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LIER L'ALIMENTATION, LA CONDITION PHYSIOLOGIQUE ET LA VALEUR ADAPTATIVE DES INDIVIDUS AUX RELATIONS TROPHIQUES ENTRE ESPÈCES POUR EXPLIQUER LE DÉCLIN D'UNE POPULATION ANIMALE

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

$\delta^{13}C$ Signature isotopique du carbone

$\delta^{15}N$ Signature isotopique de l'azote

$\Delta^{13}C$ Facteur d'enrichissement trophique du carbone

$\Delta^{15}N$ Facteur d'enrichissement trophique de l'azote

‰ Partie par mille

RÉSUMÉ

Le déclin des populations animales sauvages peut être attribué à un grand nombre de facteurs pouvant influencer la valeur adaptative. Certains facteurs tels que l'alimentation et la condition physiologique ont toutefois été moins étudiés. L'objectif principal de ma thèse était de mieux comprendre le rôle de l'alimentation, de la condition physiologique et des relations trophiques sur la dynamique d'une population menacée à l'aide de marqueurs biochimiques et physiologiques. Pour ce faire, j'ai utilisé les signatures isotopiques du carbone ($\delta^{13}C$), de l'azote ($\delta^{15}N$) et des éléments traces, tout en investissant des efforts supplémentaires pour parfaire la validation de ces méthodes et améliorer notre compréhension des limites de leur utilisation. À ce titre, mon deuxième objectif général visait à mieux comprendre les sources de variation des signatures isotopiques.

La présence des lipides dans les tissus peut influencer les signatures isotopiques et, potentiellement, affecter l'interprétation biologique de la composition du régime alimentaire et des relations trophiques. Par contre, les études antérieures ont supposé que lorsque les taux de lipides étaient faibles, le biais associé pouvait être ignoré. Mon premier chapitre visait à vérifier cette supposition en évaluant l'effet des lipides dans les tissus sur les valeurs de $\delta^{13}C$, de $\delta^{15}N$ et du rapport carbone : azote (CN) ainsi que de proposer un modèle de correction mathématique spécifique à l'espèce et au tissu. Mes résultats montrent que l'extraction des lipides est nécessaire même si les rapports CN étaient < 4 et que la précision de quatre modèles de normalisation des lipides fréquemment utilisés dans la littérature était moindre qu'attendu. Je recommande donc l'utilisation d'un modèle de correction des lipides adapté au tissu, à l'espèce et à la méthode d'extraction chimique. Mes chapitres suivants ont donc utilisé le modèle paramétré pour le caribou (*Rangifer tarandus caribou*).

Des informations sur les facteurs d'enrichissement trophique sont également nécessaires pour l'estimation du régime alimentaire et du partitionnement des niches trophiques. Toutefois, ces facteurs sont manquants pour de nombreuses espèces et types de tissus. Mon deuxième chapitre avait pour objectif d'estimer les facteurs d'enrichissement trophique de cinq espèces de mammifères terrestres dans deux types de tissus afin d'augmenter la précision des modèles mixtes isotopiques Bayésiens. Ce chapitre a permis de définir ces facteurs pour le caribou, l'orignal (*Alces americanus*), le cerf de Virginie (*Odocoileus virginianus*), le coyote (*Canis latrans*) et l'ours noir

(*Ursus americanus)* et a noté des différences importantes dans les facteurs entre les cinq espèces et les deux types de tissus analysés. Ces variations renforcent la nécessité de bien estimer les facteurs d'enrichissement trophique. Les facteurs que j'ai estimés se sont avérés très précis, comme en témoigne leur faible coefficient de variation respectif, et ont été utilisés tout au long de ma thèse afin d'obtenir des estimations précises des relations trophiques et de la composition du régime alimentaire de quatre de ces espèces sympatriques.

La compréhension des relations trophiques des espèces sympatriques au sein d'une communauté est essentielle pour mieux comprendre les mécanismes de coexistence, de compétition ou de prédation. Mon troisième chapitre visait donc à évaluer le partitionnement des resources et des niches trophiques entre le caribou, l'orignal et leurs prédateurs, le coyote et l'ours noir, ainsi que la composition de leur régime alimentaire. Le potentiel de compétition entre les deux cervidés s'est avéré relativement faible en raison de régimes alimentaires et de niches trophiques différents. Cependant, les fortes densités d'orignaux pourraient modifier la stratégie d'isolement du caribou et augmenter la compétition pour les ressources alimentaires de bonne qualité. La contribution du caribou dans le régime alimentaire des prédateurs s'est avérée faible, suggérant des taux de prédation occasionnels. Toutefois, le chevauchement important entre la niche trophique du caribou et de ses prédateurs (principalement l'ours noir) suggère qu'ils exploitent en partie la même niche, ce qui pourrait faire augmenter le risque de co-occurence et, par conséquent, le risque de prédation opportuniste pour le caribou. Il importe de prendre en considération les liens trophiques entre les espèces pour améliorer la compréhension des facteurs impliqués dans le déclin des populations.

L'alimentation et la condition physiologique sont également reconnues pour influencer les performances individuelles et la dynamique d'une population en déclin. Mon quatrième chapitre visait à évaluer l'influence des différences individuelles dans l'alimentation et la condition physiologique sur la valeur adaptative du caribou de la Gaspésie à l'aide des isotopes stables et des éléments traces. Une relation a été mise en évidence entre l'accumulation en éléments traces dans les poils de caribous et les signatures isotopiques, tout comme un lien entre le régime alimentaire, les éléments traces et les taux vitaux. Une signature élevée en $\delta^{13}C$ chez les femelles caribous en été et automne semblait liée à de haut taux de gestation et de survie des faons dans la population. De plus, certains éléments traces étaient corrélés à une meilleure survie des adultes et à une plus longue longévité. Mes résultats ont mis en évidence le lien potentiel entre l'alimentation, la condition physiologique et la valeur adaptative d'une population menacée.

Cette thèse comble en partie quelques zones d'ombre de la littérature scientifique. En effet, très peu de données existent quant à l'effet des lipides sur les signatures isotopiques et relativement aux facteurs d'enrichissement trophique pour les grands mammifères terrestres. De plus, l'utilisation des isotopes stables a aidé la compréhension des relations trophiques entre ces quatre espèces sympatriques, tout en favorisant un échantillonnage non invasif et une approche non létale. Dans le contexte d'une meilleure compréhension des facteurs influençant les performances individuelles, ma thèse a souligné l'importance de reconnaître les effets cumulatifs de plusieurs facteurs influençant le déclin d'une population tels que l'alimentation, la condition physiologique et les relations trophiques. J'estime que de suivre les changements dans la condition physique, physiologique et les indicateurs de santé qui pourraient refléter des changements dans la santé globale d'une population permettraient d'améliorer la gestion et la conservation des espèces menacées.

Mots clés : caribou, éléments traces, isotopes stables, niche trophique, performances individuelles

ABSTRACT

Decline of wild animal populations can be attributed to many factors, but some factors that may influence fitness, such as diet and physiological condition, have been less studied. The main objective of my dissertation was to better understand the role of diet, physiological condition and trophic relationships on the dynamics of a threatened population using biochemical and physiological markers. I used stable isotope ratios of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and trace elements, and invested efforts to improve our understanding of their use and limitations. My second objective was thus to better understand the sources of variation in isotopic signatures.

The presence of lipids in tissues is one underestimated aspect that may influence isotopic signatures. High lipid content in tissues may potentially bias future interpretation of trophic relationships or diet composition. Many studies have assumed that such a bias may be ignored when lipid content is low. My first chapter aimed to evaluate the effect of lipids on stable isotope ratios and to propose a species- and tissue-specific lipid normalization model. My results revealed that lipid extraction was required even if the carbon : nitrogen (CN) ratios were < 4 and that the accuracy of lipid normalization models frequently used in the literature was lower than expected. I then recommend using a lipid normalization model that is tissue-, method-, and species-specific. My following chapters have used this model parameterized for caribou (*Rangifer tarandus caribou*).

Estimating diet composition and trophic interactions using Bayesian stable isotope mixing models requires a species- and tissue-specific trophic discrimination factor (TDF). However, these factors are still missing for many species and tissues because only a few controlled studies have been carried out on captive animals. My second chapter aimed to estimate TDFs for caribou, moose (*Alces americanus*), white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), and black bear (*Ursus americanus*) in two types of tissue (hair and blood) to increase the accuracy of the models. I noted significant differences in TDFs among the five species and the two types of tissue, which reinforces the need to properly estimate TDFs. I have used these species- and tissue-specific TDFs throughout my dissertation to obtain precise estimates of trophic relationships and diet composition for four of these sympatric species.

Documenting the resource use and trophic relationships of sympatric species within a community is essential to assess underlying mechanisms of coexistence, competition or predation. My third chapter thus aimed to assess resource and trophic niche partitioning in summer/autumn between caribou, moose, and their incidental predators, the coyote and black bear, and the diet composition of their predators, and to what extent they consumed caribou. A low potential for resource competition between the two cervids was observed. However, high moose densities may modify the "spacing-away" antipredator strategy of caribou while increasing competition for high-quality food resources. The contribution of caribou to the diet of predators was relatively low, but the trophic niche overlap between caribou and their predators (mainly black bear) suggest that they exploit the same niche, which could increase the encounter rate and associated mortality risk for caribou. These results highlighted the importance of considering trophic relationships to increase our understanding of population decline.

Diet and physiological condition have the potential to impact individual performance and population dynamics. My fourth chapter aimed at evaluating how diet composition and physiological condition influence individual performance in an endangered population using stable isotopes and trace elements. A relationship was found between accumulation of trace elements in caribou hair and stable isotope ratios, but also a relationship between diet, trace elements and vital rates. This suggested that a high $\delta^{13}C$ signature of female caribou in summer/autumn appeared to be related to high pregnancy and calf survival probabilities in this population. Moreover, the concentration in some trace elements was correlated with higher adult survival and lifespan. This chapter revealed that nutrition may play a key role in the decline of endangered populations.

This dissertation filled some gaps in the scientific literature, considering that little empirical data exist regarding the effect of lipids on stable isotope ratios and TDFs for large terrestrial mammals. Also, using stable isotopes helped document the trophic relationships between four sympatric species using non-invasive tissue sampling and a non-lethal approach. As we highlighted the importance of considering multiple factors in the population decline, my dissertation contributed to document the factors influencing individual performance in large mammals, such as diet, physiological condition, and trophic relationships. Based on my results, I consider that monitoring changes in body condition, physiological status, and health indicators could reveal changes in the overall health of a population and will allow for improved management and conservation of threatened species.

Keywords: caribou, individual performances, stable isotopes, trace elements, trophic niche

INTRODUCTION

L'empreinte laissée par les activités anthropiques a été observée dans tous les écosystèmes à l'échelle du globe (Dirzo *et al.*, 2014; Sanderson *et al.*, 2002). Ces activités sont considérées comme l'une des principales menaces pour la biodiversité (Pelletier et Coltman, 2018). En effet, une sixième vague d'extinction massive a été déclenchée principalement par les activités humaines au cours des 500 dernières années (Pimm et Raven, 2000; WWF, 2016). Plusieurs facteurs peuvent contribuer au déclin des populations animales sauvages. Parmi les plus documentés, notons la surexploitation des espèces (Myers et Worm, 2003; Wittemyer *et al.*, 2014), la pollution (Croxall *et al.*, 2012), la prédation (Wittmer *et al.*, 2005a), les espèces invasives (Dueñas *et al.*, 2018), les changements climatiques (Zimova *et al.*, 2016) ainsi que la perte, la fragmentation et la dégradation de l'habitat (Baillie *et al.*, 2010). À titre d'exemple, le déclin de l'éléphant d'Afrique (*Loxodonta africana*) a été attribué à la perte et la dégradation de leurs habitats qui a contraint leur aire de distribution, et ce déclin a été accentué par le braconnage de l'ivoire entraînant une forte diminution de l'effectif des populations (Wittemyer *et al.*, 2014).

La perte et la dégradation de l'habitat représentent les facteurs les plus souvent cités dans le déclin des populations animales sauvages, principalement en raison de pratiques agricoles ou d'exploitation pétrolière, minière et forestière non soutenables (Baillie *et al.*, 2010; Czech *et al.*, 2000; Fahrig, 1997). Plus précisément, l'exploitation forestière entraîne des changements importants de qualité des habitats fauniques et modifie la composition et la structure des peuplements forestiers (McRae *et al.*, 2001), en plus de s'accompagner de la création de perturbations linéaires (p. ex.

routes) qui modifient l'environnement physique et chimique ainsi que le comportement d'utilisation de l'espace des animaux (Lesmerises *et al.*, 2013; Trombulak et Frissell, 2000). Ces changements sur l'habitat peuvent également influencer le comportement animal (Leblond *et al.*, 2013; Lesmerises *et al.*, 2013), l'alimentation (Birnie-Gauvin *et al*., 2017) et la condition physiologique (Wikelski et Cooke, 2006) des individus composant une population. Afin d'éviter la perturbation, un animal augmentera ses déplacements, ce qui résultera en une réduction des apports caloriques, mais aussi à une réduction de l'accessibilité ou de la disponibilité des ressources importantes ou rares (Bradshaw *et al.*, 1998). L'animal ne sera pas en mesure de combler ses besoins énergétiques et d'assurer sa reproduction, sa survie et de celle de ses jeunes (Wikelski et Cooke, 2006). Dans les cas les plus extrêmes, la modification de l'habitat pourra influencer la dynamique d'une population (Johnson et St-Laurent, 2011) et entraîner son déclin ou son extinction (Mattson et Merrill, 2002).

Le déclin des populations animales sauvages peut donc être attribué aux effets des activités anthropiques sur des facteurs largement moins étudiés, tels que l'alimentation ou la condition physiologique (voir les définitions dans le glossaire) (Birnie-Gauvin *et al.*, 2017; Carlsson *et al.*, 2019a) en influençant les performances et la valeur adaptative individuelle, la dynamique des populations et ultimement leur pérennité (Birnie-Gauvin *et al.*, 2017; Macbeth et Kutz, 2019; Mattson et Merrill, 2002). Par exemple, les tortues du désert (*Gopherus agassizii*) étaient plus susceptibles de souffrir d'une maladie respiratoire mortelle lorsque leurs besoins alimentaires n'étaient pas comblés puisque le niveau de stress pouvait augmenter et compromettre l'efficacité du système immunitaire (Tracy *et al.*, 2006). Cette forte mortalité associée à la maladie respiratoire a entraîné le déclin de cette population (Tracy *et al.*, 2006). Il importe donc de faire le lien entre les différents facteurs pouvant entraîner ou influencer le déclin des populations. Ceci nous permettra de

mieux comprendre leurs impacts et nous permettra de cibler des stratégies de gestion et de conservation efficaces chez les populations en déclin. Par conséquent, ma thèse se concentrera principalement sur le rôle de l'alimentation, de la condition physiologique ainsi que sur les relations trophiques, tels que la prédation et la compétition, sur le déclin des populations (Figure 0.1).

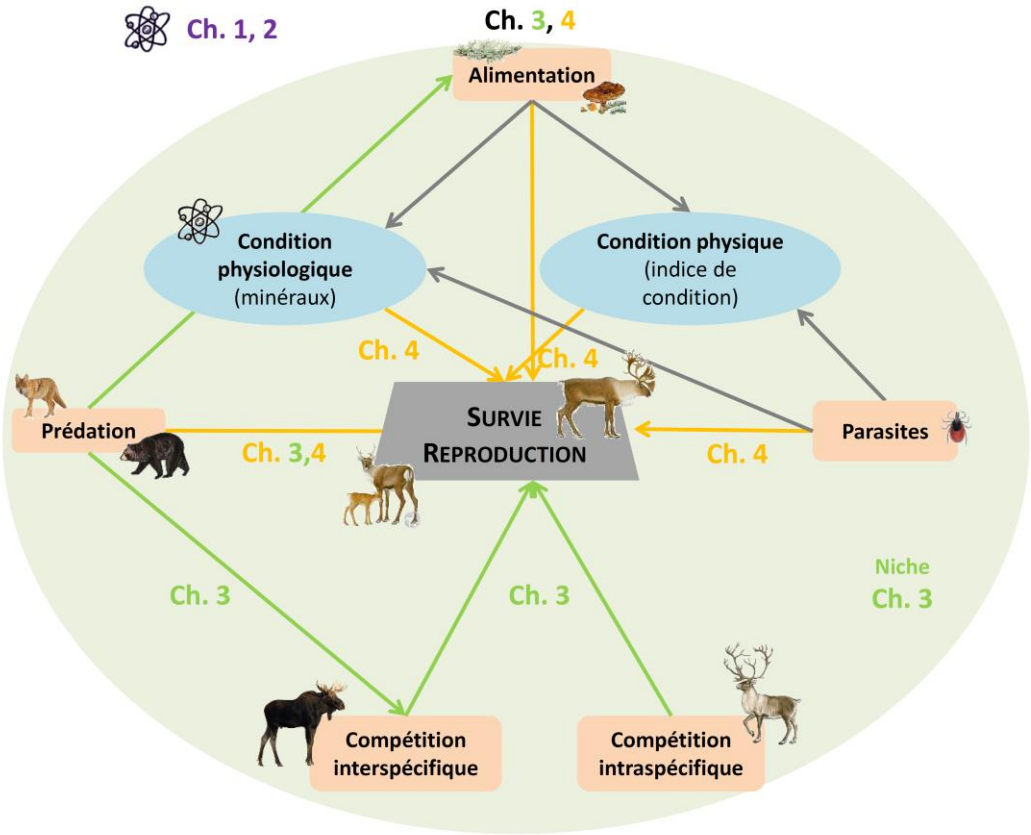

Figure 0.1. Représentation des différents facteurs extrinsèques (en orange) et intrinsèques (en bleu) (voir les définitions dans le glossaire) pouvant influencer la reproduction et la survie d'un individu, d'une population ou d'une espèce (en gris), mais également la niche écologique (en vert). Ces différents facteurs seront abordés au cours de cette thèse.

0.1 L'alimentation

L'alimentation est un facteur extrinsèque souvent mal connu, mais d'une grande importance puisqu'il qui permet d'expliquer ce qui relie l'animal à son environnement à travers les interactions nutritionnelles (Parker *et al.*, 2009) de même que les relations trophiques (Schweiger *et al.*, 2015). Chez plusieurs espèces, la quantité et le type de nourriture consommée ne sont pas très bien connus. En plus, la composition du régime alimentaire varie souvent entre les individus (Newsome *et al.*, 2009), le sexe (Lesage *et al.*, 2001; Voigt *et al.*, 2018), les populations (Carmichael *et al.*, 2001; Hoelzel *et al.*, 1998; O'Donovan *et al.*, 2018), la période de l'année (Milakovic et Parker, 2011; Mosbacher *et al.*, 2016; Roth et Hobson, 2000) ainsi que l'abondance et la disponibilité des ressources (Mowat *et al.*, 2017; Newsome *et al.*, 2009). L'alimentation est étroitement liée à la répartition saisonnière des individus et à leur abondance (Barboza *et al.*, 2009; Bowen et Siniff, 1999). Elle peut aussi être influencée par les facteurs environnementaux (Thompson et Barboza, 2013) tels que la disponibilité et la qualité des plantes et des proies (Mowat *et al.*, 2017), la température, la disponibilité en eau et l'abondance des précipitations (Mowat et Heard, 2006; Newman, 2007; Parker *et al.*, 2009). De plus, les ressources ne sont pas toujours distribuées uniformément et peuvent être très rares (Yahner, 2012).

L'accès à des ressources alimentaires de bonne qualité et en quantité suffisante permet à l'individu de maintenir une bonne condition physique et d'accumuler des réserves de graisse lui permettant de survivre lors des périodes de disettes où il doit faire face à une diminution de la disponibilité et de la qualité des ressources (Parker *et al.*, 2005; Stephenson *et al.*, 2020; Thompson et Barboza, 2013). Chez les femelles, la condition physique des individus est déterminante pour la reproduction puisqu'elle influence notamment la probabilité d'ovuler, de concevoir et de porter à terme un fœtus qui aura un poids adéquat à la naissance (Côté et Festa-Bianchet, 2001; Schai-

Braun *et al.*, 2021) ainsi que d'avoir l'énergie nécessaire pour assurer la lactation (Parker *et al.*, 2009; Robbins, 1993; Stephenson *et al.*, 2020). Chez les mâles, une bonne condition physique s'associe au développement de caractères sexuels secondaires (Weladji *et al.*, 2005; Wright *et al.*, 2019) et permet d'avoir l'énergie nécessaire aux comportements de cour, de compétition pour l'accès aux femelles (Lidgard *et al.*, 2005; Pelletier *et al.*, 2006) et au maintien des structures de harem lors de la reproduction (Mysterud *et al.*, 2004). Par exemple, les mâles phoques gris (*Halichoerus grypus*) ayant une masse corporelle plus importante et de grandes réserves adipeuses s'accouplent avec plus de femelles et engendrent plus de chiots lors de la saison de reproduction (Lidgard *et al.*, 2005).

Une acquisition insuffisante de nutriments, de protéines, de minéraux, de fibres et un contenu énergétique insuffisant via l'alimentation a été corrélé à une faible condition physique (Parker *et al.*, 2009), à un faible taux de reproduction (Barboza et Reynolds, 2004; Flueck *et al.*, 2012; Flynn *et al.*, 1977), à une mortalité élevée (Cook *et al.*, 2004a) et même à un déclin de certaines populations d'ongulés (Barboza et Reynolds, 2004; Post et Klein, 1999). L'alimentation est donc un facteur déterminant pour la croissance, la reproduction et la survie d'un individu (Parker *et al.*, 2009; Post et Klein, 1999; Stephenson *et al.*, 2020; Thompson et Barboza, 2013). En effet, il a été observé que les faons wapitis (*Cervus elaphus nelsoni*) qui avaient accès à des ressources alimentaires de meilleure qualité atteignaient une masse corporelle plus importante au début de l'hiver et donc, survivaient plus longtemps (Cook *et al.*, 2004a). Ultimement, l'alimentation peut également influencer la valeur adaptative (Abramsky *et al.*, 2002; Brown, 1992) ou la pérennité d'une population ou d'une espèce (Birnie-Gauvin *et al.*, 2017; Macbeth et Kutz, 2019; Mattson et Merrill, 2002). Par exemple, il a été montré que les limitations nutritionnelles jouaient un rôle important sur la dynamique d'une population de koala (*Phascolarctos cinereus*) à très faible densité et sur sa pérennité (Stalenberg *et al.*, 2014).

0.2 La condition physiologique des individus

L'alimentation est aussi étroitement reliée à la condition physiologique d'un individu (Homyack, 2010; Kitaysky *et al*., 2007; Ricklefs et Wikelski, 2002; Wikelski et Cooke, 2006). Il n'existe pas de définition unique de condition physiologique dans la littérature (mais voir la définition dans le glossaire) et je la définirai donc comme un indice de la condition de santé ou physique d'un individu (Carlsson *et al.*, 2016; Macbeth et Kutz, 2019; Minias, 2015; Ricklefs et Wikelski, 2002). Plusieurs marqueurs permettent d'évaluer la condition physiologique tels que les réserves de graisse (Homyack, 2010), l'analyse des taux de cortisol dans l'organisme (Wikelski et Cooke, 2006), l'analyse des éléments traces (Åhman et White, 2019; Åhman *et al.*, 2019) et l'analyse des profils biochimiques et hématologiques sanguins (Minias, 2015; Trumble et Castellini, 2002). Ces différents marqueurs fournissent de l'information sur un aspect précis de la condition physiologique. Par exemple, l'analyse du taux de cortisol mesure la réponse au stress chez les organismes (Sheriff *et al.*, 2011), l'analyse des agents pathogènes et infectieux renseigne sur l'état de santé de l'individu (Carlsson *et al.*, 2019b; Macbeth et Kutz, 2019) tandis que l'analyse des éléments traces est quant à lui un indicateur de l'état nutritionnel (Åhman et White, 2019; Becker *et al.*, 2010; Underwood et Suttle, 1999), du niveau de santé (Åhman *et al.*, 2019; Takeuchi *et al.*, 2016) et de la performance physiologique de l'individu (Bhattacharya *et al.*, 2016).

Ces indicateurs d'état de santé ou de la condition physiologique influencent également les performances individuelles et la valeur adaptative. Par exemple, des niveaux élevés et persistants de cortisol chez l'animal sont reconnus pour causer du stress à long terme et ont des effets négatifs sur l'efficacité du système immunitaire (Charbonnel *et al.*, 2008; Romero, 2004), la croissance (Reeder et Kramer, 2005), l'alimentation (Bradshaw *et al.*, 1998; Duchesne *et al.*, 2000) ainsi que sur la valeur

adaptative de l'animal (Ellenberg *et al.*, 2007; Preisser, 2009; Wingfield et Sapolsky, 2003). Ce stress chronique peut ultimement affecter la dynamique d'une population et entraîner son déclin (Charbonnel *et al.*, 2008; Reeder et Kramer, 2005). Des carences ou des concentrations trop élevées en certains éléments traces peuvent aussi entraîner des conséquences sur la croissance (Pollock, 2005), la reproduction (Flynn *et al.*, 1977; O'Hara *et al.*, 2001) et la survie des individus (Flueck, 1994; Flueck *et al.*, 2012; O'Hara *et al.*, 2001) de même que sur le déclin des populations (Barboza et Reynolds, 2004; Post et Klein, 1999). Par exemple, une carence en sélénium a été reliée à une forte mortalité des faons en raison de dystrophie musculaire chez une population de cerfs à queue noire (*Odocoileus hemionus columbianus*) en Californie (Flueck, 1994; Flueck *et al.*, 2012).

0.3 Les interactions trophiques

Les interactions trophiques, telles que la prédation et la compétition, sont omniprésentes dans tous les écosystèmes et peuvent également influencer les performances individuelles d'un animal ainsi que la valeur adaptative et la pérennité d'une population ou d'une espèce (Bryant et Page, 2005; Gurnell *et al.*, 2004; Wittmer *et al.*, 2005b). Les prédateurs peuvent avoir différentes conséquences sur la dynamique d'une population (Lima, 1998; Mahoney *et al.*, 2016; Mumma *et al.*, 2018), que ce soit par la mortalité directe de la proie induite par le prédateur (Bryant et Page, 2005; Stuart-Smith *et al.*, 1997) ou encore de manière indirecte, en entraînant une modification des patrons de sélection d'habitat des proies (Latham *et al.*, 2011a), un changement dans les patrons de vigilance et de la prise alimentaire (Blanchard et Fritz, 2007) ou par l'entremise de la compétition apparente (Holt, 1977).

Ce phénomène de compétition apparente intervient lorsque deux proies ne sont pas nécessairement en compétition directe pour les ressources (voir la définition dans le

glossaire), mais qu'elles partagent un prédateur commun (Holt, 1977). La proie principale supporte une grande densité de prédateurs, ce qui se traduit par une augmentation du taux de prédation sur la proie la moins productive (DeCesare *et al.*, 2010; Holt, 1977). Le caractère opportuniste du prédateur aura un effet plus marqué sur la proie alternative qui est plus susceptible de s'éteindre (DeCesare *et al.*, 2010; Křivan et Sikder, 1999). Un des exemples les mieux étudiés est celui impliquant le loup gris (*Canis lupus*), l'orignal (*Alces americanus*) et le caribou des bois (*Rangifer tarandus caribou*; James *et al.*, 2004; Seip, 1992). En effet, une augmentation d'abondance d'orignaux entraîne une augmentation d'abondance des loups, résultant en une augmentation de la pression de prédation sur l'orignal, mais également sur le caribou, qui lui produit moins de jeunes par année que l'orignal (Bergerud, 1974).

Néanmoins, la coexistence de ces proies peut être possible, soit par une sélection préférentielle de la proie principale par le prédateur, guidée par la faible abondance de la proie alternative qui s'avère ainsi moins profitable (Gleeson et Wilson, 1986; Latham *et al.*, 2013), ou encore par une ségrégation spatiale ou temporelle des proies résultant à une prédation opportuniste sur la proie alternative (Holt, 1984; Schmidt, 2004). Bien qu'opportuniste, cette pression de prédation sur la proie alternative peut jouer un rôle important dans le déclin d'une population précaire (Wittmer *et al.*, 2005b). Par exemple, malgré les efforts du caribou des bois pour s'isoler spatialement des autres ongulés afin de réduire le risque d'être détecter par les loups (Bergerud, 1985; James *et al.*, 2004; Seip, 1992) et le fait que les patrons de chasse des loups sont centrés sur l'orignal (Tremblay-Gendron *et al.*, Manuscrit en préparation), les rencontres opportunistes entre les loups et les caribous résultent davantage en des événements de prédation puisque cette proie est davantage vulnérable (par sa taille) que l'orignal (James *et al.*, 2004; McLoughlin *et al.*, 2005; Wittmer *et al.*, 2005a). En utilisant cette stratégie d'isolement, les caribous sélectionnent davantage les habitats

plus fréquemment utilisés par les ours noirs (*Ursus americanus*), augmentant ainsi leur risque de mortalité (Leblond *et al.*, 2016).

La coexistence entre les espèces n'est cependant pas toujours possible et peut résulter en une compétition par exploitation. La compétition par exploitation est présente lorsqu'il existe un chevauchement dans l'utilisation de l'habitat et des ressources alimentaires limitées par les espèces (de Boer et Prins, 1990; Latham, 1999). Cette compétition peut elle aussi influencer la valeur adaptative. En effet, Gurnell *et al.* (2004) ont montré que la présence d'écureuil gris (*Sciurus carolinensis*) diminuait la fécondité des femelles écureuils roux (*Sciurus vulgaris*), car elles avaient une masse corporelle plus faible en raison d'une compétition alimentaire pour les graines d'arbres. Le taux de recrutement des écureuils roux était également plus faible en raison d'une diminution du nombre annuel de portées et du nombre de petits. Les résultats suggéraient également une exclusion des écureuils roux des forêts décidues par les écureuils gris.

Les espèces sympatriques (voir la définition dans le glossaire) ont toutefois évolué de manière à limiter la compétition interspécifique, que ce soit en se partageant les ressources ou encore l'habitat (Latham, 1999). Par exemple, Jung *et al.* (2015) ont observé que la population de bisons (*Bison bison*) réintroduits avait un faible potentiel de compétition pour les ressources alimentaires avec l'orignal et le caribou en raison des différences morphologiques de leur système digestif. À ce titre, Hofmann (1989) classifie les grands herbivores en trois catégories en fonction de leur comportement de recherche de nourriture et de leur physiologie digestive. On distingue les brouteurs (lib. *browser*), qui s'alimentent principalement d'arbres, d'arbustes et d'espèces ligneuses (tels que l'orignal et la girafe *Giraffa camelopardalis*), des paisseurs (lib. *grazer*) qui eux s'alimentent de plantes herbacées et de graminées (tels que le bison et l'oryx *Oryx gazella*; Hofmann, 1989). Il existe

aussi une classe intermédiaire (lib. *intermediate mixed feeders*) qui s'alimente d'un mélange d'arbustes et d'herbacées, un groupe auquel appartiennent le caribou et l'impala (*Aepyceros melampus*) (Hofmann, 1989).

Les espèces sympatriques partitionnent ainsi les ressources en s'alimentant sur des items alimentaires différents (Gavrilchuk *et al.*, 2014; Merkle *et al.*, 2017), mais elles peuvent également s'alimenter à des endroits ou à des moments différents (Hobson *et al.*, 2000; Merkle *et al.*, 2017). Ce partitionnement des ressources minimise donc la compétition interspécifique et permet aux espèces de coexister. Par exemple, les quatre espèces de rorquals (bleu *Balaenoptera musculus*, commun *B. physalus*, petit *B. acutorostrata* et à bosse *Megaptera novaeangliae*) fréquentant le golfe du Saint-Laurent en été se partagent l'habitat en consommant une proportion différente de proies malgré un certain chevauchement de leurs niches trophiques (Gavrilchuk *et al.*, 2014).

0.4 Le concept de niche

La niche écologique est un concept théorique central en écologie (Lamotte, 1979) qui permet de décrire l'interaction d'une population avec son écosystème (Newsome *et al.*, 2007). J'utiliserai le concept de niche afin de mieux comprendre l'effet des différents facteurs extrinsèques et intrinsèques pouvant influencer les performances individuelles et la dynamique d'une population. Il importe donc de bien le décrire puisqu'il fait partie intégrante de ma thèse. La niche écologique représente l'ensemble des conditions environnementales et des ressources abiotiques et biotiques nécessaires à la reproduction, à la survie et au maintien d'une population ou d'une espèce (*sensu* Hutchinson, 1957). On distingue la *niche fondamentale*, qui est l'ensemble de toutes les conditions optimales sous lequel un organisme peut vivre en l'absence de compétiteurs et de prédateurs, de la *niche réalisée*, qui prend en compte

toutes les restrictions auxquelles l'animal est soumis puisque les écosystèmes sont faits d'un assemblage d'espèces entrant en compétition ou en coexistence (Bolnick *et al.*, 2003; Hutchinson, 1957; Schoener, 1986).

La niche écologique peut être représentée comme un hypervolume à *n* dimensions dont les axes décrivent les conditions environnementales et les ressources nécessaires à la survie et à la pérennité d'une espèce (Figure 0.2). Plusieurs facteurs peuvent contraindre l'expansion de la niche, par exemple, des barrières physiques (Grinnell, 1917; Nakazawa, 2013; Pyron et Burbrink, 2009), mais également des facteurs extrinsèques et intrinsèques, tels que la prédation (Hernandez-Santin *et al.*, 2016; Kinnear *et al.*, 2002; Roughgarden et Feldman, 1975), la compétition (Bearhop *et al.*, 2004; Roughgarden, 1972, 1976), l'alimentation (Bolnick *et al.*, 2007) et les parasites (Burke, 2012).

Hutchinson (1957) considère que tous les individus d'une population généraliste sont généralistes, plus spécifiquement qu'ils utilisent les mêmes habitats et les mêmes ressources. Toutefois, il est irréaliste de supposer que tous les individus d'une même population soient identiques. Certaines études pionnières portant sur la niche écologique ne tenaient pas compte de la variation individuelle ou croyaient que cette variation était rare ou qu'elle n'avait pas d'effet (Abrams, 1980; Case, 1981; Hutchinson, 1957; Schoener, 1986). Cependant, la variabilité individuelle est maintenant reconnue par plusieurs études plus récentes (Araújo *et al.*, 2011; Bolnick *et al.*, 2003; Dall *et al.*, 2012; Layman *et al.*, 2015).

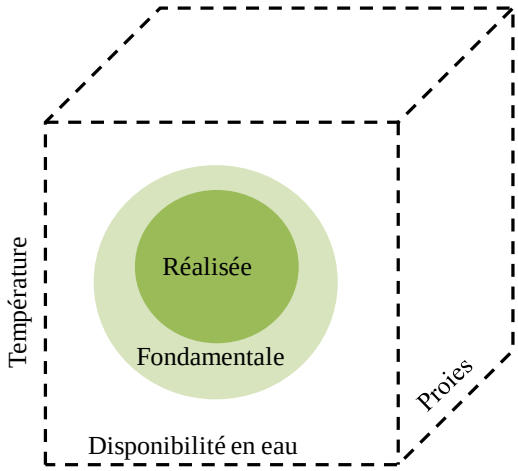

Figure 0.2. Exemple de représentation graphique du concept de niche écologique de Hutchinson (1957). Par souci de simplification dans sa représentation, l'hypervolume représenté ici présente trois dimensions (cube pointillé) et les axes décrivent les conditions environnementales (p. ex. température et disponibilité en eau) et les ressources nécessaires (p. ex. les proies) à la survie et à la pérennité d'une espèce donnée. La niche fondamentale est représentée en vert pâle tandis que la niche réalisée est montrée en vert foncé.

0.5 Les différences individuelles

Darwin (1859) a été l'un des pionniers dans la reconnaissance du fait que les individus d'une même espèce ne sont pas écologiquement égaux, mais bien des congénères qui diffèrent dans leurs traits individuels tels que le sexe, l'âge, la morphologie, la physiologie et le comportement. Les traits héritables, soit morphologiques ou comportementaux, peuvent donc être sélectionnés s'ils permettent à l'individu d'exploiter des ressources moins utilisées ou nouvelles de manière à diminuer la compétition intraspécifique (Bolnick *et al.*, 2007). Cette prédiction vient de l'hypothèse de la variation de la niche (lib. *Niche variation hypothesis*) de Van Valen (1965). Celle-ci propose qu'une population que l'on croit généraliste peut être composée, en fait, de plusieurs individus spécialistes présentant peu de

chevauchement dans leur alimentation (Bolnick *et al.*, 2003; Van Valen, 1965). Ainsi dans cette population généraliste, les individus se déclinent selon un gradient d'individus qui consomment une grande diversité de ressources (c.-à-d. les *vrais* généralistes type A) jusqu'aux individus spécialistes de quelques ressources spécifiques (c.-à-d. les généralistes type B; voir Figure 0.3) (Bearhop *et al.*, 2004).

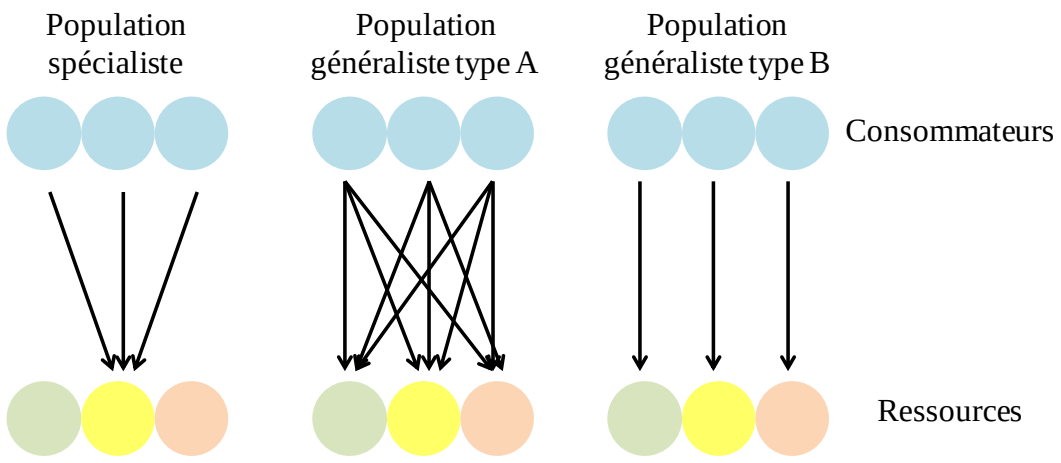

Figure 0.3. La population spécialiste est composée d'individus qui s'alimentent tous sur le même type de ressource alimentaire (c.-à-d. les *vrais* spécialistes), la population généraliste de type A est composée d'individus qui s'alimentent sur des ressources différentes en fonction de plusieurs facteurs tels que la disponibilité ou l'abondance des ressources (c.-à-d. les *vrais* généralistes) tandis que la population généraliste de type B est en fait composée d'individus qui sont spécialistes de quelques ressources spécifiques (modifiée de Bearhop *et al.*, 2004).

Une des prédictions rattachées à la variation de la niche stipule que les populations qui occupent des niches écologiques plus larges devraient montrer une variation entre les individus qui est plus grande que les populations occupant une niche plus étroite (Van Valen, 1965). L'autre prédiction stipule que cette variation individuelle dans l'alimentation devrait conférer un avantage adaptatif (Van Valen, 1965) et apporter des changements écologiques et évolutifs au niveau de l'espèce. Si les contraintes interspécifiques diminuent, la compétition intraspécifique devrait permettre

l'expansion de la niche écologique en favorisant l'utilisation de nouvelles ressources (Figure 0.4) (Bolnick *et al.*, 2010; Van Valen, 1965). Toutefois, si cette nouvelle exploitation des ressources réduit la valeur adaptative, les traits phénotypiques qui favorisent l'utilisation de ces ressources ne seraient plus sélectionnés puisqu'ils ne sont pas adaptés (Grémillet *et al.*, 2008). Ces différences individuelles dans l'utilisation des ressources amènent donc une spécialisation individuelle qui est principalement due au type ou à la quantité de nourriture consommée (Toscano *et al.*, 2016). Par exemple, il a été montré chez les blaireaux européens (*Meles meles*) que la disponibilité des ressources jouait un rôle dans la détermination de la variation de la niche individuelle au sein des groupes sociaux (Robertson *et al.*, 2015). Cette spécialisation individuelle a donc des implications importantes sur la réduction de la compétition intra- et interspécifique des ressources (Svanbäck et Bolnick, 2007), sur la prédation (Hernández et Laundré, 2005; Lima et Dill, 1990) et sur la dynamique et la structure de la chaine trophique (Araújo *et al.*, 2011; Layman *et al.*, 2015).

Les interactions écologiques intra- et interspécifiques peuvent donc influencer la sélection ou la diversité des ressources alimentaires et ainsi modifier la niche écologique (Araújo *et al.*, 2011). La compétition permet la diversification de la niche alimentaire par les individus ou les espèces en élargissant la niche écologique de la population (Svanbäck et Bolnick, 2007). Ceci entraîne une spécialisation individuelle dans l'utilisation des ressources et diminue par le fait même la compétition (Svanbäck et Bolnick, 2007). Cependant, le contraire peut aussi être observé; si la diversité des ressources est moindre ou si la population est retrouvée à forte densité, l'étendue de la niche diminuera tout comme la variabilité individuelle dans l'utilisation des ressources (Araújo *et al.*, 2011; Darimont *et al.*, 2009; Layman *et al.*, 2007a; Semmens *et al.*, 2009). Ceci peut amener un chevauchement dans l'utilisation de l'habitat et des ressources alimentaires qui peuvent être limitées (de Boer et Prins, 1990; Latham, 1999; Layman *et al.*, 2007a). Ces individus partageant un habitat et

des ressources peuvent entrer en compétition (Gurnell *et al.*, 2004). Toutefois, la coexistence entre des espèces potentiellement compétitrices peut être possible en partitionnant les niches écologiques ou les ressources alimentaires (Gavrilchuk *et al.*, 2014; Jung *et al.*, 2015).

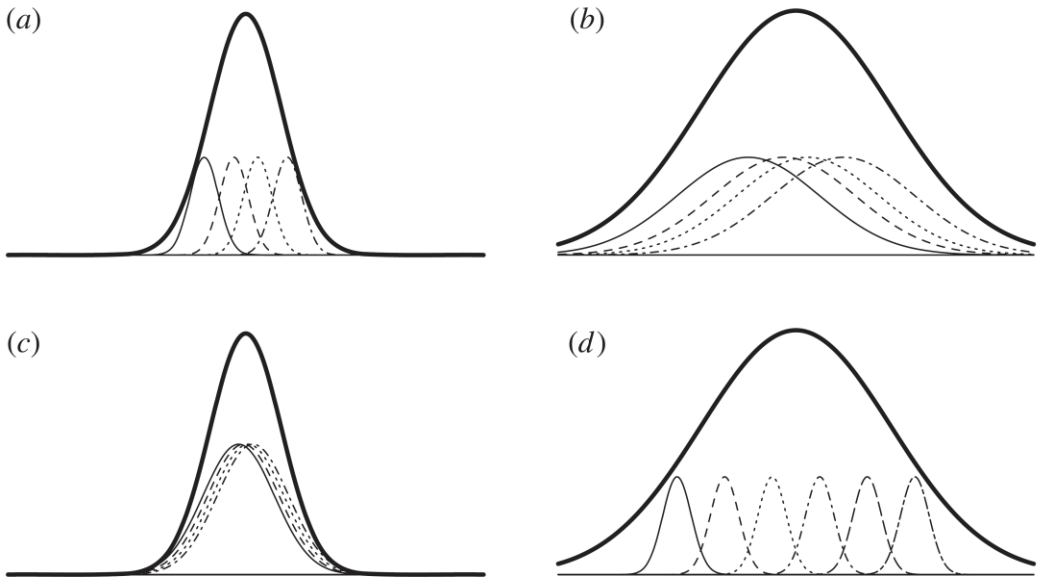

Figure 0.4. Illustration de trois scénarios d'expansion de la niche écologique. La population initiale en (a) coexiste avec un compétiteur interspécifique, la largeur de la niche de la population (sur l'axe des x) est indiquée par une courbe épaisse et les largeurs des niches de quatre individus sont indiquées par des lignes plus courtes et fines. Si la compétition interspécifique diminue, trois scénarios peuvent se produire, soit (b) une augmentation de la largeur des niches des individus et de la population, (c) une augmentation de la largeur des niches des individus mais pas de la population, car l'expansion est compensée par une diminution de la largeur des niches entre les individus ou encore (d) une augmentation de la largeur des niches de la population mais pas des niches individuelles, par le biais d'une augmentation de la variation interindividuelle (hypothèse de la variation de la niche) (tirée de Bolnick *et al.*, 2010).

La spécialisation individuelle permet aussi d'expliquer la présence de comportements alimentaires sous-optimaux (Toscano *et al.*, 2016) contrairement à la théorie de la quête alimentaire optimale (lib. *Optimal foraging theory*) qui prédit que les individus modifient leur comportement ou leur régime alimentaire en fonction des conditions écologiques afin de maximiser leur valeur adaptative (MacArthur et Pianka, 1966; Stephens et Krebs, 1986). Un animal peut donc concentrer ses activités alimentaires dans un habitat ayant des ressources alimentaires de moins bonne qualité ou en moins grande quantité en raison de la pression de prédation (Hernández et Laundré, 2005; Lima et Dill, 1990) ou de compétition intra- ou interspécifique (Araújo *et al.*, 2011; Estes *et al.*, 2003). Un des concepts de la spécialisation alimentaire suggère donc que les individus font face à des contraintes qui limitent leur comportement de quête alimentaire ou l'utilisation optimale des ressources (Toscano *et al.*, 2016). À titre d'exemple, Hernández et Laundré (2005) ont montré que les wapitis avaient modifié leur alimentation quand ils ont délaissé l'utilisation des prairies ouvertes du parc national de Yellowstone en faveur des abords de la forêt, considérés plus sécuritaires après la réintroduction des loups.

0.6 Objectif principal de la thèse

Il m'apparaît donc essentiel de mieux comprendre le rôle de ces différents facteurs extrinsèques et intrinsèques (abordés précédemment) sur la valeur adaptative d'une population en déclin (Figure 0.1). L'objectif principal de ma thèse est par conséquent de mieux comprendre le rôle de ces différents facteurs déterminants la dynamique d'une population, plus précisément le rôle de l'alimentation, de la condition physiologique et des relations trophiques à l'aide de différents marqueurs biochimiques (p. ex. isotopes stables, éléments traces).

0.7 Survol général de la méthodologie préconisée

Comprendre les relations trophiques et la diversité du régime alimentaire, de manière à faire ressortir les différences individuelles dans les liens unissant la condition physiologique aux variations des taux vitaux, nécessite une approche de pointe dont la résolution temporelle et spatiale est suffisante. En effet, plusieurs approches existent afin de déterminer la composition du régime alimentaire et de la condition physiologique, mais aucune n'est parfaite d'où l'importance de bien la choisir et de contrôler leurs différentes limitations (Nielsen *et al.*, 2018). La section suivante présente une synthèse détaillée du développement de ces méthodes et de leurs limitations puisque la validation de certaines d'entre elles pour le caribou est centrale à cette thèse.

0.7.1 Revue des méthodes d'étude du régime alimentaire

Les observations directes ont traditionnellement été utilisées afin de documenter le comportement de quête alimentaire et la composition du régime alimentaire des espèces en observant l'individu ou un groupe d'individus s'alimentant sur une carcasse ou en broutant la végétation (Sanders *et al.*, 1980; Smith et Hubbard, 1954). Bien que cette technique ait l'avantage d'être peu coûteuse, elle ne peut être réalisée qu'en plein jour, dans les habitats ouverts et elle est plus facilement applicable aux espèces grégaires (Litvaitis, 2000). De plus, pour certaines espèces, la présence des observateurs peut biaiser l'estimation en affectant les activités du consommateur et de ses proies potentielles (Barboza *et al.*, 2009; Birnie-Gauvin *et al.*, 2017). Cette approche demeure toutefois limitée dans de nombreux systèmes, notamment chez les espèces aquatiques. Par exemple, les mammifères marins sont présents dans des régions difficiles d'accès et passent la majeure partie de leur temps sous l'eau, rendant l'observation difficile (Bowen et Siniff, 1999). Depuis quelques décennies, de

nouvelles approches ont été développées afin d'améliorer les connaissances actuelles sur l'alimentation des espèces animales et sont basées sur des mesures indirectes du régime alimentaire.

Les analyses de contenus stomacaux (Bergerud, 1972; Hammill *et al.*, 2005; Mahfouz *et al.*, 2017) et de fèces (Dowd et Gese, 2012; Thompson et McCourt, 1981) permettent quant à elles d'obtenir de l'information récente (c.-à-d. quelques heures, jours) sur la composition du régime alimentaire à l'échelle individuelle (Newmaster *et al.*, 2013; Tollit *et al.*, 2003). Elles reposent sur l'identification des structures dures et des parties non digestibles retrouvées dans les contenus stomacaux (Bergerud, 1972; Deb, 1997) et les fèces (McInnis *et al.*, 1983) puisque les structures molles sont plus rapidement digérées et difficilement disponibles (McInnis *et al.*, 1983). Les structures qui se digèrent plus lentement amènent un biais puisqu'elles seront surestimées par rapport à celles qui se digèrent plus facilement (Hewitt et Robbins, 1996; McInnis *et al.*, 1983; Steenweg *et al.*, 2015). Il peut aussi être difficile de reconnaître certaines parties ou structures selon le type de nourriture consommé, ce qui peut entraîner un autre biais (Hewitt et Robbins, 1996; Morin *et al.*, 2019). Par exemple, dans le cas des herbivores, la technique est moins précise chez les consommateurs d'un régime alimentaire mixte (p. ex. le caribou) puisque les arbustes sont surestimés tandis que les plantes herbacées et le feuillage, qui se digèrent plus rapidement, seront sous-estimés (Gill *et al.*, 1983; McInnis *et al.*, 1983; Nielsen *et al.*, 2018). De plus, l'analyse des contenus stomacaux n'est pas applicable dans le cas des espèces en péril où la mort des individus n'est pas envisageable.

