UNIVERSITÉ DU QUÉBEC À RIMOUSKI

NICHE ALIMENTAIRE ET ÉCOLOGIE DU LOUP ET DU CARCAJOU DANS L'ARCTIQUE CANADIEN : DES ANALYSES ISOTOPIQUES AU SAVOIR INUIT

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RÉSUMÉ

Les grands carnivores jouent un rôle clé dans la structure et le fonctionnement des écosystèmes. Ils sont souvent utilisés comme indicateurs écologiques puisqu'ils répondent rapidement aux changements dans l'environnement. Les grands carnivores vivent depuis très longtemps à proximité des populations humaines et ont été longtemps perçus de façon très négative, mais revêtent une valeur spirituelle et culturelle et représentent une importante composante de l'économie de subsistance pour les communautés autochtones. En dépit de leur importance, l'écologie des grands carnivores est en général beaucoup moins connue que celle d'autres groupes trophiques en raison de leur faible densité et des difficultés logistiques qu'implique le suivi des populations sauvages.

L'objectif général de cette étude était de mieux comprendre le rôle de deux espèces de grands carnivores, le loup gris *Canis lupus* et le carcajou *Gulo gulo* dans le fonctionnement de l'écosystème de la toundra arctique et d'examiner leur importance pour les communautés inuit. Pour ce faire, nous avons développé un programme de suivi de ces deux espèces basé sur l'analyse de carcasses récoltées par des chasseurs inuit. Notre suivi impliquait 13 communautés inuit réparties sur la partie continentale du territoire du Nunavut (Canada), soit environ 900 000 km^2. Notre suivi multiannuel (2010-13) et multisaisonnier nous a permis d'obtenir des tailles d'échantillons inégalées pour ces espèces (287 loups et 376 carcajous). Les trois objectifs spécifiques de cette étude consistaient à:

1) quantifier, à l'aide des isotopes stables et des contenus stomacaux, les variations dans l'utilisation des ressources alimentaires par deux grands carnivores arctiques en fonction des fluctuations spatio-temporelles de la diversité des ressources alimentaires et de l'abondance des grands herbivores, et également en fonction des contraintes biologiques inhérentes aux deux espèces étudiées;
2) déterminer expérimentalement les taux de fractionnement isotopique entre la nourriture et les poils de grands carnivores afin d'augmenter la précision de nos analyses isotopiques;

3) examiner la relation entre les grands carnivores et les populations inuit dans un contexte de changements socio-économiques importants.

Dans le premier chapitre (objectif 1), nous avons examiné les hypothèses selon lesquelles les opportunités écologiques (*c.-à-d.* la diversité des ressources déterminée par les variations environnementales), l’abondance de la proie préférée (caribou) et les contraintes biologiques déterminent la niche alimentaire des populations et la variation interindividuelle chez le carcajou et le loup. Le carcajou présentait une plus grande niche alimentaire et variation interindividuelle lorsque les ressources marines étaient disponibles et là où l’abondance du caribou était faible. Cependant, sa niche alimentaire variait peu dans les régions où le caribou migrateur était disponible, même en présence des ressources marines. À l’inverse, la niche alimentaire du loup ne variait pas dans les régions où l’abondance des caribous était faible, mais plutôt dans le nord-ouest de notre aire d’étude où le caribou et les ressources marines étaient accessibles. À l’été, la diversité et l’abondance des ressources influençaient la niche alimentaire des loups et carcajous, mais pas la variation interindividuelle.

Dans le second chapitre (objectif 2), nous avons déterminé, à l’aide d’animaux en captivité nourris à partir de sources contrôlées, le taux de fractionnement du carbone et de l’azote entre la nourriture et les poils de quatre grands carnivores : le loup, le carcajou, l’ours grizzly *Ursus arctos* et l’ours blanc *Ursus maritimus*. Les taux de fractionnement obtenus chez le loup étaient comparables aux rares résultats présents dans la littérature. Notre étude est toutefois la première à avoir déterminé le fractionnement isotopique chez le carcajou et les loups juvéniles, et la première sur les poils d’ours grizzly et d’ours blanc, un tissu qui est très utilisé dans les études non invasives des mammifères.

Dans le troisième chapitre (objectif 3), nous avons examiné une hypothèse émise localement (par les chasseurs de Qamani’tuaq) reliant la pression de chasse à l’état d’une population de loups vivant à proximité de la communauté. Nous avons aussi analysé les facteurs environnementaux et socio-économiques qui déterminent cette pression de chasse. Nos résultats issus de données biologiques et d’observations effectuées par des chasseurs indiquent une moins bonne condition corporelle, une perturbation de la taille et de la structure des groupes, et une réaction de fuite à l’homme augmentée chez les loups vivant à proximité de la communauté *versus* ceux vivant au loin. Les perceptions des chasseurs suggèrent une importante contribution du développement minier à l’augmentation de l’efficacité de la chasse au loup, la modification des pratiques de chasse entraînant une plus grande pression locale, ainsi que la perturbation de l’habitat et le comportement des caribous.

En conclusion, cette thèse a permis de mieux comprendre comment deux espèces sympatriques de grands carnivores peuvent montrer des réponses très contrastées

dans leur niche alimentaire, incluant les variations interindividuelles, en réponse aux patrons régionaux et saisonniers de disponibilité des ressources. Ces résultats permettent de mieux comprendre le fonctionnement et la capacité de résilience aux changements de l’écosystème de la toundra arctique. Par exemple, les flux d’énergie et éléments nutritifs entre l’écosystème marin et toundrique peuvent augmenter les densités de prédateurs et ainsi influencer les interactions prédateur-proie terrestres. La thèse souligne l’importance de collaborer avec les communautés autochtones et d’utiliser des savoirs locaux afin d’approfondir nos connaissances en écologie tout en respectant l’identité et les priorités des cultures holistiques.

Mots-clés : Grands carnivores terrestres, loup, carcajou, niche alimentaire, ressources allochtones, fractionnement isotopique, chasse de subsistance, savoir local

INTRODUCTION

0.1 Le cadre théorique

0.1.1 Le rôle des grands carnivores dans les écosystèmes

Les prédateurs forment une composante essentielle des écosystèmes puisqu'ils modulent les flux d'énergie qui traversent les différents niveaux trophiques (Estes et al., 2011; Halpern, Cottenie, & Broitman, 2006; Legagneux et al., 2014). Pour combler les besoins énergétiques essentiels à leur survie et à leur reproduction, les prédateurs peuvent prélever d'importantes quantités de proies, et peuvent ainsi réguler leurs populations (Carbone & Gittleman, 2002; Krebs, Boonstra, Boutin, & Sinclair, 2001; Krebs, Gaines, Keller, Myers, & Tamarin, 1973; Lack, 1954; O'Donoghue, Boutin, Krebs, & Hofer, 1997; Solomon, 1949; Thirgood, Redpath, Rothery, & Aebischer, 2000).

En régulant l'abondance des herbivores, les prédateurs peuvent contribuer à relâcher la pression de broutement sur la production primaire par le biais de cascades trophiques (Borer et al., 2005; Gauthier, Bety, Giroux, & Rochefort, 2004; Hamback et al., 2004; Hebblewhite et al., 2005; Jefferies, 2000; C. N. Johnson, 2010; B. E. McLaren & Peterson, 1994). De plus, la prédation intraguilde (lorsqu'un grand prédateur limite l'abondance de mésoprédateurs) peut également générer des cascades trophiques, mais avec un effet inverse sur les herbivores et la productivité primaire (Berger, Gese & Berger 2008). Dans certains cas, l'importance du rôle régulateur d'un prédateur est telle que son déclin peut entraîner des modifications profondes de l’écosystème (Estes & Palmisano 1974; Schmitz, Hamback & Beckerman 2000; Terborgh *et al.* 2001; Frank *et al.* 2005). Dans les écosystèmes où les grands prédateurs ont été exclus par l’homme, il est également commun d’observer une augmentation de l’abondance des mésoprédateurs, qui contribuent à limiter les populations d’herbivores (Ritchie & Johnson 2009; Prugh *et al.* 2009; Elmhagen *et al.* 2010), ce qui peut même mener à des extinctions locales (Crooks & Soule 1999). La prédation peut donc être perçue comme une force de régulation descendante (*top down*), par opposition à la régulation ascendante (*bottom-up*) qui s’effectue à partir de la production primaire (Hunter & Price 1992; Power 1992; Meserve *et al.* 2003; Legagneux *et al.* 2012). Le fait qu’un écosystème soit régulé par le haut ou par le bas (ou par les deux à la fois) dépendrait vraisemblablement de sa productivité primaire (Oksanen & Oksanen 2000), du ratio de taille entre les prédateurs et leurs proies (Carbone & Gittleman 2002; Hopcraft, Sinclair & Packer 2005; Legagneux *et al.* 2014) et de sa connectivité avec d’autres écosystèmes (Leroux & Loreau 2008; Legagneux *et al.* 2012).

Les cas où la prédation par les grands carnivores terrestres est la principale force de régulation dans l’écosystème sont relativement plus rares que ceux où les prédateurs de plus petite taille ont cet effet (Fowler 1987; Skogland 1991). Plusieurs exemples ont cependant été documentés (McLaren & Peterson 1994; Crête & Manseau 1996; Terborgh *et al.* 2001; Hopcraft, Olff & Sinclair 2010; Pierce *et al.* 2012). De manière très intéressante, la prédation par les grands carnivores terrestres ne serait pas en mesure de réguler l’abondance des ongulés migrateurs (Fryxell, Greever & Sinclair 1988; Legagneux *et al.* 2014), alors qu’une telle régulation est possible avec les ongulés résidents, qui vivent à de plus faibles densités. Par exemple, bien qu’il ait été démontré que le loup puisse réguler l’abondance du caribou, *Rangifer tarandus*, dans l’écosystème de la forêt boréale (Bergerud 1988; Seip 1991; Crête & Manseau 1996; Hegel *et al.* 2010), ce type de régulation semble complètement absent chez le caribou toundrique (Messier *et al.* 1988; Ballard *et al.* 1997; Haskell & Ballard 2007). De par leur faible densité et leur niveau trophique élevé, les grands carnivores sont plus sensibles aux perturbations environnementales et sont donc considérés comme des indicateurs de la santé des écosystèmes (Estes *et al.* 2011). Étant donné leur rôle clé dans les écosystèmes (et l'intérêt qu'ils suscitent auprès du public), ils sont souvent au cœur des programmes de conservation visant à protéger la biodiversité (Saether 1999; Sergio, Newton & Marchesi 2005). Les grands carnivores sont également perçus comme une importante composante de résilience des écosystèmes dans le contexte des changements climatiques (Weaver, Paquet & Ruggiero 1996; Wilmers & Getz 2005; Sala 2006).

0.1.2 La niche alimentaire

Les stratégies d'approvisionnement des prédateurs peuvent être déterminantes pour la dynamique des populations d'herbivores (Oaten & Murdoch 1975). Les prédateurs très mobiles ayant un régime alimentaire généraliste peuvent créer des liens entre des écosystèmes spatialement distincts, exerçant d'importants effets stabilisateurs sur la dynamique des communautés (McCann, Rasmussen & Umbanhowar 2005; Rooney *et al.* 2006). À l'inverse, les prédateurs ayant une mobilité plus réduite et un régime spécialiste ont moins tendance à se disperser entre écosystèmes et ne peuvent exercer le même rôle (Matich, Heithaus, & Layman, 2011a; Quevedo, Svanback, & Eklov, 2009). Par exemple, dans les écosystèmes relativement simples tels que la taïga et la toundra, la prédation par les prédateurs spécialistes résidents (p. ex. hermine, *Mustela erminea*) peut causer et entretenir la cyclicité des populations de proies (p. ex. lemming, *Dicrostonyx groenlandicus*) alors que les prédateurs mobiles généralistes (p. ex. renard arctique, *Vulpes lagopus*) peuvent induire un effet stabilisateur sur ces mêmes populations (Hanski *et al.* 2001; Gilg, Hanski & Sittler 2003). De plus, dans de tels systèmes, il semble que certaines espèces de spécialistes nomades (p. ex. harfang des neiges, *Bubo scandiacus* et faucons gerfauts, *Falco rusticolus)* puissent également exercer un rôle stabilisateur (Korpimaki et al., 2003; O. K. Nielsen, 1999).

Afin de mieux comprendre les interactions prédateurs-proies et leurs conséquences sur la structure et le fonctionnement des écosystèmes, il importe donc de s'intéresser aux stratégies d'approvisionnement des prédateurs et de comprendre comment elles peuvent varier au sein même d'une espèce ou d'une population donnée (Bolnick *et al.* 2011).

La composition du régime alimentaire des prédateurs est typiquement déterminée en fonction du nombre d'espèces consommées. Les spécialistes (monophages et oligophages) consomment un nombre très restreint d'espèces de proies alors que les généralistes (polyphages) en consomment un plus grand éventail (Begon, Colin & Harper, 2006). La définition de Holling (1959) est toutefois la plus utilisée en écologie empirique puisqu'elle associe le type de régime alimentaire à la forme de la réponse fonctionnelle démontrée par un prédateur, qui est définie par le nombre de proies consommées *per capita* en fonction de la densité de la proie (Figure 0.1). Selon cette définition, un prédateur spécialiste est celui qui démontre une réponse de 'type II', alors qu'un prédateur généraliste démontre une réponse de 'type III' (pour plus de détails, voir la description de la Figure 0.1).

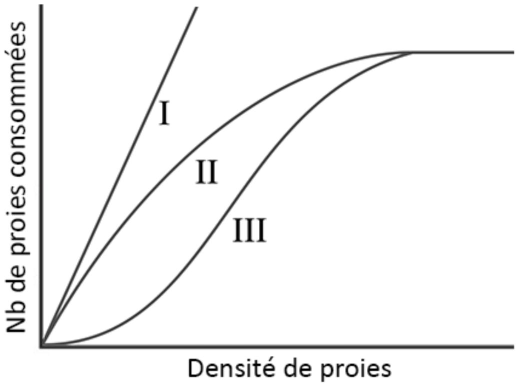

Figure 0.1 Représentation des types de réponse fonctionnelle (graphique d'après Holling 1959) : le nombre de proies capturées par un prédateur varie selon la densité des proies. Les réponses de type I et II sont typiques des prédateurs

spécialistes qui utilisent leur proie préférée de manière linéaire en situation de faible densité, mais de manière linéaire (type I) ou logarithmique (type II) à haute densité. La réponse de type III est typique des prédateurs généralistes qui utilisent leur proie préférée de manière exponentielle à faible densité (utilisant donc des ressources alternatives) et de manière logarithmique à haute densité.

Bien que la dichotomie entre prédateurs généralistes et spécialistes soit utile, les espèces et populations généralistes peuvent être constituées d'individus pouvant grandement varier en termes de stratégie d'approvisionnement et pouvant donc se situer à différents niveaux sur un gradient de spécialisation (Van Valen 1965; Roughgarden 1972; Smith & Skulason 1996). Par conséquent, un nombre croissant d'études empruntent le concept de variation des niches alimentaires formulé par Roughgarden (1972). Selon ce concept, le niveau de spécialisation est indiqué par la proportion des ressources utilisées par un individu relativement à l'ensemble des ressources utilisées par la population (Figure 0.2). L'étendue de la niche de la population est alors la somme des niches individuelles (Figure 0.2). À ce jour, plus de 200 études auraient démontré l'existence de spécialisation individuelle (Bolnick *et al.* 2003; Araujo, Bolnick & Layman 2011). Certaines auraient démontré des conséquences de cette spécialisation individuelle sur des populations (Annett & Pierotti 1999; Golet *et al.* 2000; Votier *et al.* 2004), des communautés et des écosystèmes (Quevedo *et al.* 2009), et même des processus évolutifs (Hughes *et al.* 2008; Bolnick *et al.* 2011).

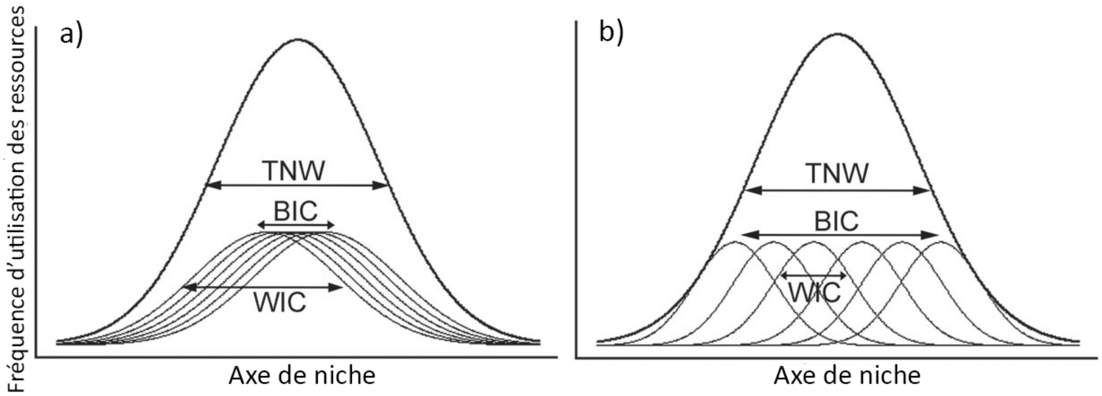

Figure 0.2 Représentation conceptuelle de la variation de la niche alimentaire pour les populations généralistes, telle que définie par Roughgarden (1972) et adapté par Bolnick et coll. (2003). Une espèce ou une population généraliste donnée peut-être composée d'individus généralistes (a) dont la niche alimentaire (*Within Individual Component*, WIC) est presque aussi vaste que celle de la population (*Total Niche Width*, TNW), ou d'individus spécialistes (b) dont la niche alimentaire (WIC) est nettement plus étroite que cette de la population (TNW). Les individus généralistes (a) sont également caractérisés par une faible variabilité interindividuelle (*Between Individual Component,* BIC) alors que les individus spécialistes (b) sont caractérisés par une forte variabilité interindividuelle (BIC). L'axe des abscisses représente la niche alimentaire, soit l'éventail des types de ressources utilisées.

Quels sont les facteurs déterminant la niche alimentaire des individus? Les variations de niche individuelle ont souvent été attribuées à des différences morphologiques et physiologiques dues au sexe ou à l'âge (Edwards, Derocher, Hobson, Branigan, & Nagy, 2011; S. Lewis et al., 2002; Schoener, 1986; T. B. Smith & Skulason, 1996; Gregory W. Thiemann, Iverson, Stirling, & Obbard, 2011) ou à des différences d'accès aux ressources dues par exemple au statut reproducteur (Kernaléguen *et al.* 2015; Horswill *et al.* 2016). Toutefois, la niche alimentaire des individus peut également varier dans un même groupe d'âge ou de sexe (Bolnick *et al.* 2003), principalement en fonction de la disponibilité des ressources alimentaires et de variations phénotypiques (Taper & Case 1985; Ackermann, Doebeli & Gomulkiewicz 2004; Hughes *et al.* 2008; Araujo *et al.* 2011).

La théorie de l'approvisionnement optimal (*Optimal Foraging Theory, OFT*, (MacArthur & Pianka 1966; Pyke 1984; Sih & Christensen 2001), peut aider à mieux comprendre comment la disponibilité des ressources influence la niche alimentaire. L'*OFT* prédit qu'un individu va se nourrir de la ressource la plus profitable (préférée), c.-à-d. celle qui confère le plus grand gain énergétique en fonction de l'énergie investie pour sa recherche, sa capture et sa digestion. D'autres ressources jugées moins rentables seront largement ignorées et ce, peu importe leur disponibilité. Par contre, lorsque les ressources les plus rentables deviennent moins abondantes dans l'environnement, l'*OFT* prédit que les individus vont élargir leur niche alimentaire pour intégrer les ressources dites alternatives, même si elles sont moins rentables (la réponse fonctionnelle de type III, voir Figure 0.1). Certains individus peuvent cependant poursuivre l'utilisation exclusive de la ressource préférée (réponse fonctionnelle de type I ou II, voir Figure 0.1) ou encore utiliser exclusivement un certain type de ressource alternative, ce qui contribue alors à la diversification des niches alimentaires et à la spécialisation individuelle. Le fait que les individus utilisent une ou l'autre des stratégies peut dépendre de variations phénotypiques (Taper & Case 1985; Ackermann *et al.* 2004; Hughes *et al.* 2008) qui déterminent les compromis fonctionnels dans la capacité des individus à utiliser les ressources alternatives. Chez les espèces grégaires, la dominance de certains individus peut également provoquer des différences dans l'utilisation des ressources (Sol *et al.* 2005).

Les interactions écologiques intra et interspécifiques peuvent influencer l'abondance des ressources préférées et la diversité des ressources disponibles et, de ce fait, influencer la niche alimentaire (Araujo *et al.* 2011). La compétition intraspécifique peut forcer les individus à diversifier leur niche alimentaire, ce qui provoque l'élargissement de la niche de la population (Evangelista, Boiche, Lecerf, & Cucherousset, 2014; R. Svanback & Bolnick, 2005, 2007a). La compétition intraspécifique serait également une force déterminant l'évolution de la niche individuelle et pourrait promouvoir la diversification adaptative de la niche (spécialisation individuelle) en situation de hauts niveaux de compétition (Ackermann *et al.* 2004; Bolnick *et al.* 2007; Parent & Crespi 2009). À l'opposé, la compétition interspécifique contraindrait la diversité des ressources disponibles et ainsi rétrécirait l'étendue de la niche des populations et diminuerait la variation interindividuelle (Bolnick *et al.* 2010). Cependant, lorsqu'une population s'émancipe d'un compétiteur, par exemple en colonisant une nouvelle aire, la niche de la population a tendance à s’élargir soit par spécialisation individuelle (Van Valen 1965; Bolnick *et al.* 2007), soit par élargissement de la niche individuelle (Bolnick *et al.* 2010).

