + basal area of black spruce, balsam fir, white birch + lateral cover + density of black spruce shrubs + % ground cover of forbs, grasses, lichens
ROAD	NATURAL + distance to the nearest road
CUTOVER	ROAD + distance to the nearest young cutover + distance to the nearest old cutover
COMPLETE	CUTOVER + Elevation × distance to the nearest young cutover + Elevation × distance to the nearest old cutover

Table 3. Results of the model selection process (see Table 2 for models' description) to assess calving location selection by female caribou at the annual home-range scale, calving home-range scale, and forest – stand scale in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011. Candidate models are listed with their Log-likelihood (LL), number of parameters (K), the difference in Quasi-likelihood under Independence Criterion compared to the best model (Δ QIC), and the model weight (w_i).

Model	LL	K	Δ QIC	w_i
Annual home-range scale (n=51)				
ELEVATION	-99.49	1	37.00	0.00
NATURAL	-85.63	4	13.73	0.00
ROAD	-77.88	5	0.00	0.58
CUTOVER	-77.38	7	1.70	0.25
COMPLETE	-77.07	9	2.38	0.17
Calving home-range scale (n=55)				
ELEVATION	-114.85	1	21.45	0.00
NATURAL	-111.28	4	19.74	0.00
ROAD	-101.11	5	0.00	0.82
CUTOVER	-100.68	7	3.51	0.14
COMPLETE	-99.88	9	6.30	0.04
Forest stand scale (n=48)				
ELEVATION	-59.14	1	17.75	0.00
NATURAL	-50.84	9	13.00	0.00
ROAD	-45.87	10	2.39	0.20
CUTOVER	-44.92	12	2.80	0.16
COMPLETE	-42.73	14	0.00	0.64

Table 4. Mean (± SE) use and availability of the variables included in the best supported models, along with their coefficients calculates trough conditional logistic regression to assess calving location selection by female caribou at the annual home-range scale, calving home-range scale, and forest stand scale in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011. Each variable is presented with its coefficient (β), robust standard error (SE), and 95% confidence interval of odds ratio.

					95% confidence interval	
Variable	**Use (mean ± SE)**	**Availability (mean ± SE)**	**β**	**SE**	**Lower limit**	**Upper limit**
Annual home-range scale (n=51)						
Elevation (m)	652 ± 10	591 ± 4	0.016	0.003	1.010	1.023
% coniferous	0.599 ± 0.037	0.386 ± 0.011	2.193	1.336	0.613	131.165
% open lichen woodland	0.018 ± 0.007	0.031 ± 0.003	-2.510	2.656	>0.001	16.809
% peatlands	0.014 ± 0.002	0.030 ± 0.003	-14.048	7.719	>0.001	4.258
Road density (km/km^2)	0.399 ± 0.111	1.162 ± 0.052	-0.925	0.289	0.222	0.709
% young cutovers	0.067 ± 0.023	0.086 ± 0.008	-0.360	0.457	0.279	1.747
% old cutovers	0.156 ± 0.026	0.319 ± 0.013	-0.497	0.708	0.147	2.518
Calving home-range scale (n=55)						
Elevation (m)	652 ± 9	616 ± 3	0.022	0.005	1.013	1.031
% coniferous	0.596 ± 0.036	0.529 ± 0.011	-0.163	0.995	0.121	5.969
% open lichen woodland	0.016 ± 0.007	0.015 ± 0.002	-0.533	2.678	0.003	111.714
% peatlands	0.014 ± 0.002	0.024 ± 0.002	-17.350	6.871	<0.001	0.021
Road density (km/km^2)	0.417 ± 0.108	0.862 ± 0.048	-1.385	0.378	0.119	0.525
Forest stand scale (n=48)						
Elevation (m)	655 ± 9	634 ± 5	0.015	0.009	0.998	1.032
Lateral cover below 1m (%)	79 ± 3	80 ± 1	-0.025	0.013	0.952	1.000
Basal area of black spruce trees (m^2/ha)	15.5 ± 2.1	16.8 ± 1.2	-0.037	0.017	0.933	0.995
Basal area of balsam fir trees (m^2/ha)	3.5 ± 0.9	6.4 ± 0.7	-0.099	0.037	0.842	0.974
Basal area of white birch trees (m^2/ha)	0.5 ± 0.4	0.3 ± 0.1	-0.056	0.067	0.829	1.078
Black spruce shrub density (stems/4m^2)	7.6 ± 0.9	7.3 ± 0.6	0.041	0.031	0.980	1.107
Forbs ground cover (%)	16.7 ± 2.6	16.3 ± 1.6	-0.014	0.015	0.959	1.015
Grass ground cover (%)	3.4 ± 0.9	3.2 ± 0.8	-0.055	0.028	0.896	0.998
Terrestrial lichens ground cover (%)	2.8 ± 1.1	4.7 ± 1.1	-0.065	0.028	0.887	0.990
Distance to the nearest road (km)	1.7 ± 0.3	1.4 ± 0.1	1.621	0.666	1.371	18.678
Distance to the nearest young cutover (km)	2.1 ± 0.3	1.8 ± 0.2	-5.277	2.376	<0.001	0.537
Distance to the nearest old cutover (km)	1.1 ± 0.2	1.1 ± 0.1	-3.479	4.142	<0.001	103.395
Elevation × Distance to the nearest young cutover	-	-	0.008	0.003	1.001	1.015
Elevation × Distance to the nearest old cutover	-	-	0.004	0.006	0.993	1.016