Depuis quelques décennies, afin de surmonter ces limites, de nouvelles approches moins intrusives ont été développées afin d'améliorer les connaissances actuelles sur l'alimentation des espèces sauvages. Ce sont, entre autres, l'analyse des acides gras (Budge *et al.*, 2006; Iverson *et al.*, 2004), le codage à barre de l'ADN (lib. *DNA*

barcoding) (Deagle *et al.*, 2007; Newmaster *et al.*, 2013) et l'analyse des rapports de certains isotopes stables (Ben-David et Flaherty, 2012; Gannes *et al.*, 1998; Kelly, 2000; Peterson et Fry, 1987). J'utiliserai principalement les marqueurs isotopiques du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) comme outil méthodologique afin de répondre à mon objectif. Les isotopes stables s'avèrent être de bons marqueurs biochimiques afin d'étudier l'alimentation (Ben-David *et al.*, 1997; Caut *et al.*, 2009; Phillips *et al.*, 2005) et les relations trophiques (Hobson et Welch, 1992; Newsome *et al.*, 2007; Post, 2002).

À ce titre, les signatures isotopiques du carbone et de l'azote peuvent, entre autres, informer sur la composition du régime alimentaire de l'animal (Hammill *et al.*, 2005; Lesage *et al.*, 2001; Milakovic et Parker, 2011), sur la position trophique du consommateur (Lesage *et al.*, 2001; Post, 2002; Ruiz-Cooley *et al.*, 2004), sur l'utilisation de l'habitat (Post, 2002) ainsi que sur les relations trophiques (Jackson *et al.*, 2011; Newsome *et al.*, 2007; Phillips *et al.*, 2014). Les rapports des isotopes stables reflètent la nourriture consommée et assimilée sur une période assez longue (p. ex. semaines, mois, années) en comparaison à l'analyse des fèces qui reflète la nourriture consommée sur une plus courte période de temps (p. ex. heures, jours) (Hilderbrand *et al.*, 1996; Jones *et al.*, 1979; Sponheimer *et al.*, 2003a). Chaque tissu intègre la signature isotopique sur des périodes différentes selon le taux de renouvellement des protéines du tissu (représenté par la demi-vie, c.-à-d. le temps requis pour que 50% des tissus soient renouvelés) (Hobson et Clark, 1992a; Rubenstein et Hobson, 2004; Tieszen *et al.*, 1983). Le taux de renouvellement peut varier selon les tissus (Lecomte *et al.*, 2011; Zilversmit *et al.*, 1943), mais aussi entre les individus selon les caractéristiques individuelles telles que l'âge et le sexe (Lecomte *et al.*, 2011).

Les muscles et les globules rouges intègrent l'information sur une période de quelques mois suivant l'échantillonnage tandis que le plasma intègre l'information sur une période de quelques jours (Lecomte *et al.*, 2011; Tieszen *et al.*, 1983). Le poil, quant à lui, intègre l'information au moment de sa croissance (Hilderbrand *et al.*, 1996; Schwertl *et al.*, 2003) et est reconnu pour être un tissu biologiquement inactif une fois synthétisé (Dunnett, 2005; Pragst et Balikova, 2006). Il peut également être récolté facilement, de manière non invasive et avec un minimum de stress chez l'animal et entreposé à température ambiante pendant de longue période (Duffy *et al.*, 2005; Pacyna *et al.*, 2018).

Plus précisément, le rapport des isotopes de l'azote mesuré dans les tissus permet de déterminer la position trophique du consommateur puisqu'un enrichissement prédictible en ^{15}N est observé à chaque niveau trophique (Figure 0.5) (DeNiro et Epstein, 1981; Minagawa et Wada, 1984; Post, 2002). En effet, les tissus du consommateur sont généralement enrichis de 3 à 5‰ par rapport à ceux de ses proies (Peterson et Fry, 1987; Post, 2002). Cette différence de rapport des isotopes de l'azote entre le consommateur et ses proies s'explique par le fait qu'il y a une proportion plus importante de ^{14}N que de ^{15}N dans les déchets azotés des consommateurs (DeNiro et Epstein, 1981). Cependant, cet enrichissement varie, entre autres, selon le taxon, le régime alimentaire et le tissu utilisé (Caut *et al.*, 2009). Le rapport isotopique de l'azote peut aussi être utilisé comme indicateur de la condition physique puisqu'on note un enrichissement en ^{15}N dans les tissus de l'animal lors d'un stress nutritionnel (Gannes *et al.*, 1998).

Le rapport isotopique du carbone est, quant à lui, généralement utilisé afin de déterminer la source de carbone et l'habitat utilisé (France, 1995; Post, 2002; Ramsay et Hobson, 1991). En effet, l'enrichissement trophique est généralement plus faible dans le cas du carbone, soit de l'ordre de 1‰, représentant ainsi un traceur plus

adéquat des sources de carbone (Figure 0.5) (DeNiro et Epstein, 1978; Peterson et Fry, 1987). Cette différence de rapport des isotopes du carbone entre les sources s'explique par le fait qu'il existe une différence dans la fixation des isotopes du carbone par les plantes terrestres en C_3, C_4, CAM et la végétation marine en C_3 (Figure 0.5) (Ben-David et Flaherty, 2012; Peterson et Fry, 1987; Rubenstein et Hobson, 2004). Dans les écosystèmes tempérés, boréaux et toundriques, où les plantes en C_4 sont pratiquement absentes, les plantes en C_3 expriment des différences isotopiques en fonction des conditions environnementales telles que la température, la luminosité, l'humidité du sol, la concentration atmosphérique en gaz carbonique et la salinité (Bonafini *et al.*, 2013; Drucker *et al.*, 2008). L'assimilation du ^{13}C par les plantes en C_3 peut être influencée par l'effet de canopée (lib. *canopy effect*). En effet, un gradient vertical en $\delta^{13}C$ est observé dans la forêt où les valeurs les plus élevées sont retrouvées en haut de la canopée et les plus faibles près du sol (Carlson et Crowley, 2016; Medina *et al.*, 1986). On observe aussi un appauvrissement en ^{13}C chez les plantes poussant dans les écosystèmes fermés par rapport aux plantes poussant dans un milieu plus ouvert (Bonafini *et al.*, 2013; Farquhar *et al.*, 1982; Giroux *et al.*, 2015; Medina *et al.*, 1986).

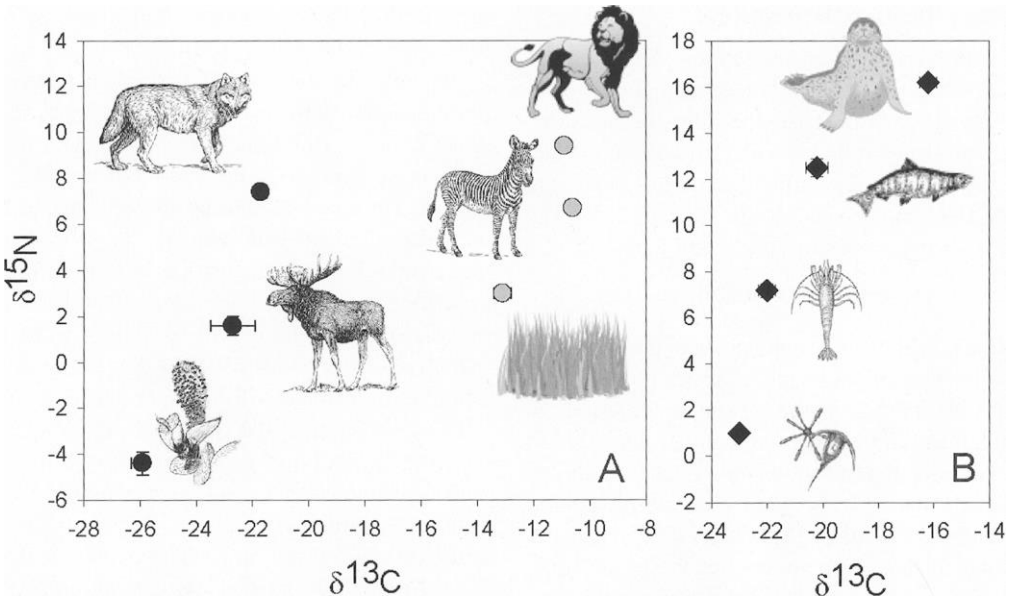

Figure 0.5. Illustration de l'enrichissement trophique en $\delta^{13}C$ et $\delta^{15}N$ des producteurs primaires (dans ce cas, plantes et diatomées), aux herbivores et aux prédateurs pour le système terrestre en A et pour le système marin en B. En A, la différence entre la chaine alimentaire basée sur des plantes en C_3 (cercles noirs) ou en C_4 (cercles gris) est aussi représentée (tirée de Ben-David et Flaherty, 2012).

0.7.2 Les isotopes pour étudier les niches trophiques

Les isotopes stables permettent également d'estimer l'étendue et le partitionnement des niches trophiques (voir la définition dans le glossaire) entre les espèces ou les populations (Jackson, 2019; Jackson *et al.*, 2011). Le concept de niche isotopique a été proposé par Newsome *et al.* (2007) en tant qu'un espace isotopique bidimensionnel des valeurs $\delta^{13}C$ et $\delta^{15}N$ dans un graphique et permet d'obtenir des informations sur la niche trophique d'une ou plusieurs espèces, populations ou groupes (Figure 0.6). Ces deux rapports isotopiques décrivent la niche trophique de l'espèce ou de la population en identifiant deux dimensions de la niche, soit l'habitat (p. ex. $\delta^{15}N$) et les ressources alimentaires consommées (p. ex. $\delta^{13}C$). Les variations

des rapports isotopiques permettent donc d'évaluer la taille de la niche trophique d'une espèce ou d'une population (Bolnick *et al.*, 2003). L'analyse des niches isotopiques permet aussi d'évaluer la façon dont les individus ou espèces se partagent les ressources alimentaires (Caut *et al.*, 2006; Hobson *et al.*, 2000; Merkle *et al.*, 2017), de mieux comprendre les relations prédateurs-proies (Urton et Hobson, 2005), la compétition interspécifique (Jung *et al.*, 2015), la coexistence (Gavrilchuk *et al.*, 2014) ainsi que la spécialisation individuelle (Newsome *et al.*, 2009).

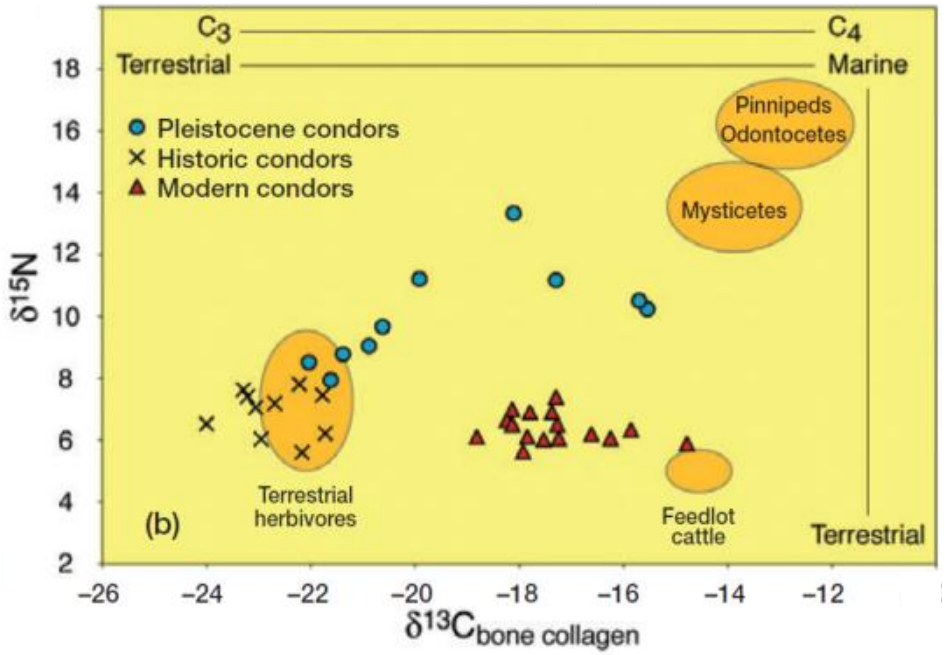

Figure 0.6. Illustration de l'espace isotopique bidimensionnel qui fournit de l'information sur l'habitat ($\delta^{15}N$, axe des y) et les ressources consommées ($\delta^{13}C$, axe des x) de la niche écologique du condor de Californie (*Gymnogyps californianus)*. Dans certain cas, l'animal peut se nourrir sur un réseau alimentaire marin ou terrestre (figure tirée de Newsome *et al.*, 2007, les données proviennent de Chamberlain *et al.*, 2005).

0.7.3 Survol des limitations des analyses isotopiques

Les isotopes stables s'avèrent donc être l'outil de prédilection afin de répondre à l'objectif principal de mon doctorat. Cependant, comme toutes les méthodes, certaines limites existent (voir Nielsen *et al.*, 2018), nécessitant des efforts pour en parfaire notre compréhension et leur utilisation. En effet, l'utilisation des isotopes stables dépend de notre capacité à contrôler les différentes sources de variation isotopique (Martínez del Rio *et al.*, 2009; Post *et al.*, 2007). Par conséquent, ma thèse a comme deuxième objectif de mieux comprendre les sources de variation des signatures isotopiques, ce à quoi s'attardent les chapitres 1 et 2.

Il est reconnu que les lipides contenus dans les tissus des organismes peuvent influencer les signatures isotopiques puisque les lipides sont appauvris en ^{13}C en comparaison aux protéines et aux glucides (DeNiro et Epstein, 1977; McConnaughey et McRoy, 1979). Le contenu variable en lipides de l'organisme peut donc influencer la signature isotopique du carbone mesurée dans le tissu (Post *et al.*, 2007). Il est donc important de prendre en compte l'effet des lipides afin de ne pas biaiser l'interprétation des relations trophiques ou de la composition du régime alimentaire (Lesage *et al.*, 2010; Tarroux *et al.*, 2010). Cependant, très peu d'études en milieu terrestre se sont intéressées à l'effet des lipides sur $\delta^{13}C$ et à la manière d'en tenir compte (mais voir Ehrich *et al.*, 2011; Post *et al.*, 2007; Tarroux *et al.*, 2010).

La reconstruction du régime alimentaire d'une espèce spécifique avec les isotopes stables suppose également une bonne compréhension au préalable des facteurs d'enrichissement trophique (c.-à-d. une différence dans les compositions isotopiques entre le consommateur et ses sources alimentaires; Ben-David et Flaherty, 2012; DeNiro et Epstein, 1978; Martínez del Rio *et al.*, 2009). Cependant, peu d'études réalisées dans des conditions contrôlées ont été entreprises chez les mammifères

(mais voir Fox-Dobbs *et al.*, 2007; Hilderbrand *et al.*, 1996; Lecomte *et al.*, 2011; Lesage *et al.*, 2002) et encore moins chez les herbivores (mais voir Darr et Hewitt, 2006; Halley *et al.*, 2010). Les facteurs d'enrichissement trophique sont en général tirés d'autres études publiées et sont souvent des moyennes obtenues de revues de littérature au lieu d'être dérivés des études expérimentales contrôlées (Caut *et al.*, 2008, 2009; Kurle *et al.*, 2014; Martínez del Rio *et al.*, 2009). De plus, plusieurs études supposent que ces facteurs d'enrichissement sont relativement constants, bien qu'ils ne le soient pas (Peterson et Fry, 1987; Post, 2002). Toutefois, les facteurs affectant ces taux sont relativement bien compris (Kelly, 2000). En effet, les facteurs d'enrichissement trophique varient entre les tissus analysés (Halley *et al.*, 2010; Sponheimer *et al.*, 2003a) en raison des taux de renouvellement des cellules qui diffèrent entre les tissus (Hobson et Welch, 1992; Tieszen *et al.*, 1983). On observe également des différences interindividuelles pour un même tissu, même lorsque les individus ont un régime alimentaire identique (Caut *et al.*, 2009; Sponheimer *et al.*, 2003b). On note de plus des variations liées à l'environnement (Caut *et al.*, 2009), à l'espèce (Sponheimer *et al.*, 2003a), à la position trophique (Lesage *et al.*, 2002; Post, 2002) et aux caractéristiques individuelles de l'individu, telles que le sexe, le statut reproducteur (Kurle *et al.*, 2014; Lecomte *et al.*, 2011; Tieszen *et al.*, 1983), le statut nutritionnel, la taille (Vanderklift et Ponsard, 2003) ainsi que les voies métaboliques des protéines, lipides et glucides (Perga et Grey, 2010; Wolf *et al.*, 2015). Cependant, les facteurs d'enrichissement trophique manquent pour plusieurs espèces et tissus, bien qu'ils soient d'une grande importance pour obtenir des estimés précis et non biaisés de la composition du régime alimentaire ou des relations trophiques (Bond et Diamond, 2011; Caut *et al.*, 2009; Phillips *et al.*, 2014).

0.7.4 L'analyse des éléments traces pour l'étude de la condition physiologique

Les isotopes stables sont de plus en plus utilisés en combinaison avec les éléments traces afin de mieux comprendre les patrons d'utilisation de l'habitat, les relations trophiques (Born *et al.*, 2003; Brookens *et al.*, 2007; Hobson et Welch, 1992; Post, 2002), distinguer les populations les unes des autres (Rioux *et al.*, 2012; Sanpera *et al.*, 1996) ou encore documenter l'état de santé de différents individus (Åhman et White, 2019; Åhman *et al.*, 2019). Les éléments traces sont des éléments présents naturellement en quantités très faibles dans le sol, l'eau et l'air (Wada, 2004). Ils ont des fonctions essentielles dans l'organisme et sont présents en très petite quantité (moins de 5%) (Robbins, 1993; Wada, 2004). Comme pour les isotopes stables, les éléments traces sont acquis par l'animal principalement par l'alimentation ou la consommation d'eau (Fontaine *et al.*, 2007; Langston et Spence, 1995; Pragst et Balikova, 2006; Reglero *et al.*, 2009; Smith *et al.*, 2007). Les éléments traces essentiels font partie de complexes protéiques (c.-à-d. métalloprotéines) et agissent comme cofacteurs pour de nombreuses voies biochimiques, métaboliques et activités enzymatiques (Bhattacharya *et al.*, 2016; O'Hara *et al.*, 2001). Certains éléments (p. ex. cadmium, mercure, plomb) sont considérés comme non-essentiels et sont considérés, jusqu'à présent, comme n'ayant pas d'autre fonction biochimique que d'interférer avec les éléments essentiels (Anderson *et al.*, 2010). Néanmoins, des effets néfastes peuvent apparaître chez un organisme si pour un élément donné, l'homéostasie est perturbée, c'est-à-dire que la concentration de cet élément n'est plus dans la limite physiologique bénéfique pour l'organisme (Bhattacharya *et al.*, 2016; Wada, 2004). Ceci peut donc entraîner une toxicité si la concentration est trop élevée ou une carence si la concentration est trop faible (Bhattacharya *et al.*, 2016; Wada, 2004).

Les concentrations requises de différents éléments essentiels ou non-essentiels pour l'organisme ne sont souvent pas bien documentées et bien souvent, pour de nombreuses espèces sauvages, les valeurs de références normales n'existent pas (Bondo *et al.*, 2019). Les études passées se sont principalement concentrées sur l'exposition aux contaminants (Smith *et al.*, 2007), la sécurité alimentaire (Hassan *et al.*, 2012) ou les carences (Flueck *et al.*, 2012; Flynn *et al.*, 1977). Par exemple, une forte concentration en éléments traces non essentiels (p. ex. cadmium, cuivre, plomb, Barboza et Parker, 2006; Sparling, 2016) ou de faibles concentrations en éléments traces essentiels (Åhman *et al.*, 2019; Underwood et Suttle, 1999) peuvent affecter la croissance (p. ex. cobalt, manganèse, zinc, Pollock, 2005), la reproduction (p. ex. calcium, cobalt, cuivre, manganèse, sélénium, Abdollahi *et al.*, 2013; Flynn *et al.*, 1977; O'Hara *et al.*, 2001; Underwood et Suttle, 1999) et le système immunitaire (p. ex. zinc, Bhattacharya *et al.*, 2016; Boland, 2003). O'Hara *et al.* (2001) ont relié une carence en cuivre à un faible taux de recrutement, une mortalité élevée des adultes et une croissance anormale des sabots dans une population d'orignaux en Alaska. Les éléments traces s'avèrent donc de bons indicateurs de l'état physiologique (Bhattacharya *et al.*, 2016) ou de santé de l'individu ou de la population (Åhman et White, 2019; Åhman *et al.*, 2019).

0.8 Objectifs spécifiques de la thèse

Il m'apparaît essentiel d'acquérir des connaissances sur l'alimentation, la condition physiologique et les relations trophiques d'une population en déclin afin de contribuer à assurer sa pérennité. Plus précisément, les deux premiers chapitres de la présente thèse visent à bonifier nos connaissances des différentes sources de variations des signatures isotopiques ainsi que de valider ces méthodes avant de les appliquer à nos modèles biologiques à l'étude. Le troisième chapitre s'intéresse aux

relations trophiques et au partage des ressources alimentaires entre quatre espèces sympatriques de grands mammifères terrestres tandis que le quatrième chapitre s'intéresse à l'influence des différences individuelles dans l'alimentation et la condition physiologique sur la valeur adaptative d'une population en déclin.

0.9 Modèles biologiques à l'étude

La plupart des populations de caribous et de rennes (*Rangifer tarandus*) sont en déclin dans leur aire de répartition circumpolaire (Vors et Boyce, 2009) et cette tendance généralisée est également documentée au Canada (Festa-Bianchet *et al.*, 2011), ce qui en fait un excellent modèle biologique afin de s'intéresser aux différents facteurs déterminants la dynamique d'une population en déclin. Selon Vors et Boyce (2009), 79 % des hardes étudiées (34/43) étaient en décroissance il y a déjà plus d'une décennie et l'abondance d'individus avait diminué d'environ 57 % par rapport aux niveaux historiques de population. Les changements climatiques et les modifications anthropiques des paysages naturels étaient les principaux facteurs évoqués pour modifier la dynamique de ces populations (Vors et Boyce, 2009). À titre d'exemple, les changements climatiques modifient la phénologie des plantes et des insectes piqueurs qui interfèrent avec la capacité d'alimentation du caribou ou du renne et entraînent une modification de sa condition physique (Post et Forchhammer, 2008; Post et Klein, 1999; Weladji *et al.*, 2003). De plus, les modifications anthropiques (p. ex. les coupes forestières ou l'exploitation minière et pétrolière) peuvent modifier l'aire de répartition des prédateurs et compétiteurs, la composition des espèces végétales, induire une compétition apparente, interférer avec son alimentation et modifier sa condition physique (Festa-Bianchet *et al.*, 2011; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005a, 2005b).

Le caribou des bois est une sous-espèce de caribou retrouvée en Amérique du Nord et est considérée comme une espèce emblématique de la forêt boréale mature. Il est actuellement en déclin et ce, depuis plusieurs années (COSEPAC, 2014), principalement en raison d'une chasse abusive au milieu du 19e siècle et par la transformation des forêts matures en jeunes forêts (Bergerud, 1974). La population de caribous des bois de la Gaspésie-Atlantique (ci-après population de caribous de la Gaspésie) est une population relique des hardes qui peuplaient jadis le nord-est des États-Unis et le Canada atlantique (Bergerud et Mercer, 1989). Cette population est distincte des autres unités désignables de caribous (COSEPAC, 2014; COSEWIC, 2011) et représente une unité de conservation à part entière (Yannic *et al.*, 2016), étant de plus la seule retrouvée au sud du fleuve Saint-Laurent (Figure 0.7). Cette population de l'écotype montagnard trouve refuge sur le massif des Chic-Chocs, dominé par les monts Albert et Logan, ainsi que sur le massif McGerrigle, dominé par le mont Jacques-Cartier et le petit mont Sainte-Anne (Figure 0.8) (Ouellet *et al.*, 1996). Cette population inclut deux sous-groupes (Logan-Albert vs McGerrigle) circonscrits sur la base des localisations géographiques et la structure génétique (Pelletier *et al.*, 2019). En été, ces caribous utilisent surtout la toundra alpine où la reconnaissance des individus est meilleure et la reproduction facilitée (Équipe de rétablissement du caribou de la Gaspésie, 2006) tandis qu'en hiver, ils se concentrent dans la forêt boréale subalpine et montagnarde présentant des conifères matures qui leur fournissent abri, protection contre les prédateurs et nourriture en hiver (Mosnier *et al.*, 2003).

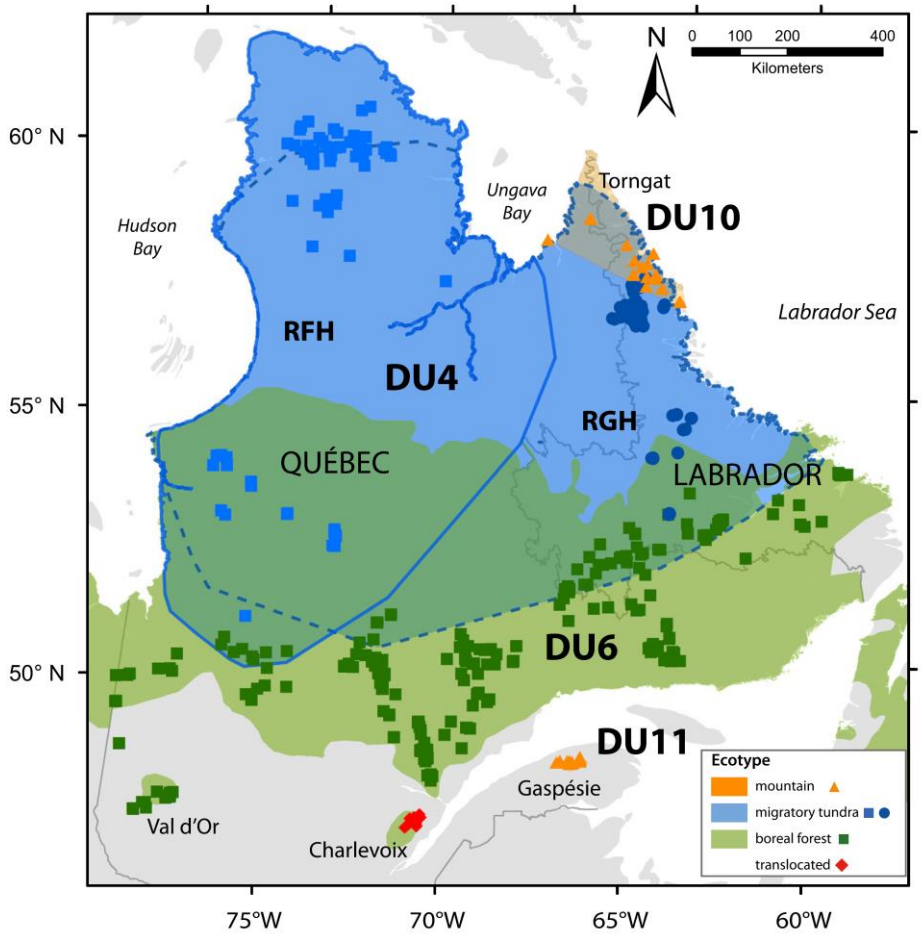

Figure 0.7. Représentation des quatre unités désignables de caribou retrouvés au Québec (DU4 : caribou migrateur de l'est, DU6 : caribou boréal, DU10 : caribou des monts Torngat et DU11 : caribou de la Gaspésie-Atlantique) et des trois écotypes (montagnard en orange, migrateur en bleu et boréal en vert) (tirée de Yannic *et al.*, 2016).

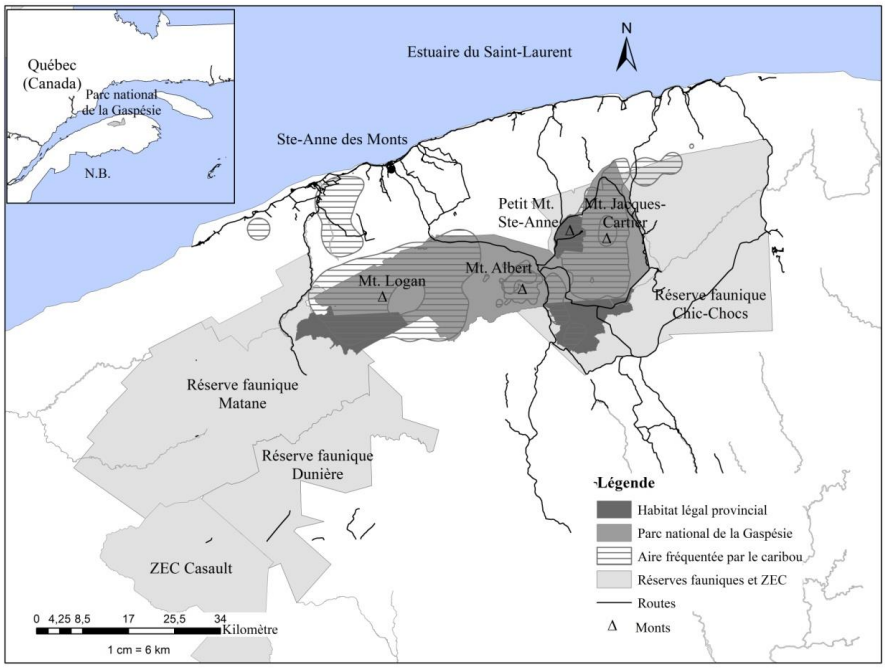

Figure 0.8. Aire de répartition de la population de caribous de la Gaspésie dans le parc national de la Gaspésie et les régions environnantes (réserves fauniques de Matane, Dunière, Chic-Chocs et zone d'exploitation contrôlée [ZEC] Casault). L'aire fréquentée par le caribou de la Gaspésie a été estimée avec la méthode des noyaux (kernel) à 99% provenant des locations télémétriques de 43 caribous suivis de 2013 à 2016.

L'effectif de la population, estimé entre 700 et 1 500 individus en 1953 (Moisan, 1956), est passé à 140 individus en 2001 (Figure 0.9) (Fournier et Faubert, 2001). La population a été désignée « *en voie de disparition* » en regard de la *Loi sur les espèces en péril* (Annexe 1), sous recommandation du Comité sur la situation des espèces en péril au Canada (COSEPAC, 2002), en plus d'être désignée comme un élément irremplaçable de la biodiversité canadienne en 2011 (COSEWIC, 2011). Ce statut a été confirmé récemment (COSEPAC, 2014). La population de caribous de la Gaspésie a été estimée entre 38 et 42 individus à l'automne 2019 par inventaire aérien et par pièges photographiques (Morin et Lesmerises, 2020).

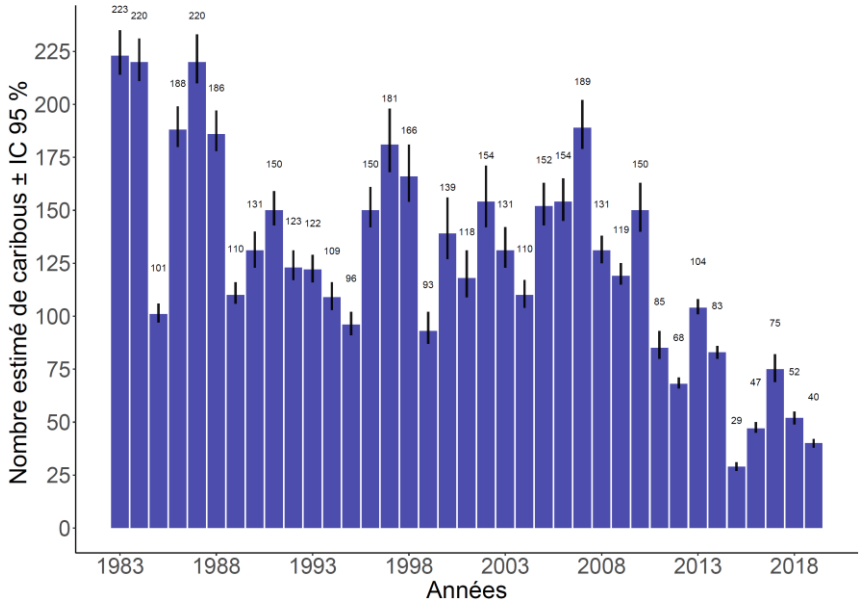

Figure 0.9. Estimation annuelle de la taille de la population de caribous de la Gaspésie (moyenne ± IC 95 %) selon les résultats d'inventaires aériens automnaux corrigés (modifiée de Morin et Lesmerises, 2020).

La perte d'habitat et la prédation sont des facteurs évoqués afin d'expliquer le déclin de la population de caribous de la Gaspésie (Frenette *et al.*, 2020). Bien que l'exploitation forestière ait cessé dans les limites du parc en 1982, elle a profondément modifié la structure et la composition des peuplements forestiers et entraîné de la perte et de la fragmentation d'habitats préférentiels pour la population de caribous (Boudreau, 2017). Les caribous sont reconnus pour sélectionner les sapinières matures et les zones subalpines et alpines (Hins *et al.*, 2009; Mosnier *et al.*, 2003) et évitent les coupes et les chemins forestiers (Leblond *et al.*, 2013). Les coupes forestières des résineux matures ont entraîné une diminution des conditions favorables au développement de fortes biomasses de lichens arboricoles en surreprésentant les milieux en régénération et les jeunes peuplements (Stone *et al.*, 2008), de même qu'une diminution de représentation d'habitats de bonne qualité (Nadeau Fortin *et al.*, 2016). Les habitats perturbés favorisent l'implantation des

feuillus, la redistribution et l'augmentation d'abondance d'autres grands mammifères. Ainsi, on y retrouve une très grande densité d'orignaux en périphérie du parc national de la Gaspésie (33 orignaux/10 km^2) (Dorais, 2015; Roussel-Garneau et Larocque, 2020), ainsi que des cerfs de Virginie (*Odocoileus virginianus*), des coyotes (*Canis latrans*; Boisjoly *et al.*, 2010) et des ours noirs (Mosnier *et al.*, 2008). La compétition apparente (Holt, 1977) entre le caribou et l'orignal pourrait être une cause de la situation précaire du caribou de la Gaspésie (Frenette *et al.*, 2020; St-Laurent *et al.*, 2009), une situation communément observée chez d'autres populations de caribous en Amérique du Nord (p. ex. : DeCesare *et al.*, 2010; Wittmer *et al.*, 2007).

De plus, les profondes modifications de composition et de structure des paysages forestiers sont reconnues pour modifier la principale stratégie anti-prédatrice du caribou, soit la ségrégation spatiale d'avec ses principaux prédateurs, tel qu'observé en Gaspésie (Boudreau, 2017; Mosnier *et al.*, 2008), à Charlevoix, au Saguenay (Leclerc *et al.*, 2014) et à Terre-Neuve (Bastille-Rousseau *et al.*, 2016). Les principaux prédateurs du caribou en Gaspésie, l'ours noir et le coyote, se sont avérés être responsables de la majorité des événements de prédation sur les faons (Crête et Desrosiers, 1995). De plus, des évidences suggèrent que le coyote peut aussi chasser des caribous adultes dans notre aire d'étude.

Selon Gaillard *et al.* (1998), la survie des adultes et le recrutement des juvéniles sont les paramètres les plus importants permettant d'expliquer les tendances démographiques de populations d'ongulés longévifs. À ce titre, le faible taux de survie des faons a été identifié comme un facteur pouvant être responsable du déclin de la population (Crête et Desrosiers, 1995; St-Laurent *et al.*, 2009). Le recrutement (estimé par le pourcentage de faons dans la population lors de l'inventaire aérien d'automne, donc à ~ 9 mois d'âge) est très variable entre les années et a été estimé à 3% en 2016, 14% en 2017, 2% en 2018 et 18% en 2019 (Figure 0.10) (Morin et

Lesmerises, 2020). Ces valeurs restent très basses par rapport à d'autres populations de caribous au Québec (Côté *et al.*, 2012; Taillon *et al.*, 2016) et au Canada (Environnement Canada, 2011; Festa-Bianchet *et al.*, 2011; Hervieux *et al.*, 2013; McLoughlin *et al.*, 2003). Ce faible recrutement de jeunes dans la population de la Gaspésie est accentué par la faible productivité du caribou (âge à primiparité élevé, production d'un jeune par année, Bergerud, 1974; Vors et Boyce, 2009) initié par la forte pression de prédation sur les faons par le coyote et l'ours noir. Frenette *et al.* (2020) ont de plus noté une tendance à la baisse du taux de survie des femelles (77%) et des mâles adultes (56%) en 2014 et 2015, ce qui est beaucoup plus faible que d'autres populations de caribous des bois en Amérique du Nord (Rettie et Messier, 1998; Stuart-Smith *et al.*, 1997; Wittmer *et al.*, 2005b), et surtout moindre que les niveaux requis pour assurer l'autosuffisance.

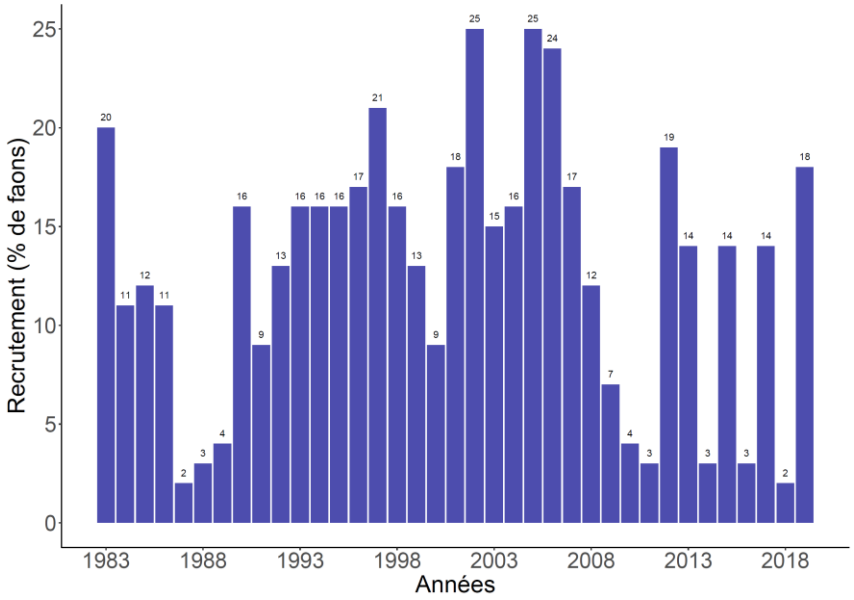

Figure 0.10. Estimation de la proportion de faons à l'automne dans la population de caribous de la Gaspésie selon les résultats d'inventaires aériens corrigés (modifiée de Morin et Lesmerises, 2020).

Tel qu'énoncé précédemment, d'autres facteurs peuvent influencer le déclin des populations animales, comme l'alimentation et la condition physiologique (Birnie-Gauvin *et al.*, 2017; Carlsson *et al.*, 2019a). Toutefois, l'influence de ces facteurs sur la population de caribous de la Gaspésie reste une facette peu explorée. Une étude antérieure a montré que l'intensité de l'infection parasitaire affectait la condition corporelle du caribou de la Gaspésie, mais aucun effet sur leur survie n'a été documenté (Turgeon *et al.*, 2018). Certaines études ont suggéré que les ressources alimentaires ne semblaient pas être limitantes pour le caribou de la Gaspésie (Mosnier *et al.*, 2003; St-Laurent *et al.*, 2009) et que la compétition par exclusion pour la nourriture s'avérait actuellement faible entre le caribou et l'orignal (Christopherson *et al.*, 2019), peut-être en raison d'une séparation passée des niches alimentaires.

Très peu d'études se sont attardées au régime alimentaire du caribou de la Gaspésie, de l'orignal et de leurs prédateurs ainsi que du chevauchement de leurs niches trophiques. En étudiant la sélection de l'habitat du caribou de la Gaspésie, Mosnier *et al.* (2003) ont observé qu'en hiver, le caribou montagnard s'alimentait principalement de lichens arboricoles et terricoles. En utilisant le codage à barre de l'ADN, Christopherson *et al.* (2019) ont observé qu'en été, le caribou montagnard s'alimentait principalement de genévrier (*Juniperus communis*), de sapin baumier (*Abies balsamea*), de bouleau (*Betula spp.*) et de prêles (*Equisetum spp.*) tandis que l'orignal s'alimentait principalement de bouleau, d'aulne rugueux (*Alnus rugosa*), de gadelier rouge (*Ribes triste*) et de sapin baumier. Ailleurs au Canada, plusieurs études se sont attardées à décrire le régime alimentaire d'autres populations de caribous (p. ex. harde de caribous Porcupine au Yukon, caribou des montagnes du Nord et caribou boréal) au moyen de différentes techniques. En hiver, les caribous forestiers et toundriques s'alimentent principalement de lichens arboricoles et terricoles (Bergerud, 1972; Rivard, 1978; Russel *et al.*, 1993; Seip, 1998), tandis qu'en été, ils s'alimentent de ressources plus variées telles que des feuilles d'arbres, d'arbustes, des plantes

herbacées et des graminées (Drucker *et al.*, 2010; Rettie *et al.*, 1997; Thompson *et al.*, 2015). À l'automne, le régime alimentaire contient également des champignons et des lichens (Bergerud, 1972; Thompson *et al.*, 2015).

Quelques études ont décrit le régime alimentaire des coyotes et des ours noirs dans l'aire de répartition du caribou de la Gaspésie à l'aide d'analyses de fèces. Boisjoly *et al.* (2010) ont observé que le coyote s'alimentait principalement d'orignaux en hiver, de petits fruits à la fin de l'été, et de lièvres (*Lepus americanus*) au début du printemps et à l'automne. Seules six fèces sur 150 analysées contenaient des poils de caribous. Boileau (1993) ainsi que Mosnier *et al.* (2008) ont observé que l'ours noir s'alimentait principalement de plantes vertes (p. ex. graminée, trèfle *Trifolium spp.*, pissenlit *Taraxacum officinale*, prêle, bouleau) et de petits fruits du printemps à l'automne, alors que très peu d'animaux étaient consommés tout au long de l'année (p. ex. faon d'orignal, lièvre, castor *Castor canadensis*). De plus, aucune des 265 fèces analysées ne contenait des restants de caribous selon Boileau (1993) et Mosnier *et al.* (2008).

Cependant, même si très peu d'évidences de consommation de caribou ont été notées, la présence d'ours noirs et de coyotes à des hautes altitudes (> 700 m) durant la période de mise bas du caribou a été rapportée à maintes reprises lors de suivis télémétriques (Boisjoly *et al.*, 2010; Mosnier *et al.*, 2005, 2008). La présence de prédateurs sur les sommets durant la période de mise bas pourrait entraîner une prédation opportuniste sur les faons, tel qu'observé dans d'autres populations (Dowd et Gese, 2012). De plus, l'ours noir et le coyote sont reconnus comme étant des prédateurs importants de faons de caribou, d'orignal et de cerf de Virginie dans plusieurs régions du Québec (Bastille-Rousseau *et al.*, 2011; Leclerc *et al.*, 2014) de même qu'en Gaspésie (Boisjoly *et al.*, 2010; Crête et Desrosiers, 1995). Il m'apparaît donc important de mieux comprendre le rôle de l'alimentation, de la condition

physiologique et des relations trophiques sur la dynamique de la population de caribous de la Gaspésie.

0.10 Plan détaillée de la thèse

Outre l'introduction générale (ce chapitre) et une conclusion générale, ma thèse est divisée en quatre chapitres distincts : les deux premiers s'intéressent aux différentes sources de variation des signatures isotopiques, le troisième chapitre s'intéresse aux relations trophiques et au partage des ressources alimentaires entre le caribou de la Gaspésie, l'orignal, l'ours noir et le coyote tandis que le quatrième chapitre s'intéresse à l'influence des différences individuelles dans l'alimentation et la condition physiologique sur la valeur adaptative de la population de caribous de la Gaspésie.

0.10.1 Survol des objectifs, hypothèses et prédictions du chapitre 1

Le contenu variable en lipides de l'organisme peut influencer les signatures isotopiques en carbone mesuré dans le tissu (Post *et al.*, 2007) puisque les lipides sont appauvris en ^{13}C en comparaison aux protéines et aux glucides (DeNiro et Epstein, 1977; McConnaughey et McRoy, 1979). Deux solutions existent afin de tenir compte du biais associé aux lipides, soit l'extraction *a priori* des lipides ou la correction *a posteriori* des valeurs obtenues à l'aide de modèles mathématiques (Fry, 2002; Lesage *et al.*, 2010; McConnaughey et McRoy, 1979; Post *et al.*, 2007). Très peu d'études en milieu terrestre se sont intéressées à l'effet des lipides ainsi qu'à l'effet de l'extraction des lipides sur les signatures isotopiques (mais voir Ehrich *et al.*, 2011; Post *et al.*, 2007; Tarroux *et al.*, 2010). Il est généralement assumé que l'extraction des lipides ou la correction mathématique ne soient pas nécessaires lors de

l'utilisation de tissus pauvres en lipides ou présentant des rapports carbone : azote (ci-après rapports CN) inférieurs à 4 en milieu terrestre (Post *et al.*, 2007), même si certaines études ne supportent pas cette affirmation (Lesage *et al.*, 2010; Yurkowski *et al.*, 2015). Les objectifs spécifiques de ce chapitre étaient donc 1) d'évaluer l'effet de l'extraction des lipides sur $\delta^{13}C$, $\delta^{15}N$ et le rapport CN dans le plasma, les cellules sanguines et les poils de caribou, 2) de proposer un modèle de normalisation des lipides spécifique au tissu et à l'espèce et 3) d'évaluer l'efficacité de quatre modèles fréquemment utilisés dans la littérature. J'ai prédit que l'effet de l'extraction des lipides variera en fonction du tissu analysé et de l'isotope ($\delta^{13}C$, $\delta^{15}N$) et que l'efficacité des modèles de normalisation varierait quant à elle entre les modèles, bien que l'extraction des lipides puisse ne pas s'avérer nécessaire chez le caribou étant donné le faible rapport CN (Post *et al.*, 2007). Finalement, aucune différence significative n'était attendue entre les valeurs réelles et ceux prédites par le modèle spécifique au tissu et à l'espèce.

0.10.2 Survol des objectifs, hypothèses et prédictions du chapitre 2

Les isotopes stables sont des outils robustes permettant d'estimer la composition du régime alimentaire d'un consommateur (Ben-David *et al.*, 1997; Caut *et al.*, 2009; Phillips *et al.*, 2005) ainsi que d'évaluer le partitionnement des ressources (Hobson et Welch, 1992; Newsome *et al.*, 2007; Post, 2002) à l'aide des modèles mixtes Bayésiens (Parnell *et al.*, 2013; Phillips *et al.*, 2014). Cependant, la précision de cette méthode dépend aussi de la capacité à contrôler les sources de variation isotopique qui ne sont pas reliés aux diverses sources alimentaires consommées (Martínez del Rio *et al.*, 2009) et nécessite l'utilisation de facteurs d'enrichissement trophique. Ces facteurs représentent la différence de rapport isotopique entre le tissu du consommateur et son régime alimentaire (Ben-David et Flaherty, 2012; DeNiro et Epstein, 1978; Martínez del Rio *et al.*, 2009) et dépendent du taux de renouvellement

des isotopes dans le tissu (Lecomte *et al.*, 2011; Zilversmit *et al.*, 1943). Les facteurs d'enrichissement trophique sont un prérequis dans les modèles mixtes isotopiques Bayésiens (Parnell *et al.*, 2013; Phillips et Gregg, 2001; Phillips *et al.*, 2014) et permettent de diminuer l'incertitude associée aux estimations (Bond et Diamond, 2011; Caut *et al.*, 2009; Phillips *et al.*, 2014). Cependant, la grande majorité des facteurs d'enrichissement trophique en carbone ($\Delta^{13}C$) et en azote ($\Delta^{15}N$) sont dérivés de la littérature et très peu d'études en milieu contrôlé ont été réalisées (Caut *et al.*, 2008, 2009; Kurle *et al.*, 2014; Martínez del Rio *et al.*, 2009). L'objectif spécifique de ce chapitre était d'estimer les facteurs d'enrichissement trophique en carbone et en azote dans deux types de tissus chez cinq espèces de mammifères élevés en captivité et nourris à partir d'un régime alimentaire connu. Ce chapitre est essentiellement descriptif, mais les valeurs obtenues sont très importantes pour les analyses liées à la poursuite de mon projet de doctorat ainsi que pour le milieu scientifique étudiant ces mêmes espèces.