0.1.3 Opportunités écologiques et variation des niches alimentaires

Les opportunités écologiques représentent la diversité des ressources disponibles aux consommateurs. Elles varient selon les conditions environnementales. À l’inverse de la compétition interspécifique, elles peuvent contribuer à augmenter la niche alimentaire d’une population en permettant la spécialisation individuelle (Araujo *et al.* 2011). L’hétérogénéité des habitats, la taille des parcelles d’approvisionnement ou encore la stabilité des conditions environnementales (Ostfeld & Keesing 2000; Yang *et al.* 2008) peuvent déterminer la diversité des ressources disponibles aux consommateurs en un lieu et à un moment donné. Les recherches les plus classiques ayant testé l’hypothèse selon laquelle les opportunités écologiques influencent la niche alimentaire ont étudié le lien entre la diversité des ressources et la variation des traits morphologiques (Roughgarden 1974) dans des environnements sans ou avec peu de compétiteurs interspécifiques(Parent & Crespi 2009), revue par (Nosil & Reimchen 2005), ou alors expérimentalement (Rainey & Travisano 1998). Les études les plus récentes utilisent des mesures directes de niche alimentaire, grâce à des contenus stomacaux ou isotopes stables, puisque les traits morphologiques ne seraient pas les seuls déterminants de l’utilisation des ressources (Bolnick *et al.* 2007). En effet, les comportements seraient également une importante composante de la niche alimentaire (Werner & Sherry 1987). Ainsi, un nombre croissant d’études quantitatives soutiennent l’hypothèse des opportunités écologiques chez différentes espèces de prédateurs (Horswill et al., 2016; Kernaléguen et al., 2015; Layman, Quattrochi, Peyer, & Allgeier, 2007; Seth D. Newsome et al., 2015; Yurkowski et al., 2016).

Par exemple, Darimont et coll. (2009) ont démontré chez des loups que la diversité des ressources contribuait à élargir la niche alimentaire et à augmenter la spécialisation individuelle. La sous-population étudiée habitait en Colombie-Britannique des îles proches du continent donnant accès à la fois aux ressources terrestres (dont le cerf mulet *Odocoileus hemionus*) et aux ressources marines (le saumon *oncorhynchus spp.*)(Figure 0.3).

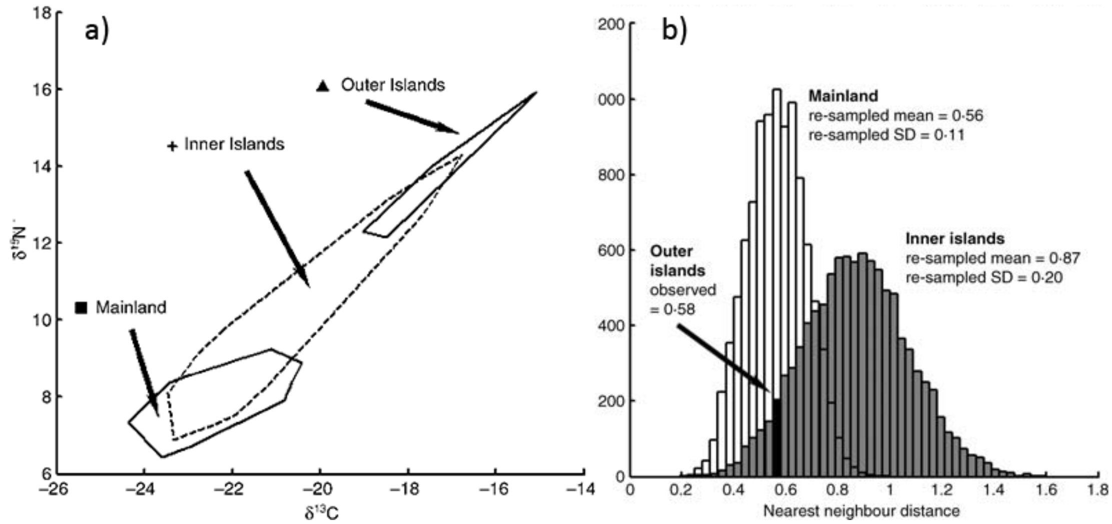

Figure 0.3 Principaux résultats issus de l'étude de Darimont et al. (2009) supportant l'hypothèse selon laquelle la diversité des ressources peut induire l'élargissement de la niche alimentaire d'une sous-population (a) par le biais de la spécialisation individuelle (b). La sous-population *Inner-Islands*, occupant un environnement avec accès à des ressources terrestres et marines, adopte une niche isotopique (l'aire totale occupée par les individus dans l'espace de l'isotope carbone, δ^{13}C et azote δ^{15}N) plus large que les sous-populations *Mainland* (donnant accès seulement aux ressources terrestres) et *Outer Islands* (accès seulement aux ressources marines). La sous-population *Inner Islands* était également caractérisée par une plus grande variation interindividuelle des niches alimentaires (et donc une plus grande spécialisation individuelle) que les deux autres sous-populations.

Très peu d'autres études ont évalué chez des prédateurs terrestres le lien entre les opportunités écologiques, la niche alimentaire et la spécialisation individuelle (voir cependant (Gerardo Herrera *et al.* 2008; Costa *et al.* 2008; L'Hérault *et al.* 2013). De telles études sont plus communes chez les prédateurs marins (Kernaléguen *et al.* 2015; Yurkowski *et al.* 2016). Toutefois, l'utilisation de ressources allochtones (marines ou non) par les carnivores terrestres semble très répandue en milieu naturel et peut contribuer à augmenter la diversité des ressources pour ces prédateurs, avec des effets potentiels sur la niche alimentaire des individus (Rose & Polis 1998; Ben-David, Titus & Beier 2004; Adams *et al.* 2010; Giroux *et al.* 2012; Tarroux *et al.* 2012). Ces effets peuvent également avoir d'importantes répercussions sur la densité et l'évolution des populations de proies, avec des effets sur l'ensemble des écosystèmes terrestres par le biais de cascades trophiques (Yang *et al.* 2008; Leroux & Loreau 2008).

0.1.4 Grands carnivores et populations humaines : persécution, conservation et impact de la chasse

En occident, la relation entre les humains et les grands prédateurs a longtemps été animée par la compétition pour les ressources, en particulier le bétail (Ciucci & Boitani 1998; Naughton-Treves, Grossberg & Treves 2003), et a ainsi été largement conflictuelle (Kellert *et al.* 1996). L'interaction homme-loup est certainement la plus viscérale et documentée et remonterait à des temps séculaires (figure 0.4a). L'abattage (Mech 1970; Moura *et al.* 2014) et la perte d'habitats due au développement anthropique (Corsi, Duprè & Boitani 1999; Terborgh *et al.* 2001; Houle *et al.* 2010) ont contribué à la disparition presque complète du loup dans les années 1970 au Mexique, aux États-Unis et au sud du Canada (Mech 1970; Wayne *et al.* 1992; Hayes & Gunson 1995). Même en territoire sauvage, par exemple au nord du Canada et en Alaska, les programmes de contrôle des prédateurs, initiés dans les années 1950 (Kulchyski & Tester 2007) afin de limiter l'impact de la prédation sur les grands herbivores (Cluff & Murray 1995; Haber 1996; Musiani & Paquet 2004) ont affecté la densité et la structure des populations de loups.

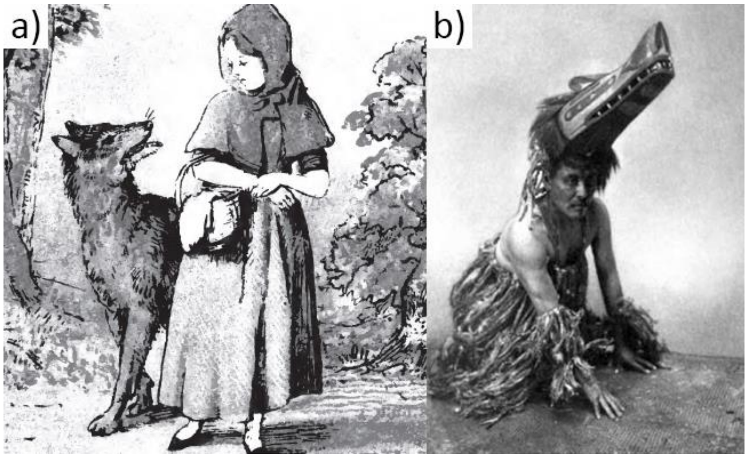

Figure 0.4 Illustration comparative des visions occidentale (a) et autochtone (b) de l'interaction entre les humains et les grands carnivores. La vision occidentale, symbolisée ici par le conte du *petit chaperon rouge* (Perrault, 1697), considère les grands carnivores, le loup en particulier, comme espèce nuisible à cause de la déprédation du bétail et des interactions agonistiques avec les humains. Cette vision a mené à la stigmatisation et à la persécution du loup par les populations humaines et à des programmes d'abattage subventionnés dès le 17^{e} siècle. D'un autre point de vue, les cultures autochtones percevaient traditionnellement les grands carnivores avec respect et égalité. Ces derniers faisaient souvent l'objet de figures sacrées et leurs qualités étaient admirées. La chasse de subsistance des grands carnivores est également une composante culturelle importante dans les communautés autochtones, bien qu'elle se soit progressivement transformée en activité commerciale avec la traite des fourrures.

Dans les années 1960, en partie suivant la publication de l'influant ouvrage '*Never Cry Wolf'* (Mowat 1963) décrivant ces programmes de contrôle par empoisonnement aux Territoires du Nord-Ouest, l'attitude du public à l'égard du loup changea drastiquement (Williams, Ericsson & Heberlein 2002; Kulchyski & Tester 2007). On passa ainsi de la stigmatisation à la conservation du loup et d'autres grands carnivores, voire à leur réintroduction (Kellert *et al.* 1996). Ce courant porté par le public fut aussi soutenu par la science, nombre d'études théoriques et empiriques s'intéressant aux processus de régulation des écosystèmes. Ces études mettaient en lumière l'importance de la productivité primaire dans la régulation ascendante des populations d'herbivores (Hairston, Smith & Slobodkin 1960; Hunter & Price 1992;

Power 1992), répliquant aux théories en place qui suggéraient un contrôle par les prédateurs (Solomon 1949; Lack 1954). Le rôle clé des grands carnivores dans les écosystèmes, et les conséquences de leur absence, fut également établi et donna une assise scientifique solide pour justifier les programmes de conservation. Toutefois, cette attitude moins conflictuelle envers les grands prédateurs ne fut pas nécessairement adoptée par les utilisateurs du territoire, qui affrontaient certains inconvénients liés à la réintroduction des carnivores (Rodriguez *et al.* 2003; Ericsson & Heberlein 2003; Bowman *et al.* 2004; Sponarski *et al.* 2013). De nouveaux programmes, comme des compensations pour dédommager les pertes causées par la déprédation du bétail ou du gibier furent ainsi adoptés pour inciter les utilisateurs à prendre part aux efforts de conservation (Wagner, Schmidt & Conover 1997; Wabakken *et al.* 2001; Naughton-Treves *et al.* 2003; Agarwala *et al.* 2010). Ces efforts ont contribué à la restauration de nombreuses populations de loup au Canada et à travers le monde, bien que la relation entre loups et les utilisateurs locaux demeure le véritable enjeu de conservation pour le maintien des populations à long terme (Musiani & Paquet 2004).

À l’inverse de la situation occidentale, la relation entre les communautés autochtones et les grands carnivores reposait traditionnellement sur une cohabitation durable basée sur la tolérance et le respect. Dans cette relation, les grands carnivores représentaient une importante composante culturelle et spirituelle (Figure 0.4b) (Nelson 1983; Berkes 1999; Clark & Slocombe 2009; Laugrand & Oosten 2010).

Il subsiste toujours un débat quant à l’impact des pratiques autochtones traditionnelles sur la faune (Kay 1998), mais l’impact de ces pratiques sur les grands carnivores était vraisemblablement variable selon le lieu et l’époque considérée. Par exemple, avant l’arrivée des pièges à patte métalliques et des armes à feu au début du 20^{e} siècle, et des modes de transport motorisés dans les années 1960, l’impact des chasseurs inuit sur les populations de loups était très limité étant donné la rapidité de ces prédateurs (Kulchyski & Tester 2007). Par contre, encore suivant l'exemple inuit, l'avènement de la motoneige et la croissance de la demande pour les fourrures de loups a contribué à une augmentation importante de la récolte de cette espèce et, par conséquent, représente une préoccupation pour les biologistes de la conservation (Cluff *et al.* 2010). De plus, en vertu des droits ancestraux reconnus au Canada, les communautés autochtones ne sont pas assujetties à des quotas pour la chasse au loup. Malgré tout, contrairement aux populations du sud du Canada et des États-Unis, les populations de loups du nord du Canada et de l'Alaska sont demeurées abondantes. Toutefois, les mesures de conservation du loup sont strictement basées sur des décomptes numériques (lorsque disponibles) et reposent sur la conception selon laquelle les loups seraient très résilients à l'exploitation de par leur capacité à ajuster leur reproduction (Haber 1996). Conséquemment, il est généralement admis que les populations de loups du Nord pourraient soutenir des taux de récoltes annuels de 25 à 50%, allant même jusqu'à 90% dans le cas de programmes de contrôle de courte durée (Haber 1996). Pourtant, si l'exploitation des loups ne semble vraisemblablement pas affecter ta taille des populations, un nombre croissant d'études tendent à démontrer des impacts importants sur d'autres aspects de la biologie de l'espèce. Ces impacts incluent le stress physiologique et la structure sociale des groupes (Haber 1996; Sidorovich *et al.* 2007; Rutledge *et al.* 2010; Bryan *et al.* 2015), les comportements d'approvisionnement et efficacité à la chasse (Haber 1996), ou encore la génétique des populations exploitées (Moura *et al.* 2014). Il devient donc impératif de déterminer ces impacts sur les populations de loups.

À ce jour, le loup est classé comme espèce « non en péril » au Canada (COSEPAC, 1999), mais en « danger d'extinction » aux États-Unis dans les états contigus sauf le Minnesota, l'Idaho et le Montana où il est classé 'menacé' (Endangered Species Act, 1978).

0.2 La toundra arctique

0.2.1 Productivité primaire, subsides allochtones et prédateurs

L’écosystème de la toundra arctique contient une faible diversité d’espèces (Callaghan *et al.* 2004) et celles-ci forment des réseaux trophiques parmi les plus simples au monde (Krebs *et al.* 2003). Pourtant, la combinaison des nombreuses forces descendantes et ascendantes qui en assurent le fonctionnement serait beaucoup plus complexe qu’attendu (Gauthier *et al.* 2011; Legagneux *et al.* 2012). Selon l’hypothèse de l’exploitation des écosystèmes (*Exploitation Ecosystem Hypothesis*, EEH, (Oksanen *et al.* 1981), la productivité primaire d’un écosystème détermine la longueur des chaînes trophiques et les forces de régulation. Ainsi, les systèmes peu productifs comme la toundra arctique ne devraient supporter que les plantes et les herbivores. Lorsque la productivité primaire devient plus élevée (p. ex. dans la forêt boréale), les écosystèmes devraient supporter des populations de prédateurs capables de réguler les populations d’herbivores, libérant ainsi la biomasse végétale du contrôle par les herbivores (Oksanen *et al.* 1981). Dans la toundra arctique, plusieurs études empiriques ont démontré un contrôle important des plantes par les herbivores en absence de prédateurs, supportant la EEH (Crête & Manseau 1996; Moen & Oksanen 1998; Jefferies 2000; Hamback *et al.* 2004; Aunapuu *et al.* 2008) En complément à la EEH, l’hypothèse des subsides (Subsidy Hypothesis, SH, Polis & Hurd 1996), stipule que les écosystèmes sont perméables aux flux d’énergie, ceux-ci traversant leurs frontières. Conséquemment, la SH prédit que même les écosystèmes peu productifs peuvent supporter des populations de prédateurs si ceux-ci bénéficient de subsides allochtones provenant d’écosystèmes plus productifs (Huxel, McCann & Polis 2002; Gauthier *et al.* 2011). La SH permettrait donc d’expliquer la raison pour laquelle on trouve des prédateurs résidents dans la toundra arctique, ce qui concorde avec les études récentes démontrant l’utilisation de ressources allochtones chez différentes espèces et populations arctiques (Samelius *et al.* 2007; Wiebe *et al.* 2009;

Therrien, Gauthier & Bety 2011; Tarroux *et al.* 2012). L’augmentation des densités de prédateurs par les subsides allochtones a des effets importants pour les chaînes trophiques terrestres, car cela affecte directement les proies autochtones (Bety *et al.* 2002; Roth 2003; Giroux *et al.* 2012) via des cascades trophiques (Croll *et al.* 2005). Leroux et Loreau (2008) suggèrent également que la force des interactions trophiques entre les prédateurs bénéficiant de subsides allochtones et les proies autochtones dépendrait de l’importance de l’apport allochtone et de son utilisation par le prédateur. Cette dernière dépend de la niche alimentaire des prédateurs et de leur degré de préférence pour les proies terrestres (voir section 0.1.3).

0.2.2 Contrastes spatio-temporels dans la disponibilité des ressources

La disponibilité des ressources de la toundra arctique est hétérogène dans le temps et dans l’espace. La toundra arctique reçoit en début d’été d’importants flux d’énergie depuis la forêt boréale (caribou migrateur; Calef & Heard 1981; Nagy *et al.* 2011) les écosystèmes tempérés (oiseaux migrateurs; Gloutney *et al.* 2001; Gauthier *et al.* 2004; McKinnon *et al.* 2010) et les écosystèmes marins (poissons anadromes; Swanson & Kidd 2010). Cependant, la disponibilité de ces ressources peut être hétérogène dans l’espace selon l’emplacement des aires de reproduction et des routes migratoires des espèces allochtones. Durant le court été arctique, les petits herbivores résidents (lemming sp., spermophile arctique *Urocitellus paryii*, lièvre arctique *Lepus arcticus*, lagopède (Sandercock, Martin & Hannon 2005; Mech 2007; Reid *et al.* 2012; Sheriff *et al.* 2012) sont prolifiques et, sans le couvert de neige, sont plus facilement accessibles aux prédateurs. L’abondance de certaines espèces comme le lemming brun *Lemmus sibiricus* (Krebs *et al.* 1973; Ims, Yoccoz & Killengreen 2011; Legagneux *et al.* 2012) et le spermophile arctique peut également varier grandement selon les années, ce qui est également le cas pour le caribou, mais à des échelles temporelles plus vastes (Ferguson, Williamson & Messier 1998; Gunn 2003; Zalatan, Gunn & Henry 2006). À l’inverse, l’hiver arctique est caractérisé par la raréfaction des ressources pour les prédateurs, puisque les espèces migratrices sont absentes et les résidentes deviennent peu abondantes ou difficiles d’accès. Par contre, des groupes de grands herbivores résidents comme le caribou (Nagy *et al.* 2011) et le bœuf musqué *Ovibos moschatus* (Fournier & Gunn 1998) demeurent disponibles en hiver, bien qu’en des lieux différents selon leurs préférences d’habitat. La banquise hivernale donne également accès aux ressources de l’écosystème marin, en particulier les phoques vivants ou leurs carcasses (Lai, Bêty, & Berteaux, 2015; Parker & Luttich, 1986; Gregory W. Thiemann et al., 2011).

Au printemps (début mars), les phoques naissants offrent également des ressources facilement accessibles pour les prédateurs terrestres (Ferguson, Stirling & McLoughlin 2005). Notons que l’accès pour les prédateurs aux ressources marines n’est pas uniforme et dans la toundra puisqu’il est limité aux habitats côtiers.

0.2.3 Stratégies des prédateurs arctiques

Les écosystèmes dont certaines ressources sont cycliques représentent un défi important pour les consommateurs, car ils doivent affronter une raréfaction récurrente des ressources (Ostfeld & Keesing 2000; Yang *et al.* 2008). Yang (2008) décrit trois alternatives offertes aux consommateurs : 1) demeurer en place et hiberner, ce qui nécessite des adaptations physiologiques, 2) demeurer en place et diversifier l’utilisation des ressources, ce qui exige des adaptations comportementales (voir la réponse fonctionnelle de type III, Figure 0.1), ou 3) migrer, ce qui exige également des adaptations comportementales. La toundra arctique est composée d’espèces employant chacune des trois stratégies. Le spermophile arctique (Sheriff *et al.* 2012) et l’ours grizzly *Ursus arctos* (McLoughlin, Cluff & Messier 2002) hibernent en hiver, les micromammifères (Reid *et al.* 2012), les petits herbivores (Klein & Bay 1991), les grands herbivores (Forchhammer & Boomsma 1995; Ihl & Klein 2001; Drucker *et al.* 2010) et les prédateurs résidents (Therrien *et al.* 2011; Tarroux *et al.* 2012) diversifient leur alimentation dans la toundra, et le caribou migrateur, certaines populations de loups (Musiani *et al.* 2007) et les oiseaux migrateurs se déplacent vers le sud. Parmi les prédateurs de la toundra résidents, mais non hibernants, on connait de mieux en mieux les stratégies hivernales d'alimentation du renard arctique *Vulpes lagopus*, lequel est souvent utilisé comme modèle biologique pour l'étude des prédateurs arctiques (Elmhagen *et al.* 2000; Roth 2002; Samelius *et al.* 2007; Tarroux, Berteaux & Bety 2010; Lai *et al.* 2015). Par contre, on ignore encore largement la stratégie des grands carnivores tels le loup et le carcajou, *Gulo gulo* (mais voir (Parker & Luttich 1986; Mulders 2001; Mech 2007).

0.2.4 L'anthropocène et les perturbations environnementales

Les écosystèmes arctiques sont le théâtre de changements environnementaux de grande envergure tels que les changements climatiques et le développement industriel (Johnson *et al.* 2005; Post *et al.* 2009). Les effets cumulatifs de ces facteurs de changement peuvent affecter les systèmes biologiques et les populations humaines (Duinker *et al.* 2013). D'un côté, les changements climatiques peuvent exercer des impacts considérables sur les composantes physiques et les processus biologiques de la toundra arctique tels que la réduction du couvert de neige (Jones *et al.* 2001), la fonte du pergélisol (Smith *et al.* 2010), l'occurrence d'événements météorologiques extrêmes (ACIA 2005) et le 'verdissement' de l'Arctique, c.-à-d. l'augmentation de la biomasse des plantes (Sturm, Racine & Tape 2001; Hudson & Henry 2009). Ces effets peuvent affecter les grands carnivores de manière directe en influençant leur thermorégulation ou utilisation de l'espace, ou de manière indirecte en influençant l'abondance de leurs proies. Les effets indirects sont sans contredit les plus préoccupants puisque l'écologie et la dynamique des populations d'herbivores semblent déjà affectées par les changements climatiques (Mech 2000; Post *et al.* 2009; Ims *et al.* 2011). Par exemple, les températures extrêmes en hiver (Tyler 2010) et en été (Vistnes *et al.* 2008; Witter *et al.* 2012) ou la réduction du couvert de glace au printemps (Poole *et al.* 2010) peuvent affecter les populations de caribous migrateurs (Vors & Boyce 2009; Festa-Bianchet *et al.* 2011). En retour, les grands carnivores peuvent répondre de façon très marquée au déclin des populations de caribous quand ils sont la principale proie consommée (Klaczek, Johnson & Cluff 2016). Toutefois, les effets directs des changements climatiques ne sont pas à négliger. Par exemple, la diminution du couvert et de la qualité de la neige peut être négative pour la distribution, les flux génétiques, et les succès de chasse et de reproduction du carcajou (Landa 1997; Copeland *et al.* 2010; Brodie & Post 2010; McKelvey *et al.* 2012), ainsi que pour le succès de chasse du loup (Post *et al.* 1999; Mech & Peterson 2003; Mech 2004; Paquet *et al.* 2010).