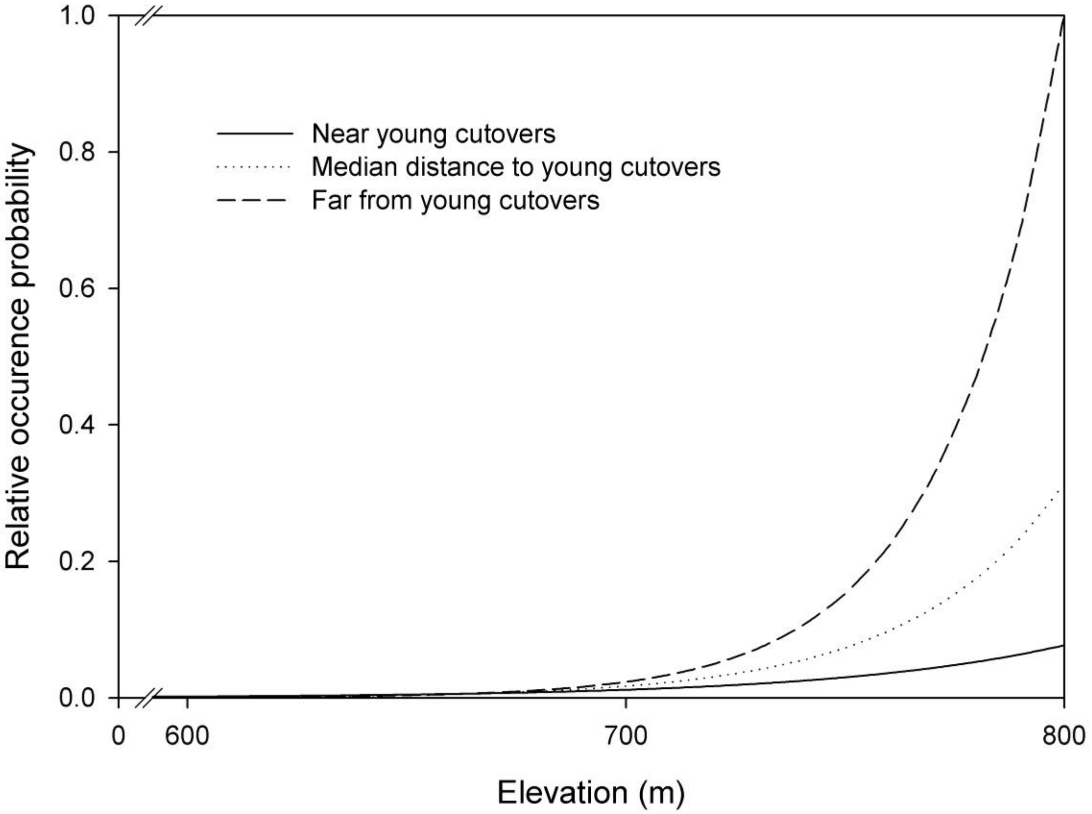

Figure 1. Relationship between the relative occurrence probability of a caribou calving location and the elevation × distance to nearest young cutover interaction, as predicted by the COMPLETE model at the forest stand scale from data collected in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011. We fitted 3 curves originating from the COMPLETE model to investigate the influence of the distance to the nearest young cutover using the 1st, 2nd, and 3rd quartile of the distance to nearest young cutover values, i.e., 0.399 km, 1.621 km, and 2.629 km, respectively.

CHAPITRE 2

LES DIFFÉRENTES STRATÉGIES COMPORTEMENTALES FACE AUX PERTURBATIONS ANTHROPIQUES EXPLIQUENT LA PERFORMANCE INDIVIDUELLE CHEZ UN GRAND ONGULÉ

Cet article sera soumis à l'été 2013 pour publication dans la revue
internationale révisée par les pairs *Journal of Applied Ecology*.

2.1 RÉSUMÉ EN FRANÇAIS DU DEUXIÈME ARTICLE

Les stratégies comportementales peuvent avoir des répercussions tant sur la valeur adaptative des individus que sur l'écologie et l'évolution des espèces. Chez le caribou des bois (*Rangifer tarandus caribou*), les perturbations anthropiques sont associées à une augmentation du risque de prédation. Nous avons étudié si la stratégie de sélection d'habitat des femelles caribous face aux perturbations anthropiques influençait leur succès reproducteur. Nous avons utilisé les données de 42 femelles munies de collier GPS et de 65 faons munis de collier VHF entre 2004 et 2011 en forêt boréale aménagée au Québec, Canada. Nous avons évalué la survie des faons avec un modèle de Cox et nous avons établi des liens entre la sélection d'habitat des femelles et le sort de leur faon à l'aide de régression logistique à trois échelles spatiales. La survie des faons (*n* = 30) a été estimée à 53 % et 43 % après 30 et 90 jours suivant la naissance, respectivement, et 53 % des faons sont morts de prédation par l'ours noir (*Ursus americanus*). La probabilité qu'une femelle perde son faon par prédation n'était pas influencée par la composition de son domaine vital annuel, mais diminuait avec l'augmentation de la proportion de dénudé sec dans son domaine vital de mise bas. À l'échelle locale, les femelles qui ont perdu leur faon par prédation ont démontré un évitement plus faible des routes et une sélection moins forte

envers les peuplements mixtes et décidus matures que les femelles dont le faon a survécu. De plus, les femelles qui ont perdu leur faon par prédation et qui avaient une faible proportion de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement absentes. Qui plus est, les femelles qui ont perdu leur faon par prédation et qui avaient une proportion élevée de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement abondantes. Nos résultats démontrent qu'il est essentiel de considérer les modifications d'habitat non seulement à l'échelle locale, mais également à l'échelle régionale pour élaborer des plans d'aménagement efficaces pour conserver le caribou. Nous avons démontré que les effets cumulés des perturbations anthropiques dans le paysage pouvaient non seulement influencer la distribution spatiale des individus, mais également leur succès reproducteur.

Cet article, intitulé « *Behavioural strategies towards human-induced disturbances explain individual performance in a large ungulate* », sera soumis à l'été 2013 pour publication dans la revue internationale révisée par les pairs *Journal of Applied Ecology*. Tout comme le premier article, j'ai réalisé la totalité des analyses géomatiques et statistiques et j'ai contribué à l'écriture du manuscrit. Les autres auteurs, soit Martin-Hugues St-Laurent et Christian Dussault, ont participé à toutes les étapes du cheminement de ce manuscrit, incluant un apport non négligeable à l'élaboration de l'idée originale, des objectifs et des hypothèses, à l'écriture du manuscrit en plus de trouver l'important financement nécessaire pour mener à terme cette recherche.

2.2 BEHAVIOURAL STRATEGIES TOWARDS HUMAN-INDUCED DISTURBANCES EXPLAIN INDIVIDUAL PERFORMANCE IN A LARGE UNGULATE

Summary

1. Behavioural strategies may have important fitness, ecological and evolutionary consequences. In woodland caribou *Rangifer tarandus caribou* (Gmelin), human disturbances are associated with higher predation risk. We investigated if habitat selection strategies of woodland caribou females towards human-induced disturbances influenced their reproductive success.

2. We used data from 42 GPS collared adult females and 65 VHF collared caribou calves between 2004 and 2011 in managed boreal forest of Québec, Canada. We evaluated calf survival using a Cox proportional hazards model and investigated the link between habitat selection of females and the fate of their calf using logistic regressions at three spatial scales.

3. Caribou calf survival was 53% and 43% after 30 and 90 days following birth, respectively and 52% of calves that died were killed by black bears *Ursus americanus* (Pallas).

4. The probability that a female lost its calf by predation was not influenced by the composition of her annual home range, but decreased with an increase in proportion of open lichen woodland within its calving home range. At the local scale, females that did not lost their calf displayed a stronger avoidance towards high road density areas and a stronger selection towards mixed and deciduous stands than females that lost their calf from predation. Further, females that lost their calf from predation and that had a low proportion of <5 years-old cutovers within their calving home range were mostly observed in areas where <5 years-old cutovers were locally absent. Also, females that lost their calf from predation and that had a high proportion of <5 years-old cutovers within their calving home range were mostly observed in areas with a high local density of <5 years-old cutovers.

5. *Synthesis and applications*. Our study demonstrated that we have to account for human disturbances at both local and regional scales in order to elaborate effective caribou management plans. We demonstrated that human-induced disturbances not only impacts spatial distribution of individuals, but also their reproductive success.

Key-words: Anthropogenic disturbances, Black bear, Caribou, Calf survival, Forest management, Functional response, Habitat selection, Québec, Reproductive success

Introduction

Anthropogenic disturbances are widely spread across both terrestrial and marine ecosystems (Sanderson et al. 2002; Halpern et al. 2008). Whereas some species benefit from anthropogenic disturbances (Fisher & Wilkinson 2005; Potvin, Breton & Courtois 2005), others like those associated with pristine habitats are often negatively affected (Vors et al. 2007; Hardus et al. 2012). As outlined by Johnson & St-Laurent (2011), anthropogenic infrastructures or disturbances may affect animal physiology (Creel et al. 2002; Wikelski & Cooke 2006), behaviour (Blumstein et al. 2005; Leclerc, Dussault & St-Laurent 2012), energetic balance (Bélanger & Bédard 1990; Williams, Lusseau & Hammond 2006), survival (Carney & Sydeman 1999; Phillips & Alldredge 2000), as well as animal populations and communities (Addessi 1994; Winfree, Grisworld & Kremen 2007).