0.10.3 Survol des objectifs, hypothèses et prédictions du chapitre 3

Il est essentiel de comprendre le partitionnement des ressources alimentaires et des niches trophiques au sein d'une population ou d'une communauté afin d'évaluer les mécanismes sous-jacents de coexistence, de compétition ou de prédation. Bien que le déclin de la population de caribous de la Gaspésie soit principalement dû à l'altération de l'habitat et à la prédation (Frenette *et al.*, 2020), le caribou de la Gaspésie est en compétition apparente avec l'orignal et se partagent des prédateurs communs. Cependant, peu d'études fournissent des évidences empiriques montrant à quel point ces prédateurs consomment du caribou. De plus, le rôle potentiel de la compétition interspécifique avec l'orignal pour les ressources alimentaires n'est pas bien compris (mais voir Christopherson *et al.*, 2019). Les objectifs spécifiques de ce chapitre étaient 1) de mieux comprendre le partitionnement des niches trophiques et

des ressources alimentaires entre le caribou, l'orignal, et leurs prédateurs afin d'améliorer notre compréhension de leurs interactions potentielles et 2) d'estimer la proportion de caribou dans le régime alimentaire des prédateurs. Notre hypothèse était qu'il y aura un partitionnement des niches trophiques entre ces quatre espèces sympatriques puisqu'ils fréquentent des types d'habitat différents. J'ai donc prédit que l'orignal aura une alimentation plus spécialisée de feuilles d'arbres et d'arbustes tandis que le caribou aura une alimentation plus variée composée de prêles, de graminées, de plantes herbacées, de champignons, de feuilles d'arbres et d'arbustes ainsi que de mousses (Christopherson *et al.*, 2019; Dussault *et al.*, 2004; Thompson *et al.*, 2015). Pour les deux prédateurs opportunistes, j'ai prédit que le régime alimentaire du coyote sera composé principalement d'animaux tandis que l'ours noir sera composé majoritairement de végétaux, bien que le coyote devrait aussi avoir une part de son régime qui sera végétale. Toutefois, les deux prédateurs auront consommé du caribou étant donné leur caractère plus généraliste. Finalement, j'ai prédit qu'il y aura peu de chevauchement de la niche trophique entre l'orignal et le caribou et un chevauchement plus important entre la niche des prédateurs et de leurs proies.

0.10.4 Survol des objectifs, hypothèses et prédictions du chapitre 4

L'alimentation et la condition physiologique sont des facteurs importants pour la santé, la croissance, la reproduction et la survie d'un individu (Parker *et al.*, 2009; Post et Klein, 1999; Thompson et Barboza, 2013) et ultimement pour la valeur adaptative (Abramsky *et al.*, 2002; Brown, 1992; Macbeth et Kutz, 2019) et la dynamique d'une population (Macbeth et Kutz, 2019). Pourtant, ces facteurs ne sont pas très bien compris chez toutes les espèces (Carlsson *et al.*, 2019a). Une alimentation pauvre en protéines, vitamines, nutriments et minéraux peut entraîner une faible condition individuelle (Parker *et al.*, 2009) et affecter le taux de reproduction (Flueck *et al.*, 2012; Flynn *et al.*, 1977), la survie (Cook *et al.*, 2004a) et

entraîner le déclin d'une population (Post et Klein, 1999). Il importe de mieux comprendre le lien entre l'alimentation et la condition physiologique et comment ils peuvent influencer la santé et les performances individuelles. Les objectifs spécifiques de ce chapitre étaient 1) d'établir une relation entre l'accumulation des éléments traces dans les poils et l'alimentation et 2) d'évaluer si la condition physiologique et l'alimentation seraient associées aux performances individuelles de la population en déclin de caribous de la Gaspésie. Comme le caribou de la Gaspésie doit faire face aux perturbations anthropiques qui influencent ses déplacements (Lesmerises *et al.*, 2018) et se retrouve ainsi impliqué dans un phénomène de compétition apparente (Frenette *et al.*, 2020), mon hypothèse voulait que les ressources alimentaires les plus nutritives ne soient pas accessibles au caribou, et que les caribous seraient par conséquent contraints d'utiliser les ressources plus pauvres qui influenceront leurs performances individuelles. J'ai donc prédit que les caribous qui s'alimenteront de ressources alimentaires pauvres en plus grande proportion à l'été et à l'automne auront des probabilités de survie et de reproduction plus faibles. Aussi, étant donné que de faibles concentrations en éléments traces essentiels peuvent affecter les performances individuelles (Bondo *et al.*, 2019; Flueck *et al.*, 2012; O'Hara *et al.*, 2001), j'ai prédit que les concentrations en éléments traces mesurées dans les poils de caribou seront faibles (p. ex. Ca, Co, Cu, Mn, Se et Zn) et pourraient expliquer les faibles taux de recrutement et de survie dans cette population (Frenette *et al.*, 2020).

CHAPITRE I

INFLUENCE DES LIPIDES SUR LES SIGNATURES ISOTOPIQUES DANS LES POILS DE MAMMIFÈRES : L'IMPORTANCE DE LA VALIDATION

INFLUENCE OF LIPIDS ON STABLE ISOTOPE RATIOS IN MAMMAL HAIR: HIGHLIGHTING THE IMPORTANCE OF VALIDATION

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1.1 Résumé

Les signatures isotopiques du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) sont de plus en plus utilisées dans les études écologiques afin d'évaluer la composition du régime alimentaire et les relations trophiques. Cependant, le contenu en lipides des tissus analysés peut biaiser l'interprétation biologique de la composition du régime alimentaire et des relations trophiques. Il est possible de corriger les valeurs de $\delta^{13}C$ par l'extraction des lipides ou encore à l'aide de modèles mathématiques lorsque des validations sont faites *a priori*. Aussi, les études antérieures supposent qu'il n'est pas

nécessaire de corriger pour l'effet des lipides lorsque le rapport carbone : azote (CN) est plus faible que 4 en milieu terrestre. Par conséquent, les objectifs de l'étude étaient d'évaluer l'effet de l'extraction des lipides sur les $\delta^{13}C$, $\delta^{15}N$ et le rapport CN mesurés chez un mammifère terrestre, le caribou (*Rangifer tarandus caribou*), et de proposer des modèles de correction mathématique spécifiques à la méthode d'extraction et au tissu. J'ai également évalué si quatre modèles mathématiques fréquemment utilisés dans la littérature étaient applicables à mon espèce à l'étude. J'ai mesuré les $\delta^{13}C$, $\delta^{15}N$ et le rapport CN dans des échantillons de poils, de plasma et de globules rouges de 44 caribous fréquentant le parc national de la Gaspésie. L'effet de l'extraction des lipides sur les rapports isotopiques a été testé à l'aide d'un test de *t* pour échantillon apparié. J'ai utilisé un modèle linéaire simple pour corriger l'effet des lipides sur les valeurs de $\delta^{13}C$ et j'ai évalué sa performance par rapport aux modèles publiés dans la littérature. La teneur en lipides a influencé de manière significative les valeurs de $\delta^{13}C$ dans les poils de caribou même si les rapports CN étaient petits. Les quatre modèles mathématiques communément utilisés dans la littérature offraient une précision inférieure pour les valeurs de $\delta^{13}C$ sans lipides mesurées dans les poils de caribou par rapport au modèle spécifique que j'ai développé pour le caribou. Sur la base de ces résultats, je recommande de corriger systématiquement le biais induit par les lipides dans les systèmes terrestres et d'analyser le $\delta^{13}C$ (sans lipides) et le $\delta^{15}N$ (avec lipides) à partir de deux échantillons différents afin d'obtenir une meilleure précision. Je recommande également d'utiliser un modèle mathématique spécifique à la méthode, au tissu et à l'espèce, ou d'appliquer un modèle qui a été précédemment validé pour le tissu et l'espèce d'intérêt.

1.2 Abstract

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios are increasingly used in ecological studies to evaluate diet composition and trophic relationships. However, lipids may influence stable isotope ratios due to the depletion of ^{13}C in adipose tissues relative to proteins and carbohydrates. $\delta^{13}C$ values can be corrected by lipid extraction or normalization models. The aims of our study were to evaluate the effects of lipid extraction on stable isotope ratios in a terrestrial mammal, the caribou (*Rangifer tarandus caribou*), and to propose relevant lipid normalization models that are method- and tissue-specific for $\delta^{13}C$ values. We also evaluated if four $\delta^{13}C$ lipid normalization and correction models proposed in the literature were applicable to our study species. Stable isotope ratios were obtained for hair, plasma and red blood cell samples of 44 caribou in the Gaspésie National Park (Québec, Canada). The effects of lipid extraction on stable isotope ratios were tested using a paired *t*-test. A simple linear model was used to correct for the effects of lipid extraction and to assess its performance compared to that of published equations. Lipid content significantly influenced $\delta^{13}C$ values in caribou hair. The four lipid normalization equations commonly used in the literature did not accurately predict $\delta^{13}C_{lipid\text{-}free}$ values of caribou hair. Based on our results, we recommend controlling systematically for lipids in terrestrial systems and analyzing $\delta^{13}C$ (lipid-free) and $\delta^{15}N$ (bulk) from two separate aliquots to reach a greater precision. We also recommend controlling for lipids in hair tissue. If not possible, we recommend using a lipid normalization model that is tissue, method and species-specific or applying a model that has been previously validated for the tissue and species of interest.

1.3 Introduction

Understanding the foraging ecology of a species, a population or an individual is a fundamental question in ecology, conservation and management. Foraging is a key behaviour as it influences the growth, reproduction and survival of an individual and may thus influence its fitness (Abramsky et al., 2002; Brown, 1992). It is thus important to improve constantly the knowledge regarding the diet of wild species. Because direct observation of feeding behaviours in wild species is difficult and often impossible (Litvaitis, 2000), other techniques were developed to acquire information about the diet of a species. Researchers often have to use indirect methods to assess diet, such as the analysis of prey parts from scats and stomach contents (Deb, 1997; Hewitt & Robbins, 1996; McInnis et al., 1983). More recently, biogeochemical markers like stable isotopes have become a key tool to study the feeding ecology of wild species (Kelly, 2000; Peterson & Fry, 1987).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios are increasingly used in ecological studies to provide information on sources of primary productivity (France, 1995; Ramsay & Hobson, 1991) and energy flow (Peterson & Fry, 1987) as well as habitat use and migratory patterns (Rubenstein & Hobson, 2004). Stable isotope ratios are useful to provide insights on trophic relationships (Hobson & Welch, 1992, Post, 2002) and diet composition (Ben-David et al., 1997; Phillips et al., 2005). Isotope analyses are based on the principle that stable isotope ratios in the tissues of consumers reflect the ratios of their diet (DeNiro & Epstein, 1978, 1981; Hobson et al., 1996). On the other hand, the relatively high (+ 3-4‰) and predictable enrichment in ^{15}N from one trophic level to the next makes nitrogen isotopes useful indicators of trophic position (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Peterson & Fry, 1987). The lower trophic enrichment for ^{13}C (typically ~ 1‰) limits the usefulness of this element as an index of trophic position but makes it particularly

suitable for delineating carbon sources (DeNiro & Epstein, 1978; Peterson & Fry, 1987).

One limitation of stable isotope analysis, however, is that lipids are more depleted in ^{13}C relative to protein and carbohydrate fractions (DeNiro & Epstein, 1977; McConnaughey & McRoy, 1979). The depleted $\delta^{13}C$ ratios result from the isotopic fractionation that occurs during the conversion of pyruvate to acetyl coenzyme A during lipid synthesis (DeNiro & Epstein, 1977). The $\delta^{13}C$ values are also influenced by the heterogeneity in lipid content among organisms (Post et al., 2007) and tissue types (McConnaughey & McRoy, 1979; Sweeting et al., 2006) and by the chemical extraction methods (Dobush et al., 1985; Elliott & Elliott, 2016; Logan & Lutcavage, 2008). Lipid extraction methods using polar solvents tend to increase the $\delta^{13}C$ values and decrease the elemental ratio of C to N (CN ratio) compared to non-polar solvents (Logan & Lutcavage, 2008). Thus, not accounting for lipids may bias future interpretation of trophic relationships or diet composition (Lesage et al., 2010; Tarroux et al., 2010). A consensus about the necessity to extract lipids or account for their effects is recognized in the literature (Kelly, 2000; Post et al., 2007). Two different approaches have been suggested to do so: controlling variability in $\delta^{13}C$ values *a priori* through lipid extraction, or, when the former is impossible, accounting for lipids *a posteriori* using a previously published normalization model (Fry, 2002; Lesage et al., 2010; McConnaughey & McRoy, 1979; Post et al., 2007).

During the past decade, lipid extraction was the approach advocated to obtain uniform samples in order to ease comparison (Post et al., 2007). It was generally assumed that the chemical solvents used to remove lipids would not alter the $\delta^{15}N$ values of tissue (Sotiropoulos et al., 2004). However, recent studies conducted on a variety of marine and freshwater vertebrates have documented an enrichment in $\delta^{15}N$ values caused by the leaching of isotopically light nitrogenous cell components

through association with extraction solvents (Lesage et al., 2010; Mintenbeck et al., 2008; Sotiropoulos et al., 2004). In contrast, other studies focusing on marine and terrestrial animals have documented negative or neutral effects of chemical solvents on $\delta^{15}N$ values (Bodin et al., 2007; Ehrich et al., 2011; Ricca et al., 2007). The effects of lipid extraction on $\delta^{15}N$ values differ considerably between species, tissues and methods, indicating the need to evaluate solvent effects on various tissues and in multiple species (Sotiropoulos et al., 2004). Some authors have recommended conducting lipid extraction on separate aliquots of samples to determine $\delta^{13}C$ and $\delta^{15}N$ values because of the variability often observed following lipid extraction (Lesage et al., 2010; Sweeting et al., 2006). However, this procedure is a time- and labor-intensive process and may be very expensive for large sample sizes (Kelly, 2000; Kiljunen et al., 2006). Lipid extraction is therefore the approach recommended when a maximum of precision is needed for calculations of diet composition involving mixing models and niche isotopic overlap (Lesage et al., 2010; Tarroux et al., 2010).

Another common strategy used to solve the problem of the 'lipid effect' refers to lipid normalization equations employed *a posteriori*; several of these equations have been established to estimate lipid-free $\delta^{13}C$ values in various aquatic organisms (Fry, 2002; McConnaughey & McRoy, 1979; Post et al., 2007). These models use the CN ratio as a proxy for lipid content and the isotopic difference between proteins and lipids (DeNiro & Epstein, 1977; McConnaughey & McRoy, 1979). However, the relationship between the CN ratio and the $\delta^{13}C$ value can vary among tissues (Logan et al., 2008) as well as between closely related species (Mintenbeck et al., 2008), thus questioning the application of these lipid normalization models. Lipid normalization models are not always applicable to all taxa and tissues, so alternative models have been proposed (Kiljunen et al., 2006; Post et al., 2007). Kiljunen et al. (2006) re-estimated the isotopic differences between proteins and lipids and improved the

precision and applicability of the lipid-normalization corrections in various aquatic and marine organisms. Errors introduced by lipids or normalization equations may bias the interpretation of trophic relationships and dietary composition (Lesage et al., 2010; Post et al., 2007; Tarroux et al., 2010). Considering this, Kiljunen et al. (2006) recommended to validate models before applying them to a particular species and tissue, or to use tissue-specific and species-specific models. These specific models have generally fit to the data better and give better predicted values of lipid-free $\delta^{13}C$ than generalized models (Lesage et al., 2010; Logan et al., 2008).

In terrestrial animals, however, only a few studies have focused on the effect of lipids on $\delta^{13}C$ and $\delta^{15}N$ values (but see Ehrich et al., 2011; Post et al., 2007; Tarroux et al., 2010). Post et al. (2007) proposed a linear normalization equation using the CN ratio but recommended validating it for terrestrial animals because their sample size was small. Before applying a model developed for another species, tissue, or a different lipid extraction protocol, it is necessary to take into account the potential biases associated with such an arithmetical correction of $\delta^{13}C$ values for lipids (Lesage et al., 2010; Tarroux et al., 2010). Furthermore, it is commonly assumed in the literature that no lipid extraction or normalization is necessary when using low-lipid tissues (CN ratio < 4 for terrestrial animals, < 3.5 for marine animals) (Post et al., 2007). However, some studies observed a significant increase in $\delta^{13}C$ after lipid extraction despite a CN ratio below 3.5, and therefore do not support this assumption (Lesage et al., 2010; Yurkowski et al., 2015).

Our study aimed to 1) evaluate the effects of lipid extraction on $\delta^{13}C$, $\delta^{15}N$ and CN ratio values in plasma, red blood cells and hair of a terrestrial mammal, the woodland caribou (*Rangifer tarandus caribou*), 2) propose tissue, species and method-specific lipid normalization models for $\delta^{13}C$ values, 3) evaluate if four of the most commonly used $\delta^{13}C$ lipid normalization and correction models throughout literature (i.e. Ehrich

et al., 2011; Fry, 2002; McConnaughey & McRoy, 1979; Post et al., 2007) are suitable to correct $\delta^{13}C$ estimates for our studied species and 4) determine if those four models are efficient to deal with varying lipid contents in different types of mammalian tissues.

1.4 Materials and methods

1.4.1 Study area

We focused our study on the range of the Atlantic-Gaspésie caribou population, a small and relict herd using bare habitats found at high elevations (> 700 m) in the Gaspésie National Park and the surrounding Matane, Dunière and Chic-Chocs Wildlife Reserves (Ouellet et al., 1996; Figure 1.1). Three groups of summits are used by caribou, namely (from west to east) the Logan ridge (Mount Logan: 1 128 m), Albert plateaus (Mount Albert: 1 154 m) and McGerrigle area (Mount Jacques-Cartier: 1 268 m). The altitudinal gradient determines three distinct ecological zones characterized by differences in vegetation type. The montane area (100-900 m) is mainly characterized by the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain, while the subalpine forest (900-1050 m) is a transition zone where tree height decreases with increasing elevation, and the alpine tundra (> 1050 m) is characterized by lichens, mosses, graminoids and ericaceous shrubs. The population was designated as Endangered in 2000 under the Canadian Species at Risk Act (SARA) and is considered as an irreplaceable component of Canada's biodiversity (COSEWIC, 2011). The estimated population size ranged between 69 and 82 caribou in the 2017 aerial survey (Morin, 2017).

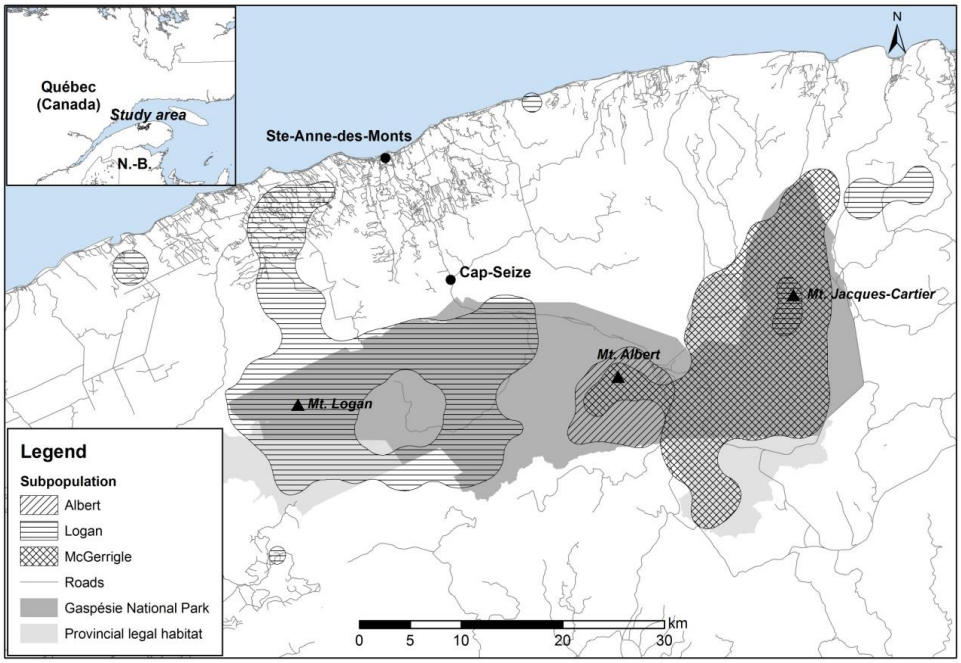

Figure 1.1. Study area of the Atlantic-Gaspésie caribou population in the Gaspésie National Park and the surrounding Matane, Dunière and Chic-Chocs Wildlife Reserves, Québec, Canada.

1.4.2 Data collection and sample preparation

We collected hair and blood samples from 44 caribou captured in 2013 and 2014 across the Gaspésie caribou range. Animals were captured using a net gun fired from a helicopter; our capture and manipulation protocol was authorized by the Animal Welfare Committee [Université du Québec à Rimouski (hereafter UQAR) certificate #CPA-52-13-112; Ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) certificate #CPA FAUNE 13-08]. We collected caribou blood with a sodium heparin tube. On the day of capture, we centrifuged whole blood kept on ice after capture to obtain plasma and red blood cells that were frozen at -20°C until they were processed.

We dried and stored hair samples in paper bags at ambient temperature until they were processed.

We washed hair samples using a solution of 2:1 chloroform-methanol in an ultrasonic bath to remove all possible surface contamination and external lipids (Hobson et al., 2000). Samples were then rinsed in distilled water and oven-dried at 50°C for 24h (Hobson et al., 2000). Hair and blood samples were freeze-dried for 48h and ground to a fine powder (Bosley & Wainright, 1999; Jardine et al., 2003). We used a CryoMill with cooling option (liquid nitrogen at -196°C) for hair samples. We divided samples into two parts: one part of the subsamples (bulk) received no further treatment prior to isotope analyses, and the second part (lipid-free) was lipid-extracted.

1.4.3 Lipid extraction and stable isotopic analyses

We conducted lipid extraction using 7 mg of powdered hair (to remove internal lipids, Dunnett, 2005; Dunnett & Lees, 2003) or 1 mL of blood material and a solvent consisting of a mixture of chloroform and methanol (2:1 v/v) (Folch et al., 1957). We shook the mixture and stored it overnight at 4°C. We centrifuged the mixture at 11,200 g for 10 min and discarded the supernatant (Folch et al., 1957). We repeated the whole procedure two times. After 3 extractions, samples were dried by evaporation overnight, rinsed with distilled water, oven-dried overnight at 50°C and powdered again.

We weighed a subsample of 0.500-0.700 mg (± 0.001 mg) of powdered tissue (bulk and lipid-free) into a tin capsule and analyzed it for stable carbon and nitrogen isotope ratios using a COSTECH ECS 4010 Elemental Analyser coupled to a DeltaPlus XP Isotope Ratio Mass Spectrometer (IRMS, Thermo Electron Co,

Marine Chemistry and Mass Spectrometry Laboratory, UQAR). By convention, ^{13}C and ^{15}N isotope abundances were expressed in delta notation (‰), as $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{13}C or ^{15}N, and R_{sample} is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$; $R_{standard}$ represents the ratios for the respective standards, i.e. Vienna Peedee Belemnite (PDB) and atmospheric nitrogen (AIR). We evaluated the accuracy of our isotopic analyses using commercially certified material (B2151) and the precision of measurement by randomly duplicating a subset of our samples. Replicates using certified materials (n = 7) indicated a systematic error of ± 0.28 and ± 0.25‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, whereas the average deviations observed between replicates of hair and blood samples (n = 24) indicated an analytical error of 0.043‰ for $\delta^{13}C$ and 0.045‰ for $\delta^{15}N$.

1.4.4 Statistical analyses

Using paired *t*-tests, we tested for an effect of lipid extraction on the $\delta^{13}C$, $\delta^{15}N$ and CN ratios while controlling for inter-individual variation. We used linear and nonlinear regression analyses to examine the relationship between $\Delta\delta^{13}C$ ($\delta^{13}C_{lipid\text{-}free}$ - $\delta^{13}C_{bulk}$), CN ratio, $\delta^{15}N_{bulk}$, $\delta^{15}N_{lipid\text{-}free}$, $\delta^{13}C_{bulk}$ and $\delta^{13}C_{lipid\text{-}free}$. We assessed the normality of residuals using normal quantile-quantile plots and assessed heteroscedasticity with a plot of standardized residuals against fitted values (Quinn & Keough, 2002).

We proposed simple linear models from our data using $\delta^{13}C_{bulk}$ values and CN ratios to correct lipid extraction effects and to assess its performance compared to published equations.

$$\delta^{13}C_{lipid-free} = \beta_1 \times \delta^{13}C_{bulk} + \beta_0 \qquad \text{(eqn 1)}$$

$$\delta^{13}C_{lipid-free} = \beta_1 \times \delta^{13}C_{bulk} + \beta_2 \times CN + \beta_0 \quad \text{(eqn 2)}$$

We used four linear and nonlinear models integrating $\delta^{13}C$ and CN ratio parameters to investigate the potential application of lipid normalization equations and their literature parameters on caribou tissues. These four models are quite commonly used in the peer-reviewed literature, but their reliability for caribou tissues has not been evaluated. The first model, developed by McConnaughey and McRoy (1979) for various marine vertebrates and invertebrates, estimated lipid-free $\delta^{13}C$ values using the following two equations:

$$L = \frac{93}{1 + \left[\left(0.246 \times CN\right) - 0.775\right]^{-1}} \quad \text{(eqn 3)}$$

$$\delta^{13}C_{lipid-free} = \delta^{13}C_{bulk} + D \times \left(I + \frac{3.90}{1 + \frac{287}{L}} \right) \quad \text{(eqn 4)}$$

where L is the lipid content, CN is the ratio of C and N in the untreated samples, D is the isotopic difference between pure lipid and pure protein and *I* is a constant. The McConnaughey and McRoy model (hereafter referred to as MM model) assumed a D of 6‰ and an I of -0.207 (McConnaughey, 1978). Post et al. (2007) developed a simplified model using the CN ratio in the untreated samples for a wide variety of aquatic and terrestrial animals (see eqn 6 in Post et al., 2007):

$$\delta^{13}C_{lipid-free} = -3.44 + 1.00 \times CN + \delta^{13}C_{bulk} \quad \text{(eqn 5)}$$

Fry (2002) developed a mass-balance approach and requires information on the CN ratio of untreated samples, pure protein ($CN_{protein}$) and D:

$$\delta^{13}C_{lipid-free} = \delta^{13}C_{bulk} + D - \frac{D \times CN_{protein}}{CN} \qquad \text{(eqn 6)}$$

where $CN_{protein}$ is determined from the lipid-extracted samples when no lipids remained in the sample and is assumed to be 3.7 (Fry, 2002) and D is assumed to be 6‰ (McConnaughey, 1978). Ehrich et al. (2011) developed a species-specific linear model for bird and mammal muscles using CN in the untreated sample:

$$\delta^{13}C_{lipid-free} = -3.113 + 0.968 \times CN + \delta^{13}C_{bulk} \qquad \text{(eqn 7)}$$

We also estimated the parameters D and I by fitting the original equations of the MM model to our observed data, the parameter D from the Fry equation and the coefficients β_0 and β_1 from the linear model of Post using the least-squares procedures in R (see section 1.9 Supplementary material,

Table S1.1).

We compared the validity of each model applied to each tissue (i.e. dried hair, blood) using the residual sums of squares obtained from a linear regression analysis between observed $\delta^{13}C_{lipid\text{-}free}$ values and predicted $\delta^{13}C_{lipid\text{-}free}$ values. We identified the most parsimonious model as the one having the lowest value of Akaike information criterion corrected for small sample size (AICc) among a set of candidate models. In addition, we calculated ΔAICc and AICc weights (ω_i), where models with ΔAICc ≤ 2 provide a relevant and interesting support to the best model (Burnham & Anderson, 2002) and ω_i provide the relative preference among a set of candidate models (Vandekerckhove et al., 2014). We assessed the fit of the most parsimonious model

using R^2. To evaluate model performance, we determined the precision of the predicted values with the proportion of predicted $\delta^{13}C_{lipid\text{-}free}$ values that were within 0.25% (systematic error) of the observed $\delta^{13}C_{lipid\text{-}free}$ values ($P_{0.25}$) and with the mean absolute error (MAE) using repeated k-fold cross validation (James et al., 2013). To do so, we calculated model coefficients using 90% of the data and withholding the remaining 10% for validation, and repeated this procedure 999 times (1000 iterations) using the library caret (Kuhn, 2018). We performed all statistical analyses using R software version 3.4.2 (R Development Core Team, 2017).

1.5 Results

1.5.1 Effect of lipid extraction on stable isotope ratios

Lipid extraction had no effect on $\delta^{13}C$ values in plasma (paired *t*-test, $t = 0.86$, $P = 0.40$) and red blood cells (paired *t*-test, $t = 1.49$, $P = 0.15$), but it increased $\delta^{13}C$ values in hair (paired *t*-test, $t = 19.42$, $P < 0.05$) by an average of 0.40‰ (Table 1.1; Figure 1.2). Lipid extraction had no effect on $\delta^{15}N$ values in red blood cells (paired *t*-test, $t = 1.72$, $P = 0.096$) but significantly increased $\delta^{15}N$ values in hair (paired *t*-test, $t = -3.09$, $P < 0.05$) and plasma (paired *t*-test, $t = -3.94$, $P < 0.05$) by an average of 0.11 and 0.18‰ (Figure 1.2). The CN ratios were relatively low, ranging from 3.93 to 4.30 for bulk samples and from 3.65 to 4.13 for lipid-free samples (Table 1.1). Lipid extraction had a negative effect on CN ratio values in all three tissues (paired *t*-test, $t = 6.28$ to 29.34, all $P < 0.05$) by an average of 0.06 for red blood cells, 0.28 for hair and 0.17 for plasma (Figure 1.2).

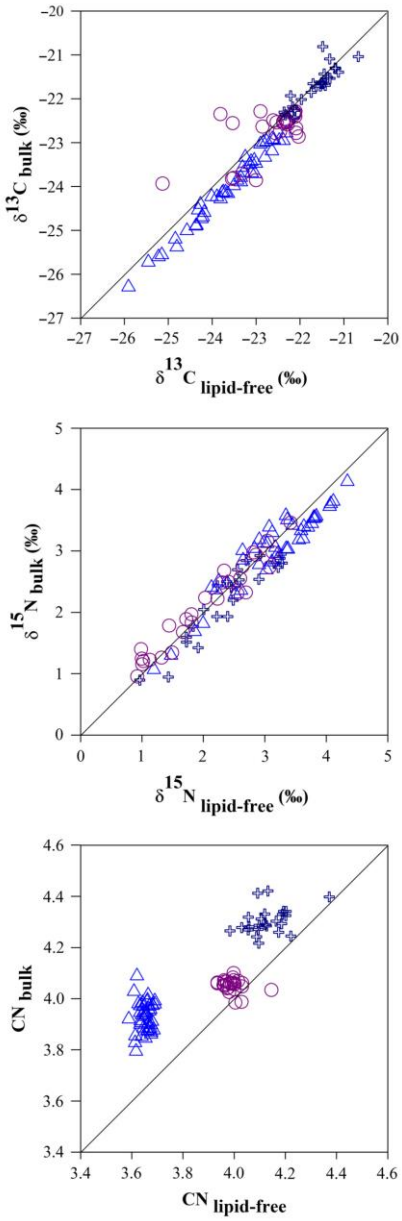

Figure 1.2. Effect of lipid extraction on $\delta^{13}C$, $\delta^{15}N$ and CN ratio values for caribou hair (Δ), red blood cells (◦) and plasma (+) with a 1:1 reference line representing values expected if there is no difference between lipid-extracted and untreated samples.

Table 1.1. Mean (± SE) values of carbon and nitrogen stable isotopes (‰) and CN ratio values of untreated (bulk) and lipid-extracted samples (lipid-free) from caribou tissues.

Tissues	n	$\delta^{13}C_{bulk}$	$\delta^{13}C_{lipid\text{-}free}$	$\delta^{15}N_{bulk}$	$\delta^{15}N_{lipid\text{-}free}$	CN_{bulk}	$CN_{lipid\text{-}free}$
Red blood cells	28	-22.76 ± 0.10	-22.67 ± 0.13	2.11 ± 0.13	2.05 ± 0.15	**4.05 ± 0.01**	**3.99 ± 0.01**
Hair	44	**-24.05 ± 0.13**	**-23.65 ± 0.13**	**2.99 ± 0.10**	**3.10 ± 0.11**	**3.93 ± 0.01**	**3.65 ± 0.01**
Plasma	24	-21.69 ± 0.09	-21.62 ± 0.09	**2.24 ± 0.13**	**2.42 ± 0.13**	**4.30 ± 0.01**	**4.13 ± 0.02**

* **Bold** values indicated significant difference (paired t-test $p < 0.05$) between bulk and lipid-free samples.

We found a subtle but significant positive linear relationship between $\delta^{13}C_{bulk}$ and CN ratios in hair samples only, but CN explained only 15% of the variation in $\delta^{13}C_{bulk}$ ($F_{1,42} = 7.46$, r = 0.39, $P < 0.05$) (Figure 1.3). No linear relationships were observed between $\Delta\delta^{13}C$ and $\delta^{13}C_{bulk}$ in all three tissues (all $R^2 < 0.1$, r < 0.02, $P > 0.05$). There were no linear or nonlinear relationships between $\Delta\delta^{13}C$ and CN ratios for all three tissues (all $R^2 < 0.08$, r < 0.30, $P > 0.05$). There was also no linear relationship between $\Delta\delta^{15}N$ and CN ratios (all tissues $R^2 < 0.10$, r < 0.40, $P > 0.05$) and between $\delta^{15}N_{bulk}$ and CN ratios (all tissues $R^2 < 0.08$, r < - 0.03, $P > 0.05$). However, a strong significant linear relationship was observed between $\delta^{15}N_{bulk}$ and $\delta^{15}N_{lipid\text{-}free}$ in all three tissues (all $R^2 > 0.87$, r > 0.93, $P < 0.001$) (Figure 1.2).

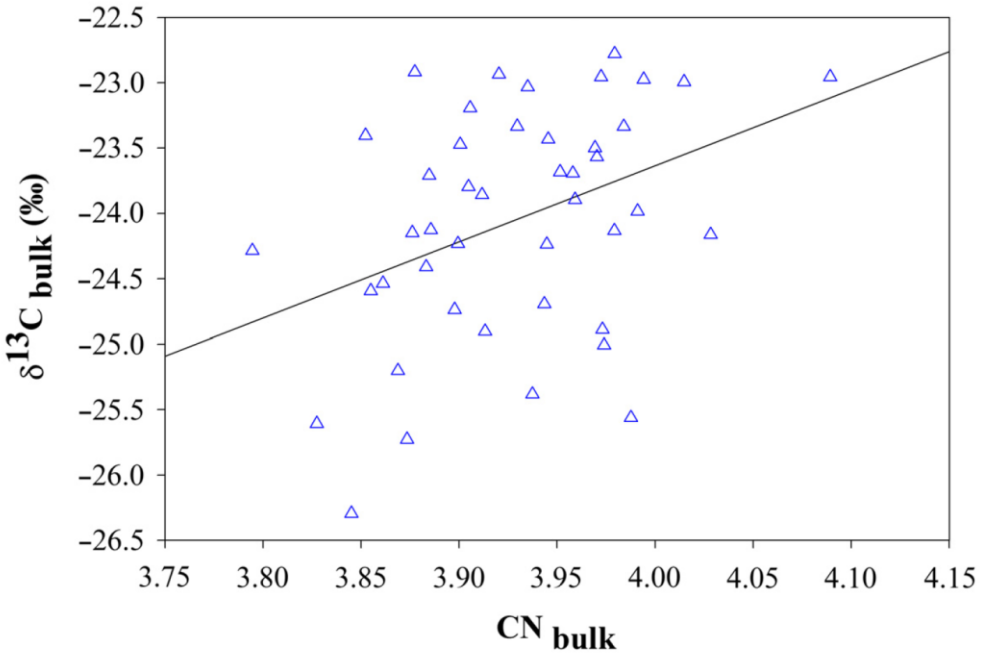

Figure 1.3. Linear relationship between CN ratio and $\delta^{13}C$ values of untreated caribou hair samples ($F_{1,42} = 7.46$, r = 0.39, p < 0.05).

1.5.2 Tissue- and caribou-specific linear models

Our best caribou-specific model to predict $\delta^{13}C_{lipid\text{-}free}$ values in hair included the $\delta^{13}C_{bulk}$ parameter alone (eqn 1) and was as follows:

$$\delta^{13}C_{lipid-free} = 0.982(\pm 0.048) \times \delta^{13}C_{bulk} - 0.028(\pm 1.15) \qquad \text{(eqn 8)}$$

In this model, $\delta^{13}C_{bulk}$ explained 98% of the variation in $\delta^{13}C_{lipid\text{-}free}$ values ($F_{1,42}$ = 1718.78, $P < 0.05$). There was an absolute error of ± 0.11‰ in the predictions of $\delta^{13}C$ values of lipid extracted samples when compared to untreated samples. This error was estimated from the cross-validation procedure previously described. The addition of the CN ratio parameter in the linear model (eqn 2) did not improve its fit to the data, this parameter having no significant effect on the relationship (t = 1.46, P = 0.15).

1.5.3 Lipid normalization models

Because models with $\Delta AIC_c \leq 2$ are generally considered to provide substantial explainable variation in the data (Burnham & Anderson, 2002), our analyses suggested that the models proposed by Ehrich et al. (2011), by Post et al. (2007), as well as the MM model (1979) along with the caribou-specific model we developed were the most parsimonious models to adjust for lipids when determining isotopic values in caribou hair. However, according to the Akaike weights, the probability that the Ehrich et al. (2011) and Post et al. (2007) models are the best models is three times higher (ω_i = 0.336 and 0.309, respectively) than for the MM (1979; 0.119) and our caribou-specific (0.181) models, although no model really outperformed the others (max ω_i = 0.336). All four models had a strong fit to the data and explained between 97 and 98% of the variability (Table 1.2). The mean absolute error estimated from the cross-validation procedure was comparable among models (0.11) and

indicated that predictions of $\delta^{13}C_{lipid\text{-}free}$ values are close to the observed lipid-extracted $\delta^{13}C$ values. Nevertheless, when comparing model performance using the percentage of $\delta^{13}C$ values predicted within 0.25‰ of the observed value, our tissue- and caribou-specific model was the most accurate. Our model predicted 93% of the $\delta^{13}C_{lipid\text{-}free}$ values compared to 43% for the equation proposed by Ehrich et al. (2011), 86% for the one found in Post et al. (2007), and 9% for the MM model (1979). Our tissue-, method-, and caribou-specific model was also the only one for which no significant differences were found between the predicted and the observed lipid-extracted $\delta^{13}C$ values (paired *t*-test, $t = -0.27$, $P = 0.79$) (Figure 1.4), suggesting our hair- and caribou-specific model is more accurate.

Table 1.2. Ranking of candidate models (based on AICc) used to assess the linear relationship between observed $\delta^{13}C_{lipid\text{-}free}$ and estimated $\delta^{13}C_{lipid\text{-}free}$ values using five lipid normalization equations for hair of 44 caribou sampled in 2013 and 2014 in Gaspésie National Park.

Models	df	LL	AICc	ΔAICc	ω_i	R^2	MAE	$P_{0.25}$
eqn 7 (Ehrich et al., 2011)	3	26.63	-46.7	0.00	0.336	0.98	0.11	43
eqn 5 (Post et al., 2007)	3	26.55	-46.5	0.17	0.309	0.98	0.11	86
eqn 8 (Our equation)	3	26.01	-45.4	1.24	0.181	0.98	0.11	93
eqn 4 (MM, 1979)	3	25.59	-44.6	2.08	0.119	0.98	0.11	9
eqn 6 (Fry, 2002)	3	24.82	-43.0	3.62	0.055	0.97	0.11	91

Model number of parameters (df), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AICc), difference in AICc values (ΔAICc), weight (ω_i), variance explained (R^2), mean absolute error (MAE), and proportion of values predicted within 0.25‰ of the observed values ($P_{0.25}$) are shown. MAE and $P_{0.25}$ were estimated from k-fold cross validation procedures.

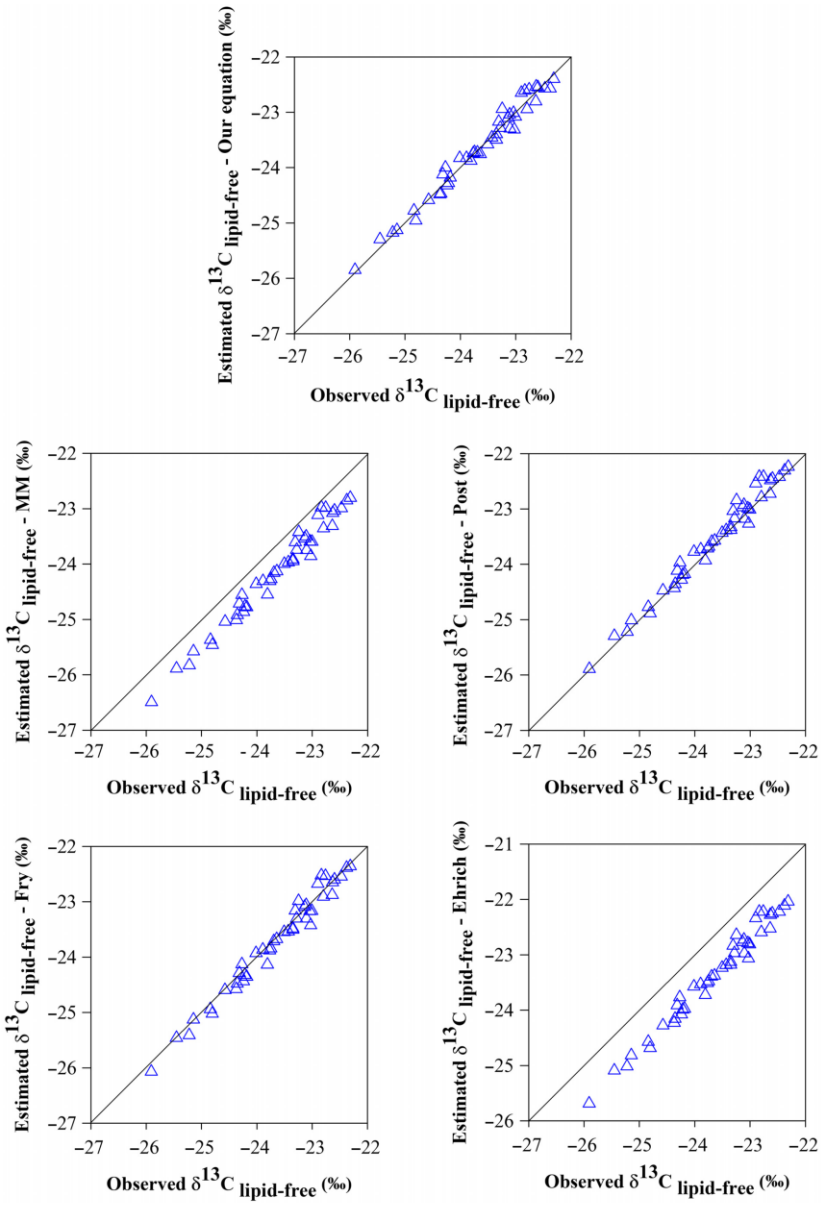

Figure 1.4. Relationships between the observed $\delta^{13}C_{lipid\text{-}free}$ values and estimated $\delta^{13}C_{lipid\text{-}free}$ values by five lipid normalization equations with 1:1 reference line representing values expected if there is no difference between observed and estimated $\delta^{13}C_{lipid\text{-}free}$ values.

The four lipid normalization equations published in the literature did not predict $\delta^{13}C_{lipid\text{-}free}$ values of caribou hair accurately (Figure 1.4). We showed that Ehrich et al. (2011) and Post et al. (2007) equations tended to overestimate $\delta^{13}C_{lipid\text{-}free}$, with 95% CI values ranging between 0.017 to 0.56‰ (coefficient of variation (CV) = 46.6%) and -0.19 to 0.36‰ (CV = 91.1%), respectively. Opposite trends were observed for the MM (1979) and Fry (2002) models: they both underestimated $\delta^{13}C_{lipid\text{-}free}$, with values ranging between -0.77 to -0.21‰ (CV = 29.5%) and -0.34 to 0.24‰ (CV = 77.8%), respectively.

1.6 Discussion

1.6.1 Effect of lipid extraction on stable isotope ratios

The decision to use lipid extraction prior to stable isotope analysis is a practice that varies across studies, taxa and tissue types (e.g. Bearhop et al., 2000; Hilderbrand et al., 1996; Hobson, 1995; Lecomte et al., 2011; Tarroux et al., 2016), and the standardization of lipid extraction in isotope studies has been recommended as a suitable alternative by Kelly (2000). In several isotopic studies, lipids were not routinely extracted in red blood cells, serum or plasma (Burns et al., 1998; Finstad & Kielland, 2011; Hobson et al., 1996; Polischuk et al., 2001). However, blood serum or plasma may have highly variable lipid contents depending on individual and physiological conditions (Hobson & Stirling, 1997; Lesage et al., 2002). The depletion of ^{13}C in adipose tissue relative to proteins and carbohydrates has been reported in the literature (DeNiro & Epstein, 1977), so it was recommended to extract lipids from all blood components (Kelly, 2000; Lesage et al., 2002). Lesage et al. (2002) observed significant depletions of ^{13}C in phocid seal species while Tarroux et al. (2016) observed similar depletions in plasma samples of Antarctic fur seals

(*Arctocephalus gazella*). However, some studies found no ^{13}C depletion in blood samples of arctic foxes (*Vulpes lagopus*, Tarroux et al., 2012), Antarctic fur seals (Tarroux et al., 2016) or various bird species (Bearhop et al., 2000). The lipid content of whole blood is usually very low, e.g. less than 5% of the dry mass of avian (Bearhop et al., 2000) and semi-domestic reindeer blood (*Rangifer tarandus tarandus*, Nieminen & Timisjärvi, 1983). Although, we did not have lipid percentage values for our caribou blood, we assume that bulk isotope signatures integrated signatures mainly from blood proteins (Bearhop et al., 2000) and that the low lipid content has not affected our $\delta^{13}C_{bulk}$ values. Based on this, lipid extraction of red blood cells and plasma samples does not appear to be a necessary step in the case of caribou.

We showed that lipid extraction influences $\delta^{13}C$ values measured in caribou hair. This is an important development in research focusing on isotopic analyses as no other study, to our knowledge, has verified the importance of accounting for the variation in lipid content when measuring $\delta^{13}C$ values in mammal hair. Internal lipids are not routinely extracted in mammal hair in the literature (but see Hilderbrand et al., 1996 who have extracted lipids in bear hair). Hair is recognized as a lipid-poor tissue (Dunnett, 2005; Dunnett & Lees, 2003; Tieszen & Boutton, 1989), and the effect of lipid extraction on $\delta^{13}C$ values is recognized to be small compared to lipid-rich tissues (e.g., muscle, liver) (Kelly, 2000). Although we still have not calculated the proportion of lipid values for our caribou hair per se, forgoing lipid extraction in our hair samples was sufficient to significantly increase $\delta^{13}C$ values.

Extracting lipids has significantly increased $\delta^{15}N$ values in caribou hair and plasma. However, the differences (0.11 and 0.18‰) were found to be below the commonly used systematic error of 0.25‰ and below the mean absolute error of ± 0.18‰ also estimated in our tissues- and caribou-specific linear model correction. We found no strong effect of lipid extraction on $\delta^{15}N$ values measured in red blood cells, plasma

and caribou hair tissues, which is supported by other studies conducted on other species. Indeed, Lesage et al. (2010) observed a small effect of lipid extraction on $\delta^{15}N$ values in cetacean skin. Ehrich et al. (2011) observed no significant changes in $\delta^{15}N$ values in bird and terrestrial mammal muscle but highlighted a positive enrichment in $\delta^{15}N$ values in bird eggs. The enrichment in $\delta^{15}N$ values is probably due to leaching of isotopically light nitrogenous cell compounds during chloroform-methanol rinsing (Bearhop et al., 2000; Søreide et al., 2006). These different results support the need to further investigate the specific mechanism of $\delta^{15}N$ alteration, in addition to testing the effects of lipid extraction protocols on $\delta^{15}N$ values for tissues and species of interest before conducting stable isotope analysis.

Some studies claimed that it is not important to account for lipids in isotopic analyses when the CN ratio is < 4.0 (i.e., lipid content around 10%) in terrestrial systems (Ehrich et al., 2011; Post et al., 2007). However, our results suggest that this recommendation is problematic. Indeed, we showed that despite low CN ratios (3.93 to 4.30), carbon and lipid contents are a potential source of bias for $\delta^{13}C$. Similar results were found for tissues of aquatic vertebrates (e.g., green turtle (*Chelonia mydas*) muscle, Bergamo et al., 2016; beluga (*Delphinapterus leucas*) muscle and liver, Choy et al., 2016). Here we showed that lipid extraction significantly influenced $\delta^{13}C$, $\delta^{15}N$ and CN values in the three tissues for caribou, supporting the necessity to correct for lipid content in tissues from terrestrial mammal species.

1.6.2 CN ratio as a model parameter

McConnaughey and McRoy (1979) suggested to use the CN ratio as a proxy of lipid content (in percentage) and observed a greater depletion in $\delta^{13}C$ associated with high lipid contents. In contrast, we observed no significant relationship between $\Delta\delta^{13}C$ and CN ratio in the three caribou tissues we analysed and no significant relationship

between $\delta^{13}C$ and CN ratio in both blood components. However, a weak relationship between $\delta^{13}C$ and CN ratio were observed in hair. High CN ratios were not associated with a greater depletion in $\delta^{13}C$ in our caribou hair samples. Post et al. (2007) also found a weak link between $\Delta\delta^{13}C$ and CN ratio in muscle of terrestrial animals and suggested to estimate empirically the derived relationship between $\Delta\delta^{13}C$ and CN when working with a new tissue and species. The strength of this relationship varies among species (Lesage et al., 2010; Post et al., 2007), so using the CN ratio as a proxy of lipid content in all taxa and tissue remains questionable (Kiljunen et al., 2006). Moreover, some authors did not recommend using CN ratios for lipid normalization of $\delta^{13}C$ values (e.g. Fagan et al., 2011 in fish muscles; Kiljunen et al., 2006 in aquatic invertebrates). Therefore, caution is required when applying lipid normalization models that use CN ratio as a model parameter for calculating $\delta^{13}C_{lipid\text{-}free}$ values. We recommend using lipid normalization based on $\delta^{13}C_{bulk}$ in relation to $\delta^{13}C_{lipid\text{-}free}$ when dealing with caribou hair, similar to results found by Lesage et al. (2010) for cetacean skin and by Choy et al. (2016) for beluga muscle and liver.