En parallèle, le réchauffement climatique et la hausse du prix des minéraux ont mené à une seconde ‘ruée vers le Nord’ (après celle des années 1950) et à la prolifération de projets d’exploration et d’exploitation minière dans l’Arctique (Tester 2016). Les effets cumulatifs de ce développement sur la toundra arctique et ses populations animales sont encore très méconnus, car particulièrement difficiles à documenter. Pourtant les projets d’exploration minière couvrent pratiquement la totalité du territoire du Nunavut (NIRB 2017). Comme décrit plus haut pour les changements climatiques, les effets du développement industriel sur les grands carnivores sont principalement de nature indirecte, car ils influencent leurs proies. Par exemple, on sait que les caribous répondent aux activités et infrastructures industrielles en changeant leur utilisation de l’habitat, leur distribution, leur comportement ou leurs patrons de migrations (Johnson *et al.* 2005; Vistnes *et al.* 2008; Polfus, Hebblewhite & Heinemeyer 2011; Boulanger *et al.* 2012; Johnson, Ehlers & Seip 2015b; Wilson *et al.* 2016). Les effets du dérangement industriel peuvent aussi avoir des conséquences sur l’approvisionnement et la reproduction du caribou (Cameron *et al.* 2005; Kuemmerle *et al.* 2014). Toutefois, il semble que certaines populations de caribou puissent s’habituer, à long terme, au dérangement industriel (Johnson & Russell 2014; Hansen & Aanes 2015). Les relations de cause à effet entre le dérangement des caribous et les grands prédateurs sont encore largement inconnues (mais voir l'exemple de (Frame, Cluff & Hik 2008). Les effets directs du développement industriel sur les grands carnivores seraient principalement associés à des changements dans l'utilisation des habitats (May *et al.* 2006) et au dérangement et à la perte d'habitats de reproduction (McLoughlin *et al.* 2004; Frame, Cluff & Hik 2007; Sazatornil *et al.* 2016). Certaines études suggèrent néanmoins que les grands prédateurs peuvent s'habituer rapidement ou même bénéficier des infrastructures industrielles (Johnson *et al.* 2005; Latham *et al.* 2011).

0.3 Modèle biologique, problématique et objectifs de recherche

0.3.1 Le carcajou et le loup toundrique

0.3.1.1 Description sommaire

Le loup est le plus grand des canidés et le mammifère terrestre ayant la plus grande répartition au monde. Il occupait historiquement presque tous les écosystèmes sauf la forêt tropicale (Paquet & Carbyn 2003). Il est sexuellement dimorphique, les mâles étant plus lourds (20-80kg) que les femelles (16-55kg) (Mech 1970). Sa taille augmente de l'équateur vers les pôles (Mech 1970; Paquet & Carbyn 2003). Le loup est digitigrade, c.-à-d. que seule l'extrémité des doigts des pattes entre en contact avec le sol, et peut donc se déplacer rapidement. Les loups sont organisés en groupes sociaux composés d'individus apparentés et dirigés par un couple dominant qui assure une reproduction exclusive, réprimant l'activité reproductrice des subordonnés (Mech & Boitani 2003). Le nombre d'individus par groupe peut fluctuer grandement selon l'habitat et la taille des proies utilisées (Mech & Boitani 2003). À l'âge d'un ou deux ans, les juvéniles quittent en général le groupe et se dispersent, bien que certains peuvent demeurer dans le groupe de naissance, où ils sont subordonnés. Les individus les plus vieux, typiquement les individus alpha déchus, vont également se disperser et vivre seuls. Bien que les groupes ont une grande capacité de déplacement (Paquet &

Carbyn 2003), ils occupent et défendent typiquement des territoires restreints (Mech 1970; Peterson, Woolington & Bailey 1984; Messier 1985). Par exemple, en milieu subarctique où la disponibilité des caribous migrateurs et des orignaux résidents est complémentaire dans le temps, ou bien dans le haut Arctique ou des assemblages de grands et petits herbivores sont présents à l'année, les groupes de loups peuvent maintenir des territoires de 1800 à 2500 km^2 (diamètre de 40-50 km) (Mech 1987; Ballard *et al.* 1997). Par contre, dans le bas Arctique, où la disponibilité des ressources est très réduite en hiver en absence du caribou migrateur, les populations continentales de loups ne maintiennent pas un territoire annuel, mais migrent plutôt avec les caribous et reviennent dans la toundra en été pour y défendre des territoires de reproduction de taille similaire à ceux des loups résidents en zone subarctique (Walton *et al.* 2001; Musiani *et al.* 2007). Dans ce cas, le domaine vital peut s'étendre jusqu'à 60,000 km^{2}chez les mâles et 45,000 km^2 chez les femelles. Aucune information n'est disponible sur la taille des domaines vitaux ou territoires chez les loups résidents de la toundra arctique, hormis dans le cas du haut Arctique. L'accouplement du loup se fait typiquement entre janvier et avril. Le temps de gestation est d'environ 60 jours et la mise bas de six petits en moyenne se fait typiquement en mai-juin en tanière. Dans l'Arctique, ces dernières sont typiquement creusées dans des sols de dépôts meubles bien drainés, aménagées sous les racines de bosquets (Heard & Williams 1992) ou sous des abris rocheux (Mech & Packard 1990). Lors de l'élevage des jeunes, la femelle et les jeunes sont limités dans leurs déplacements et utilisent donc les ressources locales (Heard & Williams 1992).

Le carcajou est le plus grand des mustélidés et occupe une distribution principalement circumboréale et circumpolaire, pouvant également se retrouver dans les chaînes montagneuses continues plus au sud. Le mâle peut être de 40 à 60% plus lourd (11 à 18kg) que la femelle (6 à 12 kg) (Banci 1994; Pasitschniak-Arts & Larivière 1995). Comme chez le loup, il existerait un patron de déclin latitudinal de la taille du carcajou du nord vers le sud (Copeland & Jackson 2003). Le carcajou est de forme compacte et très puissant musculairement. Il est plantigrade, c.-à-d. que la paume complète de ses mains et pieds entre en contact avec le sol lorsqu’il marche, ce qui le rend beaucoup plus lent que le loup. Le carcajou est typiquement solitaire et peut se déplacer sur de grandes distances, bien qu’il limite ses déplacements à un domaine vital de 100-800 km^2 (diamètre de 10-28 km) en fonction du sexe et de l’environnement (Magoun 1985; Banci & Harestad 1990; Landa *et al.* 1998). La taille du domaine vital du carcajou toundrique est très mal connue, mais, selon la seule étude publiée (Mulders 2001), elle avoisinerait 130 et 400 km^2 chez la femelle et le mâle, respectivement. L’accouplement du carcajou se fait typiquement entre mai et août, mais l’implantation utérine est différée jusqu’à l’hiver, la gestation durant 35-40 jours (Rausch & Pearson 1972). La mise bas de 2 à 4 petits se fait à la fin de l’hiver ou au début du printemps dans des tanières de neige (Pulliainen 1968; Rausch & Pearson 1972; Banci & Harestad 1988), bien que la femelle entre en tanière vers la fin janvier, début février. Lors du séjour en tanière et de l’élevage des jeunes, la femelle est limitée dans ses capacités de mouvement et l’utilisation des petits rongeurs semble être importante (Magoun 1985; Landa 1997).

0.3.1.2 Niches alimentaires

Le loup et le carcajou toundrique ont été très peu étudiés étant donné leur faible densité, de leur grande mobilité et des difficultés logistiques dues au climat arctique. Les connaissances sur l’utilisation de leurs ressources alimentaires sont limitées et typiquement inférées à partir d’autres écosystèmes et habitats. L’hypothèse généralement admise stipule que le loup est un prédateur spécialisé pour lequel les grands herbivores sont nécessaires (McLaren & Peterson 1994; Mech & Peterson 2003; Paquet & Carbyn 2003; Peterson & Ciucci 2003). Cette hypothèse repose sur des observations directes et des mesures indirectes (fèces et contenus stomacaux) de l’alimentation du loup, de même que sur ses adaptations morphologiques (dentition, endurance physique et rapidité) et comportementales (chasse en groupe) (Mech &

Boitani 2003; Paquet & Carbyn 2003). Cependant, un nombre croissant d'études, dont certaines menées dans le haut Arctique (Marquard-Petersen 1998; Mech 2005, 2007), tendent à démontrer une certaine flexibilité dans l'utilisation des ressources alimentaires chez les populations ayant un accès limité aux ongulés (Dale, Adams & Bowyer 1994; Ballard *et al.* 1997; Urton & Hobson 2005). De récentes études ont également démontré l'utilisation de ressources allochtones chez les populations de loups côtiers (Darimont & Reimchen 2002; Darimont, Paquet & Reimchen 2009) et continentaux (Adams *et al.* 2010). Par contre, chez le loup toundrique du bas Arctique vivant en forte association avec le caribou migrateur et suivant ses déplacements (Kuyt 1972; Heard & Williams 1992; Walton *et al.* 2001; Frame *et al.* 2004; Musiani *et al.* 2007), il semble que les populations n'utilisent que cette proie et démontrent peu d'intérêt pour d'autres espèces. Cette hypothèse est également supportée par l'étude récente de (Klaczek *et al.* 2016) ayant démontré une forte réponse numérique des loups aux fluctuations d'abondance des hardes de caribous, ainsi que par celle de Musiani et al. (2007) ayant révélé un profil génétique distinct de ces populations de loups par rapport au loup boréal. Toutefois, à l'exception des études du haut Arctique (Mech 1987; Mech & Packard 1990; Mech 2005, 2007), on ignore encore largement les patrons d'utilisation des ressources alimentaires chez le loup résident de la toundra, qui n'est quant à lui pas associé au caribou migrateur.

À ma connaissance, seules les études de Mulders et al. (2001) et de Samelius et coll. (2002) ont décrit l'utilisation des ressources chez le carcajou toundrique, bien que les études en milieu subarctique soient relativement communes (Rausch & Pearson 1972; Myhre & Myrberget 1975; Magoun 1985; Banci & Harestad 1990; Persson 2005; Andren *et al.* 2011; Mattisson *et al.* 2012). Contrairement au loup, le carcajou est généralement perçu comme un prédateur opportuniste sur l'ensemble de son aire de distribution (Copeland, 1996; Copeland and Jackson, 2003; Gardner, 1985; Landa, 1997; Magoun, 1985). Le carcajou présenterait également des adaptations morphologiques (forme des molaires pour broyer les os et sens d'olfaction très développé; Hornocker & Hash 1981) lui permettant d'être un charognard efficace capable d'utiliser efficacement les parties d'ongulés délaissées par d'autres prédateurs, comme la viande, les os, les cartilages, la peau, etc. (Myhre & Myrberget 1975; Pasitschniak-Arts & Larivière 1995; Mattisson *et al.* 2011). Sa taille robuste et sa force musculaire lui permettraient également de dérober les prises fraîchement capturées par affrontement direct avec les compétiteurs (selon des observateurs locaux, le carcajou peut chasser un groupe de loups ou un ours grizzly d'un site de capture). Ce comportement lui aurait valu le surnom de *tigliktik* ou 'voleur' chez les communautés Inuit, ce qui réfère également à la tendance qu'ont les carcajous à dérober les appâts ou prises des trappeurs de renards. Malgré son mode d'approvisionnement typiquement solitaire, sa taille plus petite que celle du loup et sa relative lenteur, le carcajou serait même capable de capturer des ongulés (observateurs inuit, voir aussi Pulliainen (1968) et Myhre & Myrberget (1975)). En milieu côtier, il serait également porté à utiliser les ressources marines, souvent sous forme de carcasses (Rausch & Pearson 1972; Mulders 2001) ou de proies vivantes (observateurs inuit). Durant l'été arctique, le carcajou pourrait également utiliser les micros-mammifères (Landa 1997; Mulders 2001), creuser pour capturer de petits mammifères tels que les spermophiles arctiques (Mulders 2001; Copeland & Jackson 2003), ou capturer la sauvagine et ses œufs pour les cacher et les mettre en réserve à l'instar du renard arctique (Samelius *et al.* 2002). Magoun (1985) rapporte également des comportements de cache sur des restes de caribou et des spermophiles arctiques.

0.3.2 Problématique et objectifs de recherche

Dans la toundra arctique, la grande hétérogénéité spatiale et saisonnière de la disponibilité des ressources peut forcer les prédateurs résidents à diversifier leur régime alimentaire selon l'abondance de la ressource préférée et les opportunités écologiques disponibles (Holling 1959; Yang *et al.* 2008). Cependant, la capacité d'un individu à utiliser les ressources peut dépendre de contraintes biologiques propres à l'espèce, de variations phénotypiques interindividuelles ou encore d'autres facteurs pouvant influencer les compromis alimentaires. Des études récentes ont démontré l'importance des ressources allochtones marines dans le régime alimentaire hivernal de prédateurs opportunistes terrestres résidents (Roth 2003; Killengreen *et al.* 2011; Therrien *et al.* 2011). L'utilisation de telles ressources pourrait contribuer à maintenir des populations de prédateurs dans des milieux peu productifs (Polis & Hurd 1996; Rose & Polis 1998). Les études sur l'utilisation des ressources alimentaires des grands carnivores terrestres sont très rares dans l'Arctique, de sorte qu'on ignore grandement comment l'hétérogénéité spatiale et temporelle dans la disponibilité des ressources allochtones peut influencer ces espèces de haut niveau trophique, de même que la structure et le fonctionnement de la toundra arctique (Leroux & Loreau 2008).

Par ailleurs, la biologie et l'écologie des grands carnivores arctiques et le statut de leurs populations sont mal connus de manière générale, de même que les facteurs influençant ces variables (Johnson *et al.* 2005; Bryan *et al.* 2015). Pourtant cette information est cruciale pour prendre des mesures de conservation des espèces (Haber 1996). En raison des grandes difficultés logistiques associées à l'étude des animaux arctiques, un nombre croissant d'études biologiques s'intéressent au savoir écologique traditionnel (*Traditional Ecological Knowledge*, TEK, voir (Berkes 1999), comme source d'information complémentaire à la science (Gagnon & Berteaux 2009; Huntington 2011). Dans notre cas, les chasseurs inuit peuvent fournir des observations et de connaissances importantes pour détecter et comprendre les changements dans le nombre, la biologie et l'écologie des grands prédateurs arctiques (Cardinal 2004; Clark & Slocombe 2011).

Les trois objectifs spécifiques de la thèse, ainsi que les hypothèses et prédictions associées sont les suivants :

Objectif 1- quantifier, à l'aide des isotopes stables et des contenus stomacaux, les variations dans l'utilisation des ressources alimentaires par deux grands carnivores arctiques en fonction des fluctuations spatio-temporelles de la diversité des ressources alimentaires et de l'abondance des grands herbivores, et également en fonction des contraintes biologiques inhérentes aux deux espèces étudiées;

Tel que décrit précédemment, la niche alimentaire des prédateurs est déterminée par l'interaction entre les contraintes biologiques (déterminées par la morphologie et les comportements), la diversité des ressources disponibles dans l'environnement (c.-à-d. les opportunités écologiques) et l'abondance de la ou des proie(s) préférée(s) (Araujo *et al.* 2011). Un nombre croissant d'études tend à démontrer l'importance des opportunités écologiques sur la niche alimentaire et la spécialisation individuelle des prédateurs (Layman *et al.* 2007b; Newsome *et al.* 2015). Par contre, très peu d'études ont détaillé les interactions entre les opportunités écologiques et les deux autres composantes de la niche alimentaire, les proies préférées et les contraintes biologiques (mais voir Kernaléguen *et al.* 2015; Horswill *et al.* 2016). Ainsi, on connait encore mal l'importance relative de ces facteurs pour la niche alimentaire des prédateurs, particulièrement chez les grands carnivores terrestres (mais voir Darimont *et al.* 2009, Figure 0.3). Bien que les grands carnivores terrestres soient souvent fortement associés aux grands herbivores (McLaren & Peterson 1994; Sinclair, Mduma & Brashares 2003), l'utilisation de proies alternatives semble être commune lorsque l'abondance de la proie préférée diminue (Yeakel *et al.* 2009; Adams *et al.* 2010). Toutefois, la capacité de ces prédateurs à exploiter les ressources alternatives peut être très variable en fonction de contraintes biologiques associées à l'espèce, au sexe, à l'âge, au statut reproducteur ou encore à l'individu (Sinclair *et al.* 2003; Edwards *et al.* 2011; Mattisson *et al.* 2012). Pour ce premier objectif, nous avons utilisé deux grands carnivores de la toundra arctique, le loup et le carcajou, comme modèles d'étude puisqu'ils possèdent des contraintes biologiques fort différentes (adaptations morphologiques, structure sociale et mode d'approvisionnement), bien qu’ils puissent tous deux adopter un régime alimentaire généraliste. Ces prédateurs sont également très mobiles, ce qui nous permet d’examiner les variations de niche à une grande échelle spatiale (voir aire d’étude section 0.4.1). La toundra arctique est un lieu d’étude idéal puisque sa forte saisonnalité et l’hétérogénéité de ses habitats à vaste échelle spatiale permettent d’isoler des patrons distincts de diversité des ressources et d’abondance des proies préférées.

Dans un premier temps, nous avons évalué les trois hypothèses de recherche suivantes :

- H1. Les contraintes biologiques déterminent les variations de niche alimentaire des loups et des carcajous;

  Nous avons évalué quatre prédictions pour tester cette hypothèse :

  1) Les carcajous ont une plus grande niche alimentaire que les loups;
  2) Les carcajous mâles ont une plus grande niche alimentaire que les femelles;
  3) Les femelles carcajous ont une plus grande niche alimentaire durant la période de reproduction (hiver et printemps) qu’à l’automne;
  4) Les loups solitaires (jeunes adultes en dispersion et vieux adultes déchus) ont une plus grande niche alimentaire que les loups vivant en groupe (juvéniles et adultes).

- H2. Les opportunités écologiques déterminent les variations de niche alimentaire des loups et des carcajous;

  Nous avons évalué deux prédictions pour tester cette hypothèse :

  1) La niche alimentaire est plus étendue en hiver, au printemps et en été qu’en automne;
  2) Les signatures isotopiques individuelles (carbone/azote) augmentent avec l’accès aux ressources marines.

- H3. L’abondance de la proie préférée détermine les variations de niche alimentaire des loups et des carcajous;

  Nous avons évalué trois prédictions pour tester cette hypothèse:

  1) La niche alimentaire est plus étendue dans les régions de notre aire d’étude où la disponibilité des caribous est faible que dans les régions où elle est élevée;
  2) Les signatures isotopiques individuelles (carbone/ azote) diminuent avec l’accès au caribou migrateur;
  3) Les signatures isotopiques individuelles (carbone/ azote) diminuent avec l’accès au caribou résident.

Dans un deuxième temps, nous avons évalué l’hypothèse de variation des niches (*Niche Variation Hypothesis,* (Van Valen 1965) qui stipule que l’élargissement des niches alimentaires est causé par la spécialisation individuelle (Bolnick *et al.* 2007), voir Figure 0.2b). Pour tester cette hypothèse, nous avons pris le même cadre de prédictions que celui utilisé ci-haut pour les hypothèses 1-3.

Objectif 2- déterminer expérimentalement les taux de fractionnement isotopique entre la nourriture et les poils de grands carnivores afin d’augmenter la précision de nos analyses isotopiques;

Depuis le début des années 1980, les isotopes stables ont été de plus en plus utilisés en écologie pour quantifier la niche alimentaire (Peterson & Fry 1987; Gannes, del Rio & Koch 1998). Toutefois, la précision de cette méthode dépend de notre capacité à contrôler les sources de variation isotopique qui ne sont pas liées au régime alimentaire (Post *et al.* 2007; Martinez del Rio *et al.* 2009). Le fractionnement isotopique, c.-à-d. la différence de ratio isotopique entre un consommateur et sa ressource, est déterminé par des processus métaboliques survenant lors de la digestion et de l'assimilation des nutriments dans les tissus du consommateur. Pourtant les valeurs de fractionnement isotopique sont relativement rares dans la littérature, de sorte que la majorité des études menées en milieu naturel utilisent des valeurs de fractionnement déterminées chez des espèces apparentées au modèle d'étude plutôt qu'à l'espèce étudiée (Roth & Hobson 2000a). Dans ce contexte, plusieurs études expérimentales (Caut, Angulo & Courchamp 2008; Lecomte *et al.* 2011) et des revues de littérature (Martinez del Rio *et al.* 2009) ont relevé l'importance de valider les taux de fractionnement en milieu contrôlé.

Nous présentons une expérience visant à déterminer les taux de fractionnement isotopique du carbone et de l'azote entre la nourriture et les poils de loups, de carcajous, d'ours grizzly et d'ours blancs captifs. Ces deux dernières espèces sont résidentes de la toundra et de l'écosystème marin arctique, respectivement. Nous avons étudié les poils dans cette expérience, car ils sont très utilisés dans la recherche reposant sur des méthodes non invasives (Mulders, Boulanger & Paetkau 2007). Certains taux de discimination calculés dans ce chapitre (poils de loups et carcajous) ont été utilisés dans le chapitre 1 de la thèse.

Nous n'avons pas formulé d'hypothèses puisque notre objectif était simplement de déterminer des taux de fractionnement isotopique.