The boreal forest, a biome representing 33% of the Earth's forest cover, is increasingly impacted by forestry activities (Burton et al. 2003). The threatened woodland caribou *Rangifer tarandus caribou* (Gmelin) is recognized as being negatively impacted by both human-induced and natural disturbances (Vors et al. 2007; Festa-Bianchet et al. 2011). Increased predation risk in highly disturbed environments is considered the most important proximal limiting factor explaining the widespread population declines (McLoughlin et al.

2003; Wittmer et al. 2007; Festa-Bianchet et al. 2011). Forestry activities benefit wolves *Canis lupus* (L.) (Seip 1991; Potvin, Breton & Courtois 2005), the main predator of adult caribou, and black bears *Ursus americanus* (Pallas) which is another potential predator of caribou calves (Gustine et al. 2006; Pinard et al. 2012). Although adult female survival is the most important determinant of population dynamics, calf survival is highly variable among years and populations (Seip & Cichowski 1996; Gustine et al. 2006; Pinard et al. 2012), and it also has a great influence on population dynamics (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard et al. 2000; Raithel, Kauffmian & Pletscher 2007).

During the calving period, behavioural adjustments expressed by female caribou aims at reducing predation risk for their calf (Gustine et al. 2006; Pinard et al. 2012), and their habitat selection is oriented toward old-growth coniferous forests (Lantin et al. 2003; Mahoney & Virgl 2003), open lichen woodlands and peatlands (McLoughlin, Dundford & Boutin 2005; Hins et al. 2009). Females also select areas located at high elevations or in rugged terrains (Nellemann and Cameron 1996; Gustine et al. 2006; Leclerc, Dussault & St-Laurent 2012), while avoiding cutovers, regenerating areas and roads (Leclerc, Dussault & St-Laurent 2012; Leblond, Dussault & Ouellet 2013). Caribou attempt to spatially isolate themselves from predators and their habitat selection pattern appears to be effective in avoiding predation by wolves (James et al. 2004). However, calves also suffer from black bear predation in landscapes where the human footprint is extensive (Mahoney & Virgl 2003; Pinard et al. 2012). Some authors suggested that wolf-avoidance strategies displayed by caribou could result in an increased exposure to predation risk by bear (Faille et al. 2010; St-Laurent & Dussault 2012), a potentially maladaptive behaviour due to recent increases in bear density across caribou range.

During the last decade, an increasing number of studies investigated differences in behaviour (Réale et al. 2010) which can occur between and within populations of the same species (Wilson 1998). For example, individuals may express different habitat selection (Mabille et al. 2012) or movement patterns while foraging (Austin, Bowen & McMillan 2004) or different intensities of boldness or shyness (Wilson et al. 1994; Réale & Festa-

Bianchet 2003). Because different behavioural strategies may translate into different survival probability or reproductive rate, behavioural strategies may have fitness, ecological and evolutionary consequences (Sih, Bell & Johnson 2004; Smith & Blumstein 2008; Réale et al. 2010). Therefore it is important to consider the range of behavioural strategies displayed by individuals when assessing the impacts of human-induced disturbances on wildlife, particularly in caribou as human disturbances are associated with higher predation risk for that species (Courtois et al. 2008; James & Stuart-Smith 2000; Whittington et al. 2011).

The study of functional responses in habitat selection may help to highlight the different behavioural strategies within a population. A functional response in habitat selection is defined as a change in the selection of a habitat attribute as a function of its availability or the availability of other habitat attributes (Mysterud & Ims 1998; Hebblewhite & Merrill 2008). Functional responses in habitat selection have been reported to occur in large ungulates such as moose *Alces alces* (L.) (Mabille et al. 2012; Beyer et al. 2013), red deer *Cervus elaphus* (L.) (Godvik et al. 2009) and caribou (Hansen et al. 2009; Moreau et al. 2012). However, few studies have tried to link functional responses to fitness (except Dussault et al. 2012). In this study, we used a GPS telemetry program of female caribou inhabiting a highly managed landscape in the boreal forest of Québec, Canada. We investigated if habitat selection strategies of females towards major human disturbances influenced their reproductive success. Further, we examined if functional responses in habitat selection of adult females caribou towards human-induced disturbances could explain the fate of their calf.

Materials and methods

STUDY AREA

The study area included two caribou ranges, i.e. Charlevoix (5086 km^2; 47°40’ N, 71°15’ W) and Saguenay–Lac-St-Jean (26 686 km^2; 48°28’-50°59’ N, 69°59’-72°15’ W), both typical of the boreal forest. In both regions, the landscape was dominated by coniferous stands composed of black spruce *Picea mariana* (Mill.) and balsam fir *Abies* *balsamea* (L.) Mill. with few mixed or deciduous stands composed of white birch *Betula papyrifera* (Marsh.), trembling aspen *Populus tremuloides* (Michx.), and maples *Acer spp*. (L.). Topography was characterized by low rolling relief ranging between 250 and 900 m in Saguenay–Lac-St-Jean, and between 500 and 1000 m in Charlevoix (Robitaille & Saucier 1998). Mean amount of precipitations were 1500 mm/y in Charlevoix and 1 200 mm/y in Saguenay–Lac-St-Jean, and snow accumulations could reach > 3 m (Robitaille & Saucier 1998). The Charlevoix region encompassed 3 National Parks (Grands-Jardins, Jacques-Cartier, and Hautes-Gorges-de-la-Rivière-Malbaie) where forest harvesting was prohibited but also a large part of the Laurentides Wildlife Reserve where forestry activities were allowed, such as in Saguenay–Lac-St-Jean. Other large mammals inhabiting the study area were moose, black bear, and grey wolf. White-tailed deer *Odocoileus virginianus* (Zimmermann) was also occasionally seen in Charlevoix.

CAPTURE AND MONITORING

Between 2004 and 2011, we captured female caribou using a net-gun fired from a helicopter (Potvin & Breton 1988), and equipped them with GPS collars (model 2200L or 3300L from Lotek, Newmarket, Ontario, Canada or model TGW4600 from Telonics, Mesa, AZ, USA). We programmed GPS collars to attempt location fixes every 1, 2, 3 or 4 hours depending upon the collar model and study site.

From 2004 to 2007 in Charlevoix and 2009 to 2011 in Saguenay–Lac-St-Jean, we captured as many calves as possible from the sample of females equipped with GPS collars. To do so, we regularly conducted telemetry flights during the calving period (21st May – 20th June) and visually confirmed the absence or presence of a newborn calf accompanying collared females. When a calf was first detected, we evaluated if we could capture it immediately (calf standing firmly or moving with its mother) or delayed capture to the next day (wet fur, lying down, low mobility). We captured calf by hand, wearing latex gloves, determined its sex, and fitted it with a VHF expansible collar (model LMRT-3 from Lotek, Newmarket, Ontario, Canada or model M2510B from Advanced Telemetry Systems, Isanti, MN, USA) equipped with a mortality sensor. All capture and handling procedures were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (UQAR; certificates # CPA-30-08-67 and CPA-27-07-53-R2) and of the Ministère des Ressources naturelles et de la Faune du Québec (MRNF; certificate # CPA-07-00-02).

We monitored calf survival by flying over the study area and listening to VHF signals at least twice a week from birth date to the end of June (flights being on average 1.8 ± 1.5 [SD] days apart), and every 2 weeks thereafter until late August (flights being on average 10.8 ± 6.7 [SD] days apart), and finally once per month in September and October. When a mortality signal was detected, we located the collar within 72 hours and investigated the carcass and its surroundings to determine the mortality cause. We considered the presence of tooth marks, blood or disarticulated, dispersed or crushed bones as evidence of predation, and we determined the predator species with indices such as faeces, tracks, hairs, and scratching signs (Pinard et al. 2012). We used the date of telemetry flights, indices left on the mortality site, and unusual long movement of the calf's mother by looking at their GPS locations to assess the mortality date more precisely.