1.6.3 Lipid normalization models

Our results suggest that a model specific to the chemical extraction method, the tissue analysed and the species of interest usually fits the data better than generalized lipid normalization equations, a recommendation supported by Logan et al. (2008) and Lesage et al. (2010). Our tissue- and caribou-specific models were the most accurate of the five models tested in our study, as no significant difference was found between the predicted and the observed lipid-extracted $\delta^{13}C$ values. These tissue- and caribou-specific models also had a better predictive power based on cross-validation procedures. The four lipid normalization equations published in the literature performed relatively well for caribou hair, with a lower mean absolute error and a

strong fit to the data but did not predict $\delta^{13}C_{lipid\text{-}free}$ values of caribou hair accurately. Lipid normalization appears to be a good method to deal with lipids in stable isotope analyses and to apply to a variety of organisms (Lesage et al., 2010; Post et al., 2007). However, based on our results, we recommend using a tissue-, method- and species-specific model with fewer assumptions and parameters. If the former is not possible, we recommend validating general equations and parameters published in the literature before using them.

1.7 Conclusion

Choosing between conducting lipid-normalization of $\delta^{13}C$ values or extracting lipids using common laboratory techniques depends on research objectives, the level of precision required and the potential consequences of lipid-caused shifts in $\delta^{13}C$ values on the conclusions of a study. Based on our results, we consider that lipid extraction should be performed when maximum precision is needed to calculate diet composition using mixing models and niche isotopic overlap. As a next step, we recommend testing the effects of lipid extraction on $\delta^{13}C$, $\delta^{15}N$ and CN ratios for tissues and species of interest before conducting stable isotope analysis. We also support the need for further investigation regarding the effects of lipids effect on $\delta^{13}C$ values in mammal hair.

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1.9 Supplementary material

Models were fitted by least-squares procedure using nls function in R to estimate parameters. To evaluate model performance, we determined the precision of the predicted values with the proportion of predicted $\delta^{13}C_{lipid\text{-}free}$ values that where within 0.25% (systematic error) of the observed $\delta^{13}C_{lipid\text{-}free}$ values ($P_{0.25}$), the mean square error (MSE) and the mean absolute error (MAE) using repeated k-fold cross validation (James et al., 2013).

Table S1.1. Parameter estimates (95% CI) of Post, MM and Fry equations for lipid normalization of $\delta^{13}C$ values of the caribou hair. Our equation parameters are given for comparison.

Models	Equations	Parameters (95% CI)	MSE	MAE	$P_{0.25}$ (%)
eqn 8 (Our equation)	$\delta^{13}C_{lipid-free} = \beta_1 \times \delta^{13}C_{bulk} + \beta_0$	β_0 = -0.0277 (-1.178 ; 1.123) β_1 = 0.982 (0.934 ; 1.0301)	0.13	0.11	93
eqn 5 (Post et al., 2007)	$\Delta\delta^{13}C = \beta_1 \times CN + \beta_0$	β_0 = -1.0528 (-3.855 ; 1.750) β_1 = 0.370 (-0.344 ; 1.0829)	0.13	0.11	91
eqn 4 (MM, 1979)	$\delta^{13}C_{lipid-free} = \delta^{13}C_{bulk} + D \times \left(I + \frac{3.90}{1 + \frac{287}{L}} \right)$	D = 1.837 (-1.773 ; 5.448) I = 0.0246 (-0.392 ; 0.441)	0.13	0.11	91
eqn 6 (Fry, 2002)	$\delta^{13}C_{lipid-free} = \delta^{13}C_{bulk} + D - \frac{D \times CN_{protein}}{CN}$	D = 6.601 (5.818 ; 7.385)	0.14	0.12	89

CHAPITRE II

DE L'ALIMENTATION AUX POILS ET AU SANG : ESTIMATION EMPIRIQUE DES FACTEURS D'ENRICHISSEMENT TROPHIQUE POUR LES ISOTOPES STABLES DU CARBONE ET DE L'AZOTE CHEZ CINQ MAMMIFÈRES TERRESTRES

FROM DIET TO HAIR AND BLOOD: EMPIRICAL ESTIMATION OF DISCRIMINATION FACTORS FOR C AND N STABLE ISOTOPES IN FIVE TERRESTRIAL MAMMALS

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2.1 Résumé

L'estimation des relations trophiques et du régime alimentaire des consommateurs à partir des isotopes stables requiert l'utilisation de facteurs d'enrichissement trophique qui représentent la différence de rapport isotopique entre le tissu du consommateur et son régime alimentaire. Ces facteurs d'enrichissement trophique sont d'ailleurs un

prérequis des modèles mixtes isotopiques Bayésiens et permettent de diminuer l'incertitude associée aux estimations de la composition du régime alimentaire. Cependant, les facteurs d'enrichissement trophique manquent encore pour de nombreuses espèces et tissus puisque peu d'études contrôlées ont été réalisées sur des animaux nourris en captivité avec un régime alimentaire connu. Le but de cette étude était donc d'estimer les facteurs d'enrichissement trophique du carbone ($\Delta^{13}C$) et de l'azote ($\Delta^{15}N$) dans les poils de caribous (*Rangifer tarandus caribou*), d'orignaux (*Alces americanus*), de cerfs de Virginie (*Odocoileus virginianus*), de coyotes (*Canis latrans*) et d'ours noirs (*Ursus americanus*) ainsi que dans le sang de caribous et de coyotes. J'ai mesuré les signatures isotopiques de ces tissus pour 21 animaux adultes gardés en captivité ainsi que pour diverses sources alimentaires. Les valeurs de $\Delta^{13}C$ dans les poils variaient de 0,96‰ à 3,72‰ pour les cervidés, 3,01‰ à 3,76‰ pour le coyote et 5,15‰ à 6,35‰ pour l'ours noir tandis que les valeurs de $\Delta^{15}N$ variaient de 2,58‰ à 5,95‰ pour les cervidés, 2,90‰ à 3,13‰ pour le coyote et 4,48‰ à 5,44‰ pour l'ours noir. Les valeurs de $\Delta^{13}C$ dans les cellules sanguines du coyote variaient de 2,20‰ à 2,69‰ tandis que les $\Delta^{15}N$ variaient de 3,30‰ à 4,41‰. Dans le sérum de caribous, le $\Delta^{13}C$ a atteint 3,34 ± 1,28‰ tandis que le $\Delta^{15}N$ a atteint 5,02 ± 0,07‰. Les facteurs d'enrichissement trophique calculés dans cette étude permettront d'évaluer la composition du régime alimentaire et les relations trophiques entre ces cinq espèces de mammifères terrestres et auront des implications importantes pour l'étude des populations de caribous menacées pour lesquelles l'utilisation de l'échantillonnage non invasif des tissus s'avère incontournable.

2.2 Abstract

Carbon and nitrogen stable isotope ratios are used widely to describe wildlife animal diet composition and trophic interactions. To reconstruct consumer diet, the isotopic

differences between consumers and their diet items – called the trophic discrimination factor (TDF) – must be known. Proxies of diet composition are sensitive to the accuracy of TDFs. However, specific TDFs are still missing for many species and tissues because only a few controlled studies have been carried out on captive animals. The aim of this study was to estimate TDFs for hair and blood for carbon and nitrogen stable isotopes for caribou (*Rangifer tarandus caribou*), moose (*Alces americanus*), white-tailed deer (*Odocoileus virginianus*), eastern coyote (*Canis latrans*), and black bear (*Ursus americanus*). We obtained stable isotope ratios for diet items, hair, and blood samples, of 21 captive adult mammals. Diet-tissue discrimination factors for carbon in hair ($\Delta^{13}C_{LE}$) ranged from 0.96‰ to 3.72‰ for cervids, 3.01‰ to 3.76‰ for coyote, and 5.15‰ to 6.35‰ for black bear, while nitrogen discrimination factors ($\Delta^{15}N$) ranged from 2.58‰ to 5.95‰ for cervids, 2.90‰ to 3.13‰ for coyote, and 4.48‰ to 5.44‰ for black bear. The $\Delta^{13}C_{LE}$ values in coyote blood components ranged from 2.20‰ to 2.69‰ while $\Delta^{15}N$ ranged from 3.30‰ to 4.41‰. In caribou serum, $\Delta^{13}C_{LE}$ reached 3.34 ± 1.28‰ while $\Delta^{15}N$ reached 5.02 ± 0.07‰. The TDFs calculated in this study will allow the evaluation of diet composition and trophic relationships between these five mammal species and will have important implications for the study of endangered caribou populations for which the use of non-invasive tissue sampling is highly relevant.

Keywords: blood, diet, fractionation, hair, stable isotope, TDF, terrestrial mammals, $\delta^{13}C$, $\delta^{15}N$

2.3 Introduction

Understanding the foraging ecology and the diet composition of wild species is important to implement good management and conservation plans (Chapron et al., 2008; Palomares et al., 2011; Parker et al., 2009). As such, there is a growing interest

in the development of indirect techniques to document the diet of free-ranging animals, because direct observation of feeding behaviors often is difficult (Denryter et al., 2017) and sometimes impracticable (Litvaitis, 2000; Monteiro et al., 2015; Thompson et al., 2015). Indirect methods, such as the analysis of prey remains in scats and stomach contents, have been used largely to assess the diet composition of wild species (Hodder et al., 2013; Lesmerises et al., 2015; Newmaster et al., 2013; Steenweg et al., 2015). However, the technique may be invasive if it requires killing the animal, or complicated depending on the level of access to fresh carcasses or feces. In addition, indirect diet reconstruction can be biased toward hard indigestible parts, and reflects only a snapshot of a consumer's diet (Deb, 1997; Hewitt & Robbins, 1996; McInnis et al., 1983; Newmaster et al., 2013; Tollit et al., 2003). To overcome these limitations, biogeochemical markers such as stable isotopes have become a key tool to study the feeding ecology of wild species (Ben-David & Flaherty, 2012; Kelly, 2000; Newsome et al., 2007; Peterson & Fry, 1987).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios provide information on the diet once it has been assimilated into body tissues. They reflect nutrient and energy assimilation from the diet at the time of tissue synthesis (Kelly, 2000; Post, 2002). Isotope analyses are based on the principle that stable isotope ratios in the tissues of consumers reflect the ratios of their diet (DeNiro & Epstein, 1978, 1981; Hobson et al., 1996). As a result, a relatively high (+ 3-4‰) and predictable enrichment in ^{15}N from one trophic level to the next makes nitrogen isotopes useful indicators of trophic position (Caut et al., 2009; DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Peterson & Fry, 1987; Post, 2002). The lower enrichment in ^{13}C (typically ~ 1‰) makes carbon isotopes particularly suitable for delineating carbon sources (Caut et al., 2009; DeNiro & Epstein, 1978; Peterson & Fry, 1987). Thus, stable isotope signatures are useful proxies of diet composition (Ben-David et al., 1997; Caut et al.,

2009; Phillips et al., 2005) and can provide important insights on trophic relationships (Hobson & Welch, 1992; Newsome et al., 2007; Post, 2002).

The use of multiple types of tissues to study animal diet is of interest because diet information may be determined over several time scales, from a few days to the lifetime of an animal, depending on which tissue is analyzed (Hilderbrand et al., 1996; Hobson & Clark, 1992b; Tieszen et al., 1983). The turnover rate of isotopes, defined as a renewal process of stable isotopes in a given tissue, depends on the metabolic rate and the rate of incorporation of stable isotope atoms into a specific tissue (Lecomte et al., 2011; Zilversmit et al., 1943). For example, blood plasma has a faster renewal process than red blood cells. Blood plasma therefore reflects the diet assimilated over the previous days, whereas red blood cells provide dietary information from the previous months (Hilderbrand et al., 1996; Hobson & Clark, 1992b; Tieszen et al., 1983). Once synthesized, hair is an inactive biological tissue that reflects isotopic composition during its growing period (Hilderbrand et al., 1996; Schwertl et al., 2003). Hair also is a very stable medium and a good matrix for the analysis of stable isotope ratios (Beernaert et al., 2007; Dunnett, 2005; Dunnett & Lees, 2003; Pragst & Balikova, 2006). It may be sampled noninvasively, easily, and with minimal stress, and it can be stored in ambient temperature for a long time (Duffy et al., 2005; Pacyna et al., 2018). Hair sampling is particularly suitable to monitor diet composition using Bayesian stable isotope mixing models (hereafter referred to as SIMMs) when studying endangered or threatened species.

Bayesian SIMMs are a new tool to estimate the assimilated diet composition of a group of individuals (Parnell et al., 2013; Phillips et al., 2014). SIMMs use isotopic biotracer data to estimate the relative contributions of different food sources to an isotopic mixture of consumers (Parnell et al., 2013; Phillips, 2001; Phillips & Gregg, 2003; Phillips et al., 2014). To reconstruct a consumer’s diet, the isotopic values of its

tissue and of all its possible food sources as well as the trophic discrimination factors (hereafter referred to as TDFs) must be known. A TDF is the difference in the isotopic ratios between a consumer tissue and the consumer's diet, assuming that the consumer tissue is at equilibrium with the food (Ben-David & Flaherty, 2012; DeNiro & Epstein, 1978; Martínez del Rio et al., 2009).

Estimation of TDFs is a prerequisite to explore diet composition using SIMMs (Parnell et al., 2013; Phillips & Gregg, 2001; Phillips et al., 2014). An accurate estimation of TDFs is extremely important to diminish uncertainty in diet composition estimates (Bond & Diamond, 2011; Caut et al., 2009; Phillips et al., 2014). Some studies have demonstrated the importance of using appropriate TDFs: if inappropriate TDFs are used, stable isotope analyses could yield biased estimates of diet composition (Bond & Diamond, 2011; Derbridge et al., 2015). For example, they may overestimate or underestimate the relative contribution of a given food source to the consumer's diet. Due to the difficulty to quantify species- and tissue-specific TDFs, TDFs mainly are obtained from the literature and often are the product of average values calculated from large reviews rather than being experimentally derived (Caut et al., 2008, 2009; Kurle et al., 2014; Martínez del Rio et al., 2009). Moreover, TDFs often are assumed to be a constant, but they are not. TDFs may vary based on species (Hobson et al., 1996; Lesage et al., 2002), tissue (Caut et al., 2009; Kurle et al., 2014; Lesage et al., 2002; Wolf et al., 2009), nutritional status, body size (Vanderklift & Ponsard, 2003), diet composition (Caut et al., 2009; Sponheimer et al., 2003a), age, sex (Kurle et al., 2014; Lecomte et al., 2011; Tieszen et al., 1983), and the metabolic routing of proteins, lipids, and carbohydrates (Perga & Grey, 2010; Wolf et al., 2015). Little is known about how animals synthesize and metabolize proteins, lipids, and carbohydrates, and how these affect TDFs (Wolf et al., 2015). It generally is assumed that dietary carbohydrates consumed by animals are used primarily for energy metabolism, while proteins are used for building tissues, and

lipids are used for building adipose tissues or energy metabolism (Tieszen & Fagre, 1993). However, species- and tissue-specific TDFs are still missing for many species because only a few controlled studies have been carried out on captive animals. It therefore is important to conduct experimental studies under controlled conditions to measure species- and tissue-specific TDFs to obtain unbiased and precise estimates of diet composition and to understand how various factors affect TDFs.

In boreal forest and tundra ecosystems, only a few studies have determined isotopic fractionation values for carbon and nitrogen stable isotopes in herbivore and carnivore hair and blood (but see Darr & Hewitt, 2006; Halley et al., 2010; McLaren et al., 2015). Yet these ecosystems are essential to the survival of many species. Boreal forests are subject to important anthropogenic activities, especially logging, while tundra ecosystems are subject to climate change, which largely modify the habitat of wild species (Johnson et al., 2015; Vors & Boyce, 2009). Consequently, the objective of this study was to estimate TDFs for hair and blood for carbon and nitrogen stable isotopes of five terrestrial mammals common in North America: woodland caribou (*Rangifer tarandus caribou*), moose (*Alces americanus*), white-tailed deer (*Odocoileus virginianus*), eastern coyote (*Canis latrans*), and black bear (*Ursus americanus*). Estimating the isotopic TDFs for these five terrestrial mammals fed with a known diet will provide important baseline information for interpreting their diet and foraging ecology. This is particularly relevant considering the worldwide decline of *Rangifer*, which often is caused by an exacerbated predation pressure from bears and canids, and is supported by increased abundance of cervids that is triggered by anthropogenic activities (Festa-Bianchet et al., 2011; Johnson et al., 2015; Vors and Boyce, 2009).

2.4 Materials and methods

2.4.1 Sample collection and preparation

We described in detail the diets of 21 captive adult animals from March to November 2017 and from June to November 2018 at the Zoo sauvage de St-Félicien (four coyotes, nine caribou, two moose, and one black bear) and the Bioparc de la Gaspésie (one coyote, one caribou, one white-tailed deer, one moose, and three black bears). Animals had access to food and water *ad libitum*. The bulk diet given to animals during the study was specific to each species and followed veterinarian standards (see section 2.8 Supplementary material, Table S2.1). The bulk diet included a commercial ration and some additional food items (Table 2.1-2.2) that were consumed by animals. All animals were kept on the same bulk diet for the duration of the study and were considered at equilibrium with the food (DeNiro & Epstein, 1978; Lecomte et al., 2011). Zookeepers monitored the diet items given and consumed by animals on a weekly basis. The contribution of different food items to the bulk diet of caribou, moose, deer, coyotes, and black bears, is presented in Tables 2.1 (for the St-Félicien facility) and 2.2 (for the Bioparc facility) and represented the proportion of each diet item consumed and ingested by the animal. Unfortunately, it was not possible to estimate the proportion of the diet that was assimilated by each animal because of the design of our study. We collected a sample of each diet item consumed by the studied animals; we acquired these items during the previous months. We dried and stored plant samples in Whirl-Pak bags at ambient temperature until they were processed. We froze meat and fish samples at -20°C until subsequent analyses. We freeze-dried plant, meat, and fish samples for 48h and ground them to a fine powder with a CryoMill (Bosley & Wainright, 1999; Jardine et al., 2003).

Table 2.1. Proportion of different food items in the summer diet of animals at the Zoo sauvage de St-Félicien.

	Feed mix [1]	Horse meat	Poplar twigs/buds	Hay	Twigs/foliage	Plants	Fruits	Others [2]	Total mass (kg) [3]
Caribou	0.38			0.52	0.05	0.05			4.30-4.80
Moose	0.41		0.49			0.05	0.05		6.01-8.20
Coyote	0.38	0.57						0.05	0.30
Black bear	0.70					0.10	0.15	0.05	2.10-3.20

Table 2.2. Proportion of different food items in the summer diet of animals at the Bioparc de la Gaspésie.

	Feed mix [4]	Horse meat	Fish	Foliage/grass	Hay	Fruits	Vegetables	Total mass (kg)
Caribou	0.80			0.20				3.77
Moose	0.75			0.25				12.19
White-tailed deer	0.70			0.10	0.10	0.05	0.05	3.87
Coyote	0.85	0.10	0.05					0.45
Black bear	0.60		0.15			0.25		1.10-3.10

[1] Purina (Neenah, Wisconsin) 16% Deer and Elk Bir Nutrition feed mix for caribou and deer, Mazuri (St. Louis, Missouri) Moose Breeder feed mix for moose, and Moulée Tradition Agri-chien (Longeuil, Saint Hubert, Quebec, Canada) feed mix for coyote and black bear.

[2] Small mammals and deer carcass for coyotes and deer for black bears.

[3] Total mass not included plants, fruits and other items due to unavailable information on mass.

[4] Jones Feed Mills (Mitchell, Ontario) CAZA Browser Pellets feed mix for caribou and deer, Mazuri (St. Louis, Missouri) Moose Breeder Diet feed mix for moose, La Moulée Nutri-Bouffe (Île-aux-Noix, Québec) Top Champion feed mix for coyote, and Best Choice feed mix for black bear.

We collected hair samples from the rump of eight caribou, three moose, one deer, three coyotes, and four black bears, in summer at both facilities after the spring molt (June to August). Molt occurs generally at the end of the cold season (April to June), and the new fur grows in from late spring/early summer (June) to autumn (M.-J. Bernard, zookeeper, Bioparc de la Gaspésie; C. Gagnon and S. Grenier-Laroche, zookeepers, Zoo sauvage de St-Félicien, pers. comm.; also see Ling, 1970; Mowat et al., 2017). Hairs were not fully grown, but we assumed that the stable isotope signatures would represent the summer diet because stable isotopes are integrated during the period of hair growth (Hilderbrand et al., 1996; Schwertl et al., 2003). We collected blood samples from two coyotes with sodium heparin tubes in summer and from two other coyotes and two caribou with BD vacutainer red tubes in spring and autumn. It is assumed that stable isotope analyses conducted on plasma and serum likely will represent the diet consumed over the previous week while stable isotope analyses run on red blood cells will represent the diet consumed over the previous 2-3 months (Hilderbrand et al., 1996; Hobson & Clark, 1992b; Tieszen et al., 1983). Unfortunately, we could not acquire more blood samples (i.e., from more individuals) due to the ethical guidelines followed in these facilities. Whole blood was kept on ice and centrifuged shortly after its collection to divide serum, plasma, and red blood cells. These blood components were then frozen at -20°C until they were processed in the next analytical steps. Similarly, we dried and stored hair samples in paper bags at ambient temperature until they were processed. We washed hair samples using a solution of 2:1 chloroform-methanol in an ultrasonic bath to remove all possible surface contamination and external lipids (Hobson et al., 2000), rinsed them in distilled water and oven-dried them at 50°C for 24 h (Hobson et al., 2000). We cut hair samples in small pieces (about 1 mm) with stainless scissors and cleaned the scissors with ethanol 70% after cutting each sample. We freeze-dried blood samples for 48 h and ground them to a fine powder (Bosley & Wainright, 1999; Jardine et al., 2003).

Variability in the lipid content of samples has the potential to bias the stable isotope signatures measured in tissues because lipids are more depleted in ^{13}C compared to protein and carbohydrate fractions (DeNiro & Epstein, 1977; McConnaughey & McRoy, 1979). It is recommended to chemically remove lipids from tissues before analyzing for the stable isotope of carbon. However, chemical lipid extraction also may affect the nonlipid fractions and bias nitrogen stable isotope signatures (Bodin et al., 2007; Ehrich et al., 2011; Lesage et al., 2010; Ricca et al., 2007; Sotiropoulos et al., 2004). Some authors have recommended conducting lipid extraction on separate aliquots of samples to determine $\delta^{13}C_{LE}$ (lipid extracted) and $\delta^{15}N$ (nonextracted) values because of the often-observed variability following lipid extraction on $\delta^{15}N$ signatures (Lesage et al., 2010; Rioux et al., 2019; Sweeting et al., 2006). For blood samples, we divided samples into two parts to determine $\delta^{13}C_{LE}$ and $\delta^{15}N$ values separately to account for the lipid effect on stable isotope signatures. One part of the subsamples received no further treatment prior to nitrogen isotope analyses (nonextracted part), and the second part was lipid-extracted prior to carbon isotope analyses (Kelly, 2000; Lesage et al., 2010; Post et al., 2007). We conducted lipid extraction using the second part of the powdered blood samples (to remove internal lipids, Dunnett, 2005; Dunnett & Lees, 2003) and a solvent consisting of a mixture of chloroform and methanol (2:1 v/v, Folch et al., 1957). We shook the mixture and stored it overnight at 4°C. We centrifuged the mixture at 11,200 x g for 10 min and discarded the supernatant (Folch et al., 1957). We repeated the whole procedure two more times. Following these three extractions, samples were dried overnight by evaporation, rinsed with distilled water, oven-dried overnight at 50°C, and powdered again. We did not chemically extract lipids from hair samples in this study due to methodological constraints. However, we used caribou normalization models to correct the $\delta^{13}C$ values of animal hair for lipid content ($\delta^{13}C_{LE}$) using equation #8 developed by Rioux et al. (2019) for this specific caribou population.

2.4.2 Stable isotopic analyses

We weighed a subsample of 1-1.2 mg (± 0.001 mg) of hair and powdered blood tissues and 3-3.2 mg (± 0.001 mg) of powdered plants into a tin capsule and analyzed it for stable carbon and nitrogen isotope ratios using an Elemental Analyzer coupled to a Delta Plus Continuous Flow-Isotope Ratio Mass Spectrometry (Stable Isotope in Nature Laboratory, SINLAB, University of New Brunswick). By convention, ^{13}C and ^{15}N isotope abundances are expressed in delta notation (‰), as $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$, where X is ^{13}C or ^{15}N, and R_{sample} is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$; $R_{standard}$ represents the ratios for the respective standards, i.e., Vienna Peedee Belemnite (PDB) and atmospheric nitrogen (AIR). We evaluated the accuracy of our isotopic analyses using commercially certified materials (acetanilide for plant sample analyses and nicotinamide for animal sample analyses) and evaluated the precision of measurement by randomly duplicating a subset of our samples. Replicates using certified materials (n = 18) indicated a systematic error of ± 0.08‰ for $\delta^{13}C$ and ± 0.10‰ for $\delta^{15}N$, whereas the average deviations observed between replicates of hair, blood and plant samples (n = 8) indicated an analytical error of 0.25‰ for $\delta^{13}C$ and 0.08‰ for $\delta^{15}N$.

2.4.3 Statistical analyses

To account for the differential contribution of each diet item in the bulk diet of a consumer, we calculated the weighted proportion of each diet item (p_{item}) as the mass of each item to the total mass of all food items consumed by each animal (Kurle, 2002; Parng et al., 2014). We used this weighted proportion (p_{item}) and the $\delta^{13}C$ or $\delta^{15}N$ values of each diet item to calculate the mean total diet ratio using the following equation:

$$\delta X_{\text{mean total diet}} = [(p_{\text{item 1}} * \delta X_{\text{item 1}}) + (p_{\text{item 2}} * \delta X_{\text{item 2}}) + ...]$$

where p_{item} is the contribution of a specific diet item to the total diet (see section 2.8 Supplementary material, Table S2.2) and δX_{item} is the $\delta^{13}C$ or $\delta^{15}N$ values of that particular diet item. We determined the TDFs ($\Delta^{13}C$, $\Delta^{13}C_{LE}$, and $\Delta^{15}N$) as the difference in $\delta^{13}C$, $\delta^{13}C_{LE}$, or $\delta^{15}N$ values between the isotopic ratio of each species and tissue and the mean total diet ratio (TDF = $\delta X_{\text{animal}} - \delta X_{\text{mean total diet}}$, Kurle, 2002; Martínez del Rio et al., 2009; Parng et al., 2014). Unfortunately, we were not able to explore variations in isotopic discrimination factors among sexes, ages, tissues, or diet types, as recommended by Lecomte et al. (2011), due to small sample sizes (n = 21) and sampling constraints from both facilities. Indeed, it was more difficult than expected to collect hair samples because animals were kept in a large enclosure, and they were not used to being handled. In addition, the weekly monitoring of animals and their diet added up to a higher workload for zookeepers. We were not able to run statistical analyses on the discrimination factors in blood samples due to small sample sizes (n = 8). Nevertheless, we provided coefficients of variation to quantify the dispersion around the mean as well as the degree of variation among samples, as suggested by Conquest (1983). We used analysis of variance (ANOVA) models to evaluate species variability of TDFs in hair. We assessed the normality of residuals using normal quantile-quantile plots and assessed heteroscedasticity with a plot of standardized residuals against fitted values (Quinn & Keough, 2002). Statistically significant differences among ANOVA levels were explored for significant pairwise comparisons using post hoc Tukey multiple comparison of means test, using an α significance threshold of 0.05. We performed all statistical analyses using R software version 3.4.2 (R Development Core Team, 2017).

2.5 Results

Feed mixes were the principal item consumed by the captive animals we studied except for coyotes and caribou at the Zoo sauvage de St-Félicien, where coyotes mainly ate horse meat and caribou fed on hay (Table 2.1-2.2). The mean bulk diet ratio of coyotes and black bears had the highest $\delta^{13}C_{diet}$ and $\delta^{15}N_{diet}$ values at the Zoo sauvage de St-Félicien and at the Bioparc de la Gaspésie (Figure 2.1-2.2). In contrast, the mean bulk diet ratio of caribou, moose, and deer, had the lowest $\delta^{13}C_{diet}$ and $\delta^{15}N_{diet}$ values at both facilities (Figure 2.1-2.2).

Coyote and black bear hair samples were enriched in ^{13}C and in ^{15}N compared to cervid hair (Figure 2.1; Table 2.3). The $\delta^{13}C_{LE}$ for caribou serum had higher variability (± *SD*) among the individuals sampled than the $\delta^{15}N$ values (Figure 2.2; Table 2.4). Coyotes were enriched in ^{13}C and in ^{15}N compared to caribou for all blood components. We observed little variations in $\delta^{13}C_{LE}$ and $\delta^{15}N$ values between the two coyotes sampled in this study (Figure 2.2).

All animals were enriched in ^{13}C and ^{15}N relative to their diet (Figure 2.1-2.2). Trophic fractionation factors of both C and N isotopes appeared to differ between hair and blood components. Trophic enrichment was lower in ^{13}C and higher in ^{15}N in blood components compared to hair for caribou and coyotes (Tables 2.3-2.4). The $\Delta^{13}C_{LE}$ in hair differed statistically among species (ANOVA, $F_{3,14} = 30.40$, $P < 0.001$), except for caribou and coyote (Tukey, $t_{14} = -0.88$, $P = 0.82$). $\Delta^{13}C_{LE}$ were higher in black bear hair and lower in moose hair (Table 2.3; Figure 2.3). However, $\Delta^{15}N$ marginally differed between black bear and coyote hair (Tukey, $t_{14} = 2.89$, $P = 0.052$) and $\Delta^{15}N$ were higher in black bear than coyote hair.

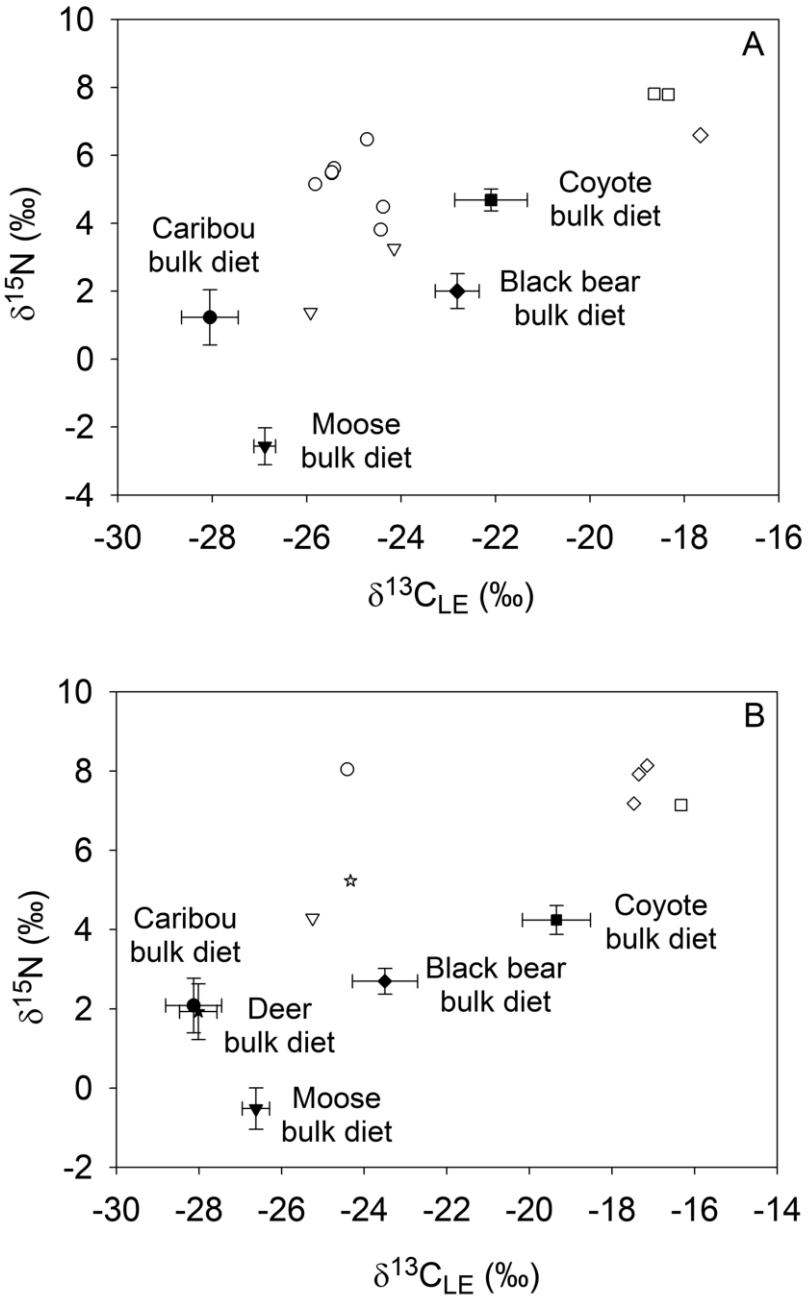

Figure 2.1. Stable isotope signatures of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) of the bulk diets (mean ± *SD*) and raw data for the consumers (○ caribou, ∇ moose, □ coyote, ◊ black bear, ☆ white-tailed deer) of hair in the St-Félicien (A) and Bioparc facilities (B).

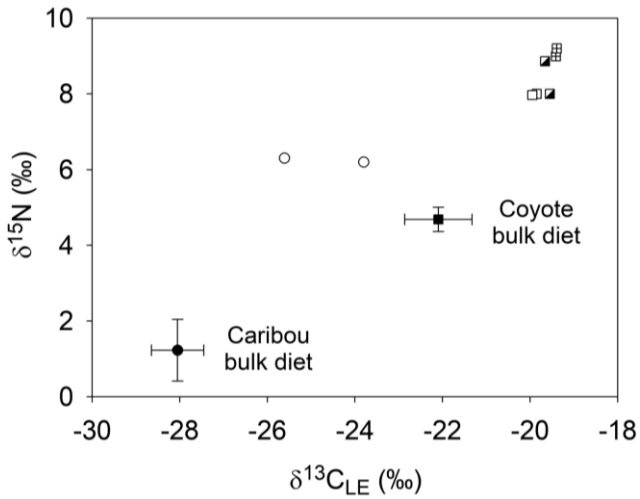

Figure 2.2. Stable isotope signatures of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) of the bulk diets (mean ± *SD*) and raw data for the consumers (○ caribou serum, □ coyote red blood cells, ⊞ coyote plasma, ◪ coyote serum) of blood components in the St-Félicien facility.

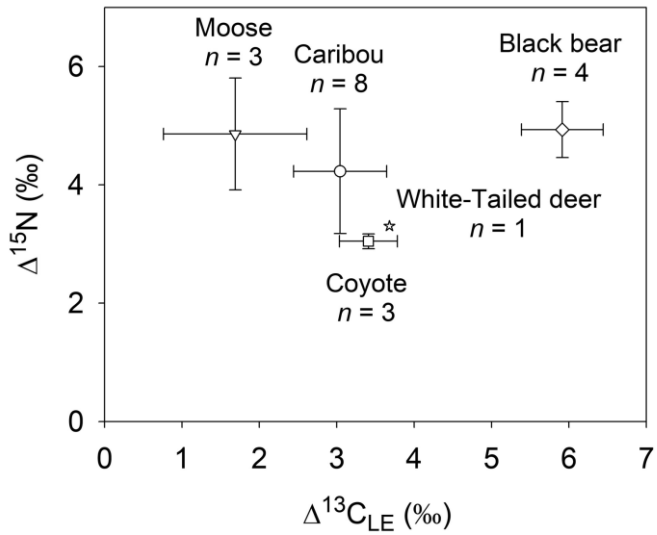

Figure 2.3. Mean (± *SD*) stable nitrogen ($\Delta^{15}N$) and carbon ($\Delta^{13}C_{LE}$) isotope discrimination factors of hair from five captive terrestrial mammals.

Table 2.3. Sex, CN ratio, $\delta^{13}C$, $\delta^{13}C_{LE}$ and $\delta^{15}N$ values of hair for the animals monitored during the experiment at the Zoo sauvage de St-Félicien and the Bioparc de la Gaspésie, mean total diet ratios ($\delta^{13}C_{diet}$ and $\delta^{15}N_{diet}$) for each species and discrimination factors ($\Delta^{13}C$, $\Delta^{13}C_{LE}$ and $\Delta^{15}N$). Means ± *SD* (in bold) are presented for species group for stable isotope values and discrimination factors.

Species	Facility	Individual	Sex	CN	$\delta^{13}C$ (‰)	$\delta^{13}C_{LE}$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C_{diet}$ (‰)	$\delta^{15}N_{diet}$ (‰)	$\Delta^{13}C$ (‰)	$\Delta^{13}C_{LE}$ (‰)	$\Delta^{15}N$ (‰)
Caribou	St-Félicien	1	F	3.21	−25.86	−25.42	5.62	−28.05 ± 0.60	1.23 ± 0.81	2.19	2.63	4.39
	St-Félicien	2	F	3.06	−25.15	−24.72	6.47			2.90	3.33	5.24
	St-Félicien	3	F	3.03	−25.91	−25.47	5.47			2.14	2.58	4.24
	St-Félicien	4		3.21	−24.85	−24.43	3.81			3.20	3.62	2.58
	St-Félicien	5		3.18	−25.91	−25.47	5.50			2.14	2.58	4.27
	St-Félicien	6	M	3.14	−24.80	−24.38	4.48			3.25	3.67	3.25
	St-Félicien	7	F	3.03	−26.27	−25.82	5.15			1.78	2.23	3.92
	Bioparc	8	F	3.11	−24.83	−24.41	8.04	−28.13 ± 0.68	2.08 ± 0.69	3.30	3.72	5.95
					−25.45 ± 0.60	**−25.02 ± 0.59**	**5.57 ± 1.27**			**2.61 ± 0.61**	**3.04 ± 0.60**	**4.23 ± 1.05**
Moose	St-Félicien	9	M	3.04	−24.57	−24.15	3.26	−26.89 ± 0.23	−2.57 ± 0.54	2.32	2.73	5.83
	St-Félicien	10	F	3.06	−26.37	−25.92	1.38			0.52	0.96	3.94
	Bioparc	11	M	3.11	−25.69	−25.25	4.29	−26.62 ± 0.33	−0.52 1 0.52	0.93	1.37	4.81
					−25.54 ± 0.91	**−25.11 ± 0.89**	**2.98 ± 1.48**			**1.26 ± 0.94**	**1.69 ± 0.93**	**4.86 ± 0.94**
Coyote	St-Félicien	12	F	2.77	−18.65	−18.34	7.79	−22.10 ± 0.77	4.68 ± 0.32	3.45	3.76	3.11
	St-Félicien	13		2.80	−18.95	−18.64	7.81			3.15	3.46	3.13
	Bioparc	14	M	2.92	−16.60	−16.33	7.14	−19.35 ± 0.82	4.24 ± 0.37	2.74	3.01	2.90
					−18.07 ± 1.28	**−17.77 ± 1.25**	**7.58 ± 0.38**			**3.11 ± 0.35**	**3.41 ± 0.37**	**3.05 ± 0.13**
Black bear	St-Félicien	15	F	2.87	−17.95	−17.66	6.59	−22.81 ± 0.46	2.00 ± 0.52	4.85	5.15	4.59
	Bioparc	16		2.92	−17.76	−17.47	7.18	−23.50 ± 0.79	2.70 ± 0.32	5.73	6.02	4.48
	Bioparc	16		2.90	−17.43	−17.15	8.14			6.06	6.35	5.44
	Bioparc	17	M	2.89	−17.64	−17.35	7.92			5.85	6.14	5.23
					−17.70 ± 0.22	**−17.41 ± 0.21**	**7.46 ± 0.71**			**5.62 ± 0.53**	**5.92 ± 0.53**	**4.94 ± 0.47**
White-tailed deer	Bioparc	18	M	2.93	−24.75	−24.33	5.23	−28.02 ± 0.45	1.93 ± 0.70	3.27	3.68	3.30
					−24.75	**−24.33**	**5.23**			**3.27**	**3.68**	**3.30**

Table 2.4. Sex, CN ratio, $\delta^{13}C_{LE}$ and $\delta^{15}N$ values of blood components for animals monitored during the experiment at the Zoo sauvage de St-Félicien, mean total diet ratios ($\delta^{13}C_{diet}$ and $\delta^{15}N_{diet}$) for each species, and discrimination factors ($\Delta^{13}C_{LE}$ and $\Delta^{15}N$). Means ± *SD* (in bold) are presented for species and tissues group for stable isotope values and discrimination factors.

Species	Tissue	Individual	Sex	CN	$\delta^{13}C_{LE}$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C_{diet}$ (‰)	$\delta^{15}N_{diet}$ (‰)	$\Delta^{13}C_{LE}$ (‰)	$\Delta^{15}N$ (‰)
Coyote	Red blood cells	13	F	3.35	−19.85	8.00	−22.10 ± 0.77	4.68 ± 0.32	2.25	3.32
		19	F	3.24	−19.95	7.97			2.14	3.28
					−19.90 ± 0.08	**7.99 ± 0.03**			**2.20 ± 0.08**	**3.30 ± 0.03**
	Plasma	13	F	3.53	−19.41	8.99			2.68	4.31
		19	F	3.22	−19.39	9.20			2.70	4.52
					−19.40 ± 0.01	**9.10 ± 0.15**			**2.69 ± 0.01**	**4.41 ± 0.15**
	Serum	13	F	3.44	−19.66	8.86			2.43	4.18
		19	F	3.39	−19.55	8.00			2.55	3.32
					−19.61 ± 0.08	**8.43 ± 0.61**			**2.49 ± 0.08**	**3.75 ± 0.61**
Caribou	Serum	20		3.32	−25.61	6.30	−28.05 ± 0.60	1.23 ± 0.81	2.43	5.07
		21	M	3.19	−23.80	6.20			4.25	4.97
					−24.71 ± 1.28	**6.25 ± 0.07**			**3.34 ± 1.28**	**5.02 ± 0.07**

Diet-tissue fractionation values for carbon and nitrogen in hair are shown in Table 2.3; they range from 0.96‰ to 6.35‰ for $\Delta^{13}C_{LE}$ and from 2.58‰ to 5.95‰ for $\Delta^{15}N$, with higher values for black bear. Specifically, the $\Delta^{13}C_{LE}$ values range from 2.23‰ to 3.72‰ in caribou hair, 0.96‰ to 2.73‰ in moose hair, 3.01‰ to 3.76‰ in coyote hair, and 5.15‰ to 6.35‰ in black bear hair. In the case of the $\Delta^{15}N$ values, they range from 2.58‰ to 5.95‰ in caribou hair, 3.94‰ to 5.83‰ in moose hair, 2.90‰ to 3.13‰ in coyote hair, and 4.48‰ to 5.44‰ in black bear hair. The $\Delta^{13}C_{LE}$ value is 3.68‰ and the value $\Delta^{15}N$ is 3.30‰ in deer hair. Finally, the $\Delta^{13}C_{LE}$ values range from 2.20‰ (coefficient of variation [*CV*] = 3.64%) to 2.69‰ (*CV* = 0.37%) while $\Delta^{15}N$ values range from 3.30‰ (*CV* = 0.91%) to 4.41‰ (*CV* = 3.40%) in coyote blood components (Figure 2.4). $\Delta^{13}C_{LE}$ and $\Delta^{15}N$ values in caribou serum are higher than in coyote blood components (Figure 2.4).

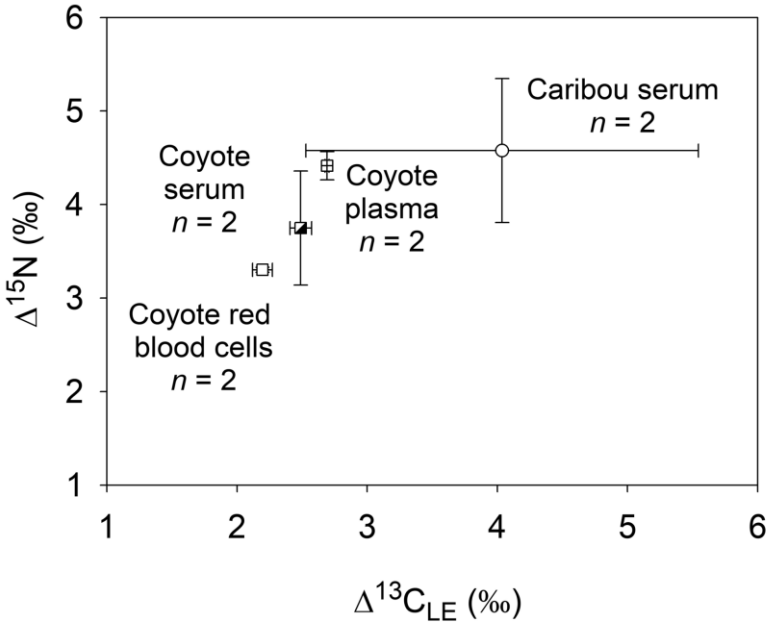

Figure 2.4. Mean (± *SD*) stable nitrogen ($\Delta^{15}N$) and carbon ($\Delta^{13}C_{LE}$) isotope discrimination factors of red blood cells, plasma and serum from two captive terrestrial mammals.

2.6 Discussion

Our study measured TDFs in caribou, moose, white-tailed deer, black bear, and eastern coyote, hair, and also in caribou and coyote blood components. Only a few studies have been conducted to estimate TDFs in wild herbivores (white-tailed deer blood components, hair and antlers, Darr & Hewitt, 2006; reindeer blood components, Barboza & Parker, 2006; Halley et al., 2010). Studies on terrestrial carnivore hair (e.g., felid species, Parng et al., 2014; gray wolves, *Canis lupus*, Derbridge et al., 2015; McLaren et al., 2015; tigers, *Panthera tigris*, and snow leopards, *Uncia uncia*, Montanari & Amato, 2015; large Arctic carnivores such as wolves, *Canis* spp., wolverines, *Gulo gulo*, grizzly, *Ursus arctos*, and polar bears, *Ursus maritimus*, L'Hérault et al., 2018) and on omnivores' blood components (black bear, Hilderbrand et al., 1996; grizzly bear, Felicetti et al., 2003) are however more common. According to the extensive literature reviews by Caut et al. (2009) and Vanderklift and Ponsard (2003), including both marine and terrestrial mammals, $\Delta^{13}C$ values ranged from -0.5‰ to 4.5‰, while $\Delta^{15}N$ values ranged from 1.4‰ to 6.4‰. The $\Delta^{13}C$ and $\Delta^{15}N$ values obtained in our study were qualitatively similar to values reported in these two reviews for other mammal species even though we observed a large variation among the five species studied and the two types of tissue analyzed. The large variation in TDFs reinforces the need to measure species- and tissue-specific TDFs and to understand how various factors affect TDFs. Indeed, a single TDF for a species or a tissue is unlikely, and we must capture variability in TDFs (± *SD*) within a species or a tissue.

2.6.1 Species variability of discrimination factors for hair

We observed a large variation in discrimination factors in hair among the five species studied, ranging from 1.69‰ to 5.92‰ for $\Delta^{13}C_{LE}$ and 3.05‰ to 4.94‰ for $\Delta^{15}N$. As

suggested by Vanderklift and Ponsard (2003), the differences in TDFs observed among species can be explained by the specific biochemical form of nitrogen excretion in the different taxonomic groups, but also by the different diet items consumed (Robbins et al., 2005). The lower nitrogen discrimination factors observed in coyote hair may be caused by the lower retention of ^{15}N during nitrogen discrimination with higher protein and lipid contents, and the lower CN ratios in fish and meat diet items (Robbins et al., 2005; Wolf et al., 2015). It also could be caused by the nitrogen availability and sources (Perga & Grey, 2010) and the different dietary amino acid profiles. Indeed, amino acid profiles are less variable in meat and fish than in plants (Robbins, 1993) and have a lower influence on the discrimination processes, thus explaining the lower variability in TDFs measured in coyote hair (Robbins et al., 2005). Herbivores had low $\delta^{13}C$ and $\delta^{15}N$ values in their tissues, low lipid and protein contents in their bulk diet, and thus lower N availability. Herbivores mainly synthesize their amino acids from the carbohydrate part of their diet, while carnivores do so from the protein and lipid components of their diet (Krueger & Sullivan, 1984; Roth & Hobson, 2000), which explains the greater isotopic fractionation of nitrogen (Perga & Grey, 2010), and the lower isotopic fractionation of carbon (Martínez del Rio et al., 2009; Wolf et al., 2015). Dietary macromolecules for metabolic demands and tissue synthesis probably affected the isotopic fractionation observed in this study (Wolf et al., 2015). Variations in the concentration of amino acids among dietary items probably influenced the consumer isotopic values we measured and variation in TDFs among species (Wolf et al., 2015).