Objectif 3- examiner la relation entre les grands carnivores et les populations inuit dans un contexte de changements socio-économiques importants;

Comme mentionné à la section 0.2.4, l'Arctique est au cœur d'importants changements environnementaux pouvant avoir des effets cumulatifs sur les populations animales et les communautés locales. Dans ce contexte, il est important de bien comprendre les interactions entre les systèmes naturels et les communautés humaines puisque ces interactions peuvent déterminer la résilience et le bien-être des deux parties (King & Hood 1999; Berkes, Colding & Folke 2003). Dans cet objectif, nous nous intéressons à la chasse de subsistance du loup toundrique dans la communauté de Qamani'tuaq (Baker Lake, Nunavut), où il est récolté principalement pour le commerce de la fourrure. Cette communauté a subi d'importantes transformations socio-économiques et culturelles au cours des dernières années, suite à l'ouverture d'une mine d'or située à approximativement 85 km au nord de la communauté. En combinant des données biologiques avec des observations des chasseurs et aînés de la communauté de Qamani'tuaq, nous visons grâce à une approche intégratrice à mieux comprendre, d'une part, l'importance de la chasse de subsistance au loup pour l'économie locale et la culture inuit et, d'autre part, l'impact de la chasse sur la biologie et l'écologie des populations de loups (voir la section 0.1.4). Nous cherchons également à mieux comprendre comment l'évolution des pratiques culturelles et le développement d'une économie minière peuvent affecter la pression de chasse, et quels impacts directs et indirects les activités industrielles et les changements climatiques peuvent avoir sur les populations de loups. La problématique de recherche a été entièrement déterminée par les chasseurs et le conseil de chasseurs et trappeurs de la communauté de Qamani'tuaq, lors de rencontres qui ont initié l'étude. Nous avons testé les hypothèses et prédictions suivantes, qui ont également été définies par la communauté.

Dans un premier temps, nous avons évalué l'hypothèse de recherche suivante :

- Les changements récents dans la pression de chasse affectent l'état des populations de loups;

  Nous avons évalué quatre prédictions pour tester cette hypothèse:

1) Les loups vivants à proximité de la communauté et de la route d'accès à la mine (zone d'impact) ont une condition physique plus faible que les loups vivant loin de la communauté (zone contrôle);
2) Les loups de la zone d'impact évitent les hommes, contrairement aux loups de la zone contrôle;
3) Les loups de la zone d'impact ont une structure sociale perturbée par rapport aux loups de la zone contrôle;
4) Les loups de la zone d'impact ont un régime alimentaire et des comportements d'approvisionnement différents des loups de la zone contrôle.

Dans un deuxième temps, nous avons utilisé le modèle de Fauchald et al. (2017) pour évaluer les perceptions de la communauté quant aux facteurs influençant la pression de chasse et la biologie et l'écologie des loups. Afin d'isoler la contribution du développement industriel sur la pression de chasse et la condition des loups, nous avons également comparé les données provenant de Qamani'tuaq avec celles obtenues dans d'autres communautés inuit où la chasse de subsistance est présente, mais le développement absent.

0.4 Méthodologie générale

0.4.1 Région d'étude

Notre aire d'étude d'approximativement 900 000 km^2 couvre la partie continentale du territoire du Nunavut (Canada), de même que l'île Victoria partiellement située dans les Territoires du Nord-Ouest (Figure 1.1 au chapitre 1). On retrouve dans l'aire d'étude 13 communautés inuit. Toutes ont activement participé à l'étude (voir section 0.4.2). Les espèces animales retrouvées dans l'aire d'étude sont typiques de la toundra arctique ((Krebs *et al.* 2003; Callaghan *et al.* 2004), voir Annexe A). Les espèces résidentes fluctuent en abondance selon les saisons et leur distribution parcellaire reflète l'hétérogénéité des habitats (section 0.2.2). L'abondance des espèces migratrices (allochtones) culmine en été et varie à une échelle régionale, voire continentale, selon l'écologie de l'espèce considérée (section 0.2.2). L'écosystème marin borde l'aire d'étude à l'Est et au Nord et fournit des ressources (surtout des phoques vivants et leurs carcasses) accessibles lorsque la banquise est consolidée, de décembre à juin. Toutefois, les ressources marines peuvent également être disponibles localement pendant l'été sous forme de carcasses de baleines ou phoques échoués. Le loup, le carcajou et l'ours grizzly sont les grands carnivores résidents de notre aire d'étude. Seuls les loups et le carcajou sont actifs à l'année.

0.4.2 Suivi écologique

En collaboration avec le ministère de l'Environnement du gouvernement du Nunavut et les conseils de chasseurs et trappeurs locaux, nous avons mis en place un programme de collecte de carcasses de loups et carcajous récoltés par les chasseurs des 13 communautés incluses dans notre aire d'étude dans le cadre de leurs activités de subsistance. La collecte des carcasses se déroulait du 1er novembre au 31 mai de chaque année, et ce en 2010-2011, 2011-2012 et 2012-2013. Au total, 287 carcasses de loups et 376 carcasses de carcajous ont été recueillies. Les gardes-chasses locaux recevaient et entreposaient les carcasses retournées par les chasseurs, lesquels devaient fournir des informations concernant l'emplacement, la date et l'heure de la capture, ainsi que des données complémentaires contextuelles. Les chasseurs recevaient une compensation monétaire pour chaque carcasse. Cette compensation représentait moins de 20% de la valeur de la fourrure de l'animal et n'incitait pas les chasseurs à augmenter leur taux de récolte (Jonzen *et al.* 2013). Pour chaque carcasse, nous avons mesuré des paramètres morphométriques et récolté des échantillons utiles aux analyses de la niche alimentaire (Killengreen *et al.* 2011) ou à d'autres analyses (voir Figure 0.5 pour les détails). Des échantillons de proies des loups et carcajous ont aussi été obtenus des chasseurs dans le cadre de leurs activités de subsistance. Tous les échantillons ont été congelés à -20°C jusqu’aux analyses.

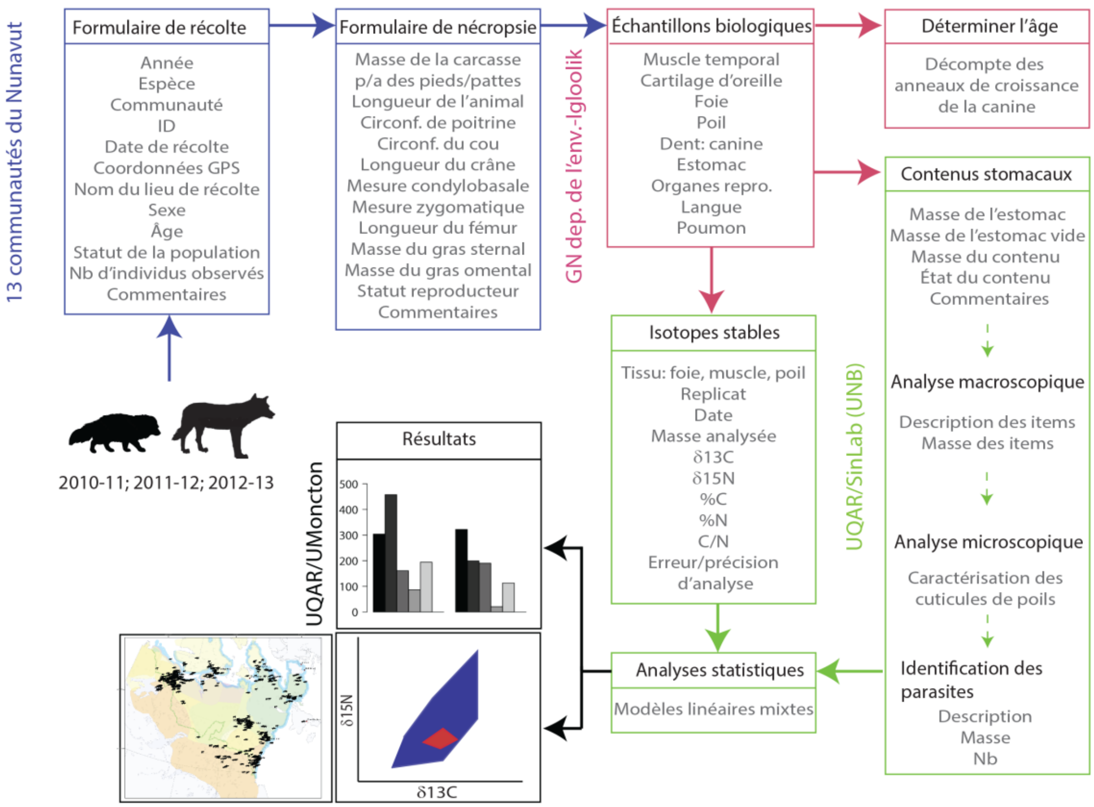

Figure 0.5 Résumé séquentiel des méthodes employées dans le cadre de cette étude. À partir de carcasses de loups et carcajous rapportées par les chasseurs inuit, nous avons mesuré différents indices morphométriques et prélevé différents échantillons qui ont été utilisés dans l’analyse des isotopes stables et des contenus stomacaux pour étudier la niche alimentaire des grands carnivores de la toundra arctique. La couleur des encadrés reflète le lieu où les activités décrites ont eu lieu.

0.4.3 Isotopes stables : les mesures de niche alimentaire

L’utilisation des isotopes stables en écologie se base sur la prémisse selon laquelle les animaux sont, isotopiquement, ce qu’ils mangent. Cette technique est répandue pour reconstruire le régime alimentaire d’un consommateur, étudier les relations trophiques ou suivre les flux d’énergie entre différents écosystèmes (revue par Peterson & Fry 1987; Gannes *et al.* 1998; Kelly 2000; Crawford, McDonald & Bearhop 2008). Les signatures isotopiques les plus fréquemment utilisées sont celles du carbone (dénotée $\delta^{13}C$) et de l’azote (dénotée $\delta^{15}N$). Les ratios sont mesurés par un spectromètre de masse et sont exprimés en parties par mille (‰), avec $\delta^{13}C = [((^{13}C/^{12}C_{\text{échantillon}})/ (^{13}C/^{12}C_{PDB}))-1] * 1000$ et $\delta^{15}N = [((^{15}N/^{14}N_{\text{échantillon}})/(^{15}N/^{14}N_{AIR}))-1] * 1000$. PDB représente le standard *Peedee belemnite carbonate* et AIR représente le standard azote atmosphérique.

Récemment, la méthode des isotopes stables a permis des avancées importantes dans l’étude des variations intraspécifique ou intrapopulation de la niche alimentaire (Bolnick *et al.* 2003; Araujo *et al.* 2011). La niche isotopique, définie comme la variation totale de $\delta^{13}C$ et $\delta^{15}N$ (Bolnick *et al.* 2003), ou comme l’aire totale occupée sur un graphique mettant en relation $\delta^{13}C$ et $\delta^{15}N$ (Layman *et al.* 2007a, voir aussi Figure 0.3a), peut être considérée comme une mesure de la niche réalisée d’une population, d’un groupe d’individus, ou d’un individu (Bearhop *et al.* 2004). Toutefois, la niche isotopique ne correspond pas nécessairement à la diversité des ressources utilisées, car elle dépend de la variabilité isotopique entre ces ressources. Il convient donc d’utiliser cette mesure dans des systèmes où les proies sont nettement différentes isotopiquement afin que la variation de niche décrite soit pertinente d’un point de vue écologique. Les mesures de niche isotopique sont aussi très communément utilisées dans les études de spécialisation alimentaire (Darimont *et al.* 2009; Jaeger *et al.* 2010; Matich *et al.* 2011a; L’Hérault *et al.* 2013) et elles ont permis de détecter plusieurs cas de spécialisation là où d'autres méthodes ont failli (voir Meiri, Dayan & Simberloff 2005 versus; Bolnick *et al.* 2007). Les différences moyennes entre les variances de $\delta^{13}C$ et $\delta^{15}N$ pour chaque individu (Bolnick *et al.* 2003), ou encore le calcul de différentes métriques de distance isotopique entre chaque individu par rapport aux autres dans l'espace $\delta^{13}C$ / $\delta^{15}N$ (Layman *et al.* 2007a, voir aussi Figure 0.3b), peuvent être utilisées pour déterminer le niveau de spécialisation individuelle.

Puisque la vitesse de renouvellent des cellules animales peut varier d'un tissu à un autre, la période durant laquelle un tissu donné reflète la signature isotopique d'une alimentation particulière est aussi variable. En connaissant les taux de renouvellement de différents tissus (Lecomte *et al.* 2011), il devient donc possible d'utiliser ces derniers pour couvrir différentes périodes (p. ex. différentes saisons) au cours desquelles on cherche à connaître l'utilisation des ressources alimentaires (Dalerum & Angerbjorn 2005; Killengreen *et al.* 2011). Les tissus métaboliquement actifs comme le foie et les muscles ont des taux de renouvellement relativement courts d'environ une semaine et un à deux mois, respectivement, alors que les tissus inertes comme les poils se renouvellent une fois l'an (Dalerum & Angerbjorn 2005).

Dans le cadre de cette étude, nous avons utilisé les signatures isotopiques $\delta^{13}C$ et $\delta^{15}N$ afin de déterminer la niche alimentaire et ses variations interindividuelles chez des loups et carcajous. Nous avons utilisé plusieurs tissus (foie, muscle et poil) afin de couvrir la presque totalité du cycle annuel des prédateurs.

0.4.4 Contenus stomacaux: validation de l'utilisation des ressources

En complément aux isotopes stables, ou avant l'avènement de cette méthode, plusieurs études ont examiné les contenus stomacaux pour évaluer la niche alimentaire des animaux (Dehn *et al.* 2007; Vulla *et al.* 2009; Killengreen *et al.* 2011). L'examen des contenus stomacaux permet de confirmer les sources de nourriture ingérées lors du dernier repas des prédateurs, bien qu'il sous-estime l'utilisation de sources digérées très rapidement, comme les petites proies et les items gras (Afik & Karasov 1995). Nous avons utilisé cette méthode pour valider les résultats de niche isotopique, ainsi que pour distinguer deux proies principales des loups et carcajous, le caribou et le bœuf musqué, qui présentent des signatures isotopiques similaires. Pour ce faire, nous avons pesé les masses humides (g) totales des items associés à chacune des espèces rencontrées dans les estomacs. La Figure 0.5 présente les étapes réalisées en laboratoire pour l'examen complet des estomacs.

0.4.5 Le savoir inuit

Malgré un historique de grandes discordes (Kulchyski & Tester 2007; Dowsley & Wenzel 2008), la connaissance scientifique et le savoir local (ou savoir écologique traditionnel; Berkes 1999) sont aujourd'hui considérés comme deux sources d'informations valables par la communauté scientifique, les gouvernements et les organisations locales (Brook & McLachlan 2008; Huntington 2011; Adams *et al.* 2014). De plus, des regroupements internationaux tels que la Plate-forme intergouvernementale sur la biodiversité et les services écosystémiques (IPBES) soulignent l'importance des savoirs locaux et promeuvent les approches intégrant ces savoirs aux connaissances scientifiques (Vohland *et al.* 2011; Diaz *et al.* 2015; Ford *et al.* 2016). Étant donné leur nature complémentaire (Gagnon & Berteaux 2009; Service *et al.* 2014), l'intégration des savoirs locaux et des connaissances scientifiques est particulièrement pertinente pour la conservation des espèces animales (Berkes 2008; Kendrick & Manseau 2008; Gutierrez, Hilborn & Defeo 2011; Cinner *et al.* 2012). Toutefois, certains auteurs (Nadasdy 1999; Tester & Irniq 2008; Vandebroek *et al.* 2011; Apgar *et al.* 2016) soulignent des risques inhérents à l'intégration des connaissances, plus particulièrement quand les chercheurs connaissent mal la culture locale ou ne valident pas leurs interprétations auprès des détenteurs de connaissances locales. Du point de vue des communautés locales, l’utilisation de leurs connaissances par les chercheurs peut aussi être mal perçue dans le cas d’études qui s’intéressent à des questions d’intérêt académique sans résonnance pratique pour la communauté. En réponse à ces difficultés, un nouveau courant de recherche (*community-based* ou *participatory research*; Hackel 1999; Leeuw, Cameron & Greenwood 2012; Johnson *et al.* 2015a) met en priorité le partenariat étroit avec les communautés et évalue des problématiques définies localement, tout en incluant la participation active des acteurs locaux dans l’ensemble du processus de recherche.

Pour notre objectif 3, nous avons collaboré avec la communauté de Qamani’tuaq (Nunavut), afin de définir les priorités locales par rapport aux grands carnivores de la toundra. À partir des observations et connaissances locales, nous avons déterminé des hypothèses de travail et avons développé un schéma d’étude avec le Conseil de chasseurs et trappeurs de Qamani’tuaq. Nous avons réalisé des entrevues avec des chasseurs et aînés locaux et combiné leurs observations (et perceptions) à des données biologiques obtenues dans le cadre de notre programme de collecte de carcasses (voir section 0.4.2). Nous avons présenté et validé notre interprétation de leurs connaissances auprès de la communauté.

0.5 Plan de la thèse

Outre l’introduction générale, cette thèse comprend trois chapitres et une conclusion générale.

Le premier chapitre répond à l’objectif 1. Il vise à déterminer comment la niche alimentaire des grands carnivores arctiques peut varier en fonction des contraintes biologiques, de la diversité des ressources disponibles et de l’accès aux proies préférées. Cette étude est la première à évaluer cette question chez plusieurs espèces de grands carnivores terrestres et à une très grande échelle spatiale. Elle permet de mieux comprendre le fonctionnement des écosystèmes en général. Ce premier chapitre est un manuscrit préparé pour la revue *Proceedings of the Royal Society B-Biological Sciences*.

Le deuxième chapitre répond à l'objectif 2. Il vise à déterminer les taux de fractionnement isotopique chez les grands carnivores afin d'augmenter la précision des analyses isotopiques en écologie animale. Les valeurs de fractionnement pourront être utiles pour d'autres études menées en milieu naturel. Ce deuxième chapitre est un manuscrit préparé pour la revue *Rapid Communications in Mass Spectrometry*.

Le troisième chapitre répond à l'objectif 3. Il vise à répondre à une problématique locale concernant l'impact de la pression de chasse sur les populations de loups toundriques, dans un contexte de développement socio-économique rapide. Cette étude démontre les impacts biologiques et écologiques de la chasse sur les populations de loups, ce qui a des implications possibles en conservation. L'étude souligne aussi l'importance d'intégrer les connaissances locales aux données scientifiques, particulièrement pour l'étude d'espèces très furtives. Ce troisième chapitre est un manuscrit préparé pour la revue *Ecology and Society*.

CHAPITRE I

ECOLOGICAL OPPORTUNITY AND NICHE VARIATION: CONTRASTING DIET OF ARCTIC TOP PREDATORS ACROSS SEASONS AND LARGE-SCALE RANGES

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Manuscrit en préparation pour soumission à *Proceedings of the Royal Society B-Biological Sciences*

Contributions des auteurs (initiales)
Mise en place du design de l'étude (VLH, NL, DB)
Récolte des données (VLH, MA, GS)
Analyse des données (VLH)
Interprétation des résultats (VLH, NL, DB)
Rédaction du manuscrit (VLH)
Commentaires et correction du manuscrit (NL, MA, GS, DB)
Financement (MA, DB)

1.1 Résumé

Afin de mieux comprendre les variations de la niche alimentaire des consommateurs, il est primordial de déterminer comment les opportunités écologiques, c.-à-d. la diversité des ressources déterminée par les variations environnementales, influencent leur utilisation des ressources. Par contre, l'étude de l'influence sur la niche alimentaire des prédateurs des facteurs qui varient à de vastes échelles spatiales demeure très complexe, car les prédateurs occupent de grands espaces, vivent à faible densité et sont furtifs.

Dans cette étude, nous avons évalué comment les contraintes biologiques, les opportunités écologiques et la disponibilité des proies principales influencent la niche alimentaire de deux prédateurs supérieurs sympatriques de la toundra arctique, le loup gris *Canis lupus* et le carcajou *Gulo gulo*. Nous avons utilisé les isotopes stables et les contenus stomacaux comme mesures complémentaires de la niche alimentaire à partir de donnée récoltées pendant trois ans (2011-13) et à une échelle continentale (ca. 900 000 km^2) dans l'Arctique canadien. Nous avons analysé les carcasses de 287 loups et 376 carcajous, une taille d'échantillon inégalée.

Les deux espèces de prédateurs utilisaient les ressources allochtones marines (surtout des phoques) au cours des mois froids, lorsque la disponibilité du caribou était faible. L'utilisation des ressources marines causait la plus large niche isotopique et la variation interindividuelle (AIV) la plus élevée chez les carcajous, particulièrement dans les régions les moins productives de la toundra. Chez les loups par contre, la niche isotopique était la plus large et AIV était la plus élevée dans une région située au nord-ouest de notre aire d'étude, là où les proies ongulées principales (caribou) et alternatives (bœuf musqué) et les ressources marines étaient disponibles. La niche isotopique était plus grande chez les carcajous mâles comparativement aux femelles, suggérant une capacité d'utilisation des opportunités écologiques qui était liée au sexe chez cette espèce. Chez les carcajous femelles, la niche isotopique était plus large au cours des mois froids qu'à l'automne, possiblement dû au comportement de reproduction en tanière. La niche isotopique des jeunes loups solitaires (des jeunes adultes en dispersion) et des vieux individus solitaires n'était pas différente de celle des loups vivant en groupe (juvéniles et adultes).

La recrudescence annuelle de proies résidentes (p. ex. lemmings) et migratrices (sauvagine) causait une variation saisonnière significative de la niche isotopique des deux prédateurs (diminution des signatures isotopiques moyennes $\delta^{13}C$ et $\delta^{15}N$ en été par rapport à l'automne), bien que l'étendue de la niche et AIV ne variait pas entre les saisons.

Nous suggérons que l'utilisation des opportunités écologiques par les grands prédateurs terrestres peut causer des variations de niche au sein des populations et au niveau individuel. La supplémentation des grands prédateurs de la toundra par des ressources provenant d'autres écosystèmes est possible et peut influencer la dynamique des écosystèmes toundriques en modifiant la force des interactions trophiques. À l'échelle continentale, les variations dans l'utilisation des ressources par les prédateurs supérieurs peuvent avoir des répercussions pour leur gestion et conservation.

<u>Mots clés :</u> Prédateurs supérieurs terrestres, niche isotopique, spécialisation individuelle, opportunités écologiques, Arctique

1.2 Abstract

How ecological opportunity, *i.e.* resource diversity determined by environmental variations, drives resource use by consumers is central to understanding niche variation. Yet deciphering the large-scale drivers behind trophic niche dynamics remains a challenge, especially in predators for which large ranges, low densities and elusiveness often complicate monitoring and diet estimation.