DATA ANALYSIS

We used 1:20 000 digital ecoforest maps, published by the MRNF, to describe caribou habitat. We updated these maps annually to include habitat modifications resulting from forestry practices and natural disturbances. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies). We combined polygons available on ecoforest maps into 10 habitat types based on caribou ecology (Table 1). We also created a digital elevation model (cell size = 30 m × 30 m) using 1:20 000 topographic maps.

We investigated the link between habitat selection of adult females and the probability that their calf die from predation at three spatial scales, i.e. annual home range, calving home range and local scales. For the habitat selection analyses, we subsampled the GPS telemetry database to get location intervals of 3 or 4 h. At the annual and calving home range scales, we used calf fate (0 = alive, 1 = dead from predation) as the dependent variable, and mean elevation, proportion of each undisturbed and disturbed habitat type

(Table 1), and road density within the female annual and calving home ranges as independent variables.

At the local scale, we contrasted habitat use and availability by comparing locations of each female caribou to an equal number of locations randomly distributed within their annual home range (3rd order of selection; Johnson 1980). We defined home ranges using 100% MCP instead of kernel which provides biased estimates when animals exhibit site fidelity behaviour (Hemson et al. 2005) such as caribou in our study area (Faille et al. 2010). MCPs are known to overestimate home range size by including unused habitats (Grueter et al. 2009). However, our objective was not to assess home range size but habitat selection, and MCP were more likely to provide the desired contrast between used and available habitat types to highlight habitat selection. We determined elevation, and calculated the proportion of each undisturbed and disturbed habitat type (Table 1), as well as road density within an 816 m radius circular buffer centred on each GPS and random locations. This allowed us to consider the influence of the surrounding environment on habitat selection at the local scale (Leblond et al. 2011). We used an 816 m buffer size as it represented the median daily distance travelled by females during the calving period. We conducted all spatial analyses using ArcGIS 10.0 (ESRI Inc., Redlands, California, USA).

STATISTICAL ANALYSIS

For the survival analysis, we only used calves from the Saguenay–Lac-St-Jean region as results for the Charlevoix region were published by Pinard et al. (2012). We assessed calf survival rate using a Cox Proportional Hazards regression model (CPH; Cox 1972; McLoughlin, Dundford & Boutin 2005; Pinard et al. 2012) and tested the effect of year, sex, and date of birth on calf survival using the “Survival” library in R 2.15.1 (R development core team 2012).

For the habitat selection analyses, we used GPS locations of radio collared females for which we captured and monitored the survival of their calf using VHF telemetry collars. Females that lost their calf from another cause than predation were removed as our study aims to focus on mortality by predation instead of total mortality (McLoughlin, Dunford &

Boutin 2005; Dussault et al. 2012). We further removed 3 other females from habitat selection analyses because we did not retrieve their GPS collar (*n* = 2) or we did not have any information on ecoforest maps at their GPS locations (*n* = 1).

At the annual and calving home range scales, we used mixed effects logistic regressions to determine the influence of the annual and calving home range composition on female reproductive success. We used calf fate (0 = alive, 1 = dead from predation) as the dependent variable and considered the region (i.e., Saguenay–Lac-St-Jean or Charlevoix) as a random effect. We performed model selection (Burnham & Anderson 2002) and evaluated different alternative hypotheses (3 candidate models; see Table 2) using the Akaike's Information Criterion (AIC; Burnham & Anderson 2002). Further, we tested if the best-supported model was statistically different from the null model using the likelihood ratio test.

At the local scale, we aimed to highlights habitat selection strategies of females and not the differences between the mortality site and previous locations (Cox model; Cox 1972). Therefore, we used Resource Selection Functions (Manly et al. 2002) to compare habitat selection between females that have lost their calf from predation and females for which the calf survived throughout the study period. Following Dussault et al. (2012), we randomly matched a female for which the calf was killed by a predator to a female for which the calf survived. We restricted the dataset of the female with the calf that survived to the same number of days as the one that died for each pairing. Doing so allowed us to compare habitat selection of the females while controlling for calf age, and prevented us to detect differences only due to increased calf mobility or environmental changes which are associated with calf age (Dussault et al. 2012). We used the resulting database to conduct mixed logistic regressions to compare habitat characteristics at the female locations (use) to those at random locations (availability) and considered the calf nested in female nested in region as a random effect. We repeated this process 999 times, each time with a different pairing of calves that died and calves that survived. On each iteration, we used the resulting database to evaluate different candidate models (Table 2) using the AIC (Burnham &

Anderson 2002). In candidate models 4 to 12, we added the interaction between calf fate and habitat type covariates in order to evaluate if habitat selection strategies of females could be linked to the fate of their calf. Further, in model 7 to 12, we added triple interactions to explore if functional responses in habitat selection could explain calf fate. Thus, for each candidate model, we obtained 1000 coefficient estimates that we used to calculate the mean coefficient and associated 95 % CIs. Prior to all habitat selection analyses, we assessed multicolinearity between independent variables using the variance inflation factor (VIF; threshold of 10; Graham 2003) and consequently removed the % of coniferous stands from the candidate models. We conducted all statistical analyses using R 2.15.1 (R development core team 2012).

Results

Between 2009 and 2011, we captured 30 calves in Saguenay–Lac-St-Jean. In this region, mean calf survival rate was 53 % and 43 % after 30 and 90 days following birth, respectively (Table 3, Fig. 1). Nine of the 17 (53%) calves that died were killed by black bear, the most important mortality agent, and no calf suffered from wolf predation (Table 3). Four calves (13%) died from an unknown natural cause (Table 3). Most calf mortalities occurred during the first month of life and survival rate stabilized after three months (Fig. 1). Survival rate did not vary with calf sex ($\chi^2 = 0.3$; df = 1; p = 0.559), year ($\chi^2 = 1.5$; df = 2; p = 0.471), and birth date ($\chi^2 = 22.2$; df = 16; p = 0.136). In Charlevoix, mean calf survival rate was 47 % after 90 days and black bear was also the primary mortality agent (see Pinard et al. 2012 for more information).

We conducted the habitat selection analyses using the GPS locations of 22 calves' mothers from the Saguenay–Lac-St-Jean region, of which 11 survived and 11 died from predation, and 35 calves' mother from Charlevoix, of which 16 survived and 19 died from predation. At the two largest spatial scales, calf fate did not depend on the reaction of their mother toward human disturbances. At the annual home range scale, the best-supported model describing calf fate only included undisturbed habitat types (model 1, Tables 2 and 4). However, this model did not differ from the null model ($\chi^2 = 2.09$; df = 4; p = 0.718), suggesting that the probability that a female lost its calf from predation was not influenced by the composition of the annual home range. At the calving home range scale, the best-supported model also included undisturbed habitat types only (model 1, Tables 2 and 4) but in this case, it was statistically better than the null model ($\chi^2 = 10.36$; df = 4; p = 0.035). The probability that a female lost its calf from predation decreased as the proportion of open lichen woodlands in its calving home range increased (Table 5).