The $\Delta^{13}C$ values obtained in black bear hair were higher (5.92 ± 0.53‰) than values reported in the literature for other mammal species (mean estimates for $\Delta^{13}C$ reached 0.75‰ ± 0.11 [*SE*], obtained from an extensive literature review by Caut et al., 2009). The $\Delta^{13}C$ and $\Delta^{15}N$ values measured in black bear hair were relatively similar to those measured by Parng et al. (2014) in felid hair (4.3-4.9 ± 0.5‰ for $\Delta^{13}C$ and 4.1-4.5

± 0.2‰ for $\Delta^{15}N$) and by McLaren et al. (2015) in gray wolf hair (4.25 ± 0.36‰ for $\Delta^{13}C$ and 3.09 ± 0.20‰ for $\Delta^{15}N$), while being higher than those measured by L'Hérault et al. (2018) in wolves, wolverines, grizzly, and polar bears (2.45 ± 0.52‰ for $\Delta^{13}C$ and 3.03 ± 0.22‰ for $\Delta^{15}N$) and by Roth and Hobson (2000) in red fox (*Vulpes vulpes*) hair (2.6‰ for $\Delta^{13}C$ and 3.3-3.5‰ for $\Delta^{15}N$). To our knowledge, no other study exists to allow us to compare our higher TDF values in hair for black bears to other values in the literature. A possible explanation for the higher $\Delta^{13}C$ values in black bear hair is the higher $\delta^{13}C$ values measured in their hair. The black bears and coyotes we sampled have probably synthesized their amino acids mainly from protein components of the ingested diet items (Krueger & Sullivan, 1984; Roth & Hobson, 2000), which, as previously mentioned, influence isotopic signatures measured in their hair and isotopic fractionation (Martínez del Rio et al., 2009; Wolf et al., 2015). These black bears and coyotes may therefore have higher $\delta^{13}C$ values than animals that ingest diet items with a higher protein content because proteins are generally enriched by about 6‰ over lipids (DeNiro & Epstein, 1977; Post et al., 2007; Roth & Hobson, 2000).

In the case of caribou, moose, and white-tailed deer hair, the $\Delta^{13}C_{LE}$ values we observed in this study were higher for all three species than those observed for white-tailed deer in Texas (Darr & Hewitt, 2006), which is, to our knowledge, the only study that was conducted on cervid hair. In contrast, the $\Delta^{15}N$ values we observed were slightly lower for the three cervid species. In our study, caribou, moose, and deer had a more diverse bulk diet, lowering the average diet signatures of carbon and nitrogen stable isotopes compared to the diet used for white-tailed deer in Darr and Hewitt (2006), which was composed of corn kernels and alfalfa. Moreover, cervids are known to have different digestive systems (grazers, browsers, and intermediate mixed feeders, with nutrient recycling system, Hofmann, 1989; Mathiesen et al., 1999) that may influence TDF values (Halley et al., 2010; Sponheimer et al. 2003a, 2003b).

Indeed, caribou have a specialized and complex digestive system that allows them to recycle ^{15}N in the urea (Barboza & Parker, 2008; Parker et al., 2005), resulting in higher $\delta^{15}N$ values than moose (Sponheimer et al., 2003b). These different $\delta^{15}N$ values between caribou and moose will influence their nitrogen TDF values (Robbins, 1993). As previously discussed by Wolf et al. (2015), the metabolic routing of macromolecules (i.e. proteins, lipids, and carbohydrates) within consumers may also explain the variation in TDFs observed between the three cervid species.

2.6.2 Individual variability of discrimination factors for hair

Although we had a relatively small sample size, we observed low individual variations in TDFs for coyote and black bear hair (less than 1‰ for both $\Delta^{13}C_{LE}$ and $\Delta^{15}N$). We interpret this as a consequence of a relatively homogenous diet mainly consisting of feed mix for black bears and feed mix and horse meat for coyotes. In order to enrich the environment for coyotes and black bears, deer carcasses were supplied a few times a year, but they were not considered an important source item in their diet (i.e., less than 5% of the different food items consumed in the summer by the animal; Table 2.1; see section 2.8 Supplementary material, Table S2.2). One limitation of our study, however, is that animals could not be maintained in experimental enclosures excluding any other food resources. As enclosures in those locations were designed to reflect the natural habitat of the captive animal, they could consume vegetation, fungi, or small mammals such as mice and squirrels that would enter the enclosure. Use of these resources is likely to differ between individuals. We were not able to quantify their contribution (because of monitoring and logistic constraints), but we consider that these sources probably only account for a small proportion of their diet (M.-J. Bernard, zookeeper, Bioparc de la Gaspésie; C. Gagnon and S. Grenier-Laroche, zookeepers, Zoo sauvage de St-Félicien, pers. comm.). Thus, some differences in discrimination factors observed among individuals from the same

species may be induced by these different diet items consumed occasionally (Parng et al., 2014). Individuals also may have different metabolic pathways or biochemical reactions, such as nitrogen excretion, which may explain some differences in TDFs among individuals (Peterson & Fry, 1987; Vanderklift & Ponsard, 2003).

In contrast with coyotes and black bears, we observed larger interindividual variation in TDFs for caribou and moose hair, ranging respectively from 1.49‰ to 1.77‰ for $\Delta^{13}C_{LE}$ and from 1.89‰ to 3.37‰ for $\Delta^{15}N$. Cervids were held on the same diet, mainly consisting of feed mix, hay, foliage, poplar twigs, and buds, for the duration of our study. We assumed that all individuals ate the same diet items in the same proportion because they stayed in the same habitat composed of the same attributes. However, we observed more variation in TDFs among individuals of the same cervid species, especially for the nitrogen TDF. Again, as for carnivores, cervids were not maintained in experimental enclosures that excluded any other vegetation and may have consumed different proportions of other source items, such as aquatic plants, forbs, deciduous foliages, and evergreen needles. Variability in cervid TDFs may be partially explained by the different consumption of dietary items (Parng et al., 2014), but also by the different amino acid, protein, lipid, or carbohydrate content in the diet items consumed by the individuals (Robbins et al., 2005) as well as by the metabolic routing of macromolecules (Wolf et al., 2015). Indeed, distribution of these constituents in plants may differ greatly (Ben-David et al., 1998; Kielland et al., 1998). When an individual consumed and assimilated different dietary items, it takes its energy from different components; this could introduce some variability in TDF values (Ben-David et al., 2001), as we noted in our study. Finally, the variability we observed in our study also could be related to different levels of N loss, which occurs through respiration or excretion via saliva, pancreatic secretion, urea N recycling (Ben-David et al., 2001), and via the different rumen microbial activity levels occurring before the fractionation process (Darr & Hewitt, 2006). Unfortunately, we

could not estimate the part of the individual variability that is associated with age (Kurle et al., 2014; Lecomte et al., 2011; Tieszen et al., 1983), reproductive status, and body size (Vanderklift & Ponsard, 2003), but we recognize that these variables may contribute to the variation observed in our study.

2.6.3 Discrimination factors for blood components

We observed a low variability of nitrogen discrimination factors in caribou serum. However, the variability of carbon discrimination factors was larger for caribou serum (3.34 ± 1.28‰ for $\Delta^{13}C_{LE}$). $\Delta^{13}C$ values in caribou serum were similar to the one reported for plasma in reindeer (3.5 ± 0.1‰, Halley et al., 2010), while they were higher than the value reported for serum in white-tailed deer (-0.36‰, Darr & Hewitt, 2006). $\Delta^{15}N$ values for caribou serum were similar to those observed for reindeer serum (5.55‰, Barboza & Parker, 2006) or plasma (4.2 ± 0.3‰, Halley et al., 2010), and also for white-tailed deer serum (5.89‰, Darr & Hewitt, 2006). The variations in $\Delta^{13}C$ and $\Delta^{15}N$ values observed between caribou tissue types differ from those of the reindeer studied by Halley et al. (2010) in Finland. This variation may be caused by the specific diet on which reindeer were fed, which consisted almost exclusively of commercial feed mixes. Indeed, caribou diet was more variable in our study, and more representative of the diet of *Rangifer* in the wild.

Finally, we noted a low variability of discrimination factors between individual coyotes for blood components (less than 1‰ for both $\Delta^{13}C_{LE}$ and $\Delta^{15}N$). TDFs of coyote blood components were relatively similar to those reported in gray wolves (*C. Lupus,* McLaren et al., 2015), but higher than those reported in red fox (Roth & Hobson, 2000). Again, this might be related to the similarity of the diets consumed by the coyotes sampled in our study compared to the diets consumed by the gray wolves studied by McLaren et al. (2015). Indeed, gray wolves were fed exclusively with

horse meat (McLaren et al., 2015), while red fox were fed exclusively with commercial pellet feed mix (Roth & Hobson, 2000). In order to better understand TDF variabilities in blood components in multiple species, we suggest that estimating TDFs on more individuals and in more studies might be required. Quantifying the contribution of each food item on TDF variations in blood components would be very useful to evaluate the effect of adding novel food items (e.g. deer carcasses, small mammals, plants) to this measure.

2.6.4 Limits and scope

Our study provides species- and tissue-specific TDF values for five large mammal species, an approach advocated to obtain accurate estimates of diet composition (Caut et al., 2008). We recognize that a single TDF value for a species–tissue combination is utopian because different factors could have an influence on it, notably sex, age (Kurle et al., 2014; Lecomte et al., 2011; Tieszen et al., 1983), and diet type (Caut et al., 2009; Sponheimer et al., 2003a). Although we provide measurements of uncertainties around our TDF values, we could not estimate the amount of variability that was related to specific variables because of our small sample size and the challenges imposed by conducting these tests on large mammals. We nevertheless recognize that some of these factors could contribute to the within-species variation we observed.

In addition, and contrary to the suggestion of Felicetti et al. (2003), we did not take into account the CN ratios in the estimates of the bulk diet isotopic signatures to derive TDF values. However, we considered this potential bias to be weak because all animals consumed the same bulk diet for at least 6 months prior sampling (DeNiro & Epstein, 1978; Lecomte et al., 2011). It therefore is important to undertake experimental studies under controlled conditions to understand how the various

factors affect TDFs. Nevertheless, we consider our TDFs to be accurate (as shown with low *CV* %), and we captured some intraspecific variation.

The principal contribution of this study is to provide a more precise estimate of TDFs and their uncertainty in hair for caribou, moose, coyote, and black bear, and to a lesser extent white-tailed deer, for which our sample size was too small to assess variability in TDF. The discrimination factors obtained in our study will be used to understand the foraging ecology and diet composition of these species, the predator–prey relationships linking caribou to coyotes and bears, but also of the diet of woodland caribou, a threatened taxon throughout North America (COSEPAC, 2014; COSEWIC, 2011; Festa-Bianchet et al., 2011). More globally, this new knowledge could have important implications for the study of threatened and endangered species for which researchers should advocate the use of noninvasive sampling (here hair) or of a non-lethal approach (here blood) to characterize diet.

2.7 Acknowledgments

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2.8 Supplementary material

Table S2.1. Guaranteed analysis and ingredients in various feed mixes.

	Mazuri Moose Breeder Diet [1]	Mazuri Moose Maintenance Diet [2]	Purina 16% Deer and Elk Bir Nutrition [3]	Tradition Agri-Chien [4]	CAZA Browser Pellets [5]	Top Champion [6]	Best Choice [7]
Guaranteed Analysis							
Crude protein (%)	16.0	11.0	16.0	21.0	13.0	26.0	26.0
Crude fat (%)	4.5	6.0	1.0	10.0	4.0	16.0	15.0
Crude fiber (%)	25.0	32.0	30.0	4.0	21.0	3.5	5.0
Minerals (Ash) (%)	9.0	7.0		7.0		8.0	
Calcium (%)	0.9-1.4	0.5-1.0	0.8	1.0	1.7		
Phosphorus (%)	0.6	0.4	0.4	0.8	1.0		
Salt (%)	0.5-1.0	0.8-1.3					
Sodium (%)		0.8	0.3		0.3		
Digestible energy	3.0	2.9					
Vitamin A (UI/kg)	13375.0	6980.0	6500.0		2000.0		
Vitamin D_3 (UI/kg)	1900.0	1280.0	1200.0		1000.0		
Vitamin E (UI/kg)	110.0	180.0	100.0		600.0		
Selenium (ppm)	0.3	0.3	0.3		0.2		

[1] Mazuri Moose Breeder Diet
Dehulled soybean meal, ground aspen, dehydrated alfalfa meal, dried beet pulp, cane molasses, oat hulls, soybean oil, sucrose, dicalcium phosphate, salt, magnesium oxide, choline chloride, calcium carbonate, l-ascorbyl-2-polyphosphate (stabilized vitamin C), pyridoxine hydrochloride, cholecalciferol (form of vitamin D3), vitamin A acetate, d-alpha tocopheryl acetate (form of vitamin E), folic acid, calcium iodate, menadione sodium bisulfite complex (source of vitamin K), calcium pantothenate, copper sulfate, biotin, vitamin B12 supplement, zinc oxide, thiamine mononitrate, nicotinic acid, riboflavin supplement, cobalt carbonate, manganous oxide, ferrous carbonate, zinc sulfate, sodium selenite.

[2] Mazuri Moose Maintenance Diet
Ground aspen, dried beet pulp, dehydrated alfalfa meal, dehulled soybean meal, soybean oil, cane molasses, sucrose, salt, magnesium oxide, dicalcium phosphate, calcium carbonate, monosodium phosphate, potassium phosphate dibasic, l-lysine, l-ascorbyl-2-polyphosphate (stabilized vitamin C), inositol, dl-methionine, choline chloride, d-alpha tocopheryl acetate (form of vitamin E), pyridoxine hydrochloride, copper sulfate, menadione sodium bisulfite complex (source of vitamin K), calcium iodate, thiamine mononitrate, zinc oxide, cholecalciferol (form of vitamin D3), folic acid, biotin, calcium pantothenate, vitamin A acetate, vitamin B12 supplement, riboflavin supplement, nicotinic acid, cobalt carbonate, sodium selenite.

[3] Purina 16% Deer and Elk Bir Nutrition
Soy scale, oat shell, soybean meal, wheat gru, dehydrated alfalfa, molasses, calcium carbonate, binder, salt, vitamins, micronutrients, flavor.

[4] Tradition Agri-chien
Ground corn, whole ground wheat, chicken by-product meal, soybean meal, chicken fat (preserved with mixed tocopherols and citric acid), dried beet pulp, natural chicken flavor, mono-dicalcium phosphate, calcium carbonate, salt, dried brewer's yeast, calcium propionate (preservative), potassium chloride, choline chloride, vitamins (vitamin E supplement, vitamin A supplement, vitamin D3 supplement, vitamin B12 supplement, niacin supplement, riboflavin supplement, calcium pantothenate, pyridoxine hydrochloride, biotin, thiamine mononitrate, menadione sodium bisulfite complex [source of vitamin K activity], folic acid), minerals (zinc amino acid complex, ferrous sulfate, zinc sulfate, iron amino acid complex, copper sulfate, manganese amino acid complex, manganese sulfate, ethylenediamine dihydriodide, sodium selenite).

[5] CAZA Browser Pellets
Ingredients list not available.

[6] Top Champion
Poultry by-products meal, whole wheat flour, but ground, poultry fat with a blend of tocopherols, corn gluten meal, beet pulp, chicken flavor, flaxseed, dried aspergillus flour fermentation (natural source of glucosamine), salt, brewery dry yeast, potassium chloride, calcium carbonate, calcium propionate, zinc and amino acid complex, ferrous sulphate, zinc sulphate, iron amino acid complex, sulphate copper, manganese complex amino acid, manganous sulfate, ethylenediamine dihydroiodide, sodium selenite, vitamin E, vitamin A, vitamin D3, vitamin B12, niacin, riboflavin, calcium pantothenate, pyridoxine hydrochloride, biotin, thiamine mononitrate, vitamin K3, folic acid.

[7] Best Choice
Whole wheat, pork meal, corn gluten meal, chicken fat stabilized with tocopherols A source of vitamin E, soybean meal, beet pulp, calcium propionate, salt, choline chloride, vitamins (vitamin E, vitamin A supplement, vitamin D3 supplement, vitamin B12 supplement, niacin supplement, riboflavin supplement, calcium pantothenate, pyridoxine hydrochloride, biotin, thiamine mononitrate, menadione sodium bisulfite complex, folic acid), minerals (zinc complex and amino acid complex, ferrous sulfate, zinc sulfate, amino acid iron complex, copper sulfate, amino acid manganese complex, manganous sulfate, ethylenediamine dihydroiodide, sodium selenite).

Table S2.2. Mean values of $\delta^{13}C_{diet}$, $\delta^{15}N_{diet}$ and CN ratios of diet items, proportion of each item in the animal's diet (p_{item}), weighted stable isotope signatures of different diet items ($p\delta^{13}C_{diet}$ and $p\delta^{15}N_{diet}$) and mean total diet ratio (in bold) for each species (± *SD*) at the Zoo sauvage de St-Félicien and the Bioparc de la Gaspésie.

Diet items per species (St-Félicien)	n	$\delta^{13}C_{diet}$ ± *SD* (‰)	$\delta^{15}N_{diet}$ ± *SD* (‰)	CN	p_{item}	$p\delta^{13}C_{diet}$ ± *SD* (‰)	$p\delta^{15}N_{diet}$ ± *SD* (‰)
Caribou							
Hay	4	-29.99 ± 0.67	1.70 ± 0.84	16.48	0.52	-15.56 ± 0.35	0.88 ± 0.44
Purina feed mix	4	-25.56 ± 0.51	1.30 ± 0.21	15.12	0.38	-9.74 ± 0.19	0.50 ± 0.08
Plants	4	-27.59 ± 0.19	-1.32 ± 3.25	19.34	0.05	-1.38 ± 0.01	-0.07 ± 0.16
Twigs/foliage	8	-27.38 ± 1.00	-1.62 ± 2.67	32.54	0.05	-1.37 ± 0.05	-0.08 ± 0.13
						-28.05 ± 0.60	**1.23 ± 0.81**
Moose							
Masuri feed mix	4	-26.93 ± 0.23	0.65 ± 0.45	19.96	0.41	-11.12 ± 0.09	0.27 ± 0.19
Poplar twigs/buds	3	-26.90 ± 0.21	-5.49 ± 0.36	38.92	0.49	-13.10 ± 0.10	-2.67 ± 0.17
Fruits (apple)	4	-25.70 ± 0.52	-1.85 ± 0.46	237.53	0.05	-1.29 ± 0.03	-0.09 ± 0.02
Plants	4	-27.59 ± 0.19	-1.32 ± 3.25	19.34	0.05	-1.38 ± 0.01	-0.07 ± 0.16
						-26.89 ± 0.23	**-2.57 ± 0.54**
Coyote							
Agri-chien feed mix	4	-19.83 ± 0.27	3.02 ± 0.20	11.46	0.38	-7.53 ± 0.10	1.15 ± 0.08
Horse meat	4	-23.40 ± 1.09	5.80 ± 0.31	6.80	0.57	-13.34 ± 0.62	3.31 ± 0.17
Small mammals (enclosure)	14	-23.22 ± 1.29	4.58 ± 1.20	3.04	0.025	-0.58 ± 0.03	0.11 ± 0.03
Deer carcass (enrichment)	4	-25.69 ± 0.42	4.61 ± 1.70	3.03	0.025	-0.64 ± 0.01	0.12 ± 0.04

						-22.10 ± 0.77	**4.68 ± 0.32**
Black bear							
Agri-chien feed mix	4	-19.83 ± 0.27	3.02 ± 0.20	11.46	0.70	-13.88 ± 0.19	2.11 ± 0.14
Fruits (berries)	15	-29.98 ± 1.47	-1.92 ± 0.94	18.97	0.15	-4.50 ± 0.22	-0.29 ± 0.14
Plants (fungi, clintonia)	6	-31.48 ± 0.33	-0.54 ± 1.52	21.04	0.10	-3.15 ± 0.03	-0.05 ± 0.15
Deer (enrichment)	4	-25.69 ± 0.42	4.61 ± 1.70	3.03	0.05	-1.28 ± 0.02	0.23 ± 0.09
						-22.81 ± 0.46	**2.00 ± 0.52**

Diet items per species (Bioparc)	n	$\delta^{13}C_{diet}$ ± *SD* (‰)	$\delta^{15}N_{diet}$ ± *SD* (‰)	CN	p_{item}	$p\delta^{13}C_{diet}$ ± *SD* (‰)	$p\delta^{15}N_{diet}$ ± *SD* (‰)
Caribou							
Foliage/grass/epilobe	10	-28.77 ± 2.06	-0.94 ± 1.97	15.02	0.20	-5.75 ± 0.41	-0.19 ± 0.39
Caza feed mix	4	-27.97 ± 0.33	2.84 ± 0.37	18.97	0.80	-22.38 ± 0.26	2.27 ± 0.29
						-28.13 ± 0.68	**2.08 ± 0.69**
Moose							
Poplar twigs/buds	3	-26.90 ± 0.21	-5.49 ± 0.36	38.92	0.25	-6.73 ± 0.05	-1.37 ± 0.09
Mazuri feed mix	4	-26.53 ± 0.37	1.14 ± 0.58	19.43	0.75	-19.90 ± 0.28	0.86 ± 0.43
						-26.62 ± 0.33	**-0.52 ± 0.52**
White-tailed deer							
Caza feed mix	4	-27.97 ± 0.33	2.84 ± 0.37	18.97	0.70	-19.58 ± 0.23	1.99 ± 0.26
Foliage	8	-27.38 ± 1.00	-1.62 ± 2.67	40.30	0.10	-2.74 ± 0.10	-0.16 ± 0.27
Hay	4	-29.99 ± 0.67	1.70 ± 0.84	16.48	0.10	-3.00 ± 0.07	0.17 ± 0.08
Vegetables (carrot)	4	-28.30 ± 0.59	0.49 ± 1.45	32.54	0.05	-1.42 ± 0.03	0.02 ± 0.07
Fruits (apple)	4	-25.70 ± 0.52	-1.85 ± 0.46	237.53	0.05	-1.29 ± 0.03	-0.09 ± 0.02
						-28.02 ± 0.45	**1.93 ± 0.70**

Coyote							
Top Champion feed mix	4	-18.27 ± 0.73	3.88 ± 0.36	9.47	0.85	-15.53 ± 0.62	3.30 ± 0.31
Horse meat	4	-23.40 ± 1.09	5.80 ± 0.31	6.80	0.10	-2.34 ± 0.11	0.58 ± 0.03
Fish (trout)	8	-29.50 ± 1.89	7.25 ± 0.55	3.06	0.05	-1.48 ± 0.09	0.36 ± 0.03
						-19.35 ± 0.82	**4.24 ± 0.37**
Black bear							
Best Choice feed mix	4	-21.08 ± 0.62	3.45 ± 0.21	9.45	0.60	-12.65 ± 0.37	2.07 ± 0.13
Fish (trout)	8	-29.50 ± 1.89	7.25 ± 0.55	3.06	0.15	-4.43 ± 0.28	1.09 ± 0.08
Fruits (apple)	4	-25.70 ± 0.52	-1.85 ± 0.46	237.53	0.25	-6.43 ± 0.13	-0.46 ± 0.12
						-23.50 ± 0.79	**2.70 ± 0.32**

CHAPITRE III

LE PARTAGE DES NICHES TROPHIQUES ENTRE DEUX PROIES ET LEURS PRÉDATEURS A RÉVÉLÉ DIVERSES MENACES POUR UNE ESPÈCE EN DANGER

TROPHIC NICHE PARTITIONING BETWEEN TWO PREY AND THEIR INCIDENTAL PREDATORS REVEALED VARIOUS THREATS FOR AN ENDANGERED SPECIES

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3.1 Résumé

Documenter le partitionnement des niches trophiques et l'utilisation des ressources au sein d'une communauté est essentiel pour évaluer les mécanismes sous-jacents de coexistence, de compétition ou de prédation. Une connaissance détaillée de l’alimentation est également primordiale puisque celle-ci peut influencer les taux vitaux qui, à leur tour, peuvent affecter la dynamique des populations. Ce chapitre

visait à reconstituer le régime alimentaire de quatre espèces sympatriques de grands mammifères, le caribou (*Rangifer tarandus caribou*), l'orignal (*Alces americanus*) et leurs prédateurs occasionnels, l'ours noir (*Ursus americanus*) et le coyote (*Canis latrans*), et de mieux comprendre le partitionnement des ressources et des niches trophiques entre elles. Les analyses isotopiques Bayésiennes ont montré un faible chevauchement de la niche trophique entre les deux espèces de cervidés, suggérant un faible potentiel de compétition pour les ressources. Mes résultats ont également révélé que le caribou occupait une plus grande niche trophique que l'orignal, ce qui sous-entend une plus grande diversité des ressources utilisées par le caribou. Comme attendu, le coyote consommait principalement des cerfs de Virginie (*Odocoileus virginianus*), des orignaux, des lièvres d'Amérique (*Lepus americanus*) et occasionnellement des caribous, tandis que l'ours consommait principalement des végétaux et, dans une moindre mesure, des orignaux et des caribous. J'ai également documenté un chevauchement plus important des niches trophiques entre le caribou et ses prédateurs. Ce fort chevauchement pourrait augmenter le taux de rencontre et le risque de mortalité qui en découle pour le caribou. Mes résultats supportent l'implication d'un tel chevauchement sur le rétablissement de cette population menacée de caribous dont le déclin est principalement lié à la pression de prédation exacerbée par la perte d'habitat. De plus, cette étude souligne l'importance de considérer les interactions trophiques entre les espèces sympatriques afin d'établir une stratégie de conservation et de gestion efficace pour assurer la persistance des populations d'espèces menacées. La comparaison des niches trophiques des espèces partageant le même habitat ou les mêmes ressources est donc fondamentale pour évaluer les relations trophiques et éventuellement prédire les conséquences des changements écosystémiques sur la communauté.

3.2 Abstract

Documenting trophic niche partitioning and resource use within a community is critical to evaluate underlying mechanisms of coexistence, competition or predation. Detailed knowledge about foraging is essential as it may influence the vital rates, which, in turn, can affect trophic relationships between species, and population dynamics. The aims of this study were to evaluate resource and trophic niche partitioning in summer/autumn between the endangered Atlantic-Gaspésie caribou (*Rangifer tarandus caribou*) population, moose (*Alces americanus*) and their incidental predators, the black bear (*Ursus americanus*) and coyote (*Canis latrans*), and to quantify the extent to which these predators consumed caribou. Bayesian isotopic analysis showed a small overlap in trophic niche for the two sympatric ungulates suggesting a low potential for resource competition. Our results also revealed that caribou occupied a larger isotopic niche area than moose, suggesting a greater diversity of resources used by caribou. Not surprisingly, coyotes consumed mainly deer (*Odocoileus virginianus*), moose, snowshoe hare (*Lepus americanus*), and occasionally caribou, while bears consumed mainly vegetation and, to a lesser extent, moose and caribou. As coyotes and bears also feed on plant species, we documented trophic niche overlap between caribou and their predators, as searching for similar resources can force them to use the same habitats and thus increase the encounter rate and, ultimately, mortality risk for caribou. Although the decline of the Gaspésie caribou population is mostly driven by habitat-mediated predation, we found evidence that the low level of resource competition with moose, added to the shared resources with incidental predators, mainly bears, may contribute to jeopardize the recovery of this endangered caribou population. Highlighting the trophic interaction between species is needed to establish efficient conservation and management strategies to insure the persistence of endangered populations. The comparison of trophic niches of species sharing the same habitat or resources is

fundamental to evaluate the mechanisms of coexistence or competition and eventually predict the consequences of ecosystem changes in the community.

Keywords: apparent competition, caribou, foraging, isotopic niche, resource partitioning, stable isotope

3.3 Introduction

Understanding ecological relationships among sympatric species is fundamental to evaluate underlying mechanisms of coexistence, competition or predation, especially for species at risk that share common predators with an alternative prey (Holt, 1977). The persistence of prey species that are least productive is compromised by the exacerbated predation pressure exerted by predators that feed primarily on the most productive prey (DeCesare et al., 2010; Holt, 1984; Latham et al., 2011a, 2011b). However, coexistence of prey may be possible if less competitive prey avoid sectors and resources that are used by the most competitive prey (Holt, 1984) through the partitioning of their respective ecological niches (Latham, 1999).

The ecological niche describes how a species interacts within an ecosystem and represents the interplay between biotic and abiotic variables that determine the conditions suitable for its survival, reproduction and persistence (Hutchinson, 1957). The *fundamental ecological niche* describes the range of optimal conditions wherein a species is able to persist in the absence of competition and predation, whereas the *realized ecological niche* considers all the constraints to which an animal is exposed, including competition and predation (Figure 3.1) (Hutchinson, 1957). It was previously assumed that all individuals belonging to a given population were using the same niche, habitat and resources (Hutchinson, 1957). However, there is increasing recognition that individuals are not identical and may have different

feeding or habitat preferences leading to niche variation among individuals (Bolnick et al., 2003, 2007; Van Valen, 1965). The niche breadth is thus a trade-off between the effect of intraspecific and interspecific competition for resources (Figure 3.1) (Roughgarden, 1972; Van Valen, 1965). If interspecific competition is low, intraspecific competition may trigger niche expansion by favoring the selection of novel resources (Lafferty et al., 2015), thereby reducing intraspecific competition, leading to an individual specialisation (Bolnick et al., 2003) and allowing the coexistence of species (Jung et al., 2015; Latham, 1999). Coexistence or exploitative competition of sympatric species can occur due to resource partitioning in different habitats, according to different temporal activity patterns and under varying consumption levels of dietary sources (or prey size for predators; Latham, 1999; Schoener, 1974).

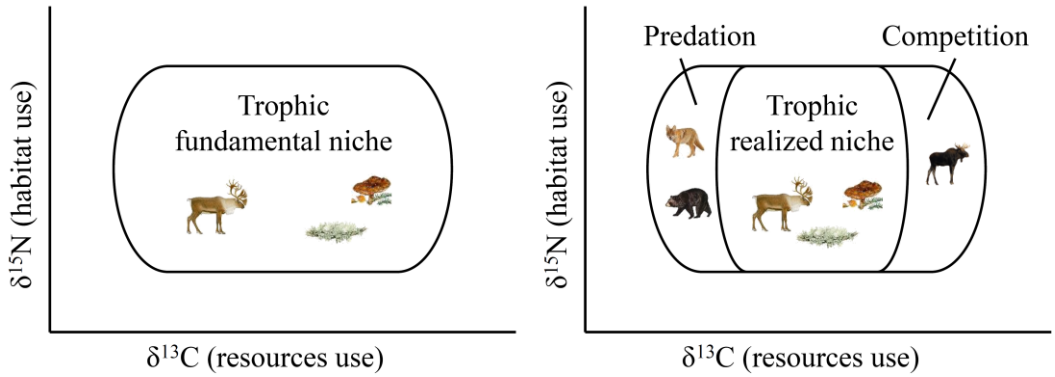

Figure 3.1. Schematic of the different trophic niche concepts presented in the bi-dimensional isotopic space of $\delta^{13}C$ (resources use) and $\delta^{15}N$ values (habitat use). The trophic *fundamental niche* describes the range of optimal conditions wherein a species is able to persist in the absence of competition and predation, whereas the trophic *realized niche* considers all the constraints to which an animal is exposed to, including competition and predation (Hutchinson, 1957).

The trophic niche of an individual or a species belongs to the ecological niche, but it is built using a subset of variables related to trophic resources (Figure 3.1). The trophic niche may thus be described as the food resources selected and the foraging behaviours exhibited to acquire them (Araújo et al., 2011). It may be influenced by the location or time at which an animal forages (Robertson et al., 2015). Documenting the diet of wild species in different habitats is needed because it may help to better understand resource partitioning and trophic interactions. Indeed, foraging may affect individual fitness (Abramsky et al., 2002), vital rates (Parker et al., 1999) and population persistence (Macbeth & Kutz, 2019). However, a trade-off between resource acquisition and predation avoidance can prevail. For example, in Yellowstone National Park, Hernández and Laundré (2005) showed that red deer (*Cervus elaphus*) moved from open meadows toward forest edges that provide lower quality forage but better protection from wolf (*Canis lupus*) predation. Characterising the partitioning and level of overlap of trophic niches between prey and its conspecific competitors is critical to inform possible ecological relationships. This type of analysis can also be applied to prey that share resources with incidental, omnivorous predators which thus act simultaneously as predator and competitor. In such complex interactions, searching for similar resources in the same area can increase the encounter rate between prey and an opportunistic predator.

Diet composition is often inferred from the analysis of prey remains in scats and stomach contents of consumers (e.g. Lesmerises et al., 2015; Popp et al., 2018), but these techniques can be biased toward indigestible hard parts (McInnis et al., 1983; Nielsen et al., 2018). To overcome this limitation, DNA metabarcoding has emerged as a good option and provides high taxonomic resolution (Newmaster et al., 2013). However, these techniques only offer a snapshot of a consumer's diet (Lesmerises et al., 2015; Nielsen et al., 2018). In contrast, stable isotope analysis has become a key tool to study the foraging ecology of wild species as it provides long-term information on diet assimilation (Kelly, 2000; Peterson & Fry, 1987). It is based on

the principle that stable isotope ratios in the tissues of consumers reflect the ratios of their diet (DeNiro & Epstein, 1978, 1981). Changes in nitrogen stable isotope ratios ($\delta^{15}N$) occur from one trophic level to the next (+ 3-4‰), making them useful indicators of trophic position (Minagawa & Wada, 1984; Peterson & Fry, 1987; Post, 2002). In contrast, the carbon stable isotope ratio ($\delta^{13}C$) is particularly useful for delineating carbon sources and foraging locations (DeNiro & Epstein, 1981; Peterson & Fry, 1987). In addition, stable isotopes can provide insights into trophic niche ecology; as proposed by Newsome et al. (2007), the isotopic niche can be delineated as the bi-dimensional isotopic space of $\delta^{13}C$ and $\delta^{15}N$ values in a bi-plot (Figure 3.1). Isotopic niche analysis has been extended to assess how individuals or species partition food resources (Hobson et al., 2000), to better understand predator-prey relationships (Urton & Hobson, 2005) and interspecific competition (Jung et al., 2015), and to get insights into individual specialization (Newsome et al., 2009). For example, using stable isotope analysis, resource partitioning attributed to different diet selection (Merkle et al., 2017) and spatial segregation (Hobson et al., 2000) has been documented in three sympatric predators that coexist in North America; the gray wolf, grizzly (*Ursus arctos*) and black bear (*Ursus americanus*).

Most woodland caribou (*Rangifer tarandus caribou*) populations are declining in Canada and some small, isolated herds are particularly at risk (Festa-Bianchet et al., 2011). This is the case of the Atlantic-Gaspésie caribou population (hereafter referred as Gaspésie caribou population), the last herd of caribou found south of the St. Lawrence River. This herd is now considered Endangered according to the Species at Risk Act (COSEPAC, 2014). Habitat-mediated predation, exacerbated by habitat alteration, is identified as the main cause of population decline in several woodland caribou populations in Canada (Festa-Bianchet et al., 2011), but also in the Gaspésie population (Frenette et al., 2020). In addition, intensive forest management occurring in the Gaspésie caribou habitat has led to a strong increase in moose (*Alces americanus*) density and was paralleled with an increase in density of black bears and

coyotes (*Canis latrans*) (Frenette et al., 2020). These two incidental predators were shown to be the main predators of moose and caribou in the area (Crête & Desrosiers, 1995) but they also feed on a variety of plant species and smaller prey (Boisjoly et al., 2010; Mosnier et al., 2008). Although the decline of the Gaspésie caribou population appears mostly driven by habitat alteration due to forestry (Frenette et al., 2020), here we focus on the foraging ecology and the resource and trophic niche partitioning between the endangered Gaspésie caribou population, moose, and their two omnivorous predators. To do so, we used Bayesian stable isotopic analysis to reconstruct the diet composition of moose, coyotes and bears, and to evaluate resource and trophic niche partitioning between caribou and these three species in the context of the apparent competition interaction (Holt, 1977). Such information is crucial to clarify the potential roles of interspecific resource competition between the endangered caribou population and moose and to determine to what extent these predators consumed (and even competed with) caribou. These omnivorous predators could theoretically enter into another type of competition (i.e. exploitation and/or interference competition) with caribou (and moose), at least for the plant species they share with both ungulates. By searching for similar food items, they could be forced to frequent similar habitat components (e.g. land- or forest-cover types), which could increase encounter rate and ultimately the associated mortality risk.

3.4 Materials and methods

3.4.1 Study area

The study area is part of the southeastern boreal forest in the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain. It is located in the Gaspésie National Park and the surrounding Matane, Dunière, and Chic-Chocs Wildlife Reserves and Casault controlled harvesting zone (hereafter referred to as

ZEC Casault) (see section 3.8 Supplementary material, Figure S3.1). The study area is characterized by three distinct vegetation zones distributed along the altitudinal gradient (see section 3.8 Supplementary material, Figure S3.1). The Gaspésie caribou population uses habitats found at high elevations (> 700m; Mosnier et al., 2003). Population size has been declining for several decades, from 130 caribou in 1990 to ~ 40 individuals in 2019 (Morin & Lesmerises, 2020). A small fine-scale genetic structure, with two subgroups (Logan-Albert vs. McGerrigle), has been documented due to limited exchanges between summits (see section 3.8 Supplementary material, Figure S3.1; Pelletier et al., 2019). Intensive forestry activities conducted in the past decades have largely modified the landscape structure within and in the surroundings of the Gaspésie National Park, increasing the proportion of early-seral forests to the detriment of mature coniferous forests (Boudreau, 2017). These changes have supported increases in moose density from 1.0 to 8.0 moose/10 km^2 between 1992 and 2011 (Dorais, 2015). This increase was accompanied by an increase in bear and coyote densities (Frenette et al., 2020) that has exacerbated the predation pressure on caribou calves (Crête & Desrosiers, 1995) and adults (Lesmerises et al., 2019) via an apparent competition phenomenon (*sensu* Holt, 1977). This habitat-mediated apparent competition is responsible for low calf recruitment rates (~ 8 calves per 100 females, Morin & Lesmerises, 2020) and low adult survival rates (77% for females and 56% for males in 2014 and 2015, Frenette et al., 2020).

3.4.2 Caribou, moose and predator sample collection

We captured 44 caribou in the winter of 2013 and 2014 across the Gaspésie caribou range using a net gun fired from a helicopter. We collected caribou hair samples from the rump of the animal, and dried and stored them in paper bags at ambient temperature until processing. We used the same sampling and conservation protocol for hair samples collected from 90 moose, 127 coyote and 57 black bear carcasses

across the three Wildlife Reserves that overlap the Gaspésie National Park (see section 3.8 Supplementary material, Figure S3.1). Moose were harvested between September and October 2018 during the sport hunting season whereas coyotes and bears were trapped during the annual predator control program between June 2016 and October 2018 across the Gaspésie caribou range. The capture and manipulation protocols were authorized by the Animal Welfare Committee [Université du Québec à Rimouski (hereafter UQAR) certificate #CPA-52-13-112; Ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) certificate #CPA FAUNE 13-08].

3.4.3 Dietary source sample collection

We collected samples opportunistically from all potential food sources consumed by moose, coyotes and bears to describe the composition of their diet. We collected hair samples from 22 individuals belonging to 6 different species that were accidentally trapped during the predator control program, including 4 white-tailed deer (*Odocoileus virginianus*), 1 snowshoe hare (*Lepus americanus*), 2 large rodents (groundhog, *Marmota monax*, North American porcupine, *Erethizon dorsatum*), 8 Canada lynx (*Lynx canadensis*) and 7 moose (*Alces americanus*). We also collected hairs from 22 individuals belonging to 6 species that were harvested by sport trappers or opportunistically collected in the ZEC Casault during summer, including five different species of rodents (1 red squirrel, *Tamiasciurus hudsonicus*, 2 common voles, *Microtus arvalis*, 5 deer mice, *Peromyscus maniculatus*, 6 Northern flying squirrels, *Glaucomys sabrinus*, and 1 pygmy shrew, *Sorex minutus*), and one species of large rodent (7 North American beaver, *Castor canadensis*). We also collected the feathers of 3 ruffed grouses (*Bonasa umbellus*) and hair from 4 snowshoe hares which were harvested by sport hunters in the ZEC Casault. We dried and stored hair and feathers in paper bags at ambient temperature until processing.

Finally, in the study area in 2017, we collected opportunistically six insects from three species belonging to the coleopteran (1 beetle) and hymenoptera orders (3 ants and 2 wasps). We also collected plant samples in July 2017 belonging to 46 different species in the montane boreal forest area of Mount Albert (*n* = 93) and Mount Logan (*n* = 72) in the Gaspésie National Park and of Petit Mount Ste-Anne (*n* = 53) in the Chic-Chocs Wildlife Reserves (see details in section 3.8 Supplementary material). Plant sampling was authorized by the Société des Établissements de Plein Air du Québec, which manages the Gaspésie National Park and the Chic-Chocs and Matane Wildlife Reserves [certificate # PNG-2017042703]. We randomly collected three replicates per species and froze them at -20°C until they were processed. We freeze-dried insect and plant samples for 48h, ground them into a fine powder using a CryoMill (Jardine et al., 2003), and stored them in a desiccator until the stable isotope analysis.

3.4.4 Hair and feather sample preparation

We washed hair samples using a solution of 2:1 chloroform-methanol in an ultrasonic bath to remove all possible surface contamination and external lipids, rinsed samples with distilled water and oven-dried them at 50°C for 24h (Hobson et al., 2000). We freeze-dried hair samples for 48h and ground them into a fine powder (Jardine et al., 2003). We used a CryoMill with a cooling system (liquid nitrogen at -196°C) for hair caribou samples only. For other animal samples, we cut the hairs and feathers into small pieces (about 1 mm) with stainless steel scissors and cleaned the scissors with ethanol 70% between samples.

3.4.5 Lipid extraction and stable isotope analyses

Stable isotope signatures measured in tissues may be biases due to the variability in the lipid content of samples because lipids are more depleted in ^{13}C relative to protein and carbohydrate fractions (DeNiro & Epstein, 1977; McConnaughey & McRoy, 1979). We divided caribou hair samples into two parts to determine $\delta^{13}C$ (lipid-extracted) and $\delta^{15}N$ (no lipid-extracted) values separately to account for lipid effect on stable isotope signatures: one part of the subsamples received no further treatment prior to nitrogen isotope analysis, and the second part was lipid-extracted prior to carbon isotope analysis (Kelly, 2000; Lesage et al., 2010; Post et al., 2007; Rioux et al., 2019). We conducted lipid extraction using the second part of powdered hair samples (to remove internal lipids) (Dunnett, 2005) and a solvent consisting of a mixture of chloroform and methanol (2:1 v/v) (Folch et al., 1957). We shook the mixture and stored it overnight at 4°C. We centrifuged the mixture at 11,200 g for 10 min and discarded the supernatant (Folch et al., 1957). We repeated the whole procedure twice. After 3 extractions, we dried samples by evaporation overnight, rinsed with distilled water, oven-dried overnight at 50°C and powdered again. Due to methodological constraints, we used previously develop models of caribou normalization to correct the $\delta^{13}C$ values of other animal hair for lipid content (equation 8 in Rioux et al., 2019).

We weighed 0.500-0.700 mg (± 0.001 mg) subsamples of powdered caribou hair and plant tissues, and 1.000-1.200 mg (± 0.001 mg) of other animal tissues and insects into a tin capsule. We analyzed samples to assess $\delta^{13}C$ and $\delta^{15}N$ using an Elemental Analyzer coupled to a Delta Plus Continuous Flow-Isotope Ratio Mass Spectrometry. Analyses were conducted in the Marine Chemistry and Mass Spectrometry Laboratory (UQAR) for caribou hair, and plant tissues and in the Stable Isotope in Nature Laboratory (SINLAB, University of New Brunswick) for other animal tissues and insects. By convention, ^{13}C and ^{15}N isotope abundances are expressed in delta

notation (‰), as $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{13}C or ^{15}N, and R_{sample} is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$; $R_{standard}$ represents the ratios of the respective standards: Vienna Peedee Belemnite (PDB) and atmospheric nitrogen (AIR). We evaluated the accuracy of our isotopic analysis using three commercially certified materials (B2151, Acetanilide, and Nicotinamide) and the precision of measurement by randomly duplicating a subset of our samples. Replicates using certified B2151 materials (n = 31) indicated a systematic error of ± 0.22 for $\delta^{13}C$ and ± 0.24‰ for $\delta^{15}N$, whereas replicates using certified Acetanilide and Nicotinamide materials (n = 36) indicated a systematic error of ± 0.08‰ for $\delta^{13}C$ and ± 0.10‰ for $\delta^{15}N$. The average deviations observed between replicates of hair, fish muscle, insect and plant samples (n = 97) indicated an analytical error of 0.16‰ for $\delta^{13}C$ and 0.20‰ for $\delta^{15}N$.

3.4.6 Estimations of diet composition

Stable isotope ratios measured in hair reflect food consumption during the period of tissue growth (Schwertl et al., 2003); consequently, we assumed that the stable isotope signatures we calculated would represent the summer/autumn diet. For the species studied, molt occurs generally at the end of the cold season (April to June), and the new fur grows between late spring/early summer (June) to autumn (Darimont & Reimchen, 2002; Ling, 1970; Mowat et al., 2017). To estimate the relative contribution of the different food sources for the summer/autumn diets of moose, coyotes and bears, we used the Bayesian stable isotope mixing model (hereafter referred to as SIMM) package in R (Parnell et al., 2013; Phillips et al., 2014). Diet composition for caribou was estimated in a companion study conducted in the same study area (Rioux et al., submitted, see details in chapter 4). SIMMs have allowed the incorporation of variability in sources and trophic discrimination factors (hereafter referred to as TDFs), and the outputs represent true probability density functions

(Moore & Semmens, 2008; Parnell et al., 2013; Phillips et al., 2014). Estimates are reported with their 95% credible intervals (hereafter referred to as 95% CI), which allow predicting within a 95% credibility level that source A represents from *x*% to *y*% of the assimilated diet (Parnell et al., 2013).

We included food sources known to be consumed by the species (moose, bears and coyotes) as prior distributions into our SIMM and added prior distributions for each source (Moore & Semmens, 2008; Stock & Semmens, 2016) based on studies conducted in our study area (see details in section 3.8 Supplementary material). For moose, priors of diet composition came from Christopherson et al. (2019), who used DNA barcoding analysis on fecal pellets, while for bears and coyotes, we used data from fecal pellet analysis (M.-H. St-Laurent, *unpublished data*) (see details in section 3.8 Supplementary material). To facilitate source distinction in SIMM, we grouped plant samples in 10 functional groups: aquatic plants, deciduous trees, ericaceous shrubs, evergreen trees, ferns, forbs, fungi, horsetails, graminoids, and shrubs. Arboreal lichens, which represent most of the lichen biomass in our study area (Stone et al., 2008), were not considered as they are almost never consumed by moose, bears and coyotes and because we were interested in describing trophic niche partitioning. We used the correlation matrix of food sources included in the SIMM package to verify the assumption of differences in isotopic signatures between sources. We combined the negatively correlated source proportions to gain precision in calculated proportions (Parnell et al., 2013; Phillips et al., 2014). We used the average TDFs (± *SD*) estimated by Rioux et al. (2020) for all the studied species during a controlled feeding trial carried out on 10 different individuals: 3 moose, 3 coyotes and 4 black bears. Estimated TDFs reached 1.69 ± 0.93‰ for $\Delta^{13}C$ and 4.86 ± 0.94‰ for $\Delta^{15}N$ for moose, 3.41 ± 0.37‰ for $\Delta^{13}C$ and 3.05 ± 0.13‰ for $\Delta^{15}N$ for coyotes, and 5.92 ± 0.53‰ for $\Delta^{13}C$ and 4.94 ± 0.47‰ for $\Delta^{15}N$ for black bears (Rioux et al., 2020). Finally, we used a concentration-dependent mixing model for bears and coyotes (Phillips & Koch, 2002) because there were considerable differences between carbon

and nitrogen concentrations in plant and animal food sources (see section 3.8 Supplementary material, Table S3.1). Incorporating concentration dependence in the model ensures that the contribution of a source is proportional to the mass it contributes to the diet (Phillips & Koch, 2002). This model was not needed for moose as their diet consists only of plants. Model convergence was verified with Gelman-Rubin diagnostic tests, and the model was considered acceptable if values were < 1.1 (Gelman et al., 2014).

3.4.7 Niche breadth and resource partitioning

We evaluated the niche breadth and food resource partitioning of our four focal species (caribou, moose, coyote and bear) by estimating the Bayesian standard ellipse area (hereafter referred as SEA_B) and the 95% CI in the bi-dimensional isotopic space of $\delta^{13}C$ and $\delta^{15}N$ values using the SIBER library (Jackson, 2019; Jackson et al., 2011). The SEA_B contains 40% of the data and represents the core isotopic niche for each species in terms of the more frequent utilization of resources. The SEA_B is robust, less sensitive to extreme values or small sample sizes, and includes uncertainty around the community metrics (Jackson et al., 2011). We calculated the degree of niche trophic overlap among species with the overlap index of the SIBER model, where a value > 1 indicates overlap between species. We also calculated the relative overlap proportion between species ellipses, where a value of 0 indicates no overlap and a value of 1 indicates complete overlap (Jackson et al., 2011). Finally, we also calculated the Layman metrics with the convex hull area to evaluate the degree of isotopic niche variability among individuals in the group (Layman et al., 2007b). Convex hull is the smallest possible area that encompasses all points. It is highly sensitive to small sample sizes and extreme values contrary to SEA_B (Jackson et al., 2011), but our sample size was relatively large for each group of species. The total area of the convex hull (TA) represents the diversity of resources used by the species,

while the mean distance to the centroid (CD) represents the dispersion and the diversity among consumers. We also calculated the mean nearest neighbor distance (NDD), which is a measure of density and clustering within a group; it represents the niche habits of an individual compared to those of other individuals in the group. Finally, we calculated the standard deviation of NND (SDNND), which is a measure of evenness of isotopic space within a group. Based on Layman et al. (2007b), the $\delta^{13}C$ range represents a proxy of the diversity of resources supporting the consumers while the $\delta^{15}N$ range represents a proxy of the vertical trophic structure of the population. We performed all statistical analysis using R software version 3.5 (R Development Core Team, 2017).