Here we examined how biological constraints, ecological opportunity and main prey availability influence niche variation in two sympatric tundra top predators, the gray wolf (*Canis lupus*) and the wolverine (*Gulo gulo*). We used stable isotopes and stomach contents as complementary measures of realized niche within a multi-year (2011-2013) and continental scale (ca. 900,000 km^2) data collection program in the Canadian Arctic. We gathered unprecedented sample sizes for such elusive species (n =287 and n=376 for wolves and wolverines, respectively).

Both predators exploited allochthonous marine resources (mainly seals) during the cold months and when the main caribou prey was less available. Such sea-based resources generated the widest isotopic niche and the highest among-individual variation (AIV) for wolverines, and this was especially true in the most unproductive tundra regions. Yet wolf niche was the widest and AIV the highest in the Northwestern region of our study area, where both the main (caribou) and alternative (muskox) ungulate prey and marine resources are potentially available. Isotopic niche was wider for males compared to female wolverines, suggesting gender-specific ability to exploit ecological opportunity in this species. For female wolverines, isotopic niche was wider in the cold months than in the fall possibly due to denning behaviour. Isotopic niche in lone wolves (young dispersers and old solitary individuals) was not different than in pack wolves (juveniles and adults).

The continent-wide surge of tundra dwelling (*e.g.* lemmings) and migratory (*e.g.* geese) prey generated significant seasonal isotopic niche variation (decreased $\delta^{13}C$

and δ^{15}N averages in summer compared to fall) in both predator species, yet with no apparent change across seasons in niche width and individual specialization.

We suggest that long-ranging terrestrial predators may respond to ecological opportunities with niche variation at both population and individual levels. The subsidization of large tundra predators by resources generated out of the tundra is likely and may impact the dynamic of tundra ecosystems by modulating the strength of trophic interactions. The range-wide variation of resource use by top predators bears implications for their conservation and management.

Keywords: Terrestrial top predators, isotopic niche, individual specialization, ecological opportunity, Arctic

1.3 Introduction

The understanding of individual variation in resource use has become a central tenet of ecology because of its implications at the population, community, and evolutionary levels (Kondoh 2003; Hughes *et al.* 2008; Bolnick *et al.* 2011). For example, individual diet specialization can increase individual reproductive performance (Annett & Pierotti 1999) or reduce food web connectivity (Quevedo *et al.* 2009; Matich *et al.* 2011a). According to the Optimal Foraging Theory framework (MacArthur & Pianka 1966, reviewed in Araujo *et al.* 2011), resource diversity and abundance of main (preferred) prey determine consumers' niche variation. In addition, individual, species, sex, or age-specific biological constraints (Lewis *et al.* 2002; Thiemann *et al.* 2011; Horswill *et al.* 2016), can determine foraging tradeoffs and the ranking criteria used by consumers to establish the most profitable resources (that is, those yielding the maximum net energy intake), as well as the ability to exploit resource diversity. When determined by environmental variations such as habitat heterogeneity or environmental stability, resource diversity is coined *ecological opportunity*.

Recent studies show the potential impact of ecological opportunity on trophic niche variation and trait evolution (Rainey & Travisano 1998; Parent & Crespi 2009, reviewed in Araujo *et al.* 2011). Using stable isotopes as quantitative measures of realized niche, recent empirical research documented that ecological opportunity generates niche expansion via individual specialization in generalist predators (for habitat heterogeneity, see Layman *et al.* 2007b; Darimont, Paquet & Reimchen 2009; L'Hérault *et al.* 2013; Louis *et al.* 2014; Newsome *et al.* 2015; Kernaléguen *et al.* 2015; Yurkowski *et al.* 2016, for environmental stability (seasonality), see Gerardo Herrera *et al.* 2008; Jaeger *et al.* 2010; Horswill *et al.* 2016). However, ecological opportunity does not always lead to niche variation (L'Hérault *et al.* 2013; Evangelista *et al.* 2014), and whether this is due to relative prey availability, biological constraints, or other reasons is unclear. For example, Kernaléguen et al. (2015) showed how species-specific traits, resource diversity, and population density (a proxy of main prey availability) can all shape niche variation and individual specialization in long-ranging marine predators.

Going beyond single predator studies is a promising avenue to unlock the determinants of niche variation, since individual niche width is a phenotypic trait that may vary among species (Taper & Case 1985; Ackermann *et al.* 2004; Svanback *et al.* 2008). However few studies have approached this phenotypic complexity in natural conditions (Jaeger *et al.* 2010; Zanden *et al.* 2010; Matich *et al.* 2011a; Yurkowski *et al.* 2016). In addition, current empirical support for the hypothesis that ecological opportunity drives niche variation originates from marine (Kernaléguen *et al.* 2015; Horswill *et al.* 2016) or aquatic generalists (Layman *et al.* 2007b), with few examples from terrestrial consumers(but see Gerardo Herrera *et al.* 2008; Costa *et al.* 2008; L'Hérault *et al.* 2013), particularly long-ranging terrestrial top predators (Darimont, Paquet & Reimchen 2009). Yet terrestrial top predators are often keystone species or environmental indicators (Saether 1999) which influence the structure and functioning of trophic webs (Terborgh *et al.* 2001; Johnson 2010). When ecological opportunity can arise, its potential effect on niche variation is extensive since the profitability of prey can differ markedly according to differences in foraging mode within and between species. These foraging modes depend on sociality (Sinclair, Mduma & Brashares 2003), scavenging (Mattisson *et al.* 212), morphological adaptations, and behavioural adaptations including learning processes (Estes *et al.* 2003; Sargeant & Mann 2009).

For top predators, the Arctic tundra is a vast and globally unproductive ecosystem with exceptionally strong spatial and seasonal contrasts in resource availability. During the short summer, photosynthetic activity and migration of animals from the south generate patches of abundant resources, with increased resource diversity via resource pulses and pulsed subsidies (Yang *et al.* 2008). In winter, main prey is scarce and determined by the distribution of barren-ground migratory caribou (*Rangifer tarandus*, Linnaeus 1758) and the tundra dwelling caribou (Nagy *et al.* 2011), yet an alternative ungulate prey, the muskox (*Ovibos moschatus*, Zimmermann 1780) can be available at high latitudes (Fournier & Gunn 1998; Mech 2005). Access to allochthonous resources from the ice-covered marine ecosystem can also create local resource diversity in coastal habitats, with potential for population and individual niche variation (Roth 2002; Tarroux *et al.* 2012). Sympatric top predators can express such variation with contrasting foraging mode and social structure. This is likely the case for the gray wolf (*Canis lupus*, Linnaeus) and the wolverine (*Gulo gulo*, Linnaeus). While the wolf is a social hunter generally considered as ungulates obligate (Peterson & Ciucci 2003, but see Mech 2007; Darimont *et al.* 2009; Adams *et al.* 2010), the wolverine is a solitary opportunist and scavenger that can feed on ungulates killed by other predators (Mattisson *et al.* 2012). Such differences in behaviour determine their foraging trade-offs. They can both exhibit a generalist diet, yet with a preference for caribou (Mulders 2001; Klaczek *et al.* 2016). Given the above, the study of these two long-ranging predators in a system characterized by strong spatiotemporal contrasts in resource variability can help to further our knowledge on the interplay between ecological opportunity, main prey availability, and biological constraints on niche variation.

Here we investigate three general hypotheses stating that biological constraints (Hypothesis 1, predictions 1-4, Table 1.1), ecological opportunity determined by seasons and habitat heterogeneity (Hypothesis 2, predictions 5-6, Table 1.1), and main prey availability (Hypothesis 3, predictions 7-9, Table 1.1) influence niche variation in large tundra top predators. For each prediction, we also examined whether niche variation arises through among-individual variation (a proxy to individual specialization) as predicted by the Niche Variation Hypothesis (Van Valen 1965). To date, this hypothesis has not yet received empirical support in terrestrial carnivores (Meiri *et al.* 2005, but see Darimont *et al.* 2009). We examine our predictions using stable isotope signatures as measures of realized niche (Layman *et al.* 2012; Ehrich *et al.* 2015) and validate and expand our results using stomach content analysis (Killengreen *et al.* 2011). Data were obtained through a carcass collection program involving Inuit hunters from Nunavut, Canada (Figure 1.1). We ran the program over 900,000 km^2 across three years (2011-2013) and multiple seasons, yielding exceptional sample sizes of 287 wolves and 376 wolverines. Such a large-scale analysis of niche variation is largely lacking in the literature.

Table 1.1 Prediction sets generated from three hypotheses stipulating that biological constraints, ecological opportunity (resource diversity across seasons and space) and main prey availability determine niche variation and among-individual variation (AIV) in wolves and wolverines studied in the Canadian Arctic tundra.We decomposed niche variation in three components: niche width, direction of variation as determined from carbon δ^{13}C and nitrogen δ^{15}N isotopic signatures, and proportion of caribou in stomachs. Bold characters identify supported predictions. Underlined predictions were supported for only one predator or one season (superscripts indicate which species or season offered support). Litterature sources are provided for each prediction.

Prediction sets	Source
Biological constraints	
1) Wolverines show more niche variation (and higher AIV) than wolves	2,4,14
2) Male wolverines show more niche variation (and higher AIV) **than females**	1,15
3) Female wolverines show more niche variation (and higher AIV) **during breeding (winter and spring) than during non-breeding (fall)**	3,16
4) Solitary wolves (young and old adults) show more niche variation (and higher AIV) than pack wolves (juveniles and adults)	9
Ecological opportunity	
5) Niche variation and AIV **are greater in winter, spring**$^{\text{wolverine}}$ and summer **than in fall**	4,11
6) Individual δ^{13}C and **δ^{15}N$^{\text{wolverine}}$ (and AIV) increase with access to allochthonous marine resources**	5,8,10
Main prey abundance	

7) Niche variation$^{\text{wolverine}}$ and AIV$^{\text{wolverine}}$ are greater in most unproductive regions (low caribou availability) than in productive regions	12,13
8) Individual δ^{13}C **and** δ^{15}**N (and AIV) decrease with access to migratory caribou**	4,11,13
9) Individual δ^{13}C and δ^{15}N (and AIV) decrease with access to tundra-dwelling caribou	13

Note: Predictions 1, 5, and 7 were tested at a large scale. Predictions 2 to 4, 6, 8, and 9 were tested at a local scale (Figure A1 in Supporting Information). Predictions were based on the following sources: 1, Inuit hunters' observations, L'Hérault et al., in prep. ; 2, Mulders 2001; 3, Magoun 1985; 4, Musiani et al. 2007; 5, Darimont et al. 2009; 6, Dale et al., 1994; 7, Ballard et al. 1997; 8, Adams et al. 2010; 9, Paquet & Carbyn 2003, 10, Araujo et al. 2011; 11,Klaczek et al. 2016; 12, Roughgarden 1974; 13, McArthur & Pianka 1966; 14, Mattisson et al. 2012; 15, Thiemann et al. 2011; 16, Landa et al. 1997.

1.4 Material and methods

1.4.1 Study design

Our study design involves a hierarchical data structure embedding two complementary spatial scales (large *vs.* local scales; Figure A1 in Appendix A). This approach allowed us to examine our three research hypotheses simultaneously and hence evaluate interactions between biological constraints, ecological opportunity and main prey availability. First, we compared species, regional, and seasonal isotopic niche width, stable isotopes (δ^{13}C and δ^{15}N), proportion of caribou in stomachs, and among-individual variation (AIV) in a large-scale model (Figure A1 in Appendix A). This model examined how the two predator species exploit large-scale variations in ecological opportunity and main prey availability beyond the range routinely travelled by individuals (Figure 1.1). This approach follows typical subpopulation analyses addressing large-scale resource gradients (Darimont *et al.* 2009; Yurkowski *et al.* 2016). Second, we analyzed in a local-scale model how individual predators exploit within their home range prey availability gradients determined by differential access to caribou and marine resources. We considered each species separately and included biological constraints (sex, reproductive status, and age, Figure A1 in Appendix A) in the model. This approach parallels those used in studies addressing local resource gradients (Killengreen *et al.* 2011; Giroux *et al.* 2012; Evangelista *et al.* 2014). Here, we use 'local scale' by opposition with continental or regional scales.

1.4.2 Study area

Our 900,000 km^2 study area located in Canada encompassed continental Nunavut and Victoria Island, from 61^{o}07'to 69^{o}13' North and from 86^{o}14' to 115^{o}05' West. This area hosts 13 Inuit communities and they all actively contributed to the research (see *Collection of animal samples* below) (Figure 1.1). Terrestrial animals in the study area are typical of the continental Arctic tundra (Callaghan et al. 2004). Distribution and abundance of species are determined by the season, with resident and migratory species being present during the short productive summer but a limited array of tundra dwelling species being present in winter (Table A1 in Appendix A). The marine ecosystem bounds the study area to the east and north and provides tundra predators with allochthonous subsidies (mostly adult and pup seals) that are hunted or scavenged.

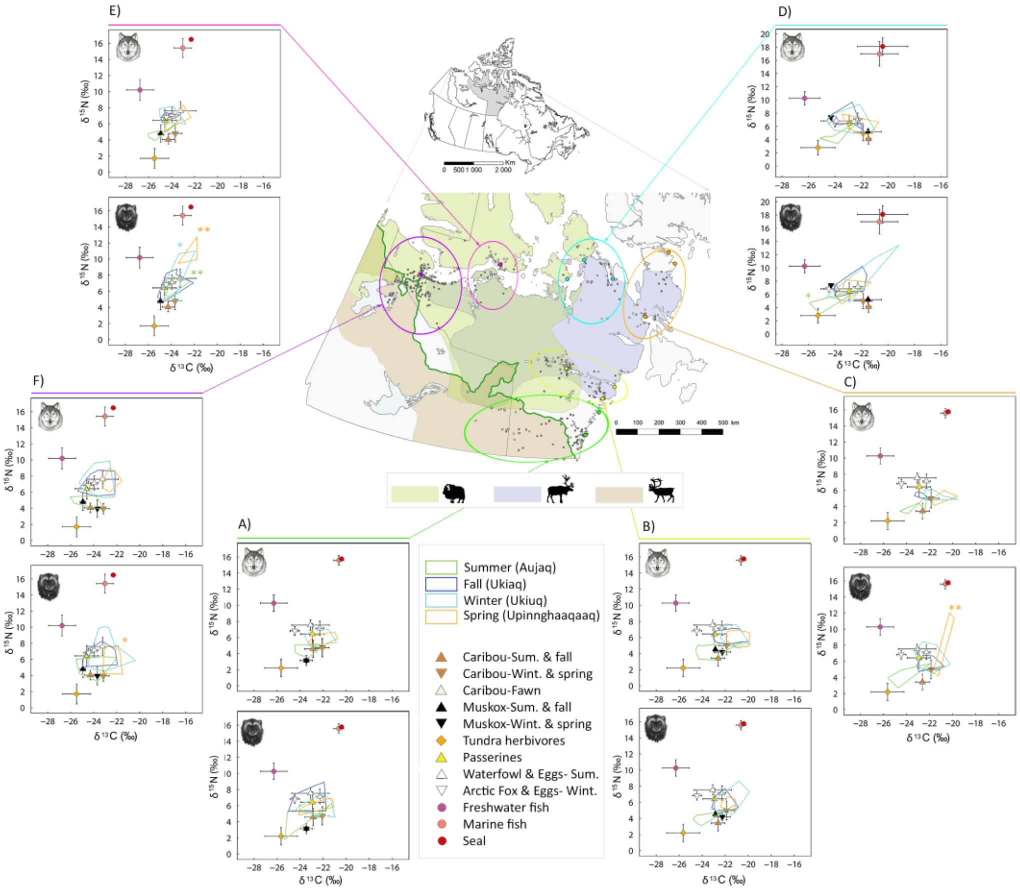

Figure 1.1 Study area and harvest locations of the wolves (white circles) and wolverines (brown circles) across 13 Nunavut communities associated to 6 regions: A) South Eastern Transition (SET), B) Eastern Barren (EB), C) North Eastern Barren (NEB), D) North Barren (NB), E) Barren Island (BI), and F) North Western Transition (NWT). Study regions were determined according to clumping of harvest locations, distribution contrasts in the three ungulate prey (brown: migratory caribou, blue: tundra-dwelling caribou, green: muskoxen) and physico-geography of the study area (see material and methods for details). The 95% Minimum Convex Polygons (MCP) drawn from the δ^{13}C and δ^{15}N signatures obtained from liver, muscle, and fur tissues of wolves (upper panels) and wolverines (lower panels) appear for each region and season. Some MCPs are marked with one (significant difference in δ^{13}C compared to the intercept (region SET and season Fall)) or two asterisks (significant difference in both δ^{13}C and δ^{15}N). δ^{13}C and δ^{15}N signatures of prey sources (muscle tissue) also appear on each panel. Raw data from predators and prey were lipid normalized whereas only raw data from predators were corrected for isotopic discrimination (see Methods and Supporting Information for details).

1.4.3 Biological constraints, ecological opportunity, and main prey availability

Foraging trade-offs related to species, sex, breeding and age (predictions 1-4)

We have not explicitly quantified foraging trade-offs among species (prediction 1 in Table 1.1), sex (predictions 2 and 3 in Table 1.1), and age classes (prediction 4 in Table 1.1) but rather based our predictions on existing biological knowledge. However, such knowledge was still very shallow for both species, especially in Arctic-dwelling populations, so that the testing of our predictions was important to validate existing observations and advance knowledge. Most predictions were thereby formulated as biological inferences and were based on the general framework provided by the Optimal Foraging Theory. Species were expected to differ based on differences in foraging mode and social structure. We expected that wolverines would show greater ability to incorporate a variety of resources to their diet than wolves given their limited ability to capture live ungulate prey (Copeland & Jackson 2003; Peterson & Ciucci 2003). Sex would determine the niche of wolverines given that males are larger and should require more energy than females (Copeland & Jackson 2003), and may have a greater ability to exploit marine resources according to Inuit hunters (prediction 2 in Table 1.1). Seasons could also determine the niche of female wolverines given that they are central-place foragers during the denning period. The denning period spans the early winter (pre-birth) to early spring (kit rearing) during which the use of small rodents would be particularly important (Magoun 1985; Landa 1997). Finally, we expected age classes (juvenile young adult, prime-age adult, and old adult) to determine the niche of wolves given their influence on sociality. Young adults during dispersal and old adults should incorporate a greater variety of resources than juveniles and prime-age adults because the latter live in packs and can hunt large ungulates (prediction 4 in Table 1.1) (Paquet & Carbyn 2003).

Seasons (prediction 5)

Based on the Inuit calendar, we studied niche variation within four time periods: 1- Summer/autumn (Upinngaaq/Aujaq/Ukiaqhaaq: 1 June to 15 October), 2- Early winter (Ukiaq: 16 October to 30 November), 3- Winter (Ukiuq: 1 December to 28 February), and 4- Spring (Upinngaaqhaaq: 1 March to 31 May) (Table A1 in Appendix A). We did so because these periods better represent changes in the Arctic tundra and animal phenology than do seasons defined from equinoxes and solstices. Based on existing knowledge on seasonal variation in caribou abundance (Nagy *et al.* 2011) and its association with large predators (Musiani *et al.* 2007; Klaczek *et al.* 2016), we expected niche expansion and highest among-individual variation in winter and spring because migratory caribou are scarce during this period, compared to fall when they are numerous. Concurrently, we also expected niche expansion in winter and spring (compared to fall) because marine resources are more available when the sea ice provides ready access to the marine ecosystem, roughly from December to June (Table A1 in Appendix A). We also expected niche expansion and higher AIV in summer compared to fall, because tundra resources are plentiful in summer (Samelius *et al.* 2002; Wiebe *et al.* 2009).

Large-scale availability of main prey (prediction 7)

The continental scale of our study area allowed important spatial contrasts in the availability of the main prey, the caribou (Nagy *et al.* 2011), but also in the availability of an alternative ungulate prey, the muskox (Kivalliq Ecological Land Classification Map Atlas 2015)(Figure 1.1). We delineated six regions that differed in the spatial distribution of tundra and migratory caribou, muskoxen, resource diversity, landforms and climate, and productivity (Kivalliq Ecological Land Classification Map Atlas 2015). For analysis purpose, we considered the wolves and wolverines from these six regions as belonging to separate subpopulations.

Prey availability gradients (predictions 6, 8 and 9)

We calculated three gradients of prey availability. They were determined as the closest Euclidean distance between each individual's harvest location and the marine ecosystem boundary (prediction 6), the distribution boundary of migratory caribou herds (prediction 8), and tundra caribou (prediction 9) (Figure 1.1). The distance to muskox distribution boundary was not considered because we could not discriminate the isotopic signatures of this prey with the ones of the caribou (Table A2 in Appendix A). Since the effects of distance typically decline beyond the home range used by individual wolves and wolverines, we transformed all Euclidean distance variables using decay functions (Nielsen, Cranston & Stenhouse 2009; Takahata *et al.* 2014) to minimize the contribution to the model of large distances. To do so, we created five transformed variables for each Euclidean distance variable using the form $e^{-\alpha/d+1}$, where α was the decay constant set at 2, 10, 20, 40, and 60, and d was the Euclidean distance (km). The smallest values of α yield the most gradual decays. To select the best fit transformed variable prior to statistical analyses, we ran single-effect linear mixed regressions and model selection between each transformed decay variable and the dependent variables of interest ($\delta^{13}C$, $\delta^{15}N$, proportion of caribou in stomachs, and AIV; see Components of niche variation below). Details on linear mixed regressions and model selection are provided in the statistical analyses section.

1.4.4 Collection of animal samples

We collected carcasses of wolves and wolverines harvested by hunters from 13 Nunavut settlements. Hunters reported carcasses between November 1st and May 31st in 2010-2011, 2011-2012 and 2012-2013 (Table A1 in Appendix A). Hunters provided information on the location, date, and time of the harvest, as well as ecological observations such as the presence of wildlife at the harvest site. They received cash subsidies as compensation. Received amounts were < 20% of the average sale price of wolf and wolverine pelts and were thus unlikely to increase hunting pressure. Other programs provided similar compensations (Agarwala *et al.* 2010). We stored all animal carcasses at -20°C until necropsies were performed to collect liver, muscle and fur samples for stable isotope analyses, to retrieve stomachs and their content, and to determine age (cementum growth layers in the canine tooth, Jensen & Nielsen 1968) and sex. Tissue and stomach samples were stored again at -20°C until further analyses were performed.