At the local scale, the best-supported model (model 12, Table 4) revealed that calf fate was linked to habitat selection strategies toward human disturbances of adult females. Three major results emerged from this analysis. First, all females avoided high road density, but females that did not lost their calf displayed a stronger avoidance towards high road density areas than females that lost their calf from predation (Table 6). Second, females that did not lost their calf from predation displayed stronger selection towards mixed and deciduous stands (Table 6). Finally, calf fate depended on the combined local (within the 816 m buffer) density of <5 years-old cutovers and on the proportion of <5 years-old cutovers within the calving home range (Table 6). This functional response towards <5 years-old cutovers highlights two different habitat selection strategies that resulted in a higher probability of calf death. Females that lost their calf from predation and that had a low proportion of <5 years-old cutovers within their calving home range were mostly observed in areas where <5 years-old cutovers were locally absent. Also, females that lost their calf from predation and that had a high proportion of <5 years-old cutovers within their calving home range were mostly observed in areas with a high local density of <5 years-old cutovers.

Discussion

Our study demonstrated that differences in behavioural strategy towards human-induced disturbances led to different outcomes on calf fate in a large ungulate, the threatened woodland caribou. Indeed, the different habitat selection strategies displayed by females toward <5 years-old cutovers and roads resulted in different reproductive success. At the local scale, all human disturbances induced behavioural changes on female caribou, but not all had consequences on the fate of their calf. Habitat selection at the largest spatial scale (annual home range) did not influence the probability a female's calf dying from predation, suggesting that females avoided predation risk at smaller spatial and temporal scales.

We further demonstrated that the functional response in habitat selection by females towards <5 years-old cutovers explained some variation in calf fate. During the lactation period, the energetic requirements of females doubled (Chan-McLoed, White & Holleman 1994) so that fine scale habitat selection might be oriented towards habitat types with higher food availability (Lantin et al. 2003; Carr, Rodgers & Walshe 2007). The use of young cutovers, a highly productive habitat type, likely resulted in more frequent foraging opportunities for female caribou (Bergerud & Nolan 1970; Bergerud 1972; Bock & Van Rees 2002). We see two plausible hypotheses to explain the adaptive use of young cutovers by female caribou after calving. Higher food availability may result in higher milk production and in more time available for maternal care, both of which should promote calf growth (White 1983; Rognmo et al. 1983), and shorten the period during which calves are highly vulnerable to predators. However, when the proportion of young cutovers within the landscape reaches higher levels, the positive effect of increased food availability is overcome by the negative effect of higher predation risk. Disturbed habitat types, such as <5 years-old cutovers, were often associated with higher predation risk (McLoughlin et al. 2003; Wittmer et al. 2007; Festa-Bianchet et al. 2011) and the proportion of disturbed habitat types within caribou habitat was negatively correlated to calf recruitment (Environment Canada 2011). The increased proportion of disturbed habitat types triggers numerical (Seip 1991; Brodeur et al. 2008) and functional (Houle et al. 2010) responses of caribou predators. Indeed, wolf is known to increase its selection of recent cutovers when these cuts are more abundant in the landscape (Houle et al. 2010). A similar functional response towards <5 years-old cutovers could also exist for other predators of caribou calves such as black bear.

Calf survival was mainly influenced by black bear predation in Saguenay–Lac-St-Jean (Pinard et al. 2012). Wolves killed 5% of calves in Charlevoix and none in Saguenay–Lac-St-Jean, suggesting that the wolf-avoidance strategy used by female caribou during the calving period is effective. This wolf-avoidance strategies mainly consisted of selecting higher elevations (Bergerud, Butler & Miller 1984; Leclerc, Dussault & St-Laurent 2012; Pinard et al. 2012) as wolves usually use lower elevations to move through the landscape (Whittington et al. 2011; Lesmerises, Dussault & St-Laurent 2012). However, avoiding wolves, the predator with which caribou co-evolved, could result in increased predation risk by black bear, as the latter also selected higher elevations during spring (Mosnier, Ouellet & Courtois 2008). Females might have difficulties in assessing predation risk by bears as they are rarely attacked by these (Ballard 1994). Although black bear killed the most calves in our system, Bastille-Rousseau et al. (2011) suggested that bear predation on caribou calves occurred on a fortuitous basis, and that bear encounter caribou along their frequent movements between food-rich habitat patches such as regenerating stands.

We also demonstrated that linear infrastructure negatively influenced caribou behaviour and calf survival. All females avoided areas with high road density, but females that avoided these linear features more strongly were less likely to lose their calf by predation. Avoidance of roads has been demonstrated to be an means of avoiding wolves by caribou (James & Stuart-Smith 2000; Leclerc, Dussault & St-Laurent 2012; Pinard et al. 2012) because roads are associated with higher predation risk by wolf (James & Stuart-Smith 2000; Whittington, St-Clair & Mercer 2005; Whittington et al. 2011). Roads may also increase black bear predation risk as roadsides are highly productive environments that are selected by bear during spring (Bastille-Rousseau et al. 2011).

Females that lost and that did not lost their calf from predation displayed different habitat selection strategies towards young cutovers. Some females selected young cutovers even if it resulted in higher predation risk for their calf. We suggest that range fidelity, as displayed by females in our study area (Faille et al. 2010), could result in an ecological trap (Schlaepfer, Runge & Sherman 2002) when an individual continues to frequent a formerly suitable habitat patch that was modified by human activities (Faille et al. 2010; St-Laurent & Dussault 2012). This maladaptive behaviour, although expressed only by some females, could jeopardize caribou recruitment, particularly in highly managed boreal forest where black bear densities are high, and at least partially explain the mechanism linking habitat alteration with the global decline of woodland caribou.

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Table 1. Description of the 10 habitat types used to assess the relationship between habitat selection of female caribou and the fate of their calf (i.e. died from predation or survived) in the boreal forest of Québec (Canada) between 2004 and 2011

Habitat type	Description
Undisturbed habitat types	
Coniferous	Coniferous stands with dominant tree strata ≥ 50-years-old
Mixed and deciduous	Mixed and deciduous stands with dominant tree strata ≥ 50-years-old
Open lichen woodland	Coniferous forest with low tree density and usually terrestrial lichens
Peatlands	Poorly drained open areas (bogs and fens)
Disturbed habitat types	
< 5 years-old cutovers	Cutovers aged ≤ 5-years-old
6-20 years-old cutovers	Cutovers aged 6-20-years-old
20-40 years-old cutovers	Cutovers aged 20-40-years-old
Open no regeneration	Areas with no dominant tree strata originating from a natural disturbance
Non-forested habitat types	
Water bodies	Lakes and rivers
Others	Others non-forested areas

Table 2. Candidate models tested to assess the relationship between the habitat selection of female caribou and the fate of their calf (i.e. died from predation or survived) in the boreal forest of Québec (Canada) between 2004 and 2011. In candidate model 4 to 12, we added the interaction between calf status and habitat covariates to investigate if habitat selection strategies could explain calf fate. In model 7 to 12, we added triple interactions to explore if functional responses in habitat selection could explain calf fate

Candidate model no.	Variables
1*	Elevation + % Peatlands + % Open lichen woodland + % Mixed and deciduous
2	% Young cutovers + % Old cutovers + % Regenerating area + % Open no regeneration + Road density
3	Model 1 + Model 2
4	Model 1 + Elevation × Calf status + % Peatlands × Calf status + % Open lichen woodland × Calf status + % Mixed and deciduous × Calf status
5	Model 2 + % Young cutovers × Calf status + % Old cutovers × Calf status + % Regenerating area × Calf status + % Open no regeneration × Calf status + Road density × Calf status
6	Model 4 + Model 5
7	Model 5 + % Young cutovers × % Young cutovers in the calving home range × Calf status
8	Model 5 + % Old cutovers × % Old cutovers in the calving home range × Calf status
9	Model 5 + % Young cutovers × % Young cutovers in the calving home range × Calf status + % Old cutovers × % Old cutovers in the calving home range × Calf status
10	Model 6 + % Young cutovers × % Young cutovers in the calving home range × Calf status
11	Model 6 + % Old cutovers × % Old cutovers in the calving home range × Calf status
12	Model 6 + % Young cutovers × % Young cutovers in the calving home range × Calf status + % Old cutovers × % Old cutovers in the calving home range × Calf status