3.5 Results

3.5.1 Diet composition estimates

Moose consumed mostly ferns (62.8% [54.1 to 72.8], mean [95% CI]), but also evergreen trees (28.8% [5.4 to 42.3]), and shrubs (4.6% [0.1 to 20.1]; Figures 3.2-3.3). Coyotes mostly had a carnivore diet and consumed deer, moose and snowshoe hare (22.7% [13.5 to 29.2], 26.4% [8.3 to 44.3], and 27.5% [4.5 to 55.1], respectively; Figures 3.2-3.3). Coyotes occasionally consumed caribou (2.6% [0 to 11.1]) as well as fruits and graminoids (14.0% [5.4 to 24.7]; Figures 3.2-3.3). Finally, bears consumed mainly plants (Figures 3.2-3.3), such as dandelions (*Taraxacum spp.*), graminoids, fruits (89.4% [62.0 to 96.8]) and willow (5.4% [0.0 to 24.4]; Figures 3.2-3.3). In a lower proportion, they also consumed moose (3.1% [3.0 to 13.3]), hare (0.9% [0 to 4.7]) and caribou (0.3% [0 to 1.7], Figures 3.2-3.3).

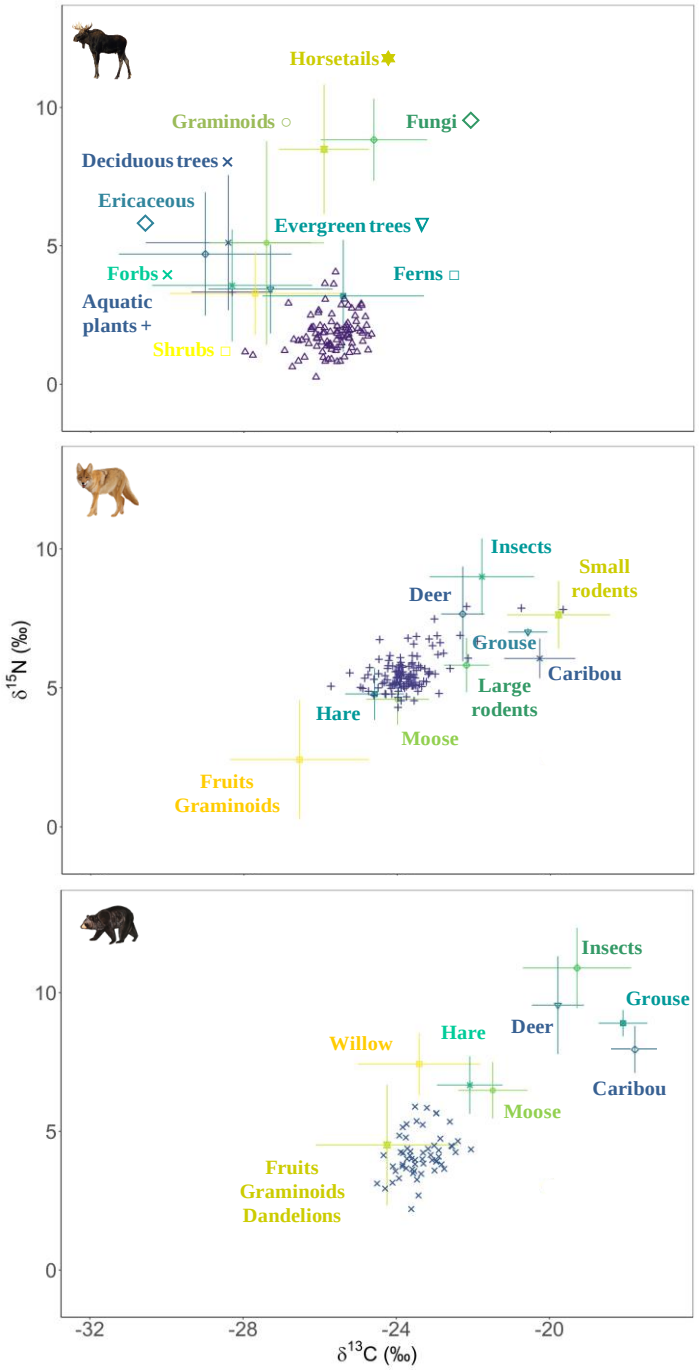

Figure 3.2. Carbon and nitrogen stable isotope signatures (mean ± SD) of dietary sources (solid points and error bars) and individual consumers (open circles ○) in the Gaspésie National Park and the surrounding area for moose, coyotes and black bears.

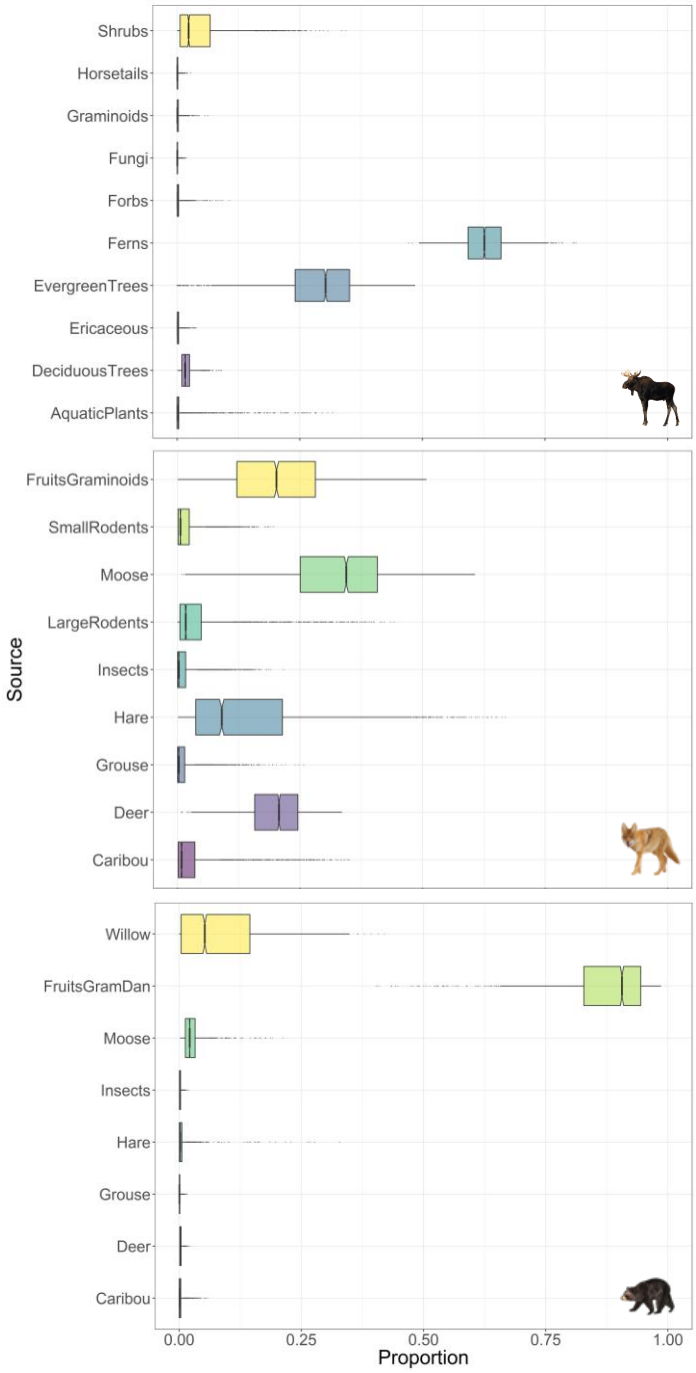

Figure 3.3. Proportional contributions of dietary sources (50, 75, and 95% CI) in the summer/autumn diet of moose, coyotes and black bears using hair stable isotope ratios of carbon and nitrogen.

3.5.2 Niche breadth and resource partitioning

Isotopic niche area (SEA_B) was larger for caribou (1.85‰^{2} [1.36-2.43], mode [95% CI]) than for moose (1.25‰^{2} [1.04-1.54]), coyotes (1.21‰^{2} [1.02-1.44]) and bears (1.18‰^{2} [0.89-1.53]) (Figure 3.4, Table 3.1). The probability of occupying a smaller isotopic niche area than caribou was 0.99 for all three species. The overlap index indicated that the caribou isotopic niche overlaps moose (1.29), coyote (1.25), and bear (4.19) niches. The isotopic niche overlap between coyotes and bears was 2.60. The relative overlap proportion between species ellipses was lower for the caribou vs. moose (0.07) and caribou vs. coyote (0.07) comparisons, but relatively higher between caribou vs. bear (0.23) and coyote vs. bear (0.18). The Layman metrics (Table 3.1) calculated with the convex hull area were larger for caribou (TA, CD, and NND reaching 0.95‰^{2}, 0.91‰, 1.36‰, respectively) than for moose, coyotes and bears. SDNND was larger for moose (0.33‰) than for caribou, coyotes and bears (Table 3.1). $\delta^{15}N$ range was lower in coyotes compared to the three other species studied, while it was higher in caribou and bear groups (Figure 3.4, Table 3.1). $\delta^{13}C$ range was higher in both cervid groups (Figure 3.4, Table 3.1).

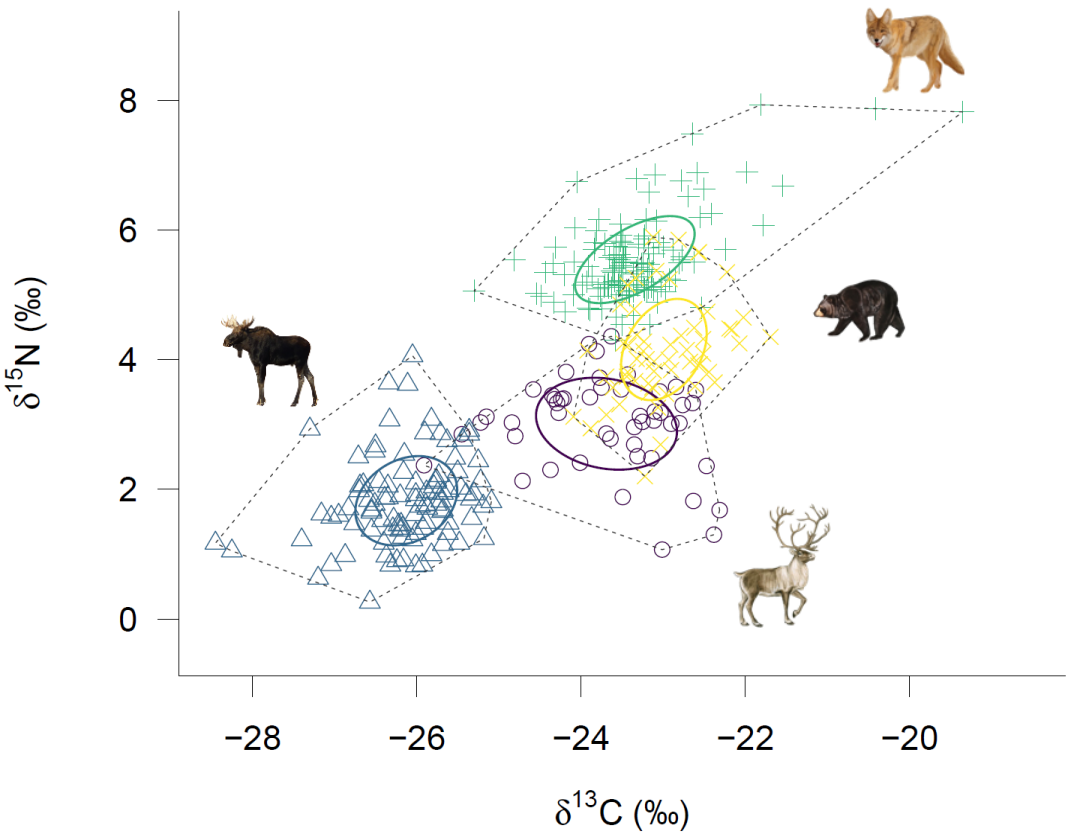

Figure 3.4. Isotopic niche areas in the bi-dimensional isotopic space of $\delta^{13}C$ and $\delta^{15}N$ values of the four groups of species (caribou, moose, coyote, and black bear) using SIBER. Circles show the Standard ellipse areas (SEA_B) and contain 40% of the data, while the dotted polygons show the Convex hull areas (TA) and are drawn around the outermost points in the cloud of data.

Table 3.1. Layman metrics calculated from the convex hull areas and Bayesian standard ellipse area (SEA_B) and their 95% credible intervals calculated from ellipse areas for caribou, moose, coyote and black bear.

Species	$\delta^{15}N$ range (‰)	$\delta^{13}C$ range (‰)	TA (‰^{2})	CD (‰)	NND (‰)	SDNND (‰)	SEA_B [95% CI] (‰^{2})
Caribou	1.30	1.66	0.95	0.91	1.36	0.08	1.85 [1.36 – 2.43]
Moose	0.66	1.48	0.38	0.55	0.54	0.33	1.25 [1.04 – 1.54]
Coyote	0.22	0.31	0.03	0.13	0.15	0.07	1.21 [1.02 – 1.44]
Black bear	0.84	0.32	0.15	0.33	0.38	0.02	1.18 [0.89 – 1.53]

3.6 Discussion

Our study highlighted the partitioning of resources among caribou, moose, and their incidental predators and improved our understanding of their potential interactions. Using isotopic analysis, we found that only a few food sources were shared between caribou and moose and the overlap in their trophic niches appears low in summer/autumn. Our analyses also revealed a highly diversified diet for two omnivorous, opportunistic predators, including a low proportion of caribou, and an overlap in their trophic niches. More interestingly, we reported a non-neglectable trophic niche overlap between caribou and their predators (mainly black bears), suggesting that the quest for similar plant species can increase the encounter rate probability between these incidental predators and caribou, explaining partially the increased mortality risk and accelerated decline for this endangered population.

3.6.1 Resource partitioning between moose and caribou

Caribou consumed a great diversity of resources in summer/autumn, and we found a high interindividual difference in diet, potentially attributed to different niche habits. In a companion study (Rioux et al., submitted, see details in chapter 4), we detailed caribou diet using the same tissue samples, and showed that caribou consumed mainly lichens, deciduous trees and shrubs, but also mosses, evergreen trees, ferns and horsetails. These results are supported by findings obtained by Christopherson et al. (2019) in the same study area where deciduous trees, shrubs and horsetails were the main food source of Gaspésie caribou identified using the DNA barcoding analysis of their scats (note that lichens and fungi were not considered in their DNA barcoding analysis). For moose, our diet analysis indicated that the diversity of resources consumed was less diversified than for caribou and that diet is more

homogenous between individuals, as seen with the narrower CI around source proportion estimates. In contrast, Christopherson et al. (2019) observed a higher diet Simpson diversity index, species richness, and food niche for moose compared to caribou. In our study, moose diet consisted mainly of ferns and, in lower proportion, of evergreen trees and shrubs, while DNA barcoding analysis of moose scats conducted by Christopherson et al. (2019) confirmed a high consumption of deciduous trees, evergreen trees, and shrubs, but they did not report consumption of ferns. However, consumption of ferns by moose is reported in other moose populations in Maine (Lautenschlager et al., 1997) and Alaska (Welch et al., 2015). As DNA barcoding analysis recorded a relatively shorter time window (~ day) compared to isotopic analysis in hair (~ months), this temporal difference in diet integration could explain the slight differences in diet composition observed between both studies.

Similar to Christopherson et al. (2019), we found a low potential for resource competition between caribou and moose in our study area, including the Gaspésie National Park and the surrounding Wildlife Reserves, as indicated by the small niche overlap between these two cervids. However, we cannot confirm that competition never occurred between these two sympatric cervids. In addition, consumers that feed on two resources with widely different isotopic compositions will always be found to have broader isotopic niches than animals that feed on food sources with less divergent δ-values (Matthews & Mazumder, 2004; Newsome et al., 2007). Newsome et al. (2007) have suggested that the trophic niche breadth does not necessarily correspond to the diversity of the resources used, because it also depends on the isotopic variability of these resources.

Some studies highlighted that resources partitioning between ungulates may be a result of past competition (caribou and moose: Christopherson et al., 2019; mule deer

Odocoileus hemionus, moose, elk: Hodder et al., 2013). Caribou and moose have lived in sympatry for a long time and coevolved to decrease exploitative competition, which may explain the different diet and the segregation of their trophic niches (Latham, 1999). Also, some studies documented spatial segregation of caribou from moose (Cumming et al., 1996; Seip, 1992), assuming that caribou select habitats less favorable to moose to reduce the encounter probability with predators that mostly focus on moose (Bergerud, 1985; James et al., 2004). This is assumed to be true in our study area, as these two cervids are thought to frequent different elevations in summer, with caribou selecting subalpine and alpine areas (> 700 m) (Mosnier et al., 2003) while moose select mixed and early seral habitats found at lower elevations. Spatial segregation is known to allow coexistence, decrease exploitative competition and reduce dietary overlap between species (Svanbäck & Bolnick, 2007). However, moose have more frequently been seen in the alpine tundra in summer in the Gaspésie National Park over the last 15 years, and an increase in the proportion of wintering grounds at high elevations (> 600 m) was observed in winter (Roussel-Garneau & Larocque, 2020) even though they prefer lower elevations with an abundance of early successional vegetative species. Spatial refuges of caribou may be compromised by high moose density and by the presence of moose in the alpine refuge habitat, potentially reducing access to highly nutritive resources and affecting physical and physiological conditions. Nutrition is known to contribute, at least partially, to the decline of this population as a secondary cause that predisposes females to poor reproductive performance and low calf survival rates (Rioux et al., submitted, see details in chapter 4). The high moose density in the area is probably harmful to caribou because these two species share common predators.

3.6.2 Coexistence of generalist predators

We found moderate niche overlap between coyotes and bears. This niche segregation may drive the partitioning of the diet, allowing a better resource and habitat partitioning between these predators. This appears to facilitate coexistence by reducing potential competition between them. Indeed, the trophic niche width of both predators may indicate a great diversity of resources consumed and the wide 95% CI for certain food sources in the diet of coyotes, highlighting the generalist behaviour of food selection or the influence of the local diversity of resources (Araújo et al., 2011; Bolnick et al., 2002).

In the boreal forest, coyotes depend mainly on human-disturbed forests such as recent (5-20-year-old) clear-cuts (Boisjoly et al., 2010). This disturbed habitat provides abundant fruit-bearing shrubs (Brodeur et al., 2008), dense understory for snowshoe hares (St-Laurent et al., 2008) and sufficient cover for moose (Dussault et al., 2005), which act as important food resources for coyotes (Boisjoly et al., 2010). As expected, we found that they had a carnivore diet and consumed mostly deer, moose and hares. Moose and snowshoe hares are found in relatively high densities in the Gaspésie caribou range, which was reflected in the coyote's diet (around 26% for each food source). This result is also supported by coyote scat analysis conducted in Gaspésie (Boisjoly et al., 2010) and in the adjacent eastern New Brunswick (Dumond et al., 2001). We also found that coyotes consumed fruits and graminoids. Other studies have reported wild berry consumption by coyotes in Gaspésie (Boisjoly et al., 2010; Samson & Crête, 1997) and on the south shore of the St. Lawrence River in southeastern Québec (Tremblay et al., 1998). Coyotes consumed caribou occasionally, as previously reported in Gaspésie (Boisjoly et al., 2010; Crête & Desrosiers, 1995).

A companion study conducted in the Gaspésie caribou range showed that bears selected barren areas and mature coniferous forests in spring, and barren areas and 5- to 20-year-old clear-cuts in summer and autumn, where abundant vegetation is found (Mosnier et al., 2008). As expected, we found that bears mostly consumed vegetation such as fruits, graminoids, dandelions and willow. The diet of bears is closely linked to plant availability (Mosnier et al., 2008), and frequent interpatch movements between vegetation-rich areas could result in a high encounter rate with moose and caribou neonates even without actively searching for them (Bastille-Rousseau et al., 2011). We noted a low consumption of caribou and moose by bears (< 3%) despite the very high moose density in the study area. Based on scat analysis, bears were shown to consume mostly vegetation (~ 95%) across the Gaspésie caribou range (Mosnier et al., 2008). A large consumption of fruits and graminoids allows bears to fulfill their daily energy requirements and allocate the remaining energy in fat reserves in anticipation of winter torpor.

3.6.3 Resource partitioning between caribou, coyotes and bears

A novel aspect of our study refers to the empirical evidence of trophic niche overlap between caribou, an endangered ungulate prey that is a strict herbivore, and its incidental predators (coyotes and bears), which are opportunistic omnivores, suggesting that cross-trophic competition might be at play between these three species. While previous studies have shown that caribou, coyotes and bears are spatially distributed in different elevation zones (Mosnier et al., 2008), our results suggest that their respective diet and foraging strategies might increase encounter rates between them.

Bears and coyotes are important predators of moose, white-tailed deer and caribou calves (and to a lesser extent adults) in Québec (Bastille-Rousseau et al., 2011;

Leclerc et al., 2014) but also specifically in the Gaspésie National Park (Boisjoly et al., 2010; Crête & Desrosiers, 1995). To isolate themselves from predators, caribou are known to select higher elevations and mountain summits in Gaspésie (Mosnier et al., 2003, 2008), a spacing-away strategy that allows caribou to reduce the risk of encounter, detection and predation (Bergerud, 1985; James et al., 2004). However, intensive forest management has led to a marked decrease in the availability of mature fir stands rich in arboreal lichens (Stone et al., 2008), which were converted into early seral stages suitable to moose (Nadeau Fortin et al., 2016). Human-driven habitat changes have been shown to support an increase in predator density (Boudreau, 2017) in response to an increase in small mammals (Etcheverry et al., 2005), fruit-bearing shrubs (Boisjoly et al., 2010; Lesmerises et al., 2015), and moose densities (Frenette et al., 2020). Moreover, an important forest road network established to support forest management, the presence of hiking trails and the movement capacities of predators facilitate coyote and bear dispersal into caribou habitat, especially in the alpine tundra where caribou are found during calving (Gaudry, 2013; Mosnier et al., 2005, 2008).

In such an altered landscape, avoiding predators might be more difficult now than it was before (1998-2004; Mosnier et al., 2008). The relative abundance of both coyotes and bears were shown to have a strong influence on caribou calf recruitment in Gaspésie, and their effect appears influenced by the relative abundance of moose, but also by habitat modifications (Frenette et al., 2020). We went a step further by showing that the respective diet of caribou and its incidental predators, which also rely on plants, may force caribou to use the same habitats where common resources shared with predators (mostly with bears) can be found, thus explaining at least partially opportunistic predation on caribou calves.

3.6.4 Conclusions, limitations and future research

Considering the low proportion of caribou found in the diet of predators in our study area, as well as the limitation of stable isotope analysis to detect scarce food sources (Nielsen et al., 2018; Phillips et al., 2014), more studies are needed to assess the diet composition of predators during other periods of the year, including the caribou neonatal stage when predation is most important (Crête & Desrosiers, 1995; Pinard et al., 2012). We also suggest that future research combines diverse dietary approaches in their analyses. Nevertheless, we found a low proportion of caribou in the diet of predators in our study area, which corresponds with their status of opportunistic predators. However, our study presented evidence suggesting that the omnivorous diet of bears and coyotes – and their trophic niche overlap with caribou – may play a key role in their predator-prey relationship with caribou. While coyotes and bears exert an incidental predation on caribou at the individual level, we consider that the high densities of these two predator species in our study area could explain the low recruitment noted for the endangered caribou in Gaspésie. In addition, we suggest that even a low level of food and habitat overlap with moose can contribute to the decline of this population or limit its potential to recover, given the precarity of the Gaspésie caribou population in the context of apparent competition interaction (Holt, 1977). Restoration (Lacerte et al., 2021) and protection of the last suitable habitat alongside other strategies like maternal penning, moose hunting and predator control (Johnson et al., 2019) are needed to establish efficient conservation and management strategies to insure the persistence of this caribou population.

3.7 Acknowledgements

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3.8 Supplementary material

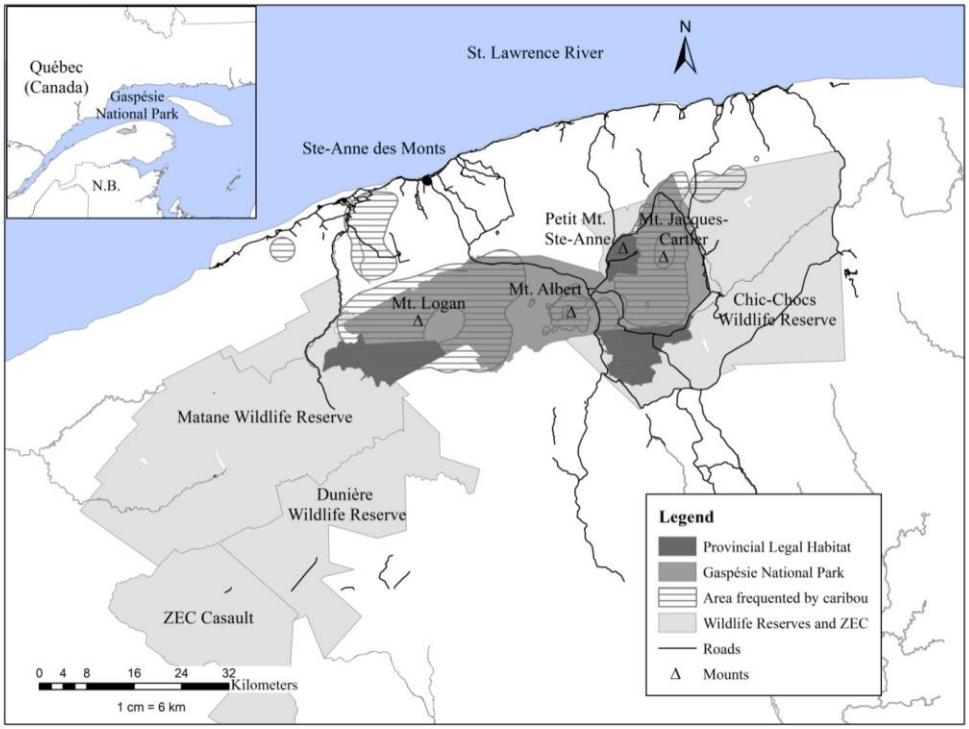

Figure S3.1. Study area of the Atlantic-Gaspésie caribou, moose, coyote and black bear populations in the Gaspésie National Park and the surrounding Wildlife Reserves and controlled harvesting zone (ZEC), Québec, Canada (Mount Logan: 1 128 m, Mount Albert: 1 154 m, Mount Jacques-Cartier: 1 268 m, and Petit Mount Ste-Anne: 1 147 m). The study area is composed of three distinct vegetation zones: the montane boreal forest belt (100-900 m) is mainly composed of balsam fir, white spruce (*Picea glauca*), black spruce (*P. mariana*), and white and yellow birch (*Betula alleghaniensis*), the transitional subalpine zone area (900-1050 m) is a krummholz belt characterized by stunted trees and shrubs, and the alpine tundra (> 1050 m) is mainly composed of lichens, mosses, graminoids and ericaceous shrubs shaped by the exposure to wind (Boudreau, 1981). The area frequented by caribou was estimated using a 95% kernel density estimator (kernelUD, package adehabitatHR, Calenge, 2019) using GPS locations of 43 Gaspésie caribou collected from a telemetry monitoring program that took place between 2013 and 2016. Three main summits are used by this caribou population; from west to east, the Logan ridge, the Albert plateau and the McGerrigle area.

3.8.1 Plant sample collection

We collected a few plant species per plant functional group: aquatic plants (3 *Nuphar variegatum*), deciduous trees (3 *Betula papyrifera*, 9 *Sorbus americana*, 9 *Salix spp.*, 3 *Populus balsamifera*), ericaceous shrubs (6 *Vaccinium spp*, 3 *Kalmia augustifolia*, 3 *Ledum groenlandicum*), evergreen trees (9 *Picea glauca*, 9 *Abies balsamea*), ferns (3 *Dryopteris spp.*, 6 *Athyrium filix-femina*), forbs (6 *Taraxacum spp.*, 3 *Hieracium pretense*, 3 *Maianthemum canadense*, 6 *Clintonia borealis*, 3 *Juncus spp.*, 9 *Epilobium angustifolium*, 3 *Aralia nudicaulis*, 6 *Cornus canadensis*, 9 *Trientalis borealis*, 3 *Ranunculus septentrionalis*, 6 *Trifolium spp.*, 3 *Fragaria Americana*, 3 *Vicia cracca*), fungi (5 *Agaricaceae* family), graminoids (2 *Carex spp*., 3 *Scirpus spp*., 4 *Agrostis borealis*, 3 *Festuca obtuse*, 6 *Habenaria dilatata*), horsetails (9 *Equisetum arvense*), and shrubs (9 *Alnus spp.*, 6 *Cornus stolonifera*, 3 *Amelanchier bartramiana*, 9 *Rubus idaeus*, 9 *Ribes spp.*, 6 *Lonicera canadensis*, 3 *Diervilla lonicera*, 6 *Viburnum spp.*, 6 *Acer spicatum*).

3.8.2 Food sources selection

The food sources that we included in the Bayesian stable isotope mixing models for the three species studied (moose, bears and coyotes) were chosen based on studies conducted in our study area and literature reviews. Briefly, DNA barcoding analyses of moose scats conducted in the same study area as ours observed a consumption of deciduous trees, evergreen trees, and shrubs in summer and autumn (Christopherson et al., 2019). Consumption of shrub and tree leaves is also reported in other moose populations in Québec (Drucker et al., 2010; Dussault et al., 2004) while consumption of ferns by moose is reported in Maine (Lautenschlager et al., 1997) and Alaska (Welch et al., 2015). Few studies described the diet of coyotes and black bears in our study area based on scat analyses and also in other adjacent regions. Coyote

scat analyses conducted in Gaspésie (Boisjoly et al., 2010), in the adjacent eastern New Brunswick (Dumond et al., 2001) and on the south shore of St. Lawrence River in southeastern Québec (Tremblay et al., 1998) reported a consumption of deer, moose, hare, fruits, and graminoids by coyotes. Boisjoly et al. (2010) found caribou hair in six coyote faeces on 150 analysed. Black bears are opportunistic omnivores, feeding on invertebrates, plants, vertebrates, and also on anthropogenic resources (Baldwin & Bender, 2009; Boileau, 1993; Boisjoly et al., 2010; Gaudry, 2013; Lesmerises et al., 2015; Mosnier et al., 2008). Diet composition also vary significantly with resource and habitat availability (Brodeur et al., 2008; Latham et al., 2011c). In our study area, Boileau (1993) and Mosnier et al. (2008) analysed 265 black bear scats and reported that black bears consumed mainly plants, such as graminoids, dandelions, horsetails, willow, and fruits. They also reported consumption of moose fawn, hare, and beaver (*Castor Canadensis*), but no trace of caribou consumption was found in the 265 faeces analysed. Crête and Desrosiers (1995) reported caribou consumption by coyotes and black bears in Gaspésie.

3.8.3 Bayesian priors

We included informative prior distributions on the dietary proportions to increase the robustness of the mixing models (Moore & Semmens, 2008; Stock & Semmens, 2016) based on studies conducted in our study area. For moose, priors of diet composition came from Christopherson et al. (2019) study that analysed 40 fecal pellets using DNA barcoding analyses, while for predators, we used data from scat analyses from 60 black bear faeces and from 115 coyote faeces (Martin-Hugues St-Laurent, *unpublished data*). Specific priors were reported in Table S.3.2.

Table S3.1. Means and standard deviations of carbon (C) and nitrogen (N) concentrations measured in dietary predator food sources.

Dietary sources	C (mg)		N (mg)	
	mean	SD	mean	SD
Animal				
Caribou	0.29	0.06	0.09	0.02
Deer	0.45	0.05	0.15	0.02
Grouse	0.47	0.01	0.16	0.01
Hare	0.47	0.02	0.16	0.01
Insects	0.51	0.06	0.12	0.02
Large rodents	0.48	0.03	0.16	0.01
Moose	0.50	0.04	0.17	0.01
Small rodents	0.48	0.03	0.16	0.01
Plant				
Dandelion	0.26	0.02	0.02	0.00
Fruits	0.29	0.03	0.02	0.01
Graminoid	0.29	0.02	0.02	0.00
Other plants	0.30	0.04	0.01	0.01
Willow	0.32	0.04	0.02	0.01

Table S3.2. Informative priors on the dietary proportions included in the mixing models for the three species studied.

Dietary sources	Priors		
	Moose	Coyote	Bear
Animal			
Caribou		0.03	0.01
Deer		0.44	0.12
Grouse		0.006	0.02
Hare		0.11	0.03
Insects		0.003	0.04
Large rodents		0.03	
Moose		0.27	0.06
Small rodents		0.02	
Plant			
Aquatic plants			
Deciduous trees	0.65		
Ericaceous	0.03		
Evergreen trees	0.07		
Ferns			
Forbs	0.01		
Fungi			
Graminoids	0.01		
Horsetails	0.02		
Shrubs	0.17		
Fruits&Graminoids		0.17	
Fruits&Graminoids&Dandelions			0.66
Willow			0.02

CHAPITRE IV

LIENS ENTRE LES PERFORMANCES INDIVIDUELLES DES CARIBOUS, LES ÉLÉMENTS TRACES ET LES ISOTOPES STABLES DANS UNE POPULATION D'ONGULÉS MENACÉE D'EXTINCTION

LINKS BETWEEN CARIBOU INDIVIDUAL PERFORMANCE, TRACE ELEMENTS AND STABLE ISOTOPES IN AN ENDANGERED UNGULATE POPULATION

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4.1 Résumé

L'alimentation et la condition physiologique sont des facteurs importants pour la santé, la croissance, la reproduction et la survie d'un individu, mais ces facteurs ne sont pas bien documentés chez plusieurs espèces sauvages. Une alimentation pauvre en protéines, vitamines, nutriments et minéraux peut entraîner une faible condition individuelle et affecter le taux de reproduction, la survie et, ultimement, entraîner le

déclin d'une population. Ce chapitre vise à mieux comprendre les liens entre l'alimentation et la condition physiologique ainsi que leurs effets combinés sur la santé et les performances individuelles chez une population de caribous (*Rangifer tarandus caribou*) en voie de disparition. J'ai mesuré les signatures isotopiques du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) ainsi que la concentration de 21 éléments traces dans les poils de 44 caribous (~ 50% de la population). Mes résultats ont montré que le régime alimentaire du caribou de la Gaspésie-Atlantique en été/automne était constitué principalement de lichens, de feuilles d'arbres décidus et d'arbustes ainsi que de fougères, de champignons et de conifères. J'ai également mis en évidence une relation étroite entre l'accumulation en divers éléments traces et les signatures isotopiques mesurées dans les poils de caribous. Une augmentation de $\delta^{13}C$ (indiquant une consommation plus élevée de lichens, champignons et arbres décidus) était liée à des concentrations plus faibles de potassium, de calcium et de manganèse dans les poils, tandis qu'une diminution de $\delta^{15}N$ (indiquant une consommation plus élevée de lichens, d'arbustes et d'arbres décidus) était liée à une concentration plus faible de césium et à une concentration plus élevée de cobalt. Les probabilités de gestation des femelles et de survie des faons étaient plus élevées lorsque les valeurs de $\delta^{13}C$ des caribous femelles étaient plus élevées. La probabilité de survie des adultes était quant à elle plus élevée chez les caribous qui avaient des concentrations plus élevées de zinc et de sodium et des concentrations plus faibles de césium et de manganèse dans les poils. Ce chapitre contribue à clarifier le lien entre certains éléments traces et une meilleure performance individuelle chez un grand mammifère. Ces résultats révèlent que la nutrition pourrait jouer un rôle clé dans le déclin de cette population de caribous en voie de disparition.

4.2 Abstract

Foraging is a key behaviour, and several aspects of foraging remain to be investigated in many wild species. Low energy gain or reduced protein, nutrient, and mineral intake may explain poor individual condition, low reproductive output, high mortality, and, in extreme cases, population declines. Our study aims at exploring how foraging ecology, diet composition, and nutritional status could influence individual performance in an endangered population of caribou (*Rangifer tarandus caribou*). We measured stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as well as the concentration of 21 trace elements in the hairs of 44 caribou (~ 50% of the population). Our results showed that the Atlantic-Gaspésie caribou population consumed mainly lichens, deciduous trees, shrubs, ferns, fungi, and evergreen trees. Using a redundancy analysis, we found a correlation between diet (described using stable isotope ratios) and accumulation of trace elements in hair, but we also detected relationships between diet, trace elements and vital rates. Pregnancy and calf survival probabilities were higher when the $\delta^{13}C$ signature of female caribou was higher, and adult survival probability was higher in caribou that had higher concentrations of zinc and sodium, and lower concentrations of cesium and manganese in hair. Our study provides empirical evidence that nutrition could be related to lower performance of caribou at the individual level and that nutrition plays a key role in the decline of this endangered caribou population.

Keywords: caribou, demography, diet, foraging ecology, reproduction, survival

4.3 Introduction

Diet diversity and quality are not fully described for several wild species (Carlsson et al., 2019a), although these are key factors that influence, growth, reproduction, and survival (Parker et al., 2009; Post & Klein, 1999; Thompson & Barboza, 2013), and that may also ultimately influence fitness (Abramsky et al., 2002; Macbeth & Kutz, 2019) and population dynamics (Macbeth & Kutz, 2019; Stephenson et al., 2020). Insufficient acquisition of energy, proteins, nutrients, and minerals via food intake has been linked to poor individual condition (Parker et al., 2009), low reproductive output (Flueck et al., 2012; Flynn et al., 1977), high mortality (Cook et al., 2004a), and even with the decline of some populations (Barboza & Reynolds, 2004; Post & Klein, 1999). It is thus important to improve our knowledge of the links between foraging ecology and diet composition, and to understand how these variables influence the health and vital rates of wild species.

Biochemical markers, such as stable isotope ratios and trace elements, have become an important tool for researchers studying foraging ecology of species in the wild (Kelly, 2000; Peterson & Fry, 1987) and to bring insights on the health status of an individual (Åhman & White, 2019; Åhman et al., 2019). While stable isotope ratios mainly provide information about trophic relationships (Hobson & Welch, 1992; Post, 2002) and diet composition (Ben-David et al., 1997; Phillips et al., 2005), coupling isotope ratios with trace elements can increase our understanding of individual or population health (Åhman & White, 2019; Åhman et al., 2019), as well as habitat use and trophic relationships (Brookens et al., 2007; Hobson & Welch, 1992; Post, 2002). As for stable isotopes, trace elements are acquired by terrestrial animals from their environment, mainly via food ingestion, water consumption (Langston & Spence, 1995; Pragst & Balikova, 2006; Reglero et al., 2009; Smith et al., 2007) and natural mineral licks (Heard & Williams, 1990). For example, lichens are known to contain highly digestible carbohydrates (Person et al., 1980), but to be poor in vitamins,

proteins, nitrogen (Bergerud, 1972; Person et al., 1980; Røed et al., 2019), and trace elements (e.g. Co, Mo, Mn, Ca, K, Cu, Staaland & White, 2001). In contrast, fungi are highly nutritive and rich in vitamins, proteins, enzymes, sugar, and fat (Nieminen & Heiskari, 1989). Deciduous trees and shrubs are a good source of energy, protein, and minerals (e.g. Co, Cu, Mn, Zn, Klein, 1990; Thompson & Barboza, 2014). Animals integrate trace elements in their tissues (e.g. skin, hair) and organs (e.g. liver, kidney) where they may also bioaccumulate (Bhattacharya et al., 2016). For example, trace elements are continuously incorporated into the hair shaft during the period of hair growth, mainly via blood flux (Flache et al., 2017; Vermeulen et al., 2009); hair thus represents an archive of what elements were available during their growth. There is empirical evidence that certain trace elements accumulate in the hair of mammals: this is the case of arsenic (As; Hopps, 1977), cadmium (Cd) and cobalt (Co; ATSDR, 2004), copper (Cu; d'Havé et al., 2006), iron (Fe; Åhman et al., 2019), magnesium (Mg) and manganese (Mn; Huckabee et al., 1972), lead (Pb; Sparling, 2006), and selenium (Se; Puls, 1988).

Essential trace elements are part of protein complexes (i.e. metalloproteins) and are required as cofactors for many biochemical pathways, metabolic routes, and enzymatic activities (Bhattacharya et al., 2016; O'Hara et al., 2001). Some elements (e.g., cadmium, lead, mercury) are considered non-essential as they typically have no biochemical function, but may interfere with essential trace elements (Anderson et al., 2010). Nevertheless, adverse effects will arise if homeostasis is disrupted for a given element, such as when essential elements are not in the required physiological range, and non-essential element exceed toxic thresholds (Bhattacharya et al., 2016). However, the trace element concentrations required in free-ranging animals are not well understood, and normal reference ranges do not exist for many species (Bondo et al., 2019). Past studies on trace elements in wildlife have largely focused on contaminant exposure (Smith et al., 2007), food safety (Hassan et al., 2012) or major deficiencies (Flueck et al., 2012; Flynn et al., 1977). It has been shown that high or

low concentrations of some trace elements can impair growth (Pollock, 2005), reproduction (Abdollahi et al., 2013; Flynn et al., 1977; O'Hara et al., 2001; Underwood & Suttle, 1999) and the immune system (Bhattacharya et al., 2016; Boland, 2003) (see Table 4.1). For example, a deficiency in copper has been linked to poor calf recruitment, high adult mortality and some abnormal keratinized hoof material in an Alaskan moose (*Alces americanus*) population (Flynn et al., 1977; O'Hara et al., 2001). Selenium deficiency has been related to high calf mortality due to muscular dystrophy in a black-tailed deer (*Odocoileus hemionus columbianus*) population in California (Flueck, 1994; Flueck et al., 2012).

Most caribou populations are declining across their circumpolar range (Vors & Boyce, 2009) including several provinces of Canada (Festa-Bianchet et al., 2011). The last caribou herd found in southeastern Québec, known as the Atlantic-Gaspésie caribou population (hereafter referred as Gaspésie caribou population) is also declining (Frenette et al., 2020). Over the last three decades, the population has declined from 130 caribou in 1990 to 40 (range 38-42) individuals in 2019 (see section 4.8 Supplementary material, Figure S4.1) (Morin & Lesmerises, 2020). Indeed, the recruitment (% of calves in the population) is highly variable between years and was estimated at 10.2% (± 7.2, [3.9 : 16.5]) (mean ± *SD*, [95% confidence interval]) for the last five years (see section 4.8 Supplementary material, Figure S4.1) (Morin & Lesmerises, 2020), and the adult survival is low (~ 77% for females and ~ 56% for males in 2014 and 2015, Frenette et al., 2020). This population is designated as Endangered since 2000 under the Canadian Species at Risk Act (SARA; COSEPAC, 2014). Habitat-mediated predation, exacerbated by increased habitat alteration, is identified as the main cause of population decline in the Gaspésie herd (Frenette et al., 2020). Coyotes (*Canis latrans*) and black bears (*Ursus americanus*) were shown to be responsible for the majority of predation events on caribou calves (Crête & Desrosiers, 1995). Anecdotal observations suggest that coyotes can kill adult caribou in Gaspésie and in Newfoundland (Huang et al., 2021; Lewis & Mahoney, 2014), but

it is unknown if this predation pressure is considered as an important factor affecting adult survival. However, a recent analysis has shown that caribou are of minor importance in both bear and coyote summer/autumn diets on an individual basis (Rioux et al., 2022), but high predator densities could nevertheless result in an important predation pressure on the caribou population (Frenette et al., 2020).

A previous study on Gaspésie caribou showed that parasite infection intensity affected body condition, however there were no reported effects on survival (Turgeon et al., 2018). A first study on diet composition in our study area has been conducted (Christopherson et al., 2019), however several aspects remain to be investigated (e.g. individual variability). Since essential trace element deficiencies could affect individual reproduction and survival (Table 4.1) (Bondo et al., 2019; Flueck et al. 2012; O'Hara et al., 2001) and that trace elements are mostly acquired via food ingestion (Smith et al., 2007), identifying links between diet composition, trace elements and demographic rates is critical to improve our understanding of the factors driving woodland caribou population dynamics.

Our study aimed at 1) describing the summer/autumn diet composition of the Gaspésie caribou using a stable isotope mixing model, 2) assessing the stable isotope and trace element levels in the hair of caribou from this population, 3) testing whether a relationship exists between the accumulation of trace elements in caribou hair and diet, and finally, 4) evaluating if trace elements and stable isotope ratios are associated with female pregnancy status, summer calf survival, and adult survival and lifespan. Given that the Gaspésie caribou population must cope not only with human disturbance activities that influence movement (Lesmerises et al., 2018), but also an apparent competition phenomenon (sensu Holt, 1977; see Frenette et al., 2020) and trophic niche overlap with bears, and to a lesser extent with coyotes and moose (Rioux et al., 2022), we hypothesized that the most nutritious food sources may not be accessible to caribou; consequently, they are constrained to feed on lower quality

resources. We expected that females foraging on lower quality resources to have a lower pregnancy probability, calf recruitment and survival. Because low concentrations of some essential elements are known to potentially impair individual performance (Table 4.1), we expected relatively low concentrations of calcium, cobalt, copper, manganese, and selenium in hair as a possible explanation of low observed values of pregnancy, calf recruitment and adult survival rates in this population (Frenette et al., 2020) as well as in other ungulate populations (Flynn et al., 1977; O'Hara et al., 2001).

Table 4.1. Previous knowledge about the possible roles or negative effects of trace elements on growth, reproduction or survival based on the literature review.

Trace elements	Essential for ...	Toxicity effect on ...	Deficiency effect on ...
Ag	-	↑ mortality [1]	
Al	-	↑ stress [2]	
As	-	Interferes with endocrine and thyroid systems, ↑ mortality, affects pregnancy [3]	Uncertain, may ↓ growth and abnormal reproduction [4]
Ba	-	Highly toxic, ↑ mortality, ↓ pregnancy rate [1,3,5]	
Ca	Pregnancy, stress, nutrition, lactation [6]		↓ antler growth, ↓ fetal development, impairs lactation [7], ↓ survival and reproduction probability [8], ↑ mortality [9]
Cd	-	↑ mortality, ↓ immune function [1,3,5]	
Co	Pregnancy, lactation, survival, hormones, metabolism, growth, B12 synthesis [10], immune system [11]		Impairs conception [2], lactation [10] and growth [1,10], anemia [13]
Cr	Associated with insulin [1]		Stresses calves and ↓ growth rate, immune response [1]
Cs	-	↑ mortality, behavioral effect [14,15]	
Cu	Pregnancy [16], lactation [6], survival, hormones, metabolism, growth, B12 synthesis [10], immune system [11]	↑ mortality, ↓ pregnancy probability [3,5]	↓ reproduction rate, antler deformity, hoof keratinization, role in population decline, ↑ calf mortality and adult [7,17],

[1] Puls (1988), [2] Underwood & Suttle (2010), [3] Sparling (2016), [4] Nielsen (1984), [5] Barboza & Parker (2006), [6] Oster (2017), [7] O'Hara et al. (2001), [8] Ropstad et al. (1997), [9] Hyvärinen et al. (1977), [10] Staaland & White (2001), [11] Åhman et al. (2019), [12] Pollock (2005), [13] ATSDR (2004), [14] Skuterud et al. (2004), [15] Papastefanou et al. (1989), [16] Gamberg et al. (2016), [17] Flynn et al. (1977), [18] Barboza et al. (2009), [19] Robbins (1993), [20] ATSDR (2012), [21] Wallisdevries (1996), [22] Flueck et al. (2012), [23] Flueck (1994), [24] Klaassen (2008), [25] Gamberg (2000), [26] Abdollahi et al. (2013), [27] Boland (2003), [28] Bhattacharya et al. (2016).

			susceptibility to infection [18], ↑ mortality [9], impacts lactation and growth [10]
Fe	Survival, immunity, lactation [6]		Impaired O_2 uptake for physical activity [18], ↓ pregnancy, survival
K	Stress, lactation, pregnancy [6]		Muscle weakness, retarded growth [19]
Mg	Pregnant, nutrition, lactation [6]		↑ mortality, ↓ reproduction probability [8], ↑ mortality [9]
Mn	Pregnancy, lactation [6], nutrition, survival, formation of cartilage, antler growth [11,19], immunity [20]	Fœtus and embryon toxicity, sperm damage [20]	Infertility, calf with poor growth [12], affects bones density [20]
Mo	Pregnancy, nutrition, survival, enzymatic reaction [19]		↓ growth [19], affects pregnancy, survival, population decline and ↑ mortality
Na	Pregnancy, lactation, growth [6]	Interferes with hormone, metabolism and growth [10]	Impacts lactation, growth of immature caribou [10], long-term survival and reproduction [21]
Pb	-	Highly toxic, effect on reproduction, ↑ mortality [3,5]	
Se	Physical condition, pregnancy, lactation, nutrition, survival, immunity, growth [22]	↑ mortality [1]	Stillborn, abortion, ↓ fertility, ↑ calf mortality, white muscle disease [17,22,23], resistance to infection [12], ↑ mortality [9]
Tl	-	↑ mortality, fetal effect [24]	
V	Growth, hormone [2]	Interferes with hormone, metabolism [2]	Incorporates into plasma transferrin, ↓ growth and reproduction performance [1]
Zn	Pregnancy [16], survival, immunity [3], lactation [6]	Anemia [25]	Affects fertility, abortion [26], ↓ survival, hair loss, wrinkled skin, growth [12], immune response [27,28], impaired reproduction [19], wound healing [25], infertility [18]

[1] Puls (1988), [2] Underwood & Suttle (2010), [3] Sparling (2016), [4] Nielsen (1984), [5] Barboza & Parker (2006), [6] Oster (2017), [7] O'Hara et al. (2001), [8] Ropstad et al. (1997), [9] Hyvärinen et al. (1977), [10] Staaland & White (2001), [11] Åhman et al. (2019), [12] Pollock (2005), [13] ATSDR (2004), [14] Skuterud et al. (2004), [15] Papastefanou et al. (1989), [16] Gamberg et al. (2016), [17] Flynn et al. (1977), [18] Barboza et al. (2009), [19] Robbins (1993), [20] ATSDR (2012), [21] Wallisdevries (1996), [22] Flueck et al. (2012), [23] Flueck (1994), [24] Klaassen (2008), [25] Gamberg (2000), [26] Abdollahi et al. (2013), [27] Boland (2003), [28] Bhattacharya et al. (2016).