When possible, we also collected muscle samples of potential prey sources from animals harvested during traditional subsistence activities. We stored these samples in 70% ethanol and at -20°C until analysis. When we were not able to obtain samples for a given prey, we used isotopic signatures from the literature (Table A2 in Appendix A).

1.4.5 Components of niche variation

Stable isotopes: niche width, direction of variation and among-individual variation

Stable isotope composition of different tissues reflects assimilated diet over different periods of time according to their respective turnover rate (Tieszen *et al.* 1983a; Dalerum & Angerbjorn 2005). In this study, liver reflected diet during November-May, muscle reflected diet during October-March, and fur reflected diet during June-October (Table A1 in Appendix A). After initial preparation of samples from predators and prey (details in Supporting Information), we performed isotopic measurements at the Stable Isotopes in Nature Laboratory (SINLAB), University of New Brunswick, Canada. We applied lipid normalization on predators and prey $\delta^{13}C$ values (Ehrich *et al.* 2010). We also applied per-tissue corrections for isotopic discrimination of $\delta^{13}C$ and $\delta^{15}N$ (Roth & Hobson 2000b; Lecomte *et al.* 2011) see the details in Appendix A).

We determined niche width (the area encompassed within a 95% Minimum Convex Polygon calculated in the δ^{13}C- δ^{15}N bi-plot; Layman *et al.* 2007a) for each level of the variables tested (Figure A1 in Appendix A). A wider 95% MCP at a given variable level indicates niche expansion and a more generalist diet than at other levels, whereas a narrower 95% MCP represents niche reduction and diet specialization. In order to test the direction and significance of niche variation, we compared average δ^{13}C and δ^{15}N among each level of the variables tested (see statistical analyses below). In models reflecting local-scale prey availability gradients (predictions 6 and 8-9 in Table 1.1), we examined niche variation using individual δ^{13}C and δ^{15}N solely. For both predators, we calculated among-individual niche variation using the Nearest Neighbour Distance metrics adapted from Layman et al., (2007a). We calculated the isotopic distances (using positioning in the δ^{13}C / δ^{15}N bi-plot) between each individual and its 'n' closest spatial neighbours (using GPS coordinates of harvest locations), thus obtaining an average among-individual isotopic distance for each individual. We ran sensitivity analyses by varying 'n' between 5 and 50, in order to determine the best fit in subsequent statistical analyses (see below).

Stomach contents: proportion of caribou in stomachs

In addition to stable isotope analyses, we analyzed the stomach contents of both predators as recommended by Killengreen et al. (2011). This dual approach was particularly critical in our study because caribou and muskoxen have similar δ^{13}C and δ^{15}N signatures (Table A2 in Appendix A). The proportion of caribou and muskoxen ingested by predators was determined by calculating the wet weight of items from each species recovered from stomachs (details in Appendix A). Again based on the assumption that caribou is the main prey for both predator species, a decrease in the proportion of caribou in stomachs indicates niche expansion and a more generalist diet, whereas its increase represents niche reduction and diet specialization on caribou. Stomach content analysis also allows determining the occurrence of alternative prey sources in the diet of predators and to ground-truth stable isotopes variation ranges.

1.4.6 Statistical analyses

Statistical analyses were conducted in R, version 3.1.1 (R Development Core Team 2014). We used linear mixed effect models (*nlme* library, Pinheiro et al. 2006) to analyze variation in $\delta^{13}C$ and $\delta^{15}N$ of predator tissues, proportion of caribou in stomachs, presence of alternative prey in stomachs, and among-individual niche variation. We tested the fixed effects Species, Season, and Region (and their interactions) in large-scale models (predictions 1, 5 and 7, see Figure A1 in Appendix A). We tested the fixed effects Distance to the coastline, Distance to migratory caribou, and Distance to tundra caribou in local-scale models (transformed Euclidean distances, predictions 6, 8, and 9). We ran local-scale models independently for each species. Models used for wolverines included Sex as fixed effect (predictions 2 and 3). Models used for wolves included the fixed effect Age class (prediction 4). In both large- and local-scale models, we included years, the settlement where the animal was harvested, and individual identity (but not in the stomach contents models because we obtained only one stomach per individual) as random intercepts. Candidate models involved models with and without two-way interactions of ecological significance (*e.g.* species*region, Table A3 in Appendix A). We based model selection on AICc scores (Burnham & Anderson 2002). The best model had the lowest AICc, unless differences in AICc (ΔAICc) were smaller than 2, in which case we selected the model with fewer variables and interactions (Table A3 in Appendix A). We used maximum likelihood fitted models for model comparisons, while we used restricted maximum likelihood for parameter estimation (Pinheiro & Bates 2000).

1.5 Results

A total of 287 wolves and 376 wolverine carcasses were reported to the program, whereas 245 (240) samples of liver, 259 (284) samples of muscle and 74 (72) samples of fur were analyzed from wolves and wolverines, respectively. A total of 261 (340) stomachs were dissected and 82% (79%) of them contained prey remains, for wolves and wolverines respectively.

1.5.1 Stable isotopes

<u>Biological constraints</u>
Isotopic niche width (hereafter INW) was larger in wolverines (MCP 95% =31.1 ‰) than in wolves (25.5 ‰), thus supporting prediction 1. δ^{13}C was on average lower (-1.13 ‰ , 95% CI [-1.54:-0.71 ‰]) in wolverines than in wolves (intercept, Table 1.2) while δ^{15}N did not vary among species (Table 1.2), thus contradicting prediction 1. Among-individual isotopic variation (hereafter AIV) was 0.51 ‰ (95% CI [0.12 :0.89 ‰]) higher in wolverines than in wolves (Table 1.4), again supporting prediction 1. Male wolverines INW was slightly larger (MCP 95% =27.31‰) than that of females (25.05 ‰), supporting prediction 2. Also supporting prediction 2, δ^{13}C and δ^{15}N were on average lower (-0.44 ‰, 95% CI [-0.78: -0.11 ‰] and -0.45 ‰, 95% CI [-0.84:-0.05 ‰], respectively) in females than in males (intercept, Table 1.3). AIV was not different among sexes (sex was not selected in the best model, see Table A3 in Appendix A), which does not support prediction 2.

Supporting prediction 3, INW of female wolverines was larger in winter (MCP 95% =14.23 ‰) and in spring (MCP 95% =9.67 ‰) than in fall (MCP 95%=6.82 ‰). Contradicting prediction 3, δ^{13}C, δ^{15}N, and AIV of female wolverines did not vary among seasons, since the interaction Female*Season was not selected in the best models (see Table A3 in Appendix A).

Contradicting prediction 4, INW of wolves was larger in juveniles (MCP 95% =18.08 ‰) living in a pack than in young adults and old adults (MCP 95% =13.44‰ and 11.14 ‰, respectively) who were solitary, which were similar to prime-age adults living in packs (MCP 95% =12.7 ‰). Also contradicting prediction 4, δ^{13}C, δ^{15}N, and AIV of wolves did not differ between age classes, since age class was not selected in the best wolf models (see Table A3 in Appendix A).

Table 1.2 Results from the selected large-scale linear mixed models relating δ^{13}C and δ^{15}N signatures obtained from wolves and wolverines to species, regions, and seasons (predictions 1, 5 and 7 in Table 1.1). Intercept is wolf, region SET, and season early winter. See Table A3 in Appendix A for the list of candidate models tested. Significant coefficients (*p*<0.05) appear in bold.

	Estimate	%95 CI (-/+)		d.f.	*p*
a) δ^{13}C fixed effects					
Intercept	-22.69	-23.14	-22.23	667	**0.0001**
Species_WV	-1.13	-1.54	-0.71	667	**0.0001**
Region_EB	0.77	0.28	1.26	18	**0.01**
Region_NEB	0.32	-0.25	0.90	18	0.29
Region_NB	-0.46	-0.99	0.06	18	0.10
Region_NWT	-0.92	-1.48	-0.37	18	**0.004**
Region_BI	-1.85	-2.42	-1.28	18	**0.0001**
Season_Winter	0.36	0.17	0.55	667	**0.0003**
Season_Spring	1.21	0.99	1.42	667	**0.0001**
Season_Summer	-1.02	-1.26	-0.77	667	**0.0001**
Species_WV*Region_EB	0.45	0.08	0.82	667	**0.02**
Species_WV*Region_NEB	0.73	0.29	1.17	667	**0.001**
Species_WV*Region_NB	0.71	0.26	1.16	667	**0.002**
Species_WV*Region_NWT	0.80	0.43	1.17	667	**0.0001**
Species_WV*Region_BI	1.59	1.16	2.02	667	**0.0001**
Species_WV*Season_Winter	0.29	0.03	0.54	667	**0.03**
Species_WV*Season_Spring	-0.06	-0.36	0.24	667	0.71
Species_WV*Season_Summer	0.25	-0.08	0.59	667	0.14
Random effects					

Year/Settlement/Id/Residual (SD):	0.0001/0.3/0.2/0.7				
b) δ^{15}N fixed effects					
Intercept	6.41	5.74	7.07	667	**0.0001**
Species_WV	-0.44	-1.05	0.17	667	0.16
Region_EB	-0.19	-0.78	0.39	18	0.52
Region_NEB	-1.19	-1.90	-0.47	18	**0.004**
Region_NB	0.32	-0.34	0.98	18	0.36
Region_NWT	1.30	0.66	1.93	18	**0.0008**
Region_BI	0.58	-0.12	1.27	18	0.12
Season_Winter	-0.21	-0.49	0.08	667	0.15
Season_Spring	-0.41	-0.73	-0.09	667	**0.013**
Season_Summer	-2.48	-2.83	-2.12	667	**0.0000**
Species_WV*Region_EB	0.38	-0.16	0.93	667	0.17
Species_WV*Region_NEB	1.06	0.43	1.69	667	**0.0010**
Species_WV*Region_NB	1.43	0.78	2.07	667	**0.0000**
Species_WV*Region_NWT	-0.27	-0.82	0.27	667	0.33
Species_WV*Region_BI	1.17	0.55	1.78	667	**0.0002**
Species_WV*Season_Winter	0.17	-0.19	0.52	667	0.36
Species_WV*Season_Spring	0.17	-0.27	0.60	667	0.45
Species_WV*Season_Summer	0.07	-0.41	0.54	667	0.79
Random effects					
Year/Settlement/Id/Residual (SD):	0.3/0.3/0.8/0.9				

Ecological opportunity (seasons)

Supporting prediction 5, wolverines' INW was larger in winter, spring, and summer (95% MCP = 20.9 ‰, 18.2 ‰, and 13.8 ‰, respectively) than in early winter (95% MCP = 13.3 ‰). Partly supporting prediction 5, INW of wolves was larger in winter (95% MCP = 14.5 ‰) and narrower in summer (95% MCP = 6.7 ‰) than in early winter (95% MCP = 12.3 ‰), when it was similar to spring values (95% MCP = 11.2 ‰). Supporting prediction 5, δ^{13}C (both species combined) was higher in winter and spring (0.36 ‰, %95 CI [0.17:0.55 ‰] and 1.21 ‰, %95 CI [0.99:1.42 ‰], respectively) and lower in summer (-1.02 ‰, %95 CI [-1.26:-0.77 ‰]) than in early winter (intercept, Table 1.2). Also supporting prediction 5, δ^{15}N (both species combined) was lower in spring and in summer (-0.41 ‰, 95% CI [-0.73:-0.09 ‰], and -2.48 ‰, 95% CI [-2.83:-2.12 ‰], respectively), than in early winter (intercept, Table 1.2). Contradicting prediction 5 however, δ^{15}N was not significantly different in winter than in early winter (intercept, Table 1.2). Contradicting prediction 5, AIV (both species) did not vary among seasons (season effect was not selected in best models, see Table A3 in Appendix A).

Ecological opportunity (interaction between Availability of marine resources and Predator species)

In wolves, δ^{13}C variation was positively correlated with the transformed Euclidean distance (hereafter tEd) to the coastline (1.09‰, 95% CI [0.29:1.89‰]), thus contradicting prediction 6. However, supporting prediction 6, in wolverines variation in δ^{15}N was negatively correlated to the tEd to the coastline (-1.55 ‰; 95% CI [-2.29:-0.81 ‰], Table 1.3). Also supporting prediction 6, AIV in wolves and wolverines were negatively correlated to the tEd to the coastline (-0.93‰, 95% CI [-1.24:-0.64 ‰] and -1.99 ‰, 95% CI [-2.51:-1.49 ‰], respectively, Figure 1.2).

Main prey availability (interaction between Region and Predator species)

Supporting prediction 7, INW in wolverines was slightly larger (by up to 15%) in the most unproductive regions (North Eastern Barren and Barren Island, but excluding the North Barren region) than in the South Eastern Transition region (the intercept, a more productive region). INW in wolves was larger in the unproductive North Barren region, and in the most productive North Western Transition region (by 75% and 73%, respectively) than the intercept (South Eastern Transition region), partly supporting prediction 7. INW was twice as high in wolverines than in wolves in the South Eastern Transition, North Eastern Barren, and Barren Island regions (supporting prediction 1 and prediction 7), but it was similar among species in the other regions. Also supporting prediction 7 and prediction 1, δ^{13}C and δ^{15}N were generally higher in wolverines than in wolves in the most unproductive regions (North Eastern Barren, North Barren and Barren Island, Table 1.2). Supporting prediction 7 and prediction 1, AIV was higher in wolverines than in wolves in the most unproductive regions (North Barren and Barren Island, Table 1.4).

Table 1.3 Results from the selected local-scale linear mixed models relating wolverine δ^{13}C and δ^{15}N signatures to sex and sex*season (predictions 2 and 3 in Table 1.1) and wolverine and wolf δ^{13}C and δ^{15}N signatures to the distance to marine resources (prediction 6) and to main prey (predictions 8 and 9). Intercept in the wolf models is distance 0. Intercept in the wolverine models is distance 0, sex male, and season fall. Distances are transformed Euclidean distances (tEd). See Table A3 in Appendix A for the list of candidate models tested. Significant coefficients ($p<0.05$) appear in bold whereas coefficients with $p<0.1$ appear in italics.

	Value	95% CI (-/+)		d.f.	*p*
a) Wolf					
δ^{13}C fixed effects:					
(Intercept)	-22.47	-22.90	-22.05	218	**0.0001**
tEd_Coastline	1.09	0.29	1.89	208	**0.01**
tEd_Tund. Caribou	-0.08	-0.50	0.34	208	0.70
tEd_Coastline:tEd_Tund. Caribou	-1.02	-1.95	-0.09	208	**0.03**
Random effects:					
Year/ Settlement/ Id/ Residual (SD):	0.0001/ 0.8/ 0.0001/ 0.8				
δ^{15}N fixed effects:					
(Intercept)	6.17	5.45	6.89	218	**0.0001**
tEd_Mig. Caribou	0.67	-0.02	1.36	209	*0.06*
tEd_Tund. Caribou	-0.47	-0.98	0.03	209	*0.07*
tEd_Mig. cbou:tEd_Tund. Cbou	3.56	2.13	4.98	208	**0.0001**
Random effects:					
Year/ Settlement/ Id/ Residual (SD):	0.0001/1.0/0.7/0.4				
b) Wolverine					
δ^{13}C fixed effects:					
(Intercept)	-23.01	-23.37	-22.65	210	**0.0001**

Sex_female	-0.44	-0.78	-0.11	202	**0.01**
Season_Winter	0.74	0.55	0.94	210	**0.0001**
Season_Spring	1.34	1.09	1.60	210	**0.0001**
Sex_female:Season_Winter	0.09	-0.26	0.44	210	0.60
Sex_female:Season_Spring	0.22	-0.22	0.66	210	0.33
Random effects:					
Year/ Settlement/ Id/ Residual (SD):	0.0001/0.7/0.5/0.6				
δ^{15}N fixed effects:					
(Intercept)	6.351	5.27	7.43	214	**0.0001**
Sex_female	-0.45	-0.84	-0.05	199	**0.03**
tEd_Coastline	-1.55	-2.29	-0.81	202	**0.0001**
tEd_Mig. caribou	1.35	-0.07	2.76	199	*0.06*
tEd_Coastline:tEd_Mig. caribou	-2.72	-5.17	-0.27	199	**0.03**
Random effects:					
Year/ Settlement/ Id/ Residual (SD):	0.0002/0.8/1.3/0.7				

Main prey availability (interaction between Availability of caribou and Predator species)

Supporting prediction 8, wolves and wolverines δ^{15}N variations (but not δ^{13}C) were positively correlated to the transformed Euclidean distance (hereafter tEd) to migratory caribou (0.67‰, 95% CI [-0.02:1.36], *p*=0.06 and 1.35‰, 95% CI [-0.07:2.76‰], *p*=0.06, respectively, Table 3). Also supporting prediction 8, wolves and wolverines AIV were positively correlated to the tEd to migratory caribou (0.51‰, 95% CI [0.11:0.90‰], and 1.80‰, 95% CI [1.18:2.43‰], respectively, Figure 1.2). Contradicting prediction 9, wolves' δ^{15}N variation was negatively correlated to the tEd to tundra caribou (-0.47‰, 95% CI [-0.98:0.03‰]). Contradicting prediction 9, wolverines' δ^{13}C and δ^{15}N variations were not correlated to the tEd to tundra caribou (Table A3 in Appendix A). Also contradicting prediction 9, wolves and wolverines AIV were not correlated to the tEd to tundra caribou (Table A3 in Appendix A).

Table 1.4 Results from the selected large-scale linear mixed models relating wolves and wolverines among-individual isotopic variation to species and regions (Predictions 1 and 7). Intercept is species wolf and region SET. See Table A3 in Appendix A for the list of candidate models tested. Significant coefficients (*p*<0.05) appear in bold.

	Value	%95 CI (-/+)		d.f.	*p*
Fixed effects					
(Intercept)	1.16	0.78	1.53	314	**0.0001**
Species_WV	0.51	0.12	0.89	221	**0.01**
Region_EB	0.21	-0.24	0.66	18	0.38
Region_NEB	0.11	-0.44	0.67	18	0.69
Region_NB	0.55	0.04	1.07	18	**0.05**
Region_NWT	0.73	0.22	1.23	18	**0.01**
Region_BI	0.05	-0.48	0.59	18	0.84
Species_WV*Region_EB	-0.56	-1.02	-0.09	221	**0.02**
Species_WV*Region_NEB	0.32	-0.24	0.88	221	0.27
Species_WV*Region_NB	0.98	0.39	1.56	221	**0.001**
Species_WV*Region_NWT	-0.27	-0.74	0.19	221	0.25
Species_WV*Region_BI	1.54	0.97	2.11	221	**0.0001**
Random effects					
Year/Settlement/Id/Residual (SD):	0.0001/0.2/0.2/0.8				

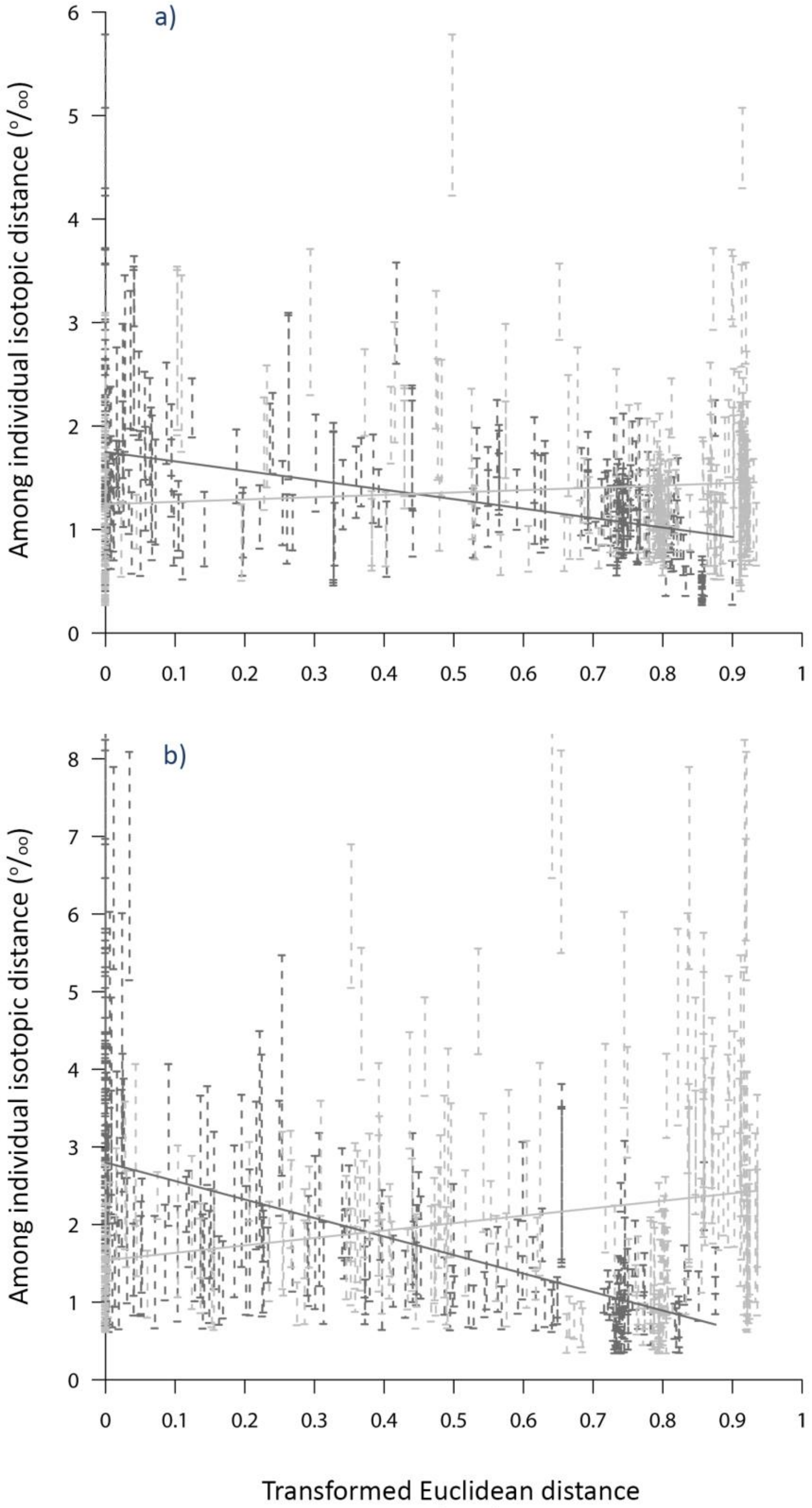
a)
b)
Among individual isotopic distance (°/oo)
Among individual isotopic distance (°/oo)
0
1
2
3
4
5
6
7
8
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Transformed Euclidean distance

Figure 1.2 Effect of distance between harvest location and marine resources (black) or migratory caribou (grey) on the among-individual isotopic distance measured in wolves (panel a) and wolverines (panel b). Coefficients and 95% CIs obtained from local-scale linear mixed models are provided for each fixed effect and species in the Results section (predictions 6 and 8). Fitted lines illustrate correlations obtained from linear models with no random effects. Whiskers show standard deviation. Distances are transformed Euclidean distances (see Methods for details).