* The % of coniferous stands was removed to prevent multicolinearity

Table 3. Survival rate and mortality agent of caribou calves monitored (n = 30) during their first 5 months of life from 2009 to 2011 in Saguenay–Lac-St-Jean, Québec, Canada

	Year			
Variable	2009	2010	2011	Total
No. of calves	9	11	10	30
Survival rate	0.444	0.364	0.500	0.433
Mortality agent (*n*)				
Black bear	3	2	4	9 (52.9 %)
Wolf	0	0	0	0 (0.00 %)
Unknown predator	2	0	1	3 (17.6 %)
Drowning	0	1	0	1 (5.88 %)
Unknown*	0	4	0	4 (23.5 %)

* Unknown mortalities occurred when the carcass was seemingly untouched and had no sign of predation.

Table 4. Results of the candidate models tested at three spatial scales to assess the relationship between the habitat selection of female caribou and the fate of their calf (i.e. died from predation or survived; *n* = 57) in the boreal forest of Québec (Canada) between 2004 and 2011. Candidate models are listed with log-likelihood (LL), numbers of parameters (K), difference in Akaike Information Criterion to the best-supported model (**Δ**AIC), and their relative weight (AICw)

Candidate model no.	Annual home range scale*				Calving home range scale*				Fine scale			
	LL	K	**Δ**AIC	AICw	LL	K	**Δ**AIC	AICw	LL	K	**Δ**AIC	AICw
1	-38.38	5	0	0.54	-34.25	5	0	0.73	-6865	5	2094	0.00
2	-37.57	6	0.38	0.44	-35.04	6	3.58	0.12	-6772	6	1910	0.00
3	-36.85	10	6.39	0.02	-30.84	10	3.18	0.15	-6146	10	666	0.00
4									-6829	10	2032	0.00
5									-6636	12	1650	0.00
6									-6004	20	402	0.00
7									-6509	16	1404	0.00
8									-6547	16	1480	0.00
9									-6429	20	1252	0.00
10									-5873	24	148	0.00
11									-5916	24	234	0.00
12									-5795	28	0	1.00

* At the annual and calving home range scales we only tested candidate model 1, 2 and 3

Table 5. Coefficients (β) and their 95% C.I. of the covariables present in the best-supported logistic regression model used to assess the link between a female's calf fate (i.e. died from predation coded 1; or survived coded 0; *n* = 57), and the composition of its calving home range in the boreal forest of Québec (Canada) between 2004 and 2011

			95 % C.I.	
Variable	β	SE	Lower limit	Upper limit
Intercept	0.768	1.970	-3.201	4.677
Elevation (km)	-0.516	2.267	-5.048	4.016
Peatlands (%)	17.278	13.567	-9.857	44.413
Open lichen woodland (%)	-34.459	14.797	-64.054	-4.865
Mixed and deciduous (%)	-1.360	5.004	-11.368	8.648

Table 6. Coefficient (β) and their 95% C.I. of the covariables present in the best-supported model at the local scale assessing the link between a female's calf fate (*n* = 57) (i.e. died from predation or survived) and its habitat selection strategy in the boreal forest of Québec (Canada) between 2004 and 2011

		95 % C.I.	
Variable	β	lower	Upper
Intercept	-4.221	-5.063	-3.745
Elevation (km)	8.457	7.956	9.272
Peatlands (%)	-8.002	-8.172	-7.814
Open lichen woodland (%)	0.729	0.673	0.809
Mixed and deciduous (%)	-2.666	-2.833	-2.521
Road density (km/km^2)	-5.286	-5.414	-5.169
Young cutovers (%)	-7.643	-7.786	-7.457
Old cutovers (%)	-5.053	-5.405	-4.680
Regenerating area (%)	-4.650	-4.709	-4.554
Open no regeneration (%)	-5.498	-5.567	-5.450
Calf alive	-0.340	-3.589	2.106
Young cutovers in calving home range (%)	-4.934	-6.439	-3.020
Old cutovers in calving home range (%)	-3.953	-5.482	-2.756
Elevation (km) × calf alive	0.755	-2.910	5.532
Peatlands (%) × calf alive	-0.104	-4.821	4.591
Open lichen woodland (%) × calf alive	-3.735	-8.732	0.375
Mixed and deciduous (%) × calf alive	4.405	0.991	7.659
Road density (km/km^2) × calf alive	-9.383	-18.472	-1.962
Young cutovers (%) × calf alive	4.501	1.918	7.193
Old cutovers (%) × calf alive	-6.312	-21.614	4.208
Regenerating area (%) × calf alive	0.657	-1.648	3.185
Open no regeneration (%) × calf alive	-1.568	-18.892	6.212
Young cutovers (%) × young cutovers in calving home range (%)	37.696	36.699	38.481
Young cutovers in calving home range (%) × calf alive	1.854	-1.202	3.984
Old cutovers (%) × old cutovers in calving home range (%)	22.386	19.505	25.259
Old cutovers in calving home range (%) × calf alive	-1.731	-6.958	2.637
Young cutovers (%) × young cutovers in calving home range (%) × calf alive	-19.936	-31.583	-3.178
Old cutovers (%) × old cutovers in calving home range (%) × calf alive	20.820	-16.650	73.138

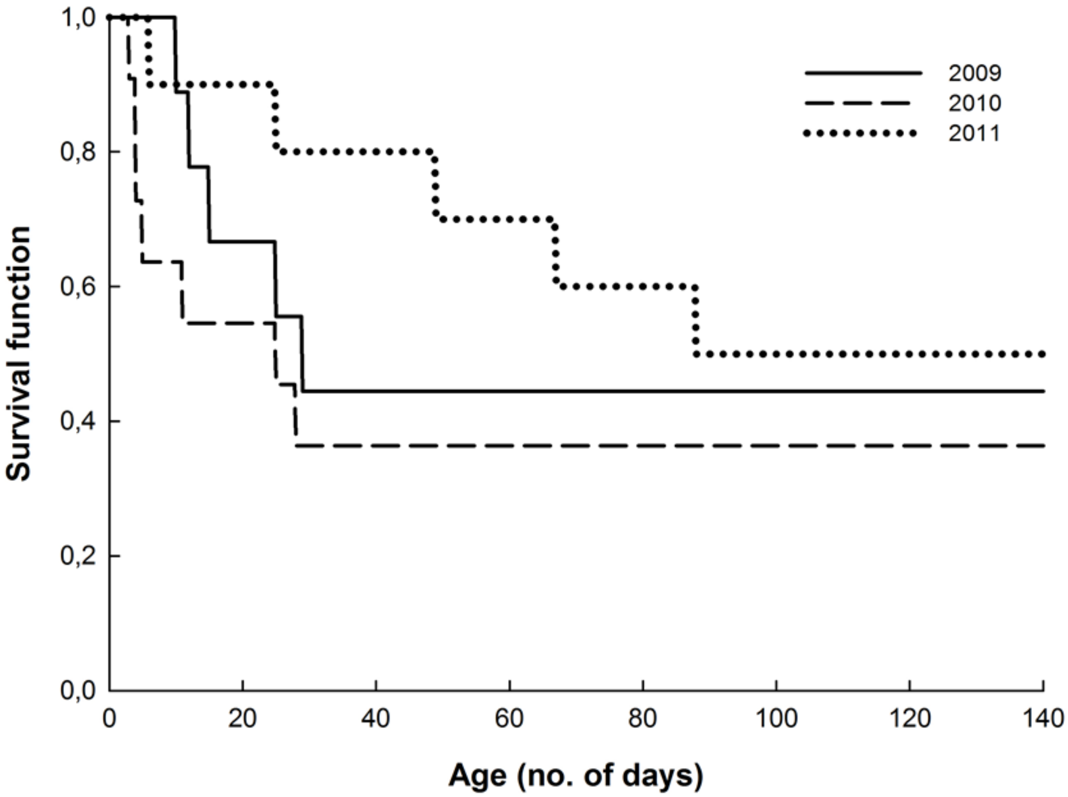

Figure 1. Survival function of caribou (*Rangifer tarandus caribou*) calves monitored in Saguenay–Lac-St-Jean, Québec, Canada, 2009-2011 (*n* = 30).