4.4 Materials and methods

4.4.1 Study area

The study area is located in the Gaspésie National Park and the surrounding Matane, Dunière and Chic-Chocs Wildlife Reserves (Figure 4.1). It is part of the southeastern boreal forest in the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain. In the past decades, intensive forestry activities have largely modified vegetation around the Gaspésie National Park, reducing the area covered by mature conifer forest by ~ 50% thus increasing the area covered by young mixed or conifer forest (Boudreau, 2017). In addition, some mining sites that were previously exploited within the Gaspésie National Park (i.e. *Madeleine* Copper-mine, exploited between 1964 and 1982 and located near the Petit Mont Ste-Anne, but also *Gîte Fédéral* Lead and Zinc-mines, exploited from 1916 to 1950 and located near Mount Albert) and in the surrounding area (i.e. Murdochville Copper-mine and smelter, exploited between 1951 and 2002) may have a historical soil contamination, and trace elements may be transferred in water and plants (Aznar et al., 2007, 2008), which could eventually have an effect on caribou (Figure 4.1). This area is used by the Gaspésie caribou population, a small, relict herd that uses bare habitats as well as montane and subalpine forests found at high elevations (> 700m). Areas located in the vicinity of the three main summits are used by this caribou population: the Logan Ridge in the west, the Albert plateaus, and the McGerrigle area in the east (Figure 4.1). This population includes two subgroups (Logan-Albert vs. McGerrigle) based on their geographical locations and genetic substructure (Pelletier et al., 2019).

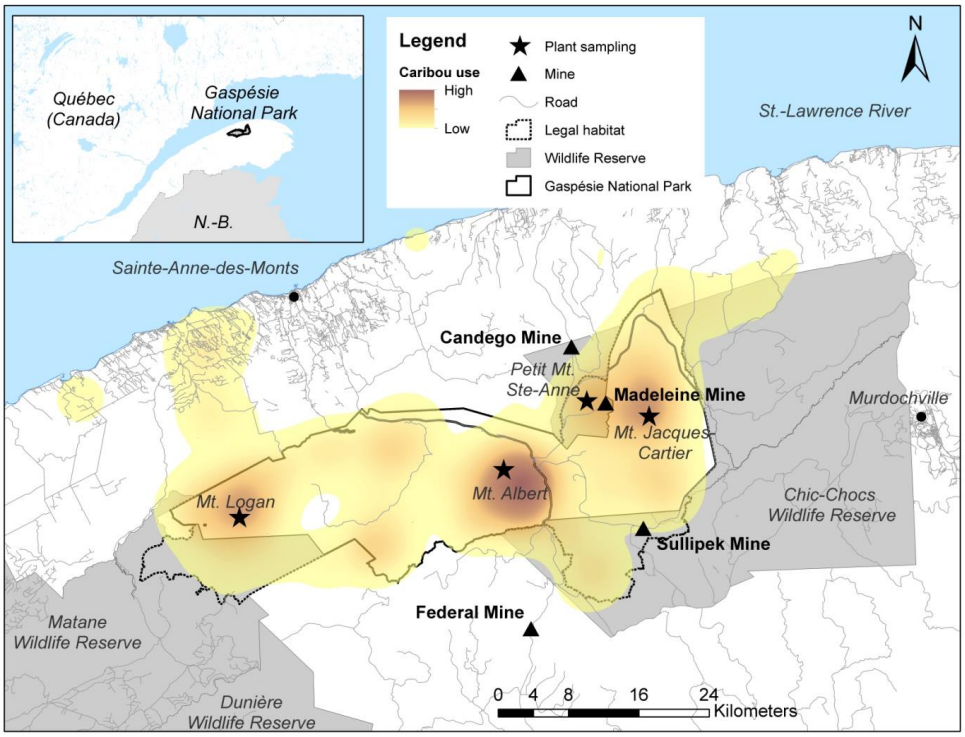

Figure 4.1. Study area of the Gaspésie caribou population in the Gaspésie National Park and the surrounding Matane, Dunière and Chic-Chocs Wildlife Reserves, Québec, Canada. Plants were sampled in the alpine tundra on the summits of Mt. Logan (1 128 m), Mt. Albert (1 154 m) and Petit Mt. Ste-Anne (1 147 m). Area frequented by caribou was estimated from 99% kernel density estimator (kernelUD, package adehabitatHR, Calenge, 2019) with GPS locations of caribou collected via a telemetry monitoring programme that took place between 2013 and 2016.

4.4.2 Caribou capture and sampling

In February and March 2013 and 2014, we captured 17 male and 27 female adult caribou (~ 50% of the population at that time) across the Gaspésie caribou range using a net-gun fired from a helicopter (Potvin & Breton, 1988). Our capture protocol was authorized by the Animal Welfare Committee [Université du Québec à Rimouski (hereafter UQAR) certificate #CPA-52-13-112; Ministère des Forêts, de la Faune et

des Parcs (hereafter MFFP) certificate #CPA FAUNE 13-08]. Each individual was marked and fitted with a GPS/Argos telemetry device (model TGW-4680, Telonics Inc., Mesa, AZ). For each capture, we noted the location, the sex of the animal and a body condition score. This score ranged from 1 to 4, where a value of 1 indicated an individual in bad condition showing signs of malnutrition, and 4 indicated an individual in good condition with a layer of fat thick enough that no prominent bones were visible (modified from Gerhart et al., 1996; Turgeon et al., 2018). Then, we classified caribou into two categories: the lower condition included the ones with a body condition score ranging from 1 to 3 and caribou in better condition with body condition score of 4. We used this approach to have a two-level factor of similar sample size discriminated above and below the average value of 3.39 (as in Turgeon et al., 2018). We collected fecal samples and used them to estimate parasite intensity (i.e. mean no. of eggs of seven parasite species per infected host; see details in Turgeon et al., 2018), and we collected 19 serum samples to evaluate the pregnancy status of female caribou using BioPRYN tests (Russell et al., 1998). We also collected 44 hair samples from the rump; these samples were dried and stored in paper bags at ambient temperature until processing.

Hair is a good matrix for analysis of trace element concentrations and stable isotope ratios (Dunnett, 2005; Pragst & Balikova, 2006) because it is a biologically inactive tissue once synthesized. Trace elements are continuously incorporated into the hair shaft during the period of hair growth, mainly via blood flux (Flache et al., 2017; Vermeulen et al., 2009). Thus, concentrations of trace elements and isotopic composition in hair reflect levels during the period of tissue growth (Hilderbrand et al., 1996; Hopps, 1977; Schwertl et al., 2003). Molt occurs generally at the end of the cold season (April to June), and the new fur grows in from late spring/early summer (June) to autumn (Darimont & Reimchen, 2002; Jacoby et al., 1999; Ling, 1970; Mowat et al., 2017). We therefore assumed that trace element and isotopic composition measured in hair collected in February and March would represent the

summer/autumn period of the previous year. Nevertheless, there are still uncertainties as to whether hair trace element content is strongly correlated with whole-body levels, so trace elements observed in hair are not necessarily comparable with those found in liver or other tissues (Bhattacharya et al., 2016).

4.4.3 Caribou observations and survival

During the summer period of 2013 and 2014 (May 25th – August 20th), we conducted 30 min focal observations of 19 marked females (see details in Lesmerises et al., 2017). A total of 171 focal observations were done at the Albert plateaus and McGerrigle area. We could not conduct behavioural observation at Logan Ridge due to the difficulty of access and the poor visibility in this closed-canopy forested area. Each female was observed in average 9.67 ± 4.52 (*SD*) times (95% CI [9.53 : 9.98]) (Lesmerises et al., 2017). We used these focal observations to determine whether each of the 14 calves that accompanied the 19 females have survived or not (1 or 0) until the end of the summer (see Lesmerises et al., 2017 for more details). Mortalities of adult caribou (both males and females) were confirmed by field investigations in days following a mortality signal (GPS locations obtained via the Argos link).

4.4.4 Plant sample collection and preparation

To estimate diet composition, we collected plant samples (leaves and flowers) from potential dietary item sources consumed by caribou (see details in section 4.8 Supplementary material). We collected 223 plant samples in 2017 in the alpine tundra across the Gaspésie caribou range, 93 on Mount Albert and 78 on Mount Logan (Figure 4.1). Due to methodological and ethical constraints (i.e. collecting plants in a National Park), we focused our sampling in the McGerrigle area on the Petit Mont Ste-Anne, located in the Chic-Chocs Wildlife Reserve, and collected 52 plant samples

(Figure 4.1). Vegetation on this summit is similar that of the other areas in the McGerrigle caribou sub-population range. Our plant sampling was authorized by the Gaspésie National Park (certificate # PNG-2017042703). We randomly collected three replicates per plant species (see section 4.8 Supplementary material, Table S4.1), washed plant samples using distilled water to remove surface contamination (e.g. dust, soil), dried the plant samples at room temperature and froze them at -20°C until they were processed. Then, we freeze-dried the plant samples (~ 1 g) for 48h before they were ground to a fine powder using a CryoMill (Bosley & Wainright, 1999; Jardine et al., 2003). We stored the plant samples in a desiccator until stable isotope analyses.

4.4.5 Hair samples preparation and lipid extraction

We washed hair samples using a solution of 2:1 chloroform-methanol in an ultrasonic bath to remove all possible surface contamination, external lipids (Hobson et al., 2000) and external trace element deposition from environmental exposure (Smith et al., 2007). We then rinsed samples in distilled water and oven-dried at 50°C for 24h (Hobson et al., 2000). Before lipid extraction and stable isotope analyses, we freeze-dried hair subsamples for 48h and ground them to a fine powder using a CryoMill with cooling option (liquid nitrogen at -196°C) (Bosley & Wainright, 1999; Jardine et al., 2003). Variability in the lipid content of samples can bias stable isotope signatures measured in tissues because lipids are more depleted in ^{13}C relative to protein and carbohydrate fractions (DeNiro & Epstein, 1977; McConnaughey & McRoy, 1979). We divided hair samples into two parts to determine $\delta^{13}C$ and $\delta^{15}N$ values separately to account for lipid effect on stable isotope signatures: one part of the subsamples received no further treatment prior to nitrogen isotope analyses (bulk part), and the second part was lipid-extracted prior to carbon isotope analyses (Kelly, 2000; Lesage et al., 2010; Post et al., 2007; Rioux et al., 2019). We conducted lipid extraction using the second part of powdered hair samples (to remove internal lipids,

Dunnett, 2005; Dunnett & Lees, 2003) and a solvent consisting of a mixture of chloroform and methanol (2:1 v/v) (Folch et al., 1957). We shook the mixture and stored it overnight at 4°C. We then centrifuged the mixture at 11,200 g for 10 min and discarded the supernatant (Folch et al., 1957). We repeated the whole procedure two times. After 3 extractions, we dried samples by evaporation overnight, rinsed with distilled water, oven-dried overnight at 50°C and powdered again.

4.4.6 Stable isotope analyses

We weighed a 0.500-0.700 mg (± 0.001 mg) subsample of powdered hair tissue (bulk and lipid-free) into a tin capsule and analyzed it for stable carbon (lipid-free) and nitrogen (bulk) isotope ratios using a COSTECH ECS 4010 Elemental Analyser coupled to a DeltaPlus XP Isotope Ratio Mass Spectrometer (IRMS, Thermo Electron Co, Marine Chemistry and Mass Spectrometry Laboratory, UQAR). We also weighed a 0.500-0.700 mg (± 0.001 mg) subsample of powdered plant tissue into a tin capsule and analyzed it for both stable carbon and nitrogen isotope ratios. By convention, ^{13}C and ^{15}N isotope abundances are expressed in delta notation (‰), as $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{13}C or ^{15}N, and R_{sample} is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$; $R_{standard}$ represents the ratios for the respective standards, i.e. Vienna Peedee Belemnite (PDB) and atmospheric nitrogen (AIR). We evaluated the accuracy of our isotopic analyses using commercially certified material (B2151) and the precision of measurement by randomly duplicating a subset of our samples. Replicates using certified materials (n = 31) indicated a systematic error of ± 0.22 and ± 0.24 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, whereas the average deviations observed between replicates of hair and plant samples (n = 76) indicated an analytical error of 0.14 ‰ for $\delta^{13}C$ and 0.20 ‰ for $\delta^{15}N$.

4.4.7 Trace element analyses

We weighed previously washed and oven-dried hair subsamples (0.09 ± 0.01g) and digested them in 3.5 ml of high-purity concentrated HNO_3 and 1.5 ml of H_2O_2 (30 % v/v) at 69°C for 3 h. We diluted all samples and blanks 1:70 with deionized water, by measuring 0.15 ml of mineralized samples with 10.35 ml of deionized water to bring the original acid strength down to 1% v/v HNO_3. Then, we introduced samples into an autosampler coupled to the inductively coupled plasma-mass spectrometer (Perkin Elmer ELAN® 9000 ICP-MS, Geoscience Laboratories, Geo Labs) to analyse 21 elements known to be potentially related to vital rates: sodium [Na], magnesium [Mg], aluminium [Al], potassium [K], calcium [Ca], vanadium [V], chromium [Cr], manganese [Mn], iron [Fe], cobalt [Co], copper [Cu], zinc [Zn], arsenic [As], selenium [Se], molybdenum [Mo], silver [Ag], cadmium [Cd], caesium [Cs], barium [Ba], thallium [Tl], and lead [Pb] (Table 4.1). We quantified the element-specific detection limits as three times the standard deviation of the laboratory blank samples; limits were < 0.0001 µg/g for all elements, except for Al (0.005 µg/g), Fe (0.001 µg/g) and Zn (0.0004 µg/g). To account for the missing observations (i.e. values below the limit of detection), we substituted the estimated values by the limit of detection previously calculated and divided by 2, and used these corrected values in our statistical analyses (Quinn & Keough, 2002). We assessed the precision of the method using certified reference materials (Dogfish liver DOLT-5 and river water SLRS-6 certified reference material from National Research Council Canada). Recoveries of the trace elements ranged from 82% to 115% of the certified concentrations (see section 4.8 Supplementary material, Table S4.2). We assessed the accuracy of the method and the repeatable estimation of metal concentration using duplicate (n = 16) and replicate samples (n = 8). We calculated the coefficient of variation (hereafter referred to as CV) and considered it acceptable for all elements (see section 4.8 Supplementary material, Table S4.2); the average CV (± *SD*) was

14.7 ± 12.4 for duplicate samples and 17.7 ± 12.9 for replicate samples. We reported trace element concentrations on a µg/g dry weight basis.

4.4.8 Statistical analyses

We used Bayesian stable isotope mixing models (hereafter referred to as SIMM) to estimate the relative contribution of different food sources to caribou diet using the SIMM package in R (Parnell et al., 2013; Phillips et al., 2014). We grouped plant samples in the following 13 categorical functional groups (as classified by Marie-Victorin, 2002) to facilitate source distinction in mixing models: aquatic plants, deciduous trees, ericaceous shrubs, evergreen trees, ferns, forbs, fungi, horsetails, lichens, lycopods, graminoids, mosses and shrubs (see section 4.8 Supplementary material, Table S4.1). We used the correlation matrix of food items included in the SIMM package to meet the assumption of differences in isotopic signatures between sources. We combined the negatively correlated source proportions to gain precision in calculated proportions (Parnell et al., 2013; Phillips et al., 2014). SIMMs also require trophic discrimination factors between consumer tissue and diet (Parnell et al., 2013; Phillips et al., 2014). For caribou hair, we used average (± *SD*) trophic discrimination factors estimated in Rioux et al. (2020) based on 8 caribou monitored during a controlled feeding trial. Trophic discrimination factor estimations between caribou hair and diet reached 3.04 ± 0.60‰ for carbon and 4.23 ± 1.05‰ for nitrogen (Rioux et al., 2020). We also included prior distribution for sources in the input parameters to Bayesian models (Moore & Semmens, 2008; Stock & Semmens, 2016). This information about diet composition came from DNA barcoding analyses of caribou fecal pellets that were randomly sampled in the study area (Christopherson et al., 2019). Prior values were 0.47 for shrubs, 0.36 for horsetails, 0.10 for deciduous trees, 0.03 for evergreen trees, 0.02 for mosses, 0.01 for ericaceous shrubs, and 0.00 for all other sources. We verified model convergence with Gelman-Rubin diagnostic

tests, and the model was considered acceptable if values are < 1.1 (Gelman et al., 2014).

Using the vegan library (in R), we conducted a redundancy analysis to evaluate the relationship between stable isotopic signatures and trace elements and to estimate the proportion of the variation in carbon and nitrogen stable isotope values explained by the different trace elements (Oksanen et al., 2019). We centered and standardized variables and verified multicollinearity with the variance inflation factor (VIF). We removed highly correlated environmental variables when VIF was > 10 (Oksanen et al., 2019). We determined the significance of the model, axes and environmental variables using a permutation test implemented in the vegan package (Oksanen et al., 2019).

Finally, we tested for an association between trace elements and stable isotope signatures of hair with female pregnancy rate, summer calf survival, and adult caribou survival probabilities using logistic regressions while controlling for potential confounding variables (see below). We thus formulated a set of candidate statistical models to assess which explanatory variables best explain the variation seen in the 3 response variables (Table 4.2). Candidate models were chosen based on previous knowledge reported in literature about the possible roles or negative effects of explanatory variables on reproduction or survival in ungulates (see Table 4.1). However, we kept in mind that there are still uncertainties that hair may not indicate deficiency states unless the growth of the hair is directly related to the supply of the trace element. The explanatory variables included in these models were trace element concentrations, stable isotope ratios, the summit frequented by caribou, sex of individual, parasite infection intensity, body condition index, and regional abundance indices of caribou predators (coyotes and black bears). We estimated predator abundance indices using the number of animals harvested by trappers in three furbearer management units (*lib. Unités de Gestion des Animaux à Fourrure:* UGAF

#71, 72 and 74) that overlap the Gaspésie National Park and the number of animals harvested during the predator control program (Frenette et al., 2020). Harvest data provide a reliable proxy of abundance, although it is known to respectively underestimate and overestimate lower and higher abundance levels as a consequence of changes in harvesting effort (Cattadori et al., 2003; Winterhalder, 1980). We are aware that correcting harvest for hunting or trapping effort is recommended (Schmidt et al., 2005), but as we did not have any robust data about harvesting effort for the different species in our system, and considering the number of permits sold, we assumed effort to be relatively stable for the short period of time considered in this study (i.e. 2 years). According to a companion study conducted in the same area (Frenette et al., 2020), we thus considered that hunting and trapping records were good proxies for the fluctuating spatial abundances observed in our study area.

We identified the most parsimonious logistic regression model as the one with the lowest value of Akaike information criterion corrected for small sample size (AIC_c) among the sets of candidate models determined *a priori* (Table 4.2). In addition, we calculated ΔAIC_c and AIC_c weights (ω_i), as models with $\Delta AIC_c \leq 2$ provide a relevant and interesting support to the most parsimonious model (Burnham & Anderson, 2002) and ω_i provides the relative preference among a set of candidate models (Vandekerckhove et al., 2014). We tested if the best-supported model was statistically different from the null model using the likelihood ratio test and assessed this model's performance using the area under the ROC curve (AUC, Hosmer & Lemeshow, 2000). Finally, we also explored the relationship between the lifespan of a caribou and several explanatory variables including the time before the animal's death. We used a Cox proportional hazards regression model (Cox, 1972) using the survival library in R (Therneau, 2019). We performed all statistical analyses using R software version 3.5 (R Development Core Team, 2017).

Table 4.2. Candidate models tested to assess the relationship between female pregnancy (*n* = 15 pregnant, *n* = 5 non-pregnant), calf (*n* = 5 alive, *n* = 9 dead) and adult (*n* = 19 alive, *n* = 25 dead) survival probabilities, and caribou lifespan, and the explanatory variables.

Candidate model no.	Highlight hypotheses	Explanatory variables
Female pregnancy		
9	Past exploited mines in the park and previously reported toxicity	As + Ba + Cu + Pb + Zn
10	Increased probability to be pregnant	Ca + Mg + Na
11	Essentials for pregnancy	Co + Cu + Mo + Mn + Zn + δ^{13}C + Condition
12	Deficiency impacts on pregnancy	Co + Cu + Fe + Mo + Mn + Se + Zn
13	Increased stress	Al + Ca + K + Parasite intensity
14	Importance of nutrition	δ^{13}C
Calf survival		
15	Past exploited mines in the park	Cu + Pb + Zn + Summits
16	Female body condition	Condition + δ^{13}C + Se
17	Essentials for pregnancy and lactation	Co + Cu + Mn + Se
18	Importance in diet	Mo + Mn + Ca + Mg
19	Indicator of female nutrition	δ^{13}C + Se
20	Predation impact	Coyote abundance + Bear abundance
21	Increased stress	Al + Ca + K + Parasite intensity
Adult survival and lifespan		

1	Essential for survival	Cu + Fe + Mn + Co + Zn + Se + Mo + $\delta^{13}C$ + Condition
2	Deficiency impacts on survival	Ca + Cu + Fe + Se + Mn + Mo + Zn
3	Toxicity impacts or increase mortality	Ag + As + Ba + Cr + Cu + Cd + Cs + Pb + Tl + Zn + Summits
4	Impact immune function	Cd + Fe + Se + Zn + $\delta^{13}C$ + Condition + Parasite intensity
5	Importance of nutrition	$\delta^{13}C$ + $\delta^{15}N$
6	Increase stress	Al + Ca + K + Coyote abundance + Bear abundance + Parasite intensity
7	Interfere with hormone, metabolism or growth	Cu + Co + V + Na + $\delta^{15}N$ + Condition + Sex
8	Past exploited mines in the park	Ba + Na + Cs + Pb + Cu + As + Cd

4.5 Results

4.5.1 Diet composition of caribou

The $\delta^{13}C$ and $\delta^{15}N$ values were highly variable in plant samples, ranging from -32.82‰ to -22.41‰ for $\delta^{13}C$ and from -8.51‰ to 6.41‰ for $\delta^{15}N$ (Figure 4.2, Table S4.2). Lichens were the most enriched in ^{13}C and the most depleted in ^{15}N compared to other categorical functional groups. The aquatic plants were the most depleted in ^{13}C while horsetails were the most enriched in ^{15}N. Caribou hair samples ranged from -25.91‰ to -22.31‰ for $\delta^{13}C$ and from 1.07‰ to 4.13‰ for $\delta^{15}N$ (Figure 4.2, Table S4.3). According to the SIMM results, lichens, deciduous trees and shrubs dominated the summer/autumn diets of the Gaspésie caribou population with respective values of 22.6 [14.8 – 29.4%] (mean [95% Credible Intervals bounds]), 17.7 [5.4 – 34.9%], and 13.4 [4.1 – 24.7%], for all individuals combined. Caribou also consumed mosses (7.7 [0 – 21.1%]), evergreen trees (7.6 [0.0 – 24.8%]), horsetails (7.2 [1.1 – 16.1%]), ferns (7.0 [0.0 – 36.3%]), and fungi (4.4 [0.0 – 18.8%]) (Figure 4.3).

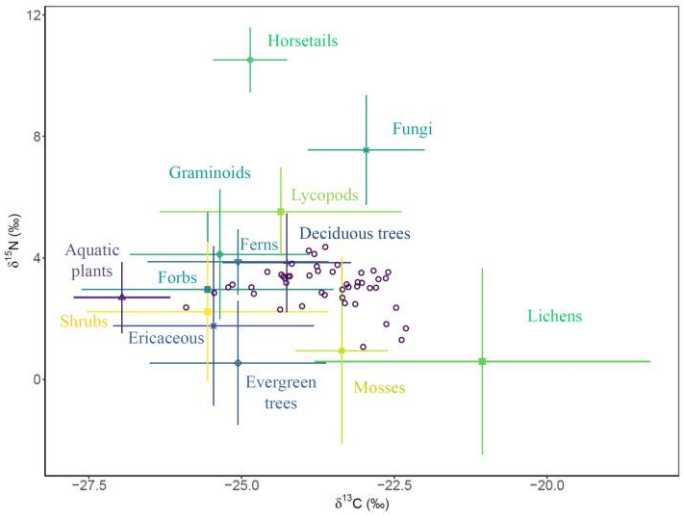

Figure 4.2. Stable isotopic signatures of carbon and nitrogen (mean ± *SD*) of plant species (solid points and error bars) and individual caribou (open circles) in the Gaspésie National Park and the surrounding Matane, Dunière and Chic-Chocs Wildlife Reserves.

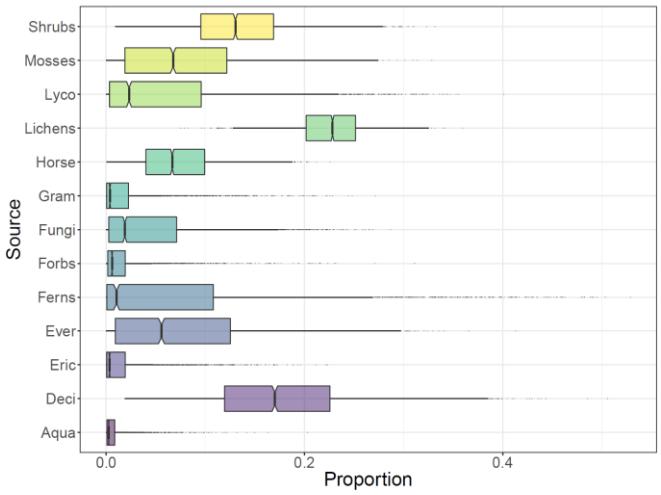

Figure 4.3. Proportional contributions of food sources (50, 75, and 95% CI) in the diet of caribou from the Gaspésie population using hair stable isotope ratios of carbon and nitrogen (Abb.: Aquatic plants (Aqua), deciduous trees (Deci), ericaceous shrubs (Eric), evergreen trees (Ever), graminoids (Gram), horsetails (Horse) and lycopods (Lyco)).

4.5.2 Relationship between trace elements and diet

We found detectable concentrations of all 21 trace elements in caribou hair samples (Table S4.3). The redundancy analysis included $\delta^{13}C$ and $\delta^{15}N$ as response variables while the summit frequented by caribou, sex, body condition, year and trace elements were included as environmental explanatory variables (except magnesium for which multicollinearity diagnoses prevent their inclusion into a candidate model, with VIF values of 16 vs. other covariates, while other variables had a VIF < 8). The model was significant ($F_{25,18} = 6.25$, $P < 0.001$), explained 89.7% of the total constrained variance, and suggested correlations between stable isotope signatures and the accumulation of different trace elements in hair (Figure 4.4). The first canonical axis was significant ($F_{1,41} = 221.01$, $P < 0.001$) and explained 55.7% of the total variance among caribou hair. The second canonical axis was also significant ($F_{1,41} = 134.80$, $P < 0.007$) and explained 34.0% of the total variance among caribou hair. The vectors for Ag, Al, Ba, Ca, Cd, Co, Cs, K, Mn, Pb, Tl, V, Zn, summit, sex, and year variables were higher and significant (ANOVA permutation test, $P < 0.05$). Higher $\delta^{13}C$ values were correlated with lower concentrations of Al, Ba, Ca, K, Mn, V, and Zn, while lower $\delta^{15}N$ values were correlated with lower concentrations of Cd and Cs and higher concentrations of Ag, Co, Pb, and Tl (Figure 4.4).

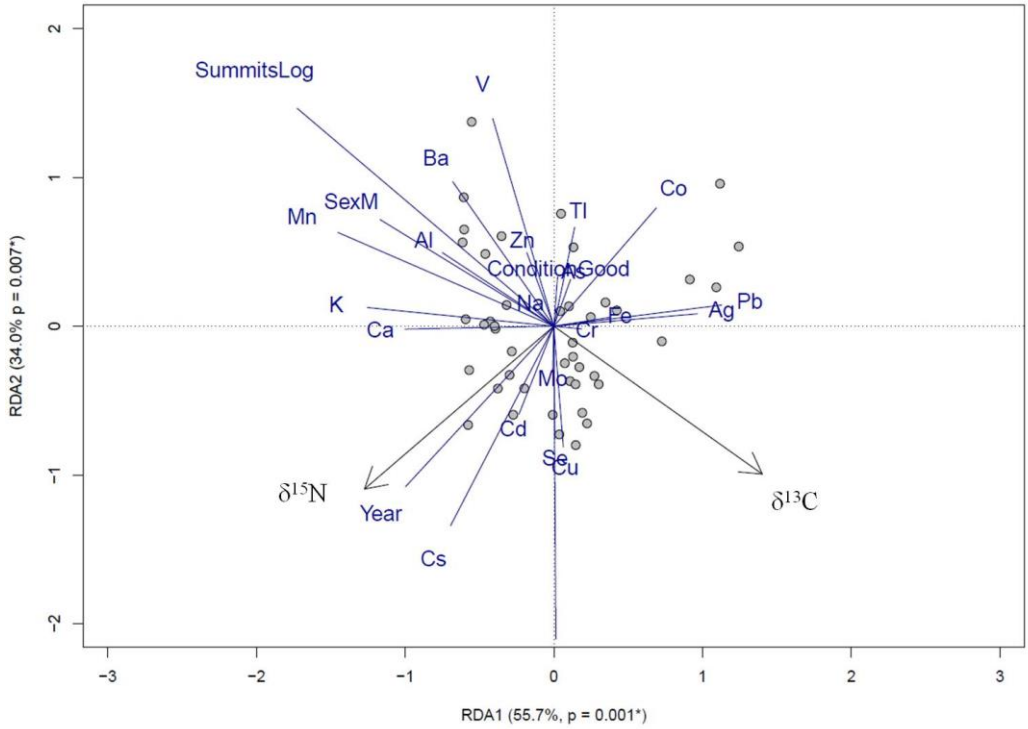

Figure 4.4. Redundancy analysis ordination tri-plot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes according to environmental variables (see the acronyms in the methods) showing the relationships between both sets of variables. Dots represent the caribou hair samples, black arrows are the stable isotopes and blue lines are the environmental variable scores. The lengths of all blue lines have been multiplied by 3 for diagram clarity.

4.5.3 Probabilities of female pregnancy, calf survival, and adult survival and lifespan

The female pregnancy probability was higher (logistic model #14, AUC = 0.80, different from the null model as χ^2 = 6.55, df = 1, P = 0.01, Table S4.4) when the $\delta^{13}C$ signatures measured in hair were higher (Table 4.3), although this effect was marginally significant (z = 1.69, P = 0.09). On average, pregnant female caribou (n = 14) had slightly higher $\delta^{13}C$ values (mean = -22.89‰) compared to non-pregnant

females (n = 5, mean = -23.65‰), but this difference was not statistically significant (one-way ANOVA, $F_{1,18}$ = 2.80, P = 0.11). Summer calf survival was also higher when the $\delta^{13}C$ signatures measured in their mother's hair (as a proxy of previous nutrition of the mother in the preceding summer) were higher (Table 4.3, Figure S4.2). However, the effect of the variable $\delta^{13}C$ was marginally significant (z = 1.77, p = 0.08) in this model (#19, AUC = 0.89, different from the null model as χ^2 = 6.58, df = 2, P = 0.04, Table S4.4). In contrast, adult caribou survival probability was higher when the Cs concentration measured in hair was lower and the Ba and Na concentrations were higher (logistic model #8, AUC = 0.89, different from the null model as χ^2 = 18.33, df = 7, P = 0.01, Tables 4.3-S4.4). The adult caribou lifespan was longer when caribou hair contained a higher concentration of Zn and a lower concentration of Mn (Cox model #2; Tables 4.3-S4.4).

Table 4.3. Coefficients (β) and their 95% confidence intervals of the covariates included in the most parsimonious logistic regression and Cox models assessing the link between female pregnancy, calf or adult survival, or lifespan, and trace elements.

	Female pregnancy		Calf survival		Adult survival (Logistic model)		Adult lifespan (Cox model)	
	β	95% CI [Lower:Upper]	β	95% CI [Lower:Upper]	β	95% CI [Lower:Upper]	β*	95% CI [Lower:Upper]*
Intercept	71.18	[-10.22 : 152.58]	137.71	[-15.48 : 290.90]	**-4.57**	**[-9.06 : -0.08]**		
$\delta^{13}C$	3.03	[-0.50 : 6.56]	6.13	[-0.65 : 12.91]				
Ba					**3.08**	**[0.38 : 5.78]**		
Na					**0.02**	**[0.00 : 0.04]**		
Cs					**-228.38**	**[-415.74 : -41.02]**		
Pb					-0.50	[-1.40 : 0.40]		
Cu					0.18	[-0.06 : 0.42]	-1.66	[-7.53 : 4.21]
As					32.02	[-25.45 : 89.49]		
Cd					4.34	[-21.32 : 30.00]		
Ca							-0.36	[-0.82 : 0.10]
Fe							-0.85	[-2.74 : 1.04]
Se			3.58	[-6.02 : 13.18]			56.46	[-180.64 : 293.56]
Mn							**54.12**	**[12.35 : 95.89]**
Mo							-186.11	[-410.20 : 37.98]
Zn							**-6.46**	**[-11.22 : -1.70]**

* Coefficients (β) and 95% CI of the caribou longevity Cox model were multiplied by 100 to lighten the presentation of the table.

Note: Bold values indicated significant variables in the model ($P < 0.05$).

4.6 Discussion

We successfully described the summer diet of the Gaspésie caribou population, and found empirical evidence of links between stable isotope signatures and accumulation of trace elements in hair, suggesting that the consumption of various dietary sources in summer and autumn can be integrated in the following winter coat. We also revealed correlations between the consumption of some specific resources by females in summer and autumn and their pregnancy rates during winter as well as higher calf survival at the end of the summer. Finally, we found associations between some trace elements and caribou survival and lifespan that could pave the way to novel research avenues.

4.6.1 Diet composition of caribou

During summer and autumn, the Gaspésie caribou consumed a diverse diet composed mainly of deciduous trees, lichens, shrubs, but also ferns, evergreen trees, fungi, horsetails and mosses. These results support the DNA barcoding results reported in Christopherson et al. (2019) for this same population using caribou feces (note that lichens and fungi were not considered in its analysis) and the larger trophic niche width for caribou than for moose reported in Rioux et al. (2022). Deciduous shrubs and lichens were also the primary food items of woodland caribou in Newfoundland (Bergerud, 1972) and barren-ground caribou (*Rangifer tarandus granti*) in Alaska (Boertje, 1984; Thompson & McCourt, 1981). However, woodland caribou in Ontario consumed a small proportion of deciduous shrubs during summer, but consumed mainly terrestrial lichens, forbs (including horsetails) and graminoids (Thompson et al., 2015). As Ohlson and Staaland (2001) mentioned, it is essential for an herbivore to feed on a variety of plants to obtain all the essential trace elements, nutrients and energy required for the organism. Deciduous trees, shrubs, horsetails

and fungi are highly nutritive and contain sufficient proteins, energy and essential trace elements for growing animals and lactation (Klein, 1990; Nieminen & Heiskari, 1989; Ohlson & Staaland, 2001; Staaland & White, 2001). Consumption of large quantity of lichens may place caribou in a negative nitrogen (Gerhart et al., 1996) and trace element balance (Staaland et al., 1980, 1982; Staaland & White, 2001) given the high nutritional demand during summer, especially for reproductive females. Lichens are rich in energy (Parker et al., 2005) but poor in protein (our study: 2.36 ± 1.45%; varying from 2-6% in Bergerud, 1972 and in Røed et al., 2019), and are thus mainly consumed in late winter for maintenance rather than during periods of growth. Our results support previous findings that caribou consume a diversified diet in summer (Rioux et al., 2022), and that the nutritional benefits gained in summer are important for caribou reproductive success and calf survival (Brown et al., 2007; Thompson et al., 2015).

4.6.2 Accumulation of trace elements in caribou hair

Trace element accumulation in caribou hair seems to be influenced by diet composition, as indicated by the correlations highlighted in the redundancy analysis. As we observed in our study, lower $\delta^{15}N$ signatures, suggesting a higher consumption of shrubs, deciduous trees, mosses and lichens, were associated with higher concentrations of cobalt and lower concentrations of cesium. Higher $\delta^{13}C$ signatures, suggesting a higher consumption of lichens and mosses, were associated with lower concentrations of potassium, manganese and calcium. Lichens are poor in nitrogen (Person et al., 1980) and macro-elements (e.g. K, Ca, Mg, Cu), while shrubs and deciduous trees are rich in essential trace elements (e.g. Co, Cu, Mn, Zn) (Klein, 1990; Ohlson & Staaland, 2001; Staaland & White, 2001).

The summits frequented by caribou may also have an influence in the accumulation of trace elements in caribou hair. Rock and soil weathering, atmospheric deposition, mine and smelter activities influenced trace element concentrations found in plants or in ungulates (Aznar et al., 2008; Sparling, 2016; Underwood & Suttle, 1999). The McGerrigle area is formed by intrusive granitic rocks rich in trace elements (e.g. As, Co, Cs, Cu, Mn, Pb, Zn), while the Chic-Chocs Mountains (Mt. Logan) are made of volcanic rocks and slates. Mount Albert is formed by a serpentine intrusion through the volcanic rocks and meta-sediments, rich in chromium and cobalt, but poor in calcium and potassium (LeSage & Paquin, 2000). This heterogenous spatial distribution of trace elements in soil may partly explain their different accumulation in plants (Aznar et al., 2008) and, as a consequence, in caribou hair following plant ingestion, as observed in this study.

4.6.3 Status of trace elements in caribou hair

Almost no information on trace element requirements, toxicity levels and normal reference ranges in caribou hair have been published (Bondo et al., 2019), thus we relied mostly on other ungulate species for comparisons. While it is currently unclear how hair may indicate deficiency states and how interspecies comparisons and differences in locations are relevant for hair element concentrations, we suggest that the concentrations documented here are low for many trace elements compared to other species and study sites. For example, the hair concentration of essential and non-essential trace elements (e.g. Ag, As, Ba, Cd, Co, Cu, Fe, Pb, V and Zn) was lower in the Gaspésie caribou population compared to the Svalbard reindeer population (*Rangifer tarandus platyrhynchus*, Pacyna et al., 2018). Based on other ungulate species, such as Italian red deer (*Cervus elaphus*, Montillo et al., 2019), non-essential element concentrations in the hair of Gaspésie caribou were also lower. However, they were qualitatively similar to concentrations reported for Wyoming

moose (*Alces alces gigas*, Becker et al., 2010). Gaspésie caribou hair also had lower concentrations of cobalt, potassium, and sodium, but higher concentrations of copper and magnesium, and similar levels of calcium, iron, manganese, selenium and zinc compared to Alaskan (Franzmann et al., 1977; O'Hara et al., 2001) and Wyoming moose hair (Becker et al., 2010). These differences in the trace element accumulation between caribou hair and other ungulate species may be due to the habitat characteristics (i.e. rock and soil types, atmospheric deposition, mine and smelter activities, Aznar et al., 2008; Sparling, 2016; Underwood & Suttle, 1999) and dietary intake. Unfortunately, we cannot conclude if the Gaspésie caribou population are contaminated or not by toxic elements or if they presented deficiencies in some elements or if the hair concentration reflects the current status of trace elements circulating in the animal. Furthermore, studies are needed to establish reference and deficiency range values in wild animals and to validate that hair concentrations reflect the animal's physiological status.

4.6.4 Diet and caribou reproduction

We found a marginally significant relationship between summer/autumn foraging and the probabilities of caribou female pregnancy and summer calf survival (Table 4.3, Figure S4.2). The small number of females (n = 19) and calves (n = 14) in our study could partially explain the low range of $\delta^{13}C$ values and the marginally significant effects we observed. Nevertheless, when female caribou had higher $\delta^{13}C$ values, representing a greater consumption of fungi and deciduous trees as well as lichens in a given summer, they tended to have a higher probability of being pregnant during the following winter and to have a calf surviving throughout the next summer. It was previously shown that female caribou rely upon the highly productive growing summer season to replenish body reserves of fat and proteins for breeding, lactation, body mass gain over the summer as well as overwinter survival (Cook et al., 2013;

Hurley et al., 2014; Parker et al., 1999). There is a trade-off between using resources for lactation or investing in direct growth and regaining body reserves (Åhman & White, 2019). Especially for female ungulates, maternal weight during pregnancy had an important role in fetal growth and early calf survival (Loison & Strand, 2005). In order to produce and wean a healthy calf, female caribou must have good body and physiological conditions, but also quality nutrition during lactation. However, Denryter (2017) has suggested that the forage biomass that caribou consume as well as the levels of digestible energy and proteins found in the biomass are too low in several habitat types to satisfy the daily nutritional requirements of caribou females, even if they increase foraging time. Consequently, the summer nutritional deficiencies that caribou are facing in some ranges may play a role in depressing population productivity, a situation that can occur in the poor montane, subalpine and alpine areas where the Gaspésie caribou females are foraging during summer and autumn. As these caribou are constrained in a small portion of the Gaspésie National Park, mainly on 3 different summits, and considering the well-demonstrated summer site fidelity of woodland caribou in Québec (Faille et al., 2010; Lafontaine et al., 2017), we could consider that the nutritional environment in which each female acquires nutrients during a given summer is similar from year to year.

We know that summer calf survival is not directly (and solely) related to the diet composition (and nutritional status) of cows during the previous summer and autumn, and that other factors might affect calf survival. As we know, predation by coyotes and black bears had an important impact on calf survival up to 6 months of age (Crête & Desrosiers, 1995) and was shown to influence calf recruitment over the last 30 years in the Gaspésie population (Frenette et al., 2020). For example, caribou calves suffered a high mortality rate in 2014, which explains the small number of calves who survived during our study (i.e. 5 out of 9 calves survived in 2013 and 0 out of 5 calves in 2014). Nonetheless, we may speculate that a healthy and heavier calf was more likely to escape from predation (Couturier et al., 2009). However, we recognize

that more efforts are needed to describe and distinguish diet composition between pregnant and non-pregnant female caribou in order to clarify the influence of nutrition and trace elements in hair on the probability of female pregnancy and calf survival, especially in this endangered population.

4.6.5 Diet and caribou survival and lifespan

Trace element concentrations in hair appeared to be associated to adult survival probability (e.g. Ba, Na, Cs) and lifespan (e.g. Zn, Mn). We observed higher adult survival and lifespan for individuals with higher concentrations of zinc, barium, and sodium, but also with lower concentrations of manganese and cesium in hair. Zinc is associated with the immune system and plays important roles in the growth and reproduction process (Robbins, 1993; Sparling, 2016), while sodium is an essential element in cervids not only for osmotic regulation (Staaland et al., 1980, 1982), but also to built-up fat reserves, reproduction and survival of free-ranging cattle (Wallisdevries, 1996). As previously mentioned by Staaland et al. (1982), reindeer need to feed on sodium-rich plants in summer to restore the negative sodium balance frequently observed in late winter and during the lactation period.

Some of the associations found in this study remain unclear. It was challenging to explain why decreasing barium, cesium, and manganese in caribou hair correlates to an increase in the probability of adult survival and lifespan. According to our redundancy analysis, lower concentrations of cesium, barium, and manganese are correlated to higher $\delta^{13}C$ and lower $\delta^{15}N$ signatures, suggesting a greater consumption of lichens, shrubs and deciduous trees. We may speculate that these animals were in better physiological conditions due to the greater diversity of plant intake consumed (Ohlson & Staaland, 2001) and the consumption of sufficient proteins, energy and essential trace elements (Klein, 1990; Ohlson & Staaland, 2001; Staaland & White,

2001; Thompson & Barboza, 2014). Cesium and barium are not known to have any essential functions in the organism and cesium is mainly absorbed via food or water (Klaassen, 2008). Because cesium can replace potassium for cellular transport, it may have deleterious effect on biological systems (Papastefanou et al., 1999). It was thus difficult to understand precisely the influence of barium, cesium, and manganese on the adult survival probability because the ranges of normal values are not known in free-ranging caribou, nor do we know if the hair concentration reflects the status of the animal. Going further would require measuring trace element concentrations in plants within the Gaspésie caribou range to better understand the potential transfer of trace elements from plants to caribou. Nevertheless, our observations can lead to novel research hypotheses for future work.

4.6.6 Limits and conclusion

Correlation does not prove causality, therefore future studies should orient their efforts in conducting controlled experiments to better understand trace element requirements, their implication for growth, reproduction and survival, their respective roles in the body physiology, as well as the transfer of trace elements between animal tissues (i.e. blood, liver and hair) and along the food chain. More specifically for (caribou) hair, the degree to which the concentration of trace elements in hair is correlated with levels found in the whole body need to be further understood (Bhattacharya et al., 2016). Nevertheless, the fact that hair incorporates trace elements mainly via blood flux (Flache et al., 2017; Vermeulen et al., 2009) during the whole period of hair growth represents an interesting way to document nutrition and physiological status over a long period. Moreover, we did not include interactions between trace elements even if some elements can interfere with the absorption of other elements (McDonald et al., 2010; Ohlson & Staaland, 2001), a complex issue that goes far beyond the scope of our study but deserves consideration in future work.

We recognize that there are probably other factors susceptible to influence individual performance, such as female age (Adams & Dale, 1998), climate (Joly et al., 2011), snow condition (Kumpula & Colpaert, 2003), interspecific interactions via apparent competition (Frenette et al., 2020), and space use (Lafontaine et al., 2017; Lesmerises et al., 2019; Losier et al., 2015). Despite limitations in our understanding of the respective role of the different trace elements we studied in hair, we provided empirical evidence showing that summer/autumn nutrition can be constraining for cervids (as seen by Cook et al., 2021; Denryter et al., 2022), even in a "green world" (Saether & Andersen, 1990). Our study brings novel information suggesting that nutrition could, as a secondary cause, predispose females to low reproductive performance and survival rates, thus raising hypotheses to be further tested in detail. From a conservation perspective, we provide a new, complementary way to explain how foraging ecology can influence the fitness of the endangered Gaspésie caribou population, the last remnant of the caribou herds that once occupied the southern shore of the St. Lawrence River (Québec), the Maritimes and New England.

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4.8 Supplementary material

We collected a few plant species per plant functional group : aquatic plants (*Nuphar variegatum*), deciduous trees (*Sorbus americana, Salix spp.*), ericaceous shrubs (*Vaccinium spp, Kalmia polifolia, Ledum groenlandicum*), evergreen trees (*Picea glauca, Abies balsamea*), ferns (*Dryopteris spp.*), forbs (*Taraxacum spp., Maianthemum canadense, Clintonia borealis, Epilobium angustifolium, Cornus canadensis, Actaea rubra, Thalictrum pubescens, Vicia cracca, Potentilla tridendata, Linnaea borealis*), fungi (Agaricaceae family), graminoids (*Agrostis borealis, Phleum pratense*), horsetails (*Equisetum arvense*), lichens (*Alectoria spp., Cladina rangiferina, Stereocaulon spp.*), lycopods (*Lycopodium spp.*), mooses (*Polytrichum spp., Dicranum spp.*), and shrubs (*Alnus rugosa, Betula glandulosa, Amelanchier bartramiana, Rubus idaeus, Ribes spp., Viburnum edule*).

Table S4.1. Mean and standard deviation of carbon and nitrogen stable isotope ratios in plant functional groups collected in the Gaspésie National Park.

Plant functional groups	n	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Aquatic plants	3	1.53 ± 0.51	-30.00 ± -0.51
Deciduous trees	18	-0.39 ± 1.24	-27.30 ± 0.86
Ericaceous shrubs	15	-2.47 ± 2.40	-28.50 ± 1.53
Evergreen trees	21	-3.69 ± 1.75	-28.10 ± 1.31
Ferns	6	-0.36 ± 0.18	-28.10 ± 1.35
Forbs	54	-1.27 ± 2.30	-28.61 ± 1.97
Fungi	7	3.32 ± 1.46	-26.00 ± 0.74
Graminoids	19	-0.11 ± 1.85	-28.40 ± 1.34
Horsetails	3	6.29 ± 0.20	-27.90 ± 0.07
Lichens	24	-4.16 ± 2.69	-23.30 ± 1.37
Lycopods	9	1.29 ± 1.01	-27.40 ± 1.89
Mosses	5	-3.29 ± 2.88	-26.40 ± 0.45
Shrubs	39	-2.00 ± 2.04	-28.60 ± 1.88

Table S4.2. Trace element measured and certified values from National Research Council Canada of certified reference materials (river water SLRS-6 and dogfish liver DOLT-5), recoveries of the trace elements of the certified concentrations, and variance coefficients (CV) for duplicate (n = 16) and replicate (n = 8) caribou hair samples.