1.5.2 Stomach contents

Contradicting prediction 1, 2 and 4, the proportion of caribou in the stomachs of predators did not vary among species, among sexes in wolverines, and among age classes in wolves (Table A4 in Appendix A). On the other hand, old adult wolves ingested a lower proportion of muskoxen (-18.2%, 95% CI [-36.6:0.2%]) than prime-age adults (intercept, Table S4b in Supporting Information). Our data did not allow examination of prediction 3 given limited sample size.

The rest of the stomach results generally illustrate that the use of caribou *vs.* muskoxen was largely compensatory in our system. In other words, we found an elevated proportion of muskoxen in stomachs when and where caribou availability decreased. Yet the proportion of caribou in the stomachs of wolves and wolverines did not vary among seasons, the proportion of muskoxen in their stomachs was higher in winter (14.5%, 95% CI [1.0:28.1%]) than in fall (intercept, Table A4a in Appendix A), and this partly supported prediction 5. In partial support to prediction 6, the correlation between the proportion of caribou in the stomachs of both predators and the tEd to the coastline was positive and approaching significance (20.1%, 95% CI [-3.4:43.7%], *p*=0.1 and 24.9%, CI 95% [-3.2:53.1%], p=0.08, in wolves and wolverines, respectively) (Table A4b in Appendix A). Conversely, the proportion of muskoxen in stomachs of wolves was negatively correlated to the tEd to the coastline (-21.4%, 95% CI [-37.8:-5.1%]). Supporting prediction 7, the proportion of caribou in the stomachs of both predators combined was the lowest in the most unproductive regions North Barren and Barren Island (-36.5%, 95% CI [-60.6:-12.4%] and -78.7%, 95% CI [-105.8:-51.5%], respectively). The proportion of caribou in the stomach of both predators was also lower (near significant) in the most productive region North Western Transition (-22.8%, 95% CI [-46.6:1.1%], *p*=0.08), than in the South Eastern Transition (intercept, Table A4a in Appendix A). On the other hand, the proportion of muskoxen in the stomach of both predators was the highest in the unproductive Barren Island region (78.2%, 95% CI [56.8:99.6%]). Supporting predictions 8 and 9, the proportion of caribou in the stomachs of wolves was negatively correlated to the tEd to migratory caribou (-41.3%, 95% CI [-65.9:-16.6%]) and to the tEd to tundra caribou (-25.1%, 95% CI [-45.9:-4.3%])(Table A4b in Appendix A). On the other hand, the proportion of muskoxen in the stomach of wolves was positively correlated to the tEd to migratory caribou (17.9%, 95% CI [0.7:35.0%]) and to the tEd to tundra caribou (19.1%, 95% CI [3.8:34.5%]) (Table A4b in Appendix A).

Finally, we found in the stomachs of both predators prey remains from lemmings *sp.*, Arctic fox *Vulpes lagopus*, Arctic hare *Lepus arcticus*, rock ptarmigan *Lagopus muta*, Arctic ground squirrel *Spermophyllus Parryii*, salmonid fishes, and seal *phoca* sp. Yet these were occasional and no pattern emerged when comparing among regions, seasons or other independent variables. However, the presence of lemmings in the stomach of both predators combined was higher in the unproductive North Barren region (21%, 95% CI [9:33%]) than in the South Eastern Transition region (intercept).

1.6 Discussion

Ecological opportunity has been associated with niche expansion and individual specialization in most recent studies (Layman *et al.* 2007b; Darimont *et al.* 2009; Kernaléguen *et al.* 2015; Yurkowski *et al.* 2016) but the applicability of the ecological opportunity framework to a multi-species and large-scale terrestrial setting remains untested. We integrated a unique set of trophic data allowing niche comparison between two sympatric and elusive large terrestrial predators, thus yielding an unprecedented evaluation of resource use at a large continental scale (ca. 900,000 km^2) and across seasons. Our results suggest that wolves and wolverines use allochthonous marine resources in addition to local tundra prey during the cold months, whereas they use tundra and allochthonous migratory resources in summer. However, the use of resource diversity by these predators varied with the availability of the main prey (caribou) and the biological constraints specific to species and sex (wolverine), reproductive status (wolves), and individuality (both species). These results provide rare empirical support, for top terrestrial predators (but see Darimont *et al.* 2009), to the long-standing suggestion that ecological opportunity can generate niche variation. Niche variation mostly arose through among-individual niche variation, proving some evidence to the niche variation hypothesis (Van Valen 1965). This had not yet been demonstrated in terrestrial carnivores (Meiri *et al.* 2005; Svanback & Bolnick 2007b).

1.6.1 Biological constraints

As anticipated, our results suggest that species-specific differences in foraging mode and behaviour may determine the capacity of predators to exploit resource diversity (prediction 1 in Table 1.1). Except in the North Western Transition region, wolves made little use of allochthonous marine resources, yet a clear use of alternative ungulate prey (muskoxen), when and where caribou were scarcer (see Results and Table A4 in Appendix A). This led to the lowest isotopic niche variation observed in wolves, as caribou and muskoxen belong to the same functional group. Except in the very northern part of their distribution (Mech 2007; Dalerum *et al.* 2017), continental wolves are typically tied to ungulates (Peterson & Ciucci 2003), with some populations even showing migratory adaptations in the southern Arctic (Walton *et al.* 2001; Musiani *et al.* 2007). In this group hunter, hunting large prey was likely more profitable than searching for marine resources, which could partly explain why wolves were less inclined than wolverines to exploit this food base. Where caribou and muskoxen were scarce (North Barren region, Figure 1.1), the use by wolves of various tundra dwelling prey such as Arctic hares, Arctic foxes, and lemmings may explain the observed high isotopic niche variation; isotopic niche width was 75% wider in wolves from the North Barren region than in those from the South Eastern Transition region, despite their apparent little use of marine resources. Yet the isotopic signatures (mostly $\delta^{15}N$) of wolves in the North Barren region were generally higher than those of small herbivores (but well aligned with the signatures of Arctic foxes; Figure 1.1). It is nonetheless possible that the signatures of herbivores were the highest in winter (from food shortage and fasting, see Drucker *et al.* 2001; Vanderklift & Ponsard 2003), what we could not measure in this study (see Table A2 in Appendix A). The use of tundra dwelling prey by wolves has also been observed in other Arctic contexts (Marquard-Petersen 1998; Mech 2005, 2007; Dalerum *et al.* 2017).

Wolverines were more prone to use marine resources when caribou were scarce (see North Barren and Barren Island regions, Figure 1.1), even when muskoxen were available (see the Barren Island region, Figure 1.1). In the most unproductive regions of our study area, searching for caribou was likely a considerable effort and wolverines increased profitability of the habitat by adding marine resources, which can be abundant and easy to access on the sea ice during winter/spring. However, phenotypic variations in the ability to detect, capture, handle or digest marine resources (reviewed in Araujo *et al.* 2011) likely existed in wolverines as only a fraction of the individuals switched diet towards these resources. Such a switch may underlie the increased AIV values observed in wolverines. Male wolverines likely included more marine resources in their diet than did females, and we suggest that this difference was linked to the larger size of males (Copeland & Jackson 2003) (prediction 2 in Table 1.1). Alternatively, males may exhibit different physiological requirements than females as they spend most of the winter and spring roaming the tundra while females are denning for reproduction (Magoun 1985; Persson 2005). The use of small herbivores during denning in winter likely determined niche variation in female wolverine (see also Magoun 1985; Landa 1997) (prediction 3 in Table 1.1). Finally, wolf niche variation did not differ among age classes since young dispersing adults and old solitary adults used resources in a similar way as pack wolves (prediction 4 in Table 1.1). This result can be explained by the capacity of lone individuals to capture ungulates or by their access to ungulate carcasses. However, some young adults do remain within packs as subordinates (Mech & Boitani 2003), and these individuals could not be distinguished from solitary young adults. Determining the social status of young and old adults is needed to further examine our prediction.

1.6.2 Ecological opportunities *vs.* main prey availability

Season and large-scale habitat heterogeneity were the two main determinants of resource diversity and main prey availability in our study area (predictions 5 to 8 in Table 1.1). A diversity of local resources was available all year-long along the coastline. Yet it was likely maximal during the cold period when the sea ice provided access to live seals, leftovers from Inuit hunters and polar bears (Lai *et al.* 2015), and potentially whale carrion. In the vicinity of the transition zone between the taiga and the tundra (South Eastern Transition and North Western Transition regions, Figure 1.1), we identified the highest resource diversity in terms of the number of prey species. Resource diversity was also elevated in summer with the continent-wide pulse of tundra dwelling and allochthonous migratory resources. Yet tundra dwelling resources (lemmings, hares, Arctic foxes, and likely hoarded waterfowl eggs) were available throughout the year. Wolverines, and also wolves to a lesser extent, generally showed the greatest niche variation and among-individual niche variation when and where they had access to allochthonous marine resources and the caribou was scarce (predictions 5 and 7 in Table 1.1). This trend was well demonstrated in local-scale models showing a progressive decrease in the proportion of caribou in stomachs (both predators), increase in $\delta^{15}N$ (wolverines), and increase in among-individual niche variation (both predators) along the inland-coastline gradient (predictions 6 and 8 in Table 1.1, also see Table 1.3, Figure 1.1, and Table A4 in Appendix A). These results parallel those reported by Darimont et al. (2009), where extensive niche variation and individual specialization was observed in coastal wolves with access to allochthonous subsidies (pacific salmon *Oncorhynchus* sp.) but decreased access to ungulate prey (mule deer *Odocoileus hemionus*). Contrasting with this study, however, our large-scale models (prediction 7 in table 1.1) showed that ca. 28% and 13% of wolves (n=30) and wolverines (n=22) from the North Western Transition region, respectively, used marine resources ($\delta^{15}N$ signatures were > 8‰, *i.e.* above the 95% CI $\delta^{15}N$ signatures Arctic foxes (Table A2 in Appendix A), which represent the second-highest winter trophic level after marine resources). This happens even when the proportion of caribou (supplemented by muskoxen) in stomach was elevated (see results section and Table A4 in Appendix A). We can potentially explain these results by the interplay between competition for main prey (see discussion on intra/inter specific competition below) and the greater access or abundance of marine resources in this particular region. The same factors may explain why wolverines from the Barren Island region used a relatively high amount of marine resources (ca. 35% of individuals, n=18, showed $\delta^{15}N$ signatures greater than 8‰) despite the elevated proportion of muskoxen found in stomachs (see Results section and Table A4 in Appendix A). Empirical data on the use of marine resources in Arctic wolves and wolverines are rare in the literature (but see Rausch & Pearson (1972); Parker & Luttich (1986); Mulders (2001)) but well acknowledged by Inuit hunters (pers. comm.). Use of marine resources by terrestrial carnivores is nonetheless widespread in the wild (Adams *et al.* 2010; Killengreen *et al.* 2011, reviewed in Rose & Polis 1998).

On the other hand, the analysis of niche variation during the summer pulse of resource diversity provided some evidence that both predator species can depart from their main prey to exploit tundra dwelling and allochthonous migratory resources (prediction 5 in Table 1.1) (see Table 1.2, Figure 1.1). Despite the fact that caribou is abundant in our study area during summer (Nagy *et al.* 2011), telemetry studies (Walton *et al.* 2001; Musiani *et al.* 2007) suggest that tundra wolves are bounded to the den area and may have limited access to high-density patches of caribou during the summer pup-rearing period. Local observers (L'Herault et al., in prep) also reported that wolves (and wolverines to a certain extent) have a lower capture rate of caribou during summer given the absence of snow cover (see also Paquet *et al.* 2010; Pozzanghera *et al.* 2016). Migratory birds, eggs and tundra dwelling prey can thus represent an easy source of food for Arctic wolves and wolverines as documented elsewhere (Marquard-Petersen 1998; Samelius *et al.* 2002; Wiebe *et al.* 2009; Dalerum *et al.* 2017). Interestingly, the use of this resource diversity by terrestrial predators did not lead to niche expansion (compared to the early winter intercept) nor to individual specialization. Kernaléguen *et al.* (2015) reported similar observations in subantarctic fur seals, whose isotopic niche width did not vary between the pup-rearing period (when they face a low resource diversity) and the non-breeding period (when they face a high resource diversity) despite an apparent increase in intra-individual niche width. Quantifying within-individual niche variation in summer would be important to determine the extent to which wolves and wolverines uniformly switch, or not, to alternative pulsed resources during that period (see Newsome *et al.* 2012).

1.6.3 The influence of competition on prey availability

Intra-specific competition may be a key determinant of niche variation and individual specialization as it influences the availability of the main prey (Svanback & Bolnick 2007b, reviewed in Araujo *et al.* 2011). Although we could not quantify predator density (a proxy for intraspecific competition), our large-scale analysis suggests an interaction between intraspecific competition and ecological opportunity, as documented elsewhere (Darimont *et al.* 2009; Yurkowski *et al.* 2016). Indeed the carrying capacity of the barren land, which largely covers the northernmost regions of our study area (Kivalliq Ecological Land Classification Map Atlas 2015), is lower than that of the transitional zone between the taiga and tundra and can thus sustain a lower number of large herbivores. This opens up the possibility of a positive south-north competition gradient in predators. In addition, intra-and interspecific variations may also contribute to niche diversification in North Western Transition where wolves showed niche expansion through among-individual variation. According to our carcass records, the number of wolverines reported to the program in the North Western Transition region was about twice the number reported in any other region of our study area, and high densities were also reported in this region (Mulders 2001 and local observers). Interestingly, local observers reported on wolverine capacity to outcompete wolf packs on feeding sites and potentially restrict their access to resources (L’Hérault et al., in prep). Whether or not wolverine (and wolf) populations are denser in this region, and whether wolverines can compete with wolves for ungulates, still remains to be tested.

1.6.4 Trophic subsidization of terrestrial top predators

Several studies suggest that food subsidies increase the density of terrestrial carnivores (Rose & Polis 1998; Roth 2003; Adams *et al.* 2010; Giroux *et al.* 2012), with potential effects on ecosystem functions (Leroux & Loreau 2008). In our study system, the subsidization of wolves and wolverines by marine and migratory tundra prey was likely, particularly in the northernmost study areas where wolverines used marine resources. Allochthonous resources were used in winter and in the summer breeding season, two energy demanding periods of the predators’ annual life cycle, which may have increased survival or reproduction. Persson et al. (2005) reported effects of winter food availability on reproduction effort in female wolverines. Comparing the reproductive performance of wolverines using marine and terrestrial resources would help to evaluate the demographic impact of subsidies on this species.

1.6.5 Methods caveats

The amount of isotopic variation among prey species does not necessarily correspond to the actual prey diversity available to consumers (Newsome et al. 2015). Prey isotopic signatures are mostly driven by the isotopic composition of primary producers (Tieszen *et al.* 1983a; Gannes *et al.* 1998) and the trophic level of the prey (Deniro & Epstein 1981; Matthews & Mazumder 2008). In our study area, variations in $\delta^{13}C$ and $\delta^{15}N$ were thus greater between tundra dwelling herbivores (typically showing low $\delta^{13}C$ and $\delta^{15}N$) and marine predators (typically showing high $\delta^{13}C$ and $\delta^{15}N$) than among tundra or marine species belonging to the same functional group (see Table A2 in Appendix A). Because we measured the highest isotopic variation in predators (wolverines) from the northernmost regions of our study area, one could argue that this result was generated by the greater isotopic variation among prey from this particular area than from other regions, rather than to actual predator dietary response. By combining stable isotope analysis to stomach content analysis, we could nonetheless connect isotopic niche variation to actual prey diversity used by predators. Specifically, predators from the northernmost regions had ingested the lowest proportion of caribou (and a diversity of non-ungulates prey) among all regions of our study area, thus suggesting the use of alternate resources (see Results and Table A4 in Appendix A).

In addition, there was no indication that the isotopic variation among prey was higher in the northernmost regions. Except for caribou and muskoxen, the tundra prey assemblages were virtually the same throughout our study area and we detected no South to North differences in prey isotopic variations (Table A2 in Appendix A). All regions provided equivalent access to the marine ecosystem, yet the isotopic signatures of ringed seals, potentially the main marine resources used by terrestrial predators in our system, are known to vary across latitude (by ca.0.5‰ and 1.5‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, Yurkowski *et al.* 2016). Whether this bias applies to our study system is unknown.

Finally, intra-population variability in isotopic discrimination of $\delta^{13}C$ and $\delta^{15}N$ is, too, a potential limitation to the use of stable isotopes analysis in the wild (Lecomte *et al.* 2011). This bias was likely minimal in our study, except for summer diet. Details are available in the Correction methods section of Supporting Information).

1.6.6 Conclusion

A better understanding of the intra-population niche variation and its underlying causes is crucial for population, community, and evolutionary ecology (Hughes *et al.* 2008; Bolnick *et al.* 2011; Araujo *et al.* 2011). Our study suggests that ecological opportunity can determine niche variation in large terrestrial predators. Yet unlike other generalist predators studied (L'Hérault *et al.* 2013; Newsome *et al.* 2015; Horswill *et al.* 2016), the trophic niche of wolves and wolverines varied very little when resources were diverse but the main prey were available. Our results also support the few available studies contrasting niche variation in sympatric long-ranging predators (Jaeger *et al.* 2010; Kernaléguen *et al.* 2015; Yurkowski *et al.* 2016). In our study, wolverines exploited marine resources and showed greater among-individual niche variation than wolves. This was likely attributed to their more flexible foraging mode. We suggest that individual specialization on marine resources may impact predator density in our study area, with trophic subsidization potentially affecting predator-prey relations (Leroux & Loreau 2008; Legagneux *et al.* 2014). Finally, we recommend accounting for and protecting niche diversity in the management of large mammalian predators, including during predator control practices.

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Research permit

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CHAPITRE II

DISCRIMINATION FACTORS OF CARBON AND NITROGEN STABLE ISOTOPES FROM DIET TO HAIR IN CAPTIVE LARGE ARCTIC CARNIVORES OF CONSERVATION CONCERN

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Manuscrit soumis à *Rapid Communications in Mass Spectrometry*

Contributions des auteurs (initiales)
Mise en place du design de l'étude (VLH, NL, MHT)
Récolte des données (VLH)
Analyse des données (VLH, MHT)
Interprétation des résultats (VLH, NL)
Rédaction du manuscrit (VLH)
Commentaires et correction du manuscrit (NL, MHT, DB)
Financement (DB)

2.1 Résumé

Les isotopes stables sont communément utilisés en écologie afin de reconstruire le régime alimentaire, déterminer les interactions trophiques ou encore étudier les flux d'énergie entre les écosystèmes. Ces inférences écologiques reposent sur l'idée générale que les animaux sont, isotopiquement, ce qu'ils mangent, mis à part une différence prévisible du ratio isotopique entre l'animal et sa nourriture (δ_{animal}-$\delta_{nourriture}$), nommée facteur de fractionnement. La mesure précise du fractionnement isotopique nourriture-consommateur en conditions contrôlées est primordiale pour une utilisation robuste de la technique des isotopes stables en nature. Cette mesure a des implications importantes pour les approches de recherche non invasives.

Nous avons déterminé le fractionnement des signatures isotopiques du carbone et de l'azote (δ^{13}C et δ^{15}N), les deux signatures les plus communément utilisées en écologie, dans les poils de garde de quatre grands prédateurs de l'Arctique, le loup gris *Canis lupus* (n=7), le carcajou *Gulo gulo* (n=2), l'ours grizzly *Ursus arctos* (n=2) et l'ours blanc *Ursus maritimus* (n=3). Tous les individus étaient gardés en captivité pour contrôler la nourriture administrée au cours d'une expérience qui dura 105 jours. La nourriture était constituée de mélanges de différentes sources afin de refléter la diversité de leurs proies. La composition isotopique (δ^{13}C et δ^{15}N) et la quantité (g) des sources de nourriture administrées à chaque individu étaient notées chaque semaine pour déterminer la signature moyenne du régime alimentaire global. Tous les individus d'une espèce donnée avaient le même régime alimentaire, sauf pour l'ours blanc pour lequel le régime était ajusté au sexe et au stade de développement.

Le fractionnement isotopique nourriture-poil variait selon l'âge et l'espèce, passant de 1,88 ±0,69‰ à 3,2 ±0,69‰ (moyenne 2,45 ±0,40‰, CI 95% [2,22: 2,68‰]) pour δ^{13}C et de 1,58 ±0,17‰ à 3,81 ±0,22‰ (moyenne 3,03 ±0,70‰, CI 95% [2,63: 3,43‰]) pour δ^{15}N. Le fractionnement moyen de δ^{13}C des loups adultes (2,03 ±0,7‰) était moins élevé que celui des jeunes loups (2,60 ±0.8‰, CI 95% [1,56:3,64‰]) et de n'importe quelle autre espèce (moyenne combinée de 2,59

±0.28‰, CI 95% [2,24: 2,94‰]), bien que similaire à celui du carcajou (2,12 ±0,23‰). Les taux de fractionnement moyens de δ^{15}N des loups (jeunes: 3,51 ±0,34‰, adultes: 3,68 ±0,28‰) étaient plus grands que ceux des autres espèces (moyenne combinée de 2,50 ±0,58‰, CI 95% [1,96: 3,04‰]). Chez l'ours blanc, le fractionnement moyen de δ^{15}N de la femelle adulte (1,58 ±0,17‰) différait grandement de celui de ses deux jeunes (M: 2,74 ±0,21‰; F: 2,90 ±0,21‰), mais ce n'était pas le cas du fractionnement de δ^{13}C. Ces derniers résultats sont typiques de la période d'allaitement.