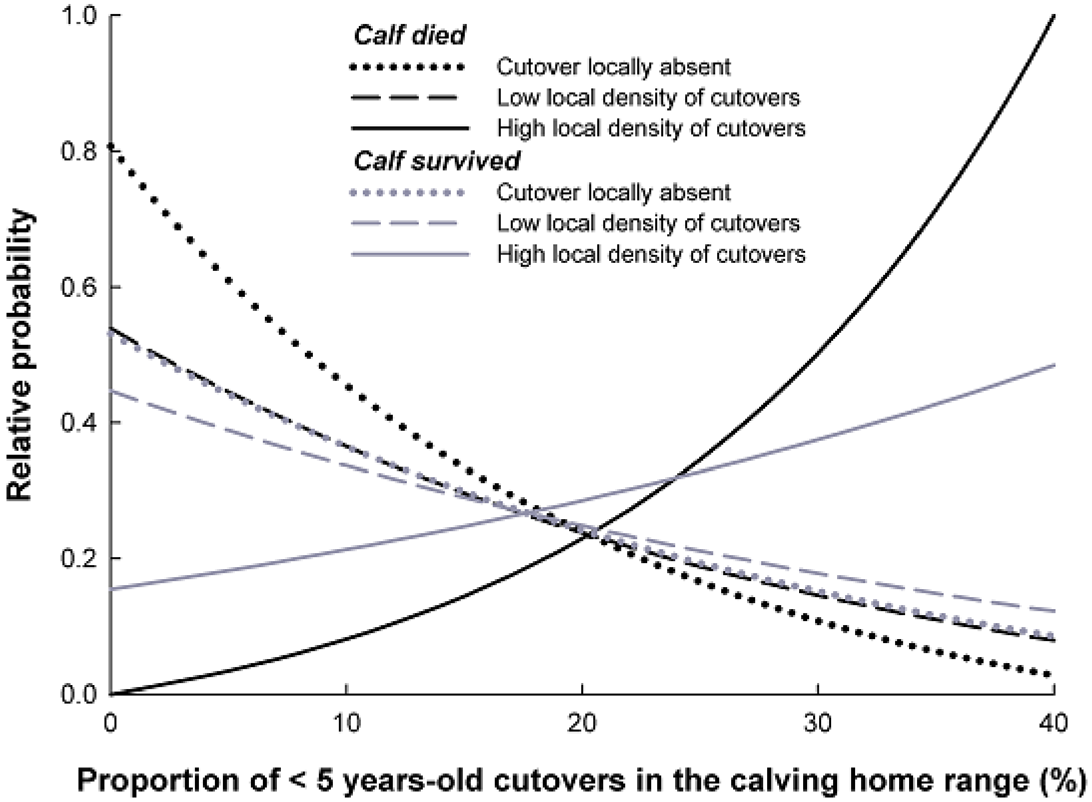

Figure 2. Relative probability of occurrence of female caribou (*Rangifer tarandus caribou*) that did or did not lost their calves (*n* = 57) from predation, as a function of the percentage of < 5 years-old cutovers within the female calving home range, for three < 5 years-old cutovers density (i.e., 0.0 %, 4.6 %, 29.1 % of 816 m radius circular buffer, corresponding to absent, low and high density of cutovers, respectively)

CHAPITRE 3
CONCLUSION

Le caribou forestier bénéficie d’un statut particulier tant au Canada (espèce menacée; COSEPAC 2002) qu’au Québec (espèce vulnérable; MRNF 2005). L’aire de répartition mondiale de cette espèce ne cesse de régresser vers le nord (Bergerud 1974; Courtois 2003; McLoughlin et al. 2003) et la majorité des populations de caribou sont en déclin (Vors & Boyce 2009). La cause proximale de ce déclin est l’augmentation de la prédation (McLoughlin et al. 2003; Festa-Bianchet et al. 2011) dû à l’altération de son habitat, la cause ultime (Wittmer et al. 2007; Courbin et al. 2009). Le loup gris est le principal prédateur des caribous adultes (Seip 1991) et peut aussi s’attaquer aux faons, ces derniers ayant également comme prédateur l’ours noir, l’aigle royal, le carcajou, le lynx et le grizzly (Bergerud 1971; Adams et al. 1995; Gustine et al. 2006; Pinard et al. 2012). La survie des faons est hautement variable d’une année à l’autre (Seip & Cichowski 1996; Gustine et al. 2006; Pinard et al. 2012) et peut influencer de manière importante le taux de croissance des populations (Gaillard et al. 1998, 2000; Raithel et al. 2007). Sachant que la majorité des événements de prédation sur les faons caribous surviennent durant les six premières semaines de vie (Adams et al. 1995; Gustine et al. 2006; Pinard et al. 2012), les périodes de mise bas et d’élevage en bas âge s’avèrent cruciales pour déterminer la trajectoire démographique et la persistance des populations de caribou.

C’est dans cette optique que cette étude s’est intéressée à ces deux périodes critiques que sont la mise bas et l’élevage en bas âge. Plus précisément, cette étude visait à mieux comprendre les impacts de l’aménagement forestier sur la sélection des sites de mise bas et sur la survie des faons caribous au cours des premiers mois de vie. Bien que certains auteurs s’étaient déjà intéressés à ces questions dans la harde réintroduite et isolée de

Charlevoix (Pinard et al. 2012; Dussault et al. 2012), il était important de faire cette même démarche pour les caribous appartenant à l'aire de répartition continue de l'espèce dans un paysage dominé par les pessières noires et où l'empreinte de l'aménagement forestier était somme toute moindre.

Les résultats du chapitre 1 ont mis en lumière certaines caractéristiques du paysage sélectionnées (*e.g.* forêt résineuse mature, altitude, peuplement ayant une faible surface terrière) et d'autres évitées (*e.g.* routes, coupes forestières, dénudés humides) par les femelles pour l'établissement du site de mise bas. Ces résultats démontrent que les femelles caribous mettent bas de manière à réduire le risque de prédation et ce, aux trois échelles spatiales étudiées. L'intégration des résultats des trois échelles spatiales suggère que les patrons de sélection d'habitat exprimés par les femelles à large échelle spatiale ne permettent pas d'atténuer suffisamment le risque de prédation. Ainsi, la conservation des sites de mise bas devrait s'orienter vers la protection de grands massifs forestiers exempts de perturbations anthropiques, ces dernières étant associées à un risque de prédation plus élevé (Courtois et al. 2007; James & Stuart-Smith 2000; Whittington et al. 2011). Bien que cette étude démontre que la prédation semble être le facteur limitant principal lors de la sélection des sites de mise bas (Barten et al. 2001; Gustine et al. 2006; Pinard et al. 2012), d'autres études dans l'aire de répartition du caribou ont également mis en évidence un effet de la disponibilité en nourriture sur le comportement des femelles (Lantin et al. 2003; Carr et al. 2007). Les besoins énergétiques des femelles sont en effet élevés durant la période de gestation et de lactation (McEwan & Whitehead 1972; Chan-McLoed et al. 1994) et il serait important de conserver des massifs forestiers qui, en plus d'être exempts de perturbations anthropiques, offriraient une disponibilité en nourriture suffisante pour couvrir les besoins énergétiques des femelles.