	SLRS-6			DOLT-5			Duplicate caribou	Replicate caribou
Elements	Measured values (µg/g)	*Certified values (µg/g)*	Recoveries (%)	Measured values (µg/g)	*Certified values (µg/g)*	Recoveries (%)	CV (%)	CV (%)
Ag	ND †			1.941	*2.05 ± 0.08*	94.7	31.1	26.8
Al	33.550	*33.9 ± 2.2*	99.0	11.220			10.9	4.8
As	0.595	*0.57 ± 0.08*	104.4	32.704	*34.6 ± 2.4*	94.5	22.0	48.7
Ba	14.045	*14.32 ± 0.48*	98.1	0.102			4.2	6.6
Ca	8528.750	*8790 ± 200*	97.0	532.139	*550 ± 80*	96.8	8.9	3.3
Cd	ND †	*0.0063 ± 0.0014*		14.606	*14.5 ± 0.6*	100.7	10.5	10.2
Co	0.051			0.249	*0.267 ± 0.026*	93.2	3.6	6.7
Cr	0.245	*0.253 ± 0.012*	96.6	0.624			9.4	2.9
Cs	0.005			0.073			3.0	12.4
Cu	25.063	*24 ± 1.8*	104.4	34.030	*35 ± 2.4*	97.2	3.9	2.4
Fe	82.650	*84.6 ± 3.6*	97.7	1045.300	*1070 ± 80*	97.7	2.9	1.8
K	639.500	*653 ± 54*	97.9	14865.320	*14400 ± 3000*	103.2	2.9	2.5
Mg	2143.000	*2140 ± 58*	100.1	874.259	*940 ± 100*	93.0	6.0	10.0
Mn	2.200	*2.12 ± 0.1*	103.8	8.374			3.8	4.7
Mo	0.178	*0.215 ± 0.018*	82.6	1.288	*1.41 ± 0.22*	91.3	12.4	6.7
Na	2784.250	*2770 ± 220*	100.5	10073.640	*9900 ± 1600*	101.8	21.5	24.2
Pb	0.163	*0.17 ± 0.026*	95.6	0.187	*0.162 ± 0.032*	115.7	80.7	3.6
Se	0.220			8.827	*8.3 ± 1.8*	106.4	18.1	35.7

Tl	0.007			0.012			30.8	26.7
V	0.354	*0.352 ± 0.006*	100.5	0.477	*0.51 ± 0.06*	93.6	19.0	17.2
Zn	1.778	*1.76 ± 0.12*	101.0	104.701	*105.3 ± 5.4*	99.4	2.0	2.6

† Not detectable

Table S4.3. Mean, standard deviation and range (min, max) of carbon and nitrogen stable isotope ratios (‰) and trace element concentrations (in µg/g units) in hair of 44 caribou captured in the Gaspésie National Park.

	Mean ± SD	Min	Max
$\delta^{13}C$	-23.65 ± 0.88	-25.91	-22.31
$\delta^{15}N$	2.99 ± 0.65	1.07	4.13
Ag	0.0053 ± 0.0075	0.00	0.046
Al	23.23 ± 7.71	11.12	49.82
As	0.050 ± 0.020	0.014	0.11
Ba	1.43 ± 0.83	0.28	6.15
Ca	438.94 ± 118.73	169.69	762.19
Cd	0.044 ± 0.035	0.007	0.17
Co	0.042 ± 0.030	0.014	0.19
Cr	0.29 ± 0.22	0.095	1.41
Cs	0.014 ± 0.0064	0.0047	0.033
Cu	7.79 ± 5.28	4.98	41.57
Fe	36.01 ± 39.62	10.01	255.81
K	212.75 ± 64.49	59.18	415.58
Mg	84.43 ± 22.43	53.5	154.79
Mn	2.27 ± 1.33	0.76	5.91
Mo	0.22 ± 0.21	0.023	0.99
Na	76.66 ± 40.03	4.27	188.01
Pb	0.92 ± 1.13	0.18	5.59
Se	0.036 ± 0.18	0.00005	0.77
Tl	0.0024 ± 0.00094	0.00076	0.0045
V	0.037 ± 0.018	0.014	0.083
Zn	78.82 ± 9.85	60.03	105.42

Table S4.4. Rankings of the candidate models to assess pregnancy, calf and adult survival probabilities, and adult lifespan, and the explanatory variables using logistic regression and Cox models.

	Female pregnancy				Calf survival				Adult survival (Logistic model)				Adult lifespan (Cox model)			
Model no.	df	LL	ΔAICc	ω_i	df	LL	ΔAICc	ω_i	df	LL	ΔAICc	ω_i	df	LL	ΔAICc	ω_i
14	**2**	**-7.68**	**0.00**	**0.96**												
10	4	-8.35	7.47	0.02												
9	6	-5.11	9.11	0.01												
13	5	-7.67	9.85	0.01												
11	8	-4.65	19.60	0.00												
12	8	-5.08	20.45	0.00												
19					**3**	**-5.84**	**0.00**	**0.45**								
20					3	-6.17	0.66	0.32								
16					4	-4.96	2.30	0.14								
17					5	-3.19	3.82	0.07								
18					5	-4.80	7.02	0.01								
21					5	-7.43	12.29	0.00								
15					5	-7.58	12.58	0.00								
8									**8**	**-19.68**	**0.00**	**0.85**	7	-63.35	13.25	0.00
5									3	-28.78	4.69	0.08	2	-65.45	2.05	0.25
4									8	-22.61	5.86	0.05	7	-60.04	6.63	0.03
6									8	-23.60	7.85	0.02	6	-61.85	6.55	0.03
7									8	-24.22	9.08	0.01	7	-64.60	15.74	0.00
2									8	-26.61	13.86	0.00	**7**	**-56.73**	**0.00**	**0.69**
1									10	-24.81	16.81	0.00	9	-57.14	9.52	0.01
3									13	-19.81	18.28	0.00	12	-55.30	23.54	0.00

Note: the most parsimonious models according to AICc and ω_i were indicated in bold.

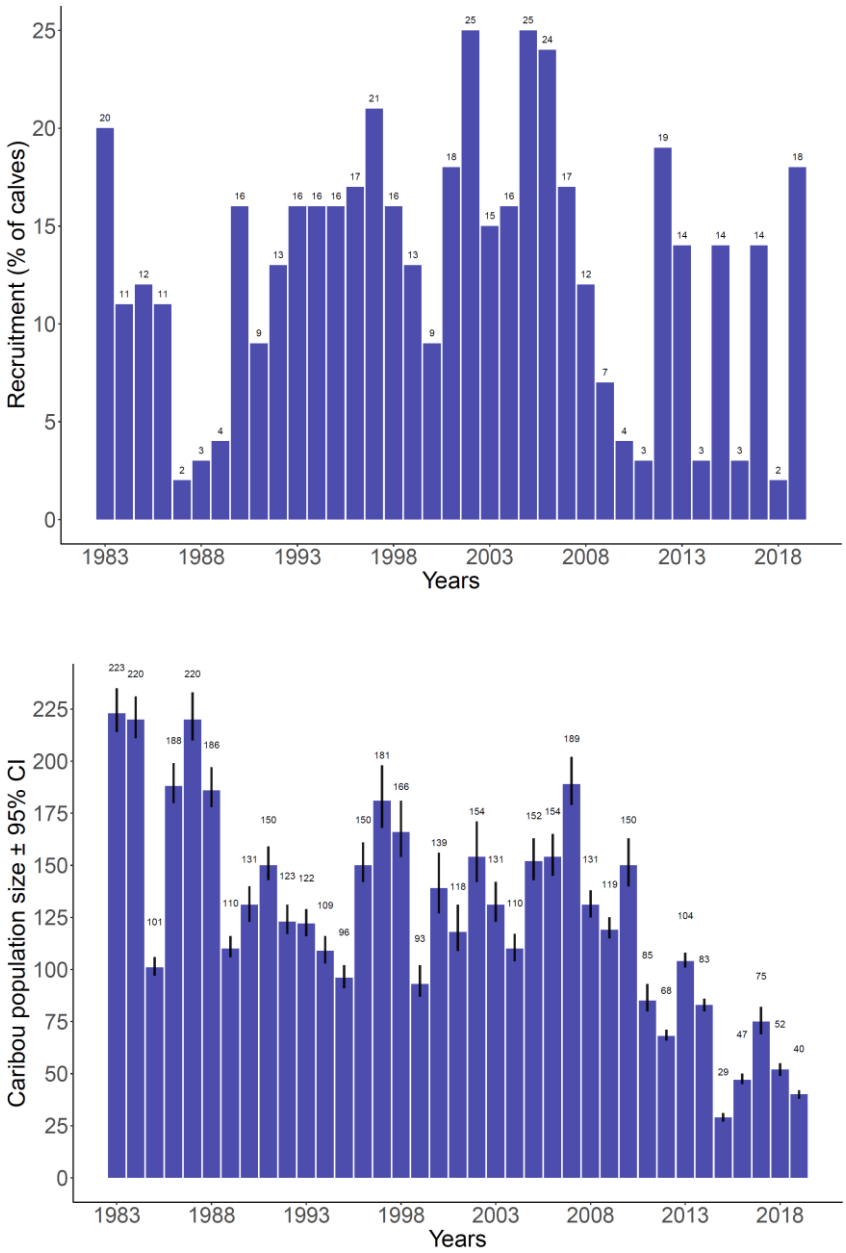

Figure S4.1. Estimates of the recruitment and the population size of the Gaspésie caribou population according to aerial surveys conducted in autumn from 1983 to 2019 (modified from Morin & Lesmerises, 2020).

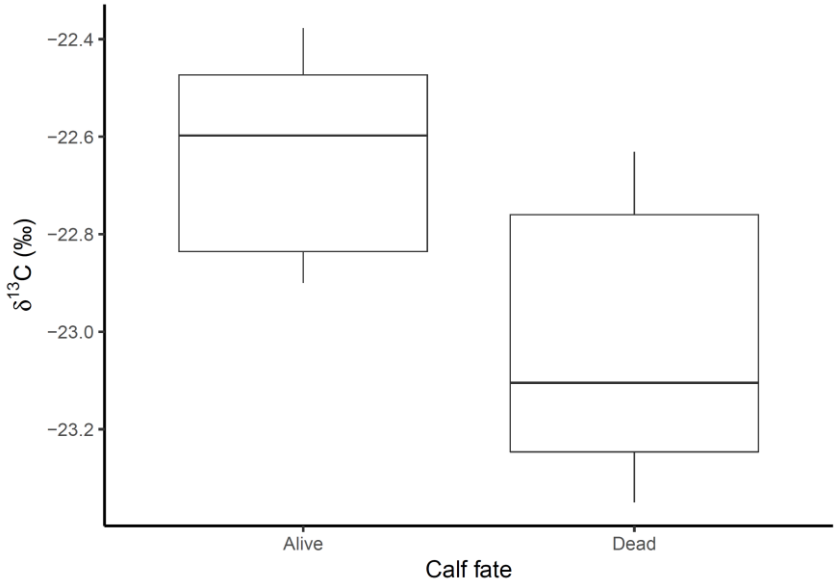

Figure S4.2. $\delta^{13}C$ signatures (50, 75, and 95% CI) of female caribou without (dead, *n* = *9*) and with (alive, *n* = *5*) a calf that survived throughout the summer period. Based on an *a posteriori* two-sample *t*-test, $\delta^{13}C$ signatures were statistically higher for females with a calf that survived compared to those that lose their calf during summer (t = -2.81, P = 0.02).

CONCLUSION

Le déclin des populations animales sauvages peut être attribué à un grand nombre de facteurs (Baillie *et al.*, 2010; Croxall *et al.*, 2012; Dueñas *et al.*, 2018; Myers et Worm, 2003; Wittemyer *et al.*, 2014; Wittmer *et al.*, 2005a; Zimova *et al.*, 2016), dont certains ont moins bien été étudiés que d'autres, soit l'alimentation et la condition physiologique (Birnie-Gauvin *et al.*, 2017; Carlsson *et al.*, 2019a; Tracy et *al.*, 2006). Ces facteurs sont pourtant connus pour influencer les performances et la valeur adaptative individuelle chez plusieurs espèces animales (Birnie-Gauvin *et al.*, 2017; Macbeth et Kutz, 2019; Mattson et Merrill, 2002; O'Hara *et al.*, 2001; Stephenson *et al.*, 2020; Thompson et Barboza, 2013). L'objectif principal de ma thèse visait par conséquent à mieux comprendre le rôle de l'alimentation, de la condition physiologique et des relations trophiques sur la dynamique d'une population en déclin (Figure 0.1) à l'aide de différents marqueurs biochimiques et physiologiques. Ma thèse avait également comme deuxième objectif de mieux comprendre les sources de variation des signatures isotopiques. Au fil des quatre chapitres principaux, ma thèse a permis de répondre aux différents objectifs fixés, plus spécifiquement d'évaluer l'effet des lipides sur les signatures isotopiques du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) et de proposer un modèle de correction mathématique spécifique à l'espèce et au tissu (chapitre 1), d'estimer les facteurs d'enrichissement trophique de cinq espèces de mammifères terrestres dans deux types de tissus afin d'augmenter la précision des modèles mixtes isotopiques Bayésiens (chapitre 2), d'évaluer les relations trophiques et le partage des ressources alimentaires entre des espèces sympatriques partageant le même habitat (chapitre 3) et d'évaluer l'influence des différences individuelles dans l'alimentation et la

condition physiologique sur la valeur adaptative d'une population en déclin (chapitre 4). Les sections suivantes synthétisent brièvement les résultats obtenus pour chacun des quatre chapitres de ma thèse, les contributions théoriques et appliquées issues de ceux-ci, les limites de la thèse ainsi que les avenues de recherche permettant de poursuivre l'acquisition de connaissances dans la foulée des résultats obtenus.

5.0 Sommaire des principaux résultats

Les deux premiers chapitres de ma thèse visaient à mieux comprendre les sources de variation des signatures isotopiques afin de mieux les contrôler pour s'assurer de la validité et de la précision des résultats obtenus pour les chapitres suivants. La présence des lipides dans les échantillons biologiques récoltés en vue des analyses isotopiques peut potentiellement biaiser les résultats et l'interprétation biologique des relations trophiques (Lesage *et al.,* 2010; Post *et al.,* 2007; Tarroux *et al.,* 2010). Toutefois, il n'existe pas de consensus au niveau de la meilleure approche à utiliser, soit de conserver les lipides, de les extraire chimiquement ou de corriger les rapports isotopiques à partir d'équations de normalisation mathématique (Fry, 2002; Lesage *et al.,* 2010; McConnaughey et McRoy, 1979; Post *et al.,* 2007). De plus, il est suggéré qu'il n'est pas nécessaire de corriger pour l'effet des lipides si le rapport carbone : azote (ci-après CN) est inférieur à 4 en milieu terrestre (ou si le pourcentage de lipides est moins de 10%) (Ehrich *et al.,* 2011; Post *et al.,* 2007). Les objectifs spécifiques du premier chapitre étaient donc 1) d'évaluer l'effet de l'extraction des lipides sur $\delta^{13}C$, $\delta^{15}N$ et le rapport CN dans le plasma, les cellules sanguines et les poils de caribou (*Rangifer tarandus caribou*), 2) de proposer un modèle de normalisation des lipides qui soit spécifique au tissu et à l'espèce et 3) d'évaluer l'efficacité de quatre modèles de normalisation mathématique fréquemment utilisés

dans la littérature. Mon premier chapitre a montré l'importance de vérifier l'effet des lipides sur les signatures isotopiques du carbone et de l'azote même si le rapport CN est inférieur à 4. De plus, contrairement à ma prédiction, l'extraction des lipides s'est avérée nécessaire dans le poil de caribou même si les valeurs des rapports CN étaient peu élevées (entre 3,93 et 4,30) (comme proxy du pourcentage de lipides). Ce chapitre a également permis de comparer l'efficacité de quatre modèles de normalisation des lipides fréquemment utilisés dans la littérature (Ehrich *et al.,* 2011; Fry, 2002; McConnaughey et McRoy, 1979; Post *et al.,* 2007). Sur ces bases, j'ai recommandé d'utiliser un modèle de correction des lipides adapté au tissu, à l'espèce et à la méthode d'extraction chimique. Finalement, j'ai aussi développé une équation adaptée à notre modèle d'étude et au tissu analysé. Ce chapitre témoigne de l'importance de valider les modèles fréquemment utilisés dans la littérature afin de s'assurer qu'ils sont applicables à notre modèle d'étude, mais aussi d'évaluer l'effet des lipides sur $\delta^{13}C$, $\delta^{15}N$ et le rapport CN puisque cet effet varie selon les espèces, les tissus et la méthode d'extraction chimique (Ehrich *et al.,* 2011; Lesage *et al.,* 2010; Ricca *et al.,* 2007; Sotiropoulos *et al.,* 2004). Les chapitres suivants ont donc utilisé le modèle paramétré pour le caribou.

L'estimation du régime alimentaire et du partitionnement des ressources d'un groupe d'individus peut être réalisée à l'aide des isotopes stables et des modèles mixtes isotopiques Bayésiens (Parnell *et al.,* 2013; Phillips *et al.,* 2014). Toutefois, la précision de ces modèles dépend, entre autres, des facteurs d'enrichissement trophique spécifiques à l'espèce et au tissu (Bond et Diamond, 2011; Caut *et al.,* 2009; Phillips *et al.,* 2014). Cependant, ces facteurs sont manquants pour de nombreux mammifères terrestres, car seules quelques études ont été réalisées en milieu contrôlé (Darr et Hewitt, 2006; Halley *et al.,* 2010; McLaren *et al.,* 2015). L'objectif

spécifique de ce deuxième chapitre était donc d'estimer les facteurs d'enrichissement trophique du carbone ($\Delta^{13}C$) et de l'azote ($\Delta^{15}N$) dans deux types de tissus chez cinq espèces de mammifères élevés en captivité et nourris à partir d'un régime alimentaire connu. Ce chapitre a permis de définir ces facteurs dans le poil de caribou, d'orignal (*Alces americanus*), de cerf de Virginie (*Odocoileus virginianus*), de coyote (*Canis latrans*) et d'ours noir (*Ursus americanus*) ainsi que dans le sang de caribou et de coyote. J'ai observé des différences importantes dans les facteurs d'enrichissement trophique entre les cinq espèces et les deux types de tissus analysés. Ces variations renforcent la nécessité de bien estimer les facteurs d'enrichissement trophique spécifique à l'espèce et au tissu. De plus, les facteurs estimés pour cinq espèces et deux types de tissus sont très précis, comme en témoigne leur faible coefficient de variation respective. Ils ont donc été utilisés tout au long des chapitres 3 et 4.

La compréhension du partitionnement des ressources alimentaires et des niches trophiques des espèces au sein d'une communauté est essentielle afin de mieux comprendre les mécanismes sous-jacents de compétition, de coexistence et de prédation (Bearhop *et al.*, 2004; Svanbäck et Bolnick, 2007). Cette compréhension est encore plus importante lorsqu'une espèce est en déclin et entre en compétition apparente avec une autre espèce principale partageant des prédateurs communs (DeCesare *et al.*, 2010; Holt, 1977). Il est donc essentiel de déterminer le rôle potentiel de la compétition interspécifique entre les deux espèces de proies, tout comme d'estimer la composition du régime alimentaire de leurs prédateurs et dans quelle mesure ils consomment l'espèce en déclin. Les objectifs spécifiques de ce troisième chapitre étaient 1) de mieux comprendre le partitionnement des niches trophiques et des ressources alimentaires entre le caribou, l'orignal, et leurs prédateurs, le coyote et l'ours noir, afin d'améliorer notre compréhension de leurs

interactions potentielles et 2) d'estimer la proportion de caribou dans le régime alimentaire des prédateurs. Ce chapitre a permis d'atteindre cet objectif en montrant un certain chevauchement des niches trophiques et un partitionnement des ressources alimentaires entre ces quatre espèces sympatriques. Le potentiel de compétition pour les ressources entre le caribou et l'orignal s'est avéré relativement faible en raison d'un régime alimentaire différent et d'un partitionnement des niches trophiques. Cependant, les observations plus fréquentes d'orignaux en hautes altitudes pourraient modifier la stratégie d'isolement du caribou (Cumming *et al.*, 1996; Seip, 1992) et augmenter la compétition pour les ressources alimentaires de bonne qualité en plus d'augmenter le risque de prédation sur le caribou. Tel qu'attendu, le régime alimentaire du coyote était principalement constitué de sources animales tandis que celui de l'ours était constitué majoritairement de sources végétales. Cependant, la contribution du caribou de la Gaspésie dans le régime alimentaire des prédateurs s'est avérée relativement faible. Toutefois, comme le coyote et l'ours noir s'alimentent aussi de sources végétales, mes résultats ont montré un chevauchement plus important entre la niche trophique du caribou et celle des prédateurs, suggérant qu'ils exploitent, du moins partiellement, la même niche trophique. Un tel chevauchement pourrait avoir des impacts négatifs pour le caribou, car la recherche des mêmes ressources alimentaires peut forcer les prédateurs et le caribou à utiliser le même habitat, et conséquemment augmenter la probabilité de rencontre et la pression de prédation exercée sur le caribou de la Gaspésie.

En plus de la prédation et de la compétition intra- et interspécifique, l'alimentation et la condition physiologique d'un individu peuvent affecter la valeur adaptative (Abramsky *et al.*, 2002; Brown, 1992; Macbeth et Kutz, 2019) et la dynamique d'une population (Macbeth et Kutz, 2019). En effet, une alimentation pauvre en protéines,

vitamines, nutriments et minéraux a été reliée à une faible condition individuelle (Parker *et al.*, 2009), à de faibles performances de reproduction (Flueck *et al.*, 2012; Flynn *et al.*, 1977), à un faible taux de survie (Cook *et al.*, 2004a) et au déclin de population (Post et Klein, 1999). Cependant, l'influence de l'alimentation et de la condition physiologique sur la santé et les performances individuelles n'est pas bien comprise pour toutes les espèces sauvages. Les objectifs spécifiques de ce quatrième chapitre étaient 1) d'établir une relation entre l'accumulation des éléments traces dans les poils et l'alimentation et 2) d'évaluer si la condition physiologique et l'alimentation seraient associées aux performances individuelles de la population en déclin de caribou de la Gaspésie. Les résultats obtenus pour ce chapitre ont témoigné d'un régime alimentaire diversifié pour le caribou à l'été et à l'automne, principalement constitué de feuilles d'arbres décidus et d'arbustes, mais aussi de lichens. J'ai également trouvé une corrélation entre l'accumulation en éléments traces dans les poils de caribou et les signatures isotopiques. Les concentrations en éléments traces mesurées dans le poil de caribou et les rapports isotopiques du carbone et de l'azote semblent être associés aux ressources alimentaires consommées en été/automne qui, en retour, pourraient avoir un effet sur le recrutement de faons dans cette population. De plus, certains éléments traces sont corrélés à une meilleure survie des adultes ainsi qu'à une longévité plus longue. Mon étude a mis en évidence le lien entre l'alimentation, la condition physiologique et les performances individuelles d'une population en déclin.

5.1 Contributions conceptuelles et théoriques

Sur les plans conceptuel et théorique, ma thèse a apporté différentes contributions novatrices. Très peu d'études se sont concentrées à étudier l'effet des lipides sur les signatures isotopiques en milieu terrestre (mais voir Ehrich *et al.,* 2011; Post *et al.,* 2007; Tarroux *et al.,* 2010). Le chapitre 1 a toutefois montré l'importance de vérifier les effets possibles des lipides sur les signatures isotopiques même s'il est généralement assumé qu'un faible rapport CN (c.-à-d. < 4, comme proxy du contenu en lipides) n'a pas ou très peu d'effet sur les signatures isotopiques en milieu terrestre. De plus, mon étude a mis en évidence l'importance de la validation des différents modèles de normalisation des lipides utilisés telle que suggérée par Post *et al.* (2007). La précision des modèles mixtes isotopiques Bayésiens est également meilleure en utilisant des signatures isotopiques corrigées avec un modèle de normalisation des lipides spécifique à l'espèce et au tissu (Lesage *et al.,* 2010; Tarroux *et al.,* 2010). Selon mes résultats, je considère que l'extraction des lipides doit être effectuée lorsque l'étude nécessite une meilleure précision dans la détermination du régime alimentaire ou des niches trophiques. Les résultats du chapitre 1 peuvent donc avoir des implications importantes dans d'autres systèmes d'étude dans des habitats aquatiques, terrestres ou toundriques ainsi qu'à d'autres espèces puisqu'il s'avère essentiel de tenir compte de l'effet des lipides sur les signatures isotopiques.

Bien que l'objectif du chapitre 2 puisse apparaître *a priori* simple, il comble un besoin important puisque très peu de données existaient dans la littérature quant aux facteurs d'enrichissement trophique pour les grands mammifères. Ce chapitre permet donc de répondre à un besoin dans l'étude de l'écologie alimentaire et des niches isotopiques. Considérant la sensibilité des modèles mixtes isotopiques Bayésiens aux

variations dans les facteurs d'enrichissement trophique, il est souvent essentiel de les estimer expérimentalement pour un système d'étude donné (Bond et Diamond, 2011). L'utilisation des facteurs d'enrichissement trophique non spécifiques au tissu et à l'espèce peut de plus mener à des conclusions erronées ou biaisées quant aux relations trophiques et à la description du régime alimentaire des espèces à l'étude, puisque les sources de variabilité ne sont pas prises en compte dans les modèles mixtes (Caut *et al.,* 2008; Wolf *et al.,* 2009). Au-delà du fait que j'ai déterminé les facteurs d'enrichissement trophique pour cinq mammifères terrestres dans deux types de tissus en particulier, la méthodologie utilisée peut être adaptée à d'autres systèmes d'étude et à d'autres espèces. Ces nouvelles connaissances peuvent également avoir des implications importantes dans l'étude des espèces menacées et en voie de disparition pour lesquelles les scientifiques devraient préconiser un échantillonnage non invasif (p. ex. les poils) et une approche non létale (p. ex. le sang) afin de caractériser la composition du régime alimentaire et les relations trophiques. De plus, ces tissus peuvent être prélevés à plusieurs moments au cours de la vie de l'animal et donc, cette approche s'avère très utile dans les études longitudinales portant sur la dynamique des populations ou sur la valeur adaptative d'une population.

Le troisième chapitre a montré que l'utilisation des isotopes stables s'avère être un bon outil pour comprendre le partitionnement des ressources entre des espèces sympatriques, mais également sur les facteurs influençant le déclin des populations. En effet, les espèces sympatriques doivent occuper des niches trophiques différentes ou s'alimenter sur des ressources différentes afin de diminuer l'intensité de la compétition interspécifique (Gavrilchuk *et al.,* 2014; Jung *et al.,* 2015). Mes résultats viennent également appuyer empiriquement une des prédictions rattachées à l'hypothèse de Van Valen (1965) qui stipule que les populations qui occupent des

niches écologiques plus larges devraient montrer une plus grande variation interindividuelle dans l'utilisation des ressources que celles occupant une niche plus étroite, ce que j'ai observé pour le caribou et le coyote. Cette niche écologique plus large implique un comportement alimentaire plus généraliste (Bolnick *et al.,* 2003; 2010) qui peut être influencé par les conditions locales et la disponibilité ou la diversité des ressources. La comparaison des niches trophiques des espèces partageant le même habitat ou les mêmes ressources est donc fondamentale pour évaluer les mécanismes de coexistence ou de compétition et éventuellement prédire les conséquences des changements de l'écosystème sur la communauté. Mon étude a également souligné l'importance de reconnaître les liens trophiques entre les espèces, une préoccupation déjà reconnue (Christopherson *et al.,* 2019; Frenette *et al.,* 2020; Gavrilchuk *et al.,* 2014; Jung *et al.,* 2015). Elle a toutefois mis en évidence l'importance de prendre en considération les effets cumulatifs de plusieurs facteurs afin de mieux comprendre les processus de déclin d'une population. Elle a de plus contribué à comprendre comment les activités humaines peuvent affecter la disponibilité des ressources alimentaires de prédateurs généralistes et par conséquent moduler leurs impacts sur la dynamique d'une population en déclin dans un contexte de compétition apparente.

Le déclin des populations est souvent attribué à la perte et l'altération de l'habitat, à la création de structures linéaires et à la prédation (voir p. ex. Baillie *et al.,* 2010; Czech *et al.,* 2000; Dirzo *et al.,* 2014; Pimm et Raven, 2000). Quelques études ont cependant attribué le déclin des populations à des facteurs moins largement reconnu tels que l'alimentation (Birnie-Gauvin *et al.,* 2017; Stephenson *et al.,* 2020), la condition physique (Turgeon *et al.,* 2018) et physiologique (Charbonnel *et al.,* 2008; Tracy *et al.,* 2006), la santé via l'intensité parasitaire et les maladies (Carlsson *et al.,*

2019b) ainsi que les relations trophiques (Bryant et Page, 2005; Gurnell *et al.*, 2004; Macbeth et Kutz, 2019). Cependant, peu d'études ont tenté de relier différents facteurs pour expliquer le déclin de certaines populations (mais voir Tracy *et al.*, 2006; Wittemyer *et al.*, 2014). Le chapitre 4 a montré empiriquement le lien potentiel entre l'alimentation, la condition physiologique et la valeur adaptative d'une population en déclin. Ce lien est important puisqu'il permet d'améliorer la compréhension des différents facteurs pouvant affecter le rétablissement d'une population. De plus, ce chapitre a permis de faire ressortir les différences individuelles dans l'alimentation et s'avère essentiel dans la compréhension des liens unissant la condition physiologique aux variations des taux vitaux. Dans le contexte d'une meilleure compréhension des facteurs influençant les performances individuelles, il apparaît essentiel de reconnaître les effets cumulatifs de plusieurs facteurs. De plus, suivre les changements dans la condition physique, physiologique et les indicateurs de la santé pourrait refléter des changements dans la santé globale d'une population et permettrait ainsi aux gestionnaires de suivre l'état de la population et de s'ajuster ou de faire des changements le cas échéant (Kutz *et al.*, 2013).

5.2 Contributions appliquées à la conservation du caribou

Ma thèse a permis d'améliorer nos connaissances générales sur la population de caribous de la Gaspésie et pourra contribuer spécifiquement à la conservation de cette population, mais également à d'autres populations de caribous au Canada. Les deux premiers chapitres de ma thèse ont permis d'augmenter la précision des modèles mixtes isotopiques Bayésiens utilisés dans les chapitres 3 et 4. Ceci a conséquemment permis de documenter le régime alimentaire de cette population en déclin en

corrigeant pour l'effet des lipides et en utilisant des facteurs d'enrichissement trophique spécifiques à nos espèces et nos tissus afin de diminuer les incertitudes associées à la détermination du régime alimentaire et l'évaluation des niches trophiques (Bond et Diamond, 2011; Derbridge *et al.,* 2015). Les deux premiers chapitres sont aussi importants dans l'étude de l'écologie alimentaire de ces cinq espèces de mammifères terrestres et des relations prédateurs-proies impliquant les populations de caribous en déclin partout en Amérique du Nord. Les modèles de normalisation des lipides dérivés du chapitre 1 et les facteurs d'enrichissement trophique calculés dans le chapitre 2 pourront être utilisés pour d'autres populations de caribous (en déclin ou non) afin de mieux comprendre et décrire leur alimentation, leur performance individuelle ou la dynamique des populations, mais également dans d'autres systèmes d'étude où le caribou est absent mais où l'on trouve de l'orignal, du coyote, du loup gris (*Canis lupus*) ou de l'ours noir. De plus, les marqueurs isotopiques et les éléments traces se sont avérés être de bons outils afin de mieux comprendre l'effet de certains déterminants (alimentation, condition physiologique) sur la valeur adaptative du caribou de la Gaspésie ainsi que les interactions trophiques qu'il entretient avec l'orignal et ses prédateurs.

La prédation et la perte d'habitat sont les principaux facteurs évoqués afin d'expliquer le déclin de la population de caribous de la Gaspésie (Frenette *et al.,* 2020). Notre étude a mis en évidence un chevauchement relativement important de la niche trophique du caribou avec celles du coyote et de l'ours noir (chapitre 3). Un tel chevauchement constitue une menace au rétablissement de cette population puisqu'il peut augmenter le taux de rencontre entre le caribou et ses prédateurs et, par conséquent, le risque de mortalité pour le caribou. La modification de la structure et de la composition des peuplements forestiers dans l'aire de répartition de la

population de caribous de la Gaspésie (Boudreau, 2017) a favorisé les jeunes peuplements et l'augmentation de l'abondance d'orignaux (Frenette *et al.*, 2020; Lamoureux *et al.*, 2012), d'ours noirs (Mosnier *et al.*, 2008) et de coyotes (Boisjoly *et al.*, 2010) entraînant un phénomène de compétition apparente (*sensu* Holt, 1977). Les fortes densités de prédateurs dans la région d'étude pourraient expliquer le faible recrutement constaté dans la population de caribous de la Gaspésie. Les coyotes et les ours noirs se sont avérés être responsable de la majorité des événements de prédation sur les faons de caribous lors d'une étude antérieure (Crête et Desrosiers, 1995). Le troisième chapitre de ma thèse a également confirmé que le caribou faisait partie du régime alimentaire des coyotes et des ours noirs de façon opportuniste, une information difficile à obtenir sur la simple base des analyses de fèces communément utilisées. Mes résultats suggèrent également un faible chevauchement des niches trophiques de l'orignal et du caribou (chapitre 3). Cependant, les orignaux sont de plus en plus observés dans la toundra alpine et davantage d'aires d'hivernage sont dénombrées en hautes altitudes (Roussel-Garneau et Larocque, 2020). La stratégie d'isolement du caribou pourrait être compromise par les densités élevées d'orignaux et le partage de l'habitat alpin, réduisant potentiellement l'accès aux ressources les plus nutritives et pouvant ainsi affecter leurs conditions physique et physiologique. De plus, les fortes densités d'orignaux peuvent s'avérer nuisibles au caribou par l'entremise d'un phénomène de compétition apparente.

Une faible compétition entre l'orignal et le caribou pour quelques items alimentaires pourrait influencer le rétablissement de cette population puisqu'une alimentation de moins bonne qualité et une condition physiologique faible pouvaient prédisposer les caribous à de faibles performances de reproduction et à un faible taux de survie (chapitre 4). Selon Gaillard *et al.* (1998), la survie des adultes et le recrutement des

juvéniles sont les paramètres les plus importants pour expliquer les trajectoires démographiques d'ongulés longévifs et, par conséquent, atteindre l'autosuffisance des populations en déclin. Mon chapitre 4 a montré le rôle important de l'alimentation et de la condition physiologique sur la productivité des femelles et sur la survie des individus. Bien que peu d'information soit disponible sur le sujet, certaines études ont suggéré que les ressources alimentaires ne semblaient pas être limitantes pour le caribou de la Gaspésie (Mosnier *et al.,* 2003; St-Laurent *et al.,* 2009). Cependant, les coupes forestières qui ont eu lieu dans l'aire de répartition de la population de caribous de la Gaspésie (Boudreau, 2017) ont entraîné une diminution des conditions favorables au développement de fortes biomasses de lichens arboricoles (Stone *et al.,* 2008) et une diminution d'habitats de bonne qualité pour le caribou (Nadeau Fortin *et al.,* 2016). Des ressources alimentaires de bonne qualité et en quantité suffisante sont toutefois nécessaires pour le caribou et aideront à son rétablissement. Considérant la précarité de cette population de caribous, la restauration de son habitat (Lacerte *et al.,* 2021) ainsi que d'autres stratégies, telles que la mise en enclos des femelles, la chasse à l'orignal et le contrôle des prédateurs (Johnson *et al.,* 2019), risquent de s'avérer nécessaires pour assurer la pérennité de cette population isolée de caribous.

5.3 Limites de l'étude

L'analyse des isotopes stables est un outil méthodologique très robuste permettant de décrire le régime alimentaire d'un consommateur et de quantifier le partitionnement des ressources entre les espèces (Merkle *et al.,* 2017; Newsome *et al.,* 2007; Post, 2002). Cependant, comme toutes les méthodes, il existe des limitations que j'ai considérées en interprétant mes résultats. En effet, l'utilisation des isotopes stables

nécessite une bonne connaissance *a priori* du système d'étude (Phillips *et al.,* 2014). Toutes les sources utilisées dans les modèles mixtes isotopiques Bayésiens doivent avoir des signatures isotopiques distinctes afin d'avoir des proportions et des intervalles de crédibilité valides (Newsome *et al.,* 2007; Phillips *et al.,* 2014). Cependant, certaines de mes sources alimentaires présentaient des zones de chevauchement isotopique. Il est donc conseillé de valider les résultats à l'aide d'approches alternatives, telles que le codage à barre d'ADN (Deagle *et al.,* 2007; Newmaster *et al.,* 2013). À cet effet, mes résultats portant sur la composition du régime alimentaire étaient cohérents avec ce qui a été observé par Christopherson *et al.* (2019) à l'aide du codage à barre d'ADN réalisé sur le caribou et l'orignal dans la même aire d'étude que la mienne (à noter que les lichens et les champignons n'ont pas été pris en compte dans leur analyse). J'ai également validé la corrélation entre les différentes sources avec la librairie SIMM (lib. *matrixplot*). Lorsque la corrélation entre deux sources alimentaires était trop élevée, nous avons combiné ces différentes sources (Jackson *et al.,* 2011; Phillips *et al.,* 2014).

De plus, il apparaît essentiel de mener d'autres études afin de bonifier notre compréhension des différences sources de variabilité pouvant affecter les facteurs d'enrichissement trophique, tels que le statut nutritionnel, la masse corporelle (Vanderklift et Ponsard, 2003), la composition du régime alimentaire (Caut *et al.,* 2009; Sponheimer *et al.,* 2003a), l'âge, le sexe (Kurle *et al.,* 2014; Lecomte *et al.,* 2011; Tieszen *et al.,* 1983), les voies métaboliques des protéines, lipides et glucides (Perga et Grey, 2010; Wolf *et al.,* 2015) ainsi que le rapport CN dans les sources alimentaires (Felicetti *et al.,* 2003). Considérant la petite taille échantillon et la difficulté de réalisation de ce type d'étude, je n'ai pas pu prendre en compte toutes ces sources de variation dans mes analyses. Sur la base du faible coefficient de

variation observé et de la variabilité intraspécifique mesurée, je considère toutefois que les facteurs d'enrichissement trophique que j'ai estimés pour cinq espèces et deux types de tissus sont très précis.

La niche trophique représente un proxy de la niche écologique réalisée qui est influencée par l'utilisation de l'habitat et des ressources (Newsome *et al.,* 2007). En effet, la position des consommateurs dans l'espace bidimensionnel isotopique est déterminée par les ressources consommées (c.-à-d. différents items alimentaires ayant des compositions isotopiques distinctes) et par les différences entre l'utilisation de l'habitat en s'alimentant (c.-à-d. les mêmes proies peuvent avoir des signatures isotopiques distinctes dans divers habitats). Le consommateur qui s'alimente sur deux items alimentaires qui ont des compositions isotopiques distinctes aura toujours une niche isotopique plus large que le consommateur qui s'alimente sur deux items alimentaires présentant des signatures isotopiques similaires (Matthews et Mazumder, 2004; Newsome *et al.,* 2007). La niche isotopique représente donc des informations quantitatives relatives à l'utilisation de l'habitat et des ressources utilisées par l'animal (Newsome *et al.,* 2007). Il s'avère par conséquent important d'estimer la niche isotopique pour des groupes d'individus ayant théoriquement accès aux mêmes ressources (ce que j'ai fait).

La faible contribution du caribou de la Gaspésie dans le régime alimentaire des prédateurs pourrait potentiellement s'expliquer par la très faible abondance de caribous dans l'aire d'étude, par la capacité limitée des analyses isotopiques à détecter des items alimentaires rares (Nielsen *et al.,* 2018; Phillips *et al.,* 2014), mais aussi par le déphasage entre la saison d'échantillonnage des poils et la période de vulnérabilité des caribous à la prédation. En effet, le poil intègre l'information du

régime alimentaire au moment de sa croissance (Hilderbrand *et al.*, 1996; Schwertl *et al.*, 2003). Les poils des prédateurs échantillonnés lors de cette étude (mai à octobre) intégraient donc le régime alimentaire d'été et d'automne. Le coyote et l'ours noir sont des prédateurs relativement efficaces des faons caribous lors de la mise bas printanière dans les régions nordiques (Bastille-Rousseau *et al.*, 2011; Leclerc *et al.*, 2014), mais aussi en Gaspésie (Boisjoly *et al.*, 2010; Crête et Desrosiers 1995). Il aurait été intéressant d'avoir des échantillons sanguins prélevés au printemps afin d'estimer la proportion de caribou consommée par ces prédateurs.

De plus, les besoins en éléments traces essentiels et les plages de référence normales des espèces sauvages ne sont pas bien établis (Pollock, 2005) et une compréhension complète de leur implication dans la croissance, la reproduction et la survie fait encore défaut (Robbins, 1993), spécialement pour le caribou (Bondo *et al.*, 2019). Davantage d'études axées sur les besoins en éléments traces et sur leurs rôles respectifs dans la physiologie du corps sont donc nécessaires, sur le transfert des éléments traces le long de la chaîne alimentaire ainsi que sur le lien entre les éléments traces mesurés dans les poils et les niveaux de référence mesurés ailleurs dans l'organisme (p. ex. le foie et le sang). Cependant, les poils incorporent les éléments traces principalement par la circulation sanguine (Flache *et al*., 2017; Vermeulen *et al*., 2009) durant leur période de croissance, laissant présager que cette corrélation existe et pourrait être représentative des niveaux observés dans les autres tissus.

Finalement, je n'ai pas pu inclure les interactions entre les éléments traces, même si certains éléments peuvent interférer avec l'absorption d'autres éléments (McDonald *et al.*, 2010; Ohlson et Staaland, 2001). Je reconnais qu'il existe probablement d'autres facteurs susceptibles d'influencer les performances individuelles que je n'ai pas inclus

dans mes différents modèles du chapitre 4, tels que le climat (Joly *et al.*, 2011), l'âge des femelles (Adams et Dale, 1998), l'état de la neige (Kumpula et Colpaert, 2003), les interactions interspécifiques (via la compétition apparente; Frenette *et al.*, 2020) et l'utilisation de l'espace (Lafontaine *et al.*, 2017; Lesmerises *et al.*, 2019; Losier *et al.*, 2015).

5.4 Avenues de recherche

Ma thèse portait principalement sur le lien entre l'alimentation, la condition physiologique et la valeur adaptative du caribou de la Gaspésie dans un système trophique et ouvre la porte à plusieurs avenues de recherche qui permettront de poursuivre l'acquisition de connaissances sur les facteurs influençant le déclin des populations. Il serait intéressant de réaliser une étude plus poussée portant sur le stress associé aux perturbations humaines (Renaud, 2012), mais également à un stress nutritionnel (Kitaysky *et al.*, 2007). En effet, de hauts niveaux persistants de cortisol chez l'animal sont reconnus pour causer du stress à long terme et ont des effets négatifs sur le système immunitaire (Charbonnel *et al.*, 2008; Romero, 2004), la croissance (Reeder et Kramer, 2005), l'alimentation (Bradshaw *et al.*, 1998; Duchesne *et al.*, 2000) ainsi que sur la valeur adaptative de l'animal (Ellenberg *et al.*, 2007; Preisser, 2009; Wingfield et Sapolsky, 2003). Ce stress chronique peut ultimement affecter la dynamique d'une population et entraîner son déclin (Charbonnel *et al.*, 2008; Reeder et Kramer, 2005).

Il serait aussi intéressant d'évaluer la disponibilité, la qualité et le contenu en éléments traces des ressources alimentaires pour le caribou. En effet, la digestibilité, la quantité de protéines, de fibres, de vitamines ou le contenu énergétique sont des

indicateurs importants de la qualité nutritionnelle d'un item alimentaire. Les ressources alimentaires de bonne qualité et en quantité suffisante sont importantes pour les ongulés (Barboza et Parker, 2008; Cook *et al.*, 2004a; Parker *et al.*, 1999, 2009), principalement pour la gestation (Cook *et al.*, 2004b), la production de lait, la croissance du fœtus et des juvéniles, la constitution des réserves de graisse (Barboza et Parker, 2008; Barboza *et al.*, 2004), ainsi que la survie hivernale (Cook *et al.*, 2004a). En effet, une acquisition de ressources alimentaires de mauvaise qualité pourrait affecter l'état nutritionnel de l'animal et affecter les performances individuelles et le déclin de la population (Barboza *et al.*, 2009; Cook *et al*., 2004a, 2004b; Parker *et al.*, 2009).

Il serait également intéressant d'effectuer un suivi des individus à long terme et d'avoir accès à des échantillons de poils annuellement afin de mesurer la variation interannuelle des éléments traces et des isotopes stables. Ces analyses pourraient aider à mieux expliquer les variations dans le taux de survie entre les années (60 à 100%, Frenette *et al.*, 2020) ainsi que les variations dans le taux de gestation des femelles. Par exemple, 90% des femelles étaient gestantes en 2013 alors que seulement 60% l'étaient en 2014. Il a été montré qu'au niveau populationnel, certains éléments traces affectent la dynamique des populations (Flueck *et al.*, 2012). Par exemple, une carence en cuivre et en sélénium a été associée à une pauvre santé globale et une faible productivité chez des populations d'ongulés (Flueck *et al.*, 2012; Flynn *et al.*, 1977).

Finalement, Bolnick *et al.* (2003) ont montré l'importance d'étudier la variabilité individuelle dans l'étude des populations et des communautés puisqu'elle a des implications importantes au niveau de l'écologie, de l'évolution et de la conservation.

Les caractéristiques de l'individu telles que son phénotype, sa physiologie et ses comportements vont déterminer ses préférences alimentaires, l'utilisation de son habitat, son statut immunologique ainsi que ses stratégies anti-prédatrice ou de reproduction (Araújo *et al.,* 2011). Conséquemment, ces variations individuelles intraspécifiques vont moduler les interactions trophiques et donc la dynamique de la population (Bolnick *et al.,* 2011; Dall *et al.,* 2012). Ultimement, les coûts et les bénéfices énergétiques de ces préférences déterminent l'énergie disponible pour la reproduction et la survie de l'individu.

5.5 Conclusion

Mes résultats mettent en lumière l'impact de nombreux facteurs sur le déclin du caribou (voir la Figure 0.1 de l'introduction générale). Puisque la majorité des populations de caribous au Canada sont en déclin (COSEPAC, 2014; Festa-Bianchet *et al.,* 2011; Vors et Boyce, 2009), investir des efforts supplémentaires pour assurer leur conservation est essentiel, d'autant que le caribou est une espèce emblématique de la forêt boréale. De plus, la sous-espèce caribou des bois est endémique au Canada et est un indicateur de changement, puisque la perte du caribou appauvrirait la diversité biologique de tous les paysages occupés par celui-ci (Bichet *et al.,* 2016; COSEWIC, 2011). Il importe de continuer à étudier l'effet des menaces et les pistes de solution permettant le rétablissement de cette espèce iconique qui fait partie intégrante de notre patrimoine naturel. Cet effort de recherche est d'autant plus criant que le caribou de la Gaspésie est désigné comme « *espèce en voie de disparition* » selon la *Loi sur les espèces en péril*, et comme un élément de la biodiversité irremplaçable au Canada par le Comité sur la situation des espèces en péril au Canada (COSEPAC, 2014; COSEWIC, 2011). Toutefois, la pérennité des populations de

caribous au Canada, et plus spécifiquement de la population de caribous de la Gaspésie, dépendra de sa résilience face à la transformation de son habitat et à la restauration de celui-ci ainsi que de notre volonté collective à renverser le déclin et assurer son autosuffisance. J'ai tout de même espoir de pouvoir observer encore des caribous de la Gaspésie avec mes futurs petits-enfants.

GLOSSAIRE

Alimentation (lib. *feeding*) : ensemble des comportements impliqués dans la prise alimentaire, action de s'alimenter, d'alimenter (Soanes, 2002).

Condition physiologique : condition ou l'état du corps ou des fonctions corporelles et peut référer au métabolisme, à la nutrition, au système endocrinien et immunitaire (Ricklefs et Wikelski, 2002).

Espèces sympatriques : espèces se partageant un habitat commun simultanément (Peters *et al*., 2013).

Facteur extrinsèque : facteur qui exerce son influence de l'extérieur et qui regroupe les conditions environnementales (p. ex. les caractéristiques de l'habitat, le climat), les facteurs abiotiques (p. ex. précipitations, pH du sol) et biotiques (p. ex. prédation, compétition, alimentation, agents infectieux et parasitaires) (Macbeth et Kutz, 2019).

Facteur intrinsèque : caractéristique biologique endogène, qui concerne directement l'individu ou la population (p. ex. la génétique, l'immunité, le comportement et la phase du cycle de vie) (Macbeth et Kutz, 2019).

Niche trophique : partie de la niche écologique qui concerne les ressources alimentaires utilisées (Bearhop *et al*., 2004).

Nutrition : ensemble des processus d'assimilation et de dégradation des aliments qui ont lieu dans un organisme lui permettant d'assurer ses fonctions essentielles et de croître, processus métabolique de modification des nutriments (Parker *et al*., 2009).

Quête alimentaire (lib. *foraging*) : activité de recherche des ressources alimentaires par les organismes (Soanes, 2002).

Ressources : éléments de l'environnement en quantité limitée utilisés par l'animal afin de se maintenir en vie et de se reproduire (p. ex. abris, nourriture, eau, partenaires) (Giraldeau et Dubois, 2015).

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