Les résultats du chapitre 1 ont également démontré que l'homme, par l'aménagement forestier qu'il exerce, influence le comportement des caribous lors de la sélection de leur site de mise bas. De plus, l'évitement des routes, à toutes les échelles spatiales étudiées, souligne l'incapacité des femelles à complètement atténuer l'impact des routes lors de la recherche d'un site de mise bas. De ce fait, les impacts causés par les routes sur l'écologie du caribou pourraient potentiellement se répercuter à des échelles biologiques supérieures telles que le budget énergétique ou la démographie de la population (Johnson & St-Laurent 2011). Ainsi, réduire l'accès aux routes et restaurer celles-ci après leur utilisation pourrait s'avérer une mesure permettant de diminuer les impacts de l'aménagement forestier sur l'écologie du caribou. De plus, il appert que cette mesure de gestion et de conservation, qui a déjà été appliquée en Norvège, semble efficace chez le caribou (Nellemann et al. 2010).

Les résultats obtenus dans le chapitre 2 confirment l'hypothèse émise par Rettie & Messier (1998) stipulant que la prédation par l'ours noir puisse être un facteur important influençant la survie des faons caribous. En effet, nos résultats démontrent que l'ours noir était le principal agent de mortalité des faons, des résultats similaires à ceux trouvés à Charlevoix (Pinard et al. 2012) et à Terre-Neuve (Mahoney & Virgl 2003). Certains auteurs suggèrent que la stratégie antiprédatrice du caribou face au loup gris pourrait s'avérer mal adaptée et conduire à une augmentation du risque de prédation par l'ours noir (Faille et al. 2010; St-Laurent & Dussault 2012). Bien que l'ours ait été le seul prédateur confirmé dans cette étude, Bastille-Rousseau et al. (2011) ont démontré que l'ours noir ne recherche pas activement les faons caribous dans le paysage. Les événements de prédation seraient plutôt fortuits et seraient causés par des déplacements fréquents de l'ours noir entre des parcelles riches en nourriture (Bastille-Rousseau et al. 2011). Ainsi, la ségrégation spatiale des habitats riches en nourriture pour l'ours noir (*e.g.* peuplements en régénération, bordures de routes; Brodeur et al. 2008; Bastille-Rousseau et al. 2011) et les habitats de mise bas et d'élevage en bas âge pour le caribou (*e.g.* forêt mature résineuse, altitude) représenterait une mesure permettant de diminuer le risque rencontre et conséquemment le risque de prédation par l'ours noir sur les faons caribous.

Les résultats du chapitre 2 démontrent également que la sélection d'habitat exprimée par les femelles influence la survie des faons et, par conséquent, la valeur adaptative de chacune d'entre elles. En effet, la probabilité qu'une femelle perde son faon par prédation n'était pas influencée par la composition de son domaine vital annuel, mais diminuait avec l’augmentation de la proportion de dénudé sec dans son domaine vital de mise bas. Les femelles qui n’ont pas perdu leur faon par prédation ont démontré un plus fort évitement des routes et une sélection plus forte envers les peuplements mixtes et décidus matures que les femelles dont le faon est mort par prédation. De plus, les femelles qui ont perdu leur faon par prédation et qui avaient une faible proportion de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement absentes. Qui plus est, les femelles qui ont perdu leur faon par prédation et qui avaient une proportion élevée de coupes forestières de moins de 5 ans dans leur domaine vital de mise bas ont été principalement observées dans les secteurs où les coupes forestières de moins de 5 ans étaient localement abondantes.

Ces résultats démontrent que le risque de prédation des caribous est associé aux perturbations anthropiques que sont les coupes forestières et les routes (Wittmer et al. 2007; Whittington et al. 2011; Dussault et al. 2012). Sachant que la survie des faons peut jouer un rôle déterminant sur la dynamique des populations et que la survie des faons est associée à la représentation des perturbations anthropiques, il appert important de stabiliser, voire réduire, la proportion de ces perturbations dans le paysage si l’on souhaite redresser ou à tout le moins stabiliser les populations de caribous forestiers dans les territoires aménagés. En effet, plus la proportion de perturbations augmente dans le territoire occupé par une harde, plus la probabilité d’autosuffisance de cette population (*i.e.* un taux de croissance stable ou positif) diminue et plus le risque d’extinction locale augmente (Environnement Canada 2011).

Cette étude a démontré que l’anthropisation de la forêt boréale a eu un impact sur le comportement et également sur la survie des faons, un paramètre démographique important. De plus, les résultats soulignent l’existence d’une réponse fonctionnelle du caribou face aux coupes forestières de moins de 5 ans. Qui plus est, cette étude a démontré l’impact de cette réponse fonctionnelle sur la survie des faons. À ma connaissance, la démonstration de l’influence d’une réponse fonctionnelle envers une perturbation anthropique surfacique sur la valeur adaptative est une première.

Bien que la littérature scientifique relative au caribou soit substantielle, développer les connaissances spécifiques au territoire québécois demeure important puisque cette espèce démontre une grande plasticité comportementale envers les différents habitats naturels qu'elle rencontre à travers son aire de répartition (COSEPAC 2011). Ainsi, les résultats obtenus sont teintés par le paysage dans lequel le caribou évolue et doivent conséquemment être extrapolés avec précaution. À titre d'exemple, dans le 1er chapitre, nos résultats indiquent que les femelles évitaient les dénudés humides (*i.e.* les tourbières ombrotrophes et minérotrophes) lors de la sélection de leur site de mise bas. Cependant, ces mêmes dénudés humides sont sélectionnés par les femelles lors de la mise bas à Terre-Neuve (Mahoney & Virgl 2003) et en Alberta (James et al. 2004). Cette différence comportementale entre les aires d'études pourrait résider dans le mécanisme de réponse fonctionnelle (Mysterud & Ims 1998). En effet, en Alberta et à Terre-Neuve, les dénudés humides forment de grands complexes qui permettent au caribou de s'isoler spatialement de ses prédateurs (James et al. 2004; McLoughlin et al. 2005). Cependant, dans notre aire d'étude, les dénudés humides sont des habitats plutôt rares et de petites tailles. Dans un tel contexte, la capacité du caribou à s'isoler spatialement de ses prédateurs en utilisant les dénudés humides est beaucoup plus faible. Ainsi, la sélection des dénudés humides pourraient être avantageuse lorsque ceux-ci se retrouvent en grande quantité dans le paysage, mais peu avantageuse lorsqu'ils sont plutôt rares.

En somme, cette étude aura permis de mieux comprendre les divers comportements de sélection d'habitat exprimés par les femelles caribous forestiers lors de la période de mise bas et d'élevage en bas âge et leurs conséquences sur leur valeur adaptative dans l'aire de répartition continue de l'espèce au Québec. Les résultats obtenus pourront aider à affiner les futures stratégies d'aménagement forestier et du territoire et pourront guider les actions à entreprendre pour la conservation du caribou forestier au Québec.

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