Les taux de fractionnement de δ^{13}C et δ^{15}N calculés dans cette étude peuvent être utilisés dans les études écologiques menées auprès d'animaux sauvages. Cependant, tout comme l'ont fait les autres études de fractionnement menées en conditions contrôlées, nous recommandons d'utiliser ces valeurs avec précaution lorsque la structure des populations est hétérogène.

Mots-clés: Fractionnement isotopique, isotopes de carbone et d'azote, grands prédateurs, Arctique

2.2 Abstract

Stable isotopes are widely used in ecology to reconstruct diet, delineate trophic interactions, and determine energy pathways. Such ecological inferences are based on the general idea that animals are, isotopically, what they eat but with a predictable difference, which is the difference in the isotopic ratio between a consumer and its diet ($\delta_{consumer}$- δ_{diet}), coined as the discrimination factor. Providing correct estimates of diet-consumer isotopic discrimination in controlled conditions is key for a robust application of the stable isotopes technique in the wild, with implications for non-invasive research approaches.

Here we investigated isotopic discrimination of carbon and nitrogen signatures ($\delta^{13}C$ and $\delta^{15}N$), the two most common isotopic signatures used in ecology, in guard hairs of four top predators of the Arctic; the gray wolf *Canis lupus* (n=7), the wolverine *Gulo gulo* (n=2), the grizzly bear *Ursus arctos* (n=2), and the polar bear *Ursus maritimus* (n=3). All individuals were captive to control their diet and, during a three-month trial, we used a mixed diet reflecting their wide range of prey. Isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) and mass (g) of diet items were monitored weekly for each individual to determine their Total Diet Average signatures. All individuals of a given species had a similar Total Diet Average signature in a given week, except polar bears for which diet was adjusted according to sex and development stage.

Diet-hair isotopic discrimination varied according to age and species, ranging from 1.88 ±0.69‰ to 3.2 ±0.69‰ (average 2.45 ±0.40‰, CI 95% [2.22: 2.68‰])) for $\delta^{13}C$ and from 1.58 ±0.17‰ to 3.81 ±0.22‰ (average 3.03 ±0.70‰, CI 95% [2.63: 3.43‰]) for $\delta^{15}N$. Adult wolves discrimination average for $\delta^{13}C$ (2.03 ±0.7‰) was lower than that of young wolves (2.60 ±0.8‰, CI 95% [1.56:3.64‰]) and any other species (combined average of 2.59 ±0.28‰, CI 95% [2.24: 2.94‰]) but equivalent to wolverine (2.12 ±0.23‰). Wolves discrimination averages for $\delta^{15}N$ (juveniles: 3.51 ±0.34‰, adults: 3.68 ±0.28‰) were higher than those of any other species (combined average of 2.50 ±0.58‰, CI 95% [1.96: 3.04‰]). In polar bears, the adult female

(1.58 ±0.17‰) contrasted markedly with her two cubs (M: 2.74 ±0.21‰; F: 2.90 ±0.21‰) in discrimination for δ^{15}N, but not for δ^{13}C, in agreement with her lactating status.

The discrimination factors for δ^{13}C and δ^{15}N calculated in this study can be used in ecological studies dealing with free-ranging animals. As in other controlled discrimination studies, we recommend caution for applying our discrimination factors when population structure is heterogeneous.

Key words: Isotopic discrimination, carbon and nitrogen isotopes, top predators, Arctic

2.3 Introduction

Stable isotopes are widely used in ecology to reconstruct diet, delineate trophic interactions, and determine energy pathways (Peterson & Fry 1987; Gannes *et al.* 1998; Crawford *et al.* 2008). Such ecological inferences are based on the general idea that animals are, isotopically, what they eat but with a predictable difference, *i.e.* the difference in the isotopic ratio between a consumer and its diet, which is coined as the discrimination factor. Prey isotopic signatures are mostly driven by the isotopic composition of primary producers (Tieszen *et al.* 1983a; Gannes *et al.* 1998) and the trophic level of the prey (Deniro & Epstein 1981; Matthews & Mazumder 2008). Predators have higher nitrogen isotopic signatures ($\delta^{15}N$) than their prey, and distinct carbon isotopic signatures ($\delta^{13}C$), due to metabolic processes involved in the digestion and assimilation of the nutrients. Correct estimates of discrimination are a prerequisite to describe trophic interactions and diet reconstruction in a robust manner since models are sensitive to the uncertainty in discrimination estimates (Lecomte et al. 2011). For example, increasing uncertainty in diet reconstruction models might overestimate or underestimate the contribution of a given prey species to the diet of predators. Several reviews (*e.g.* Martinez del Rio *et al.* 2009; Caut, Angulo & Courchamp 2009) and experimental studies (*e.g.* Caut *et al.* 2008; Robbins, Felicetti & Florin 2010; Lecomte *et al.* 2011) highlighted the need for more validation with experimental studies under controlled conditions, and the importance of species-based estimates.

Past ecological studies conducted on wild species typically relied on ‘borrowing’ discrimination factors experimentally derived from related species. For instance, farmed fox discrimination factors (Roth & Hobson 2000b) are commonly used in other wild carnivores (Urton & Hobson 2005; Samelius *et al.* 2007; Edwards *et al.* 2011). Recent experimental studies have produced robust species and tissue-specific discrimination estimates (Lecomte *et al.* 2011; Parng, Crumpacker & Kurle 2014;

Montanari & Amato 2015; Rode *et al.* 2016) enabling more accurate modelling in field studies (e.g. Giroux *et al.* 2012; Moss, Alldredge & Pauli 2016). However, species and tissue-specific discrimination factors are still lacking for many species with conservation concerns such as large carnivores (but see recent studies of Montanari and Amato (2015) and Parng et al. (2014)). Moreover, intra-population variation in isotopic discrimination among consumers' age classes, particularly for carbon discrimination, is still poorly understood (Lecomte *et al.* 2011).

In the Canadian Arctic, wolves, wolverines, grizzly bears, and polar bears are large carnivores of conservation importance. These top-predators can feed on various prey and all play important ecological roles, such as regulating prey populations (Dale *et al.* 1994; Mulders 2001; Thiemann, Iverson & Stirling 2008; Edwards *et al.* 2011; Rockwell, Gormezano & Koons 2011). The wolverine, the grizzly bear, and the polar bear are listed as species of special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2013, 2014). Despite their ecological importance and status, field studies on carnivore trophic interactions are still very scarce, largely because of the research challenges associated with their low density and wide-ranging behaviour. However, several indirect monitoring methods, such as hair snagging and carcass collection, are now increasingly used by Arctic biologists to monitor population size and structure (Mulders *et al.* 2007; Dumond *et al.* 2009), health and reproductive status (Lecomte, unpublished data), and trophic interactions (L'Hérault et al., in prep.). Taking advantage of non-invasive techniques, particularly the use of hair tissue for stable isotopes analyses, could provide a cost-effective avenue for inferring trophic interactions and resource use in these sensitive species. In this context, quantifying species-specific diet-consumer isotopic discrimination for hair tissue is essential.

We ran an experiment with captive animals to determine diet-hair discrimination estimates of carbon and nitrogen stable isotopes in wolverine, wolf, grizzly bear, and polar bear. Diet items fed to individuals matched the isotopic range of diet items potentially encountered in the wild. Following the recommendations of Lecomte et al. (2011), we explored variation in isotopic discrimination among age classes when allowed by sample sizes.

2.4 *Material and methods*

2.4.1 Hair and diet samples

The wolverines (n=2: F,M adults), wolves (n=7: F,M adults; 3F,2M juveniles), grizzly bears (n=2: F,M adults), and polar bears (n=3: F adult; F,M juveniles) lived at the Zoo Sauvage de St-Félicien (48°68' N, 72°51' W), located in the boreal ecosystem of Quebec, Canada. The experiment ran from August 1, 2011, to mid-November 2011, for a total duration of ca. 105 days. The control diet fed to animals during that period was specific to each species, following veterinarian standards developed by the Canadian Zoos and Aquarium Association (CAZA). The diet incorporated a similar range of isotopic composition to natural food. In wolverines, a CAZA meat mix for terrestrial carnivores (fresh horse meat, liver, vegetal oil, vitamins, and dry supplement from commercial mix for foxes) was provided (Table 2.1, Table B2; Appendix B). Polar bears ate a CAZA meat mix for marine carnivores (fresh horse meat, liver, fish oil, and vitamins), fresh herring, and dry supplements from commercial dog food (Table 2.1, Table B2; Appendix B). In addition, polar bear cubs, which were in their weaning phase, fed from maternal milk at least once a day. In grizzly bears, a mix of fresh herring, vegetal sources (bread, fresh apples and fresh carrots) and dry supplements from commercial dog food were provided (Table 2.1, Table B1; Appendix B). Finally, wolves consumed dry commercial dog food with occasional fresh horse meat (<1% diet). A similar proportion of each food item was provided to all individuals within a given species, except for polar bears where the proportion of each diet item was adjusted to age and sex based on veterinarian standards. The mass of diet items provided to animals was monitored weekly and 10 g of each diet item were stored at -20°C for subsequent analyses of $\delta^{13}C$ and $\delta^{15}N$.

Table 2.1 Contribution (% total mass) of different food items to large carnivores' diet

Carnivores	M#1[a]	M#2[a]	M#3[a]	M#4[a]	CAZA-tc[b]	CAZA-mc[b]	Horse meat	Herring[c]	Bread	Apple	Carrot
Grizzly	4.5	3.4	26.2	21.3	0	0	0	22.4	5.3	13.2	3.7
Wolf	11.6	9.7	46.5	32.0	0	0	0.3	0	0	0	0
Wolverine	0	0	0	0	100	0	0	0	0	0	0
Polar bear F Ad.	4.1	3.1	18.9	11.6	0	14.3	14.4	33.5	0	0	0
Polar bear F Juv.	3.0	2.7	18.9	11.6	0	18.4	20.9	24.3	0	0	0
Polar bear M Juv.	2.8	2.7	19.9	15.6	0	17.0	19.4	22.5	0	0	0

a Bulk commercial dog diet mixed with various ingredients. See Table S1 for detailed description of diet content.

b Canadian Association of Zoos and Aquarium's food for terrestrial carnivores (tc) and marine carnivores (mc). See Table S2

c Herring provided to polar bears were supplemented with fish oil

Guard hairs of wolves and wolverines were pulled out of animals' neck using tweezers during routine captures performed at the end of the experiment. Guard hair samples were collected opportunistically on grizzly bears and polar bears using snag wires deployed near the feeding area in the captive habitat. Underfur samples were also collected on animals as back-up tissue and for comparison purpose with guard hair. Hair samples were labelled and stored at -20^{o}C until lab analysis.

2.4.2 Stable isotope analysis (SIA)

Diet item samples were rinsed in ethanol 70% and cut into small pieces, put to -80°C and desiccated by vacuum lyophilization, and reduced into powder using a grindmill (Cryomill, Retsch ©). Diet sources (0.4 mg for animals and 1.2 mg for vegetal materials) were loaded in tin cups (precision ± 0.01 mg) for SIA. Guard hairs and underfur samples were manually brushed and rinsed in a 2:1 chloroform/methanol solution to remove dirt and lipid traces (Bligh & Dyer 1959). We subsampled 40 mm sections from the base of each guard hair to capture the specific 3-month trial during which the controlled diet was fed to animals (a conservative estimate assuming a consistent late summer/autumn growth rate of 0.63 mm/d (McLaren, Crawshaw & Patterson 2015), for a total of ca. 60 mm of total growth during the 105 days of the experiment). Underfur tissue was not subsampled because this tissue typically starts to grow in late summer (Ling 1970), after our experiment had started. Guard hair (40 mm sections) and whole underfur tissue were ground to fine powder using a grindmill at -196°C (Cryomill, Retsch ©). Hair powder (0.4 mg) was loaded in tin capsules for SIA.

Diet and hair samples were combusted in either a CarloErba NC2500 or a Costech 4010 elemental analyzer connected via continuous flow to a Finnigan Mat Delta Plus isotope-ratio mass spectrometer at the Stable Isotope In Nature Laboratory (SINLAB:

New Brunswick, Canada). Isotope ratios are represented as permil (‰) ratios referenced against Peedee belemnite carbonate (PDB) for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. $\delta^{13}C = [(^{13}C/^{12}C_{sample})/(^{13}C/^{12}C_{PDB})-1] X 1000$, $\delta^{15}N = [(^{15}N/^{14}N_{sample})/(^{15}N/^{14}N_{AIR})-1] X 1000$), respectively. Precision across spectrometer runs was measured at SINLAB using an internal smallmouth bass muscle standard ($\delta^{13}C$ = -23.39 ± 0.11‰ SD, $\delta^{15}N$ = 12.28 ± 0.12‰ SD, n =12). Finally, accuracy was estimated at SINLAB using a commercially available standard (Nicotinamide, Elemental Microanalysis Ltd.), where $\delta^{13}C$ = -34.51‰ ± 0.13‰ and $\delta^{15}N$ = -1.72 ± 0.08‰ SD (n = 14) as target ratios.

2.4.3 Data Analyses

Prior to calculating discrimination factors, we corrected the carbon isotopic signature of diet items for lipid content because lipid-rich tissues are typically depleted in ^{13}C, thus showing lower $\delta^{13}C$ values than lipid-free tissues (Deniro & Epstein 1978; Tieszen *et al.* 1983b). Typical procedures to account for the lipid-induced bias in $\delta^{13}C$ involve chemically removing lipids from samples, or applying mathematical normalization to standardize $\delta^{13}C$ values among diet types with various lipid contents (Sweeting, Polunin & Jennings 2006; Post *et al.* 2007; Logan *et al.* 2008). We used the latter method following Post et al. (2007). We first determined the % of lipids in diet items (Table S3, Supporting Information) and we calculated lipid correction factors ($\Delta\delta^{13}C$) using equation 5 in Post et al. (2007) ($\Delta\delta^{13}C$=-0.81+0.11*% lipid) for animal food sources, and equation 7 ($\Delta\delta^{13}C$ = 0.20 + 0.07 * % lipid) for vegetal food sources. We also used equation 13 in Post et al. (2007) ($\Delta\delta^{13}C$=-5.83+0.14*% carbon) for fresh vegetable items (bread, apple, carrot) as the % lipid was not available. For diet items with a mixed content of animal and vegetal sources, such as dry commercial dog food mix, $\Delta\delta^{13}C$ was calculated as the average of $\Delta\delta^{13}C_{Animal}$ and $\Delta\delta^{13}C_{Vegetal}$ (Table B3, Appendix B). $\Delta\delta^{13}C$ was then applied to bulk $\delta^{13}C$ items to obtain $\delta^{13}C_{LN}$ (lipid normalized carbon signature, Table B3, Appendix B). Given their low lipid content (Post et al., 2007), no correction was needed for guard hairs and underfur.

We calculated the discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) by subtracting the Total Diet Average signature ($\delta X_{\text{Total Diet Average}}$) to the isotopic signature of individual animal hair ($\delta X_{\text{consumer}}$): ΔX (±SD) = $\delta X_{\text{consumer}} - \delta X_{\text{Total Diet Average}}$ (± SD). Total Diet Average signature (±SD) was calculated as the weighted sum of each diet item's isotopic signature, as follows: $\delta X_{\text{Total Diet Average}}$ (±SD) = $\{(\delta X_{\text{item 1}} * \%_{\text{item 1}}) + (\delta X_{\text{item 2}} * \%_{\text{item 2}}) + \ldots\}$ (Table B4, Appendix B). $\delta X_{\text{consumer}}$ was based on guard hairs or on underfur tissue when the former was not available. To make sure that this method did not introduce any bias in the calculation of discrimination factors, we tested for statistical differences in $\delta^{13}C$ and $\delta^{15}N$ among guard hair and underfur tissues in linear mixed models using individual ID as random effect. We also tested for fixed effects using species, age, and sex. Results of the linear mixed effect models indicated how to cluster the isotopic data to calculate discrimination factors (with their SD) valid for groups of consumers with more than one data point. We ran statistical analyses in R 3.1.1 (R Development Team 2008).

2.5 *Results*

2.5.1 Carbon and nitrogen stable isotopes in fur

Isotopic signatures of individuals' fur ranged from -17.36 to -20.22‰ (-18.48 ± 0.98‰, CI 95% [-19.04: -17.91‰]), and from 7.01 to 9.48‰ (7.89 ± 0.73‰, CI 95% [7.47: 8.31‰]), for $\delta^{13}C$ and $\delta^{15}N$, respectively (Table 2). Results from the linear mixed effect model showed significant differences in $\delta^{13}C$ among species (wolves and wolverines showed average value 1.08‰ higher and 1.03‰ lower than grizzly bears) and age classes (juveniles showed average value 0.40‰ higher than adults) (Table B5, Appendix B). No differences were found between guard hair and underfur, which justifies the use of both guard hairs (most of the time) and underfur in the calculation of the discrimination factors (Table 2.2). Sex had no significant effect on isotopic signatures. We found significant differences in δ^{15}N among species only (polar bears showed 1.42‰ higher average values than grizzly bears) (Table B5, Appendix B). δ^{13}C was higher in juvenile wolves (-17.54 ±0.48‰) than in any other group (excluding polar bears that could not be treated as a group). δ^{15}N was higher in the wolverine group (7.91 ±0.14‰) than in any other group (excluding polar bears).

2.5.2 Carbon and nitrogen stable isotopes in diet items

The δ^{13}C lipid normalization factors calculated on diet items ranged from -0.28‰ to 3.47‰ (0.64 ±0.77‰, CI 95% [0.49: 0.79‰]) (Table B3, Appendix B). CAZA meat for marine carnivores was the diet item for which the lipid normalization factors were the highest (2.09 ±0.5‰, CI 95% [1.82: 2.36‰]), followed by the dry commercial dog food (0.68 ±0.24‰, CI 95% [0.56: 0.80‰]), bread (0.63 ±0.15‰, CI 95% [0.52:0.74‰]), CAZA meat for terrestrial carnivores (fixed at 0.51‰), horse and herring (0.35 ±0.55‰, CI 95% [0.12: 0.58‰]), and vegetal sources (-0.12 ±0.08‰, CI 95% [-0.16: -0.08]) (Table B3, Appendix B). In terms of the Total Average Diet, differences between $\delta^{13}C_{\text{Lipid Normalized}}$ and $\delta^{13}C_{\text{Bulk}}$ ranged from 0.51‰ (wolverines) to 0.85‰ (polar bear cubs) (Table 2.2).

Lipid normalized carbon signatures and nitrogen signatures of diet items were summed up according to their respective proportion in the diet to calculate the Total Diet Average isotopic signatures. Table 2.2 shows Total Diet Average $\delta^{13}C_{\text{Bulk}}$ and Total Diet Average $\delta^{13}C_{\text{Lipid Normalized}}$ values, as well as δ^{15}N (±SD) of diets used in the experiment. Total Diet Average of wolves (-20.14 ±0.69‰) and the adult female polar bear (7.19 ±0.19‰) had the highest $\delta^{13}C_{\text{Lipid Normalized}}$ and $\delta^{15}N$, respectively, whereas Total Diet Average of wolverines (-22.27 ±0.21‰) and wolves (3.87 ±0.22‰) had the lowest $\delta^{13}C_{\text{Lipid Normalized}}$ and $\delta^{15}N$ values, respectively.

Table 2.2 Stable isotope signatures (δ^{13}C and δ^{15}N) of fur and diet, and discrimination factors (Δ^{13}C and Δ^{15}N), for individuals of various species, sex and age classes used in the feeding experiment. Δ^{13}C is based on lipid-extracted diet

				Animal fur		Total Diet Average			Discrimination factors	
Species[a]	Sex	Age (years)	Mass (kg)	δ^{13}C	δ^{15}N	$\delta^{13}C_{Bulk}$	$\delta^{13}C_{LN}$[b]	δ^{15}N	Δ^{13}C	Δ^{15}N
Gb	M	22.0	na	-18.63	7.78	-22.19 ±0.39	-21.61 ±0.37	5.53 ±0.22	2.97 ±0.37	2.24 ±0.22
Gb	F	20.0	na	-19.38	7.48	_	_	_	2.23 ±0.37	1.95 ±0.22
Wf	M	15.0	43.0	-18.25	7.68	-20.90 ±0.69	-20.14 ±0.69	3.87 ±0.22	1.89 ±0.69	3.81 ±0.22
Wf	F	7.0	33.0	-17.96	7.43	_	_	_	2.19 ±0.69	3.56 ±0.22
Wf	M	1.0	52.5	-17.55	7.50	_	_	_	2.59 ±0.69	3.63 ±0.22
Wf	F	1.0	39.0	-17.36	7.01	_	_	_	2.78 ±0.69	3.14 ±0.22
Wf	M	1.0	57.0	-17.58	7.52	_	_	_	2.56 ±0.69	3.65 ±0.22
Wf	F	1.0	37.5	-18.26	7.65	_	_	_	1.88 ±0.69	3.78 ±0.22
Wf	F	1.0	42.5	-16.95	7.20	_	_	_	3.2±0.69	3.33 ±0.22
Wv	M	12.0	15.2	-20.09	7.82	-22.78 ±0.21	-22.27 ±0.21	4.87 ±0.25	2.18 ±0.21	2.95 ±0.25
Wv	F	18.0	8.4	-20.22	8.01	_	_	_	2.05 ±0.21	3.15 ±0.25
Pb	M	1.5	216.0	-18.93	9.16	-22.36 ±0.43	-21.51 ±0.42	6.42 ±0.21	2.58 ±0.42	2.74 ±0.21
Pb	F	1.5	162.0	-18.83	9.48	-22.41 ±0.46	-21.56 ±0.45	6.58 ±0.21	2.72 ±0.45	2.90 ±0.21
Pb	F	8.5	219.0	-18.68	8.76	-21.95 ±0.43	-21.14 ±0.40	7.19 ±0.19	2.46 ±0.40	1.58 ±0.17
Gb				-19.01 ± 0.53	7.63 ±0.21	_	_	_	2.60 ±0.65	2.10 ±0.30
$\mathrm{Wf}_{\mathrm{Juv.}}$				-17.54 ±0.48	7.37 ±0.26	_	_	_	2.60 ±0.84	3.51 ±0.34
$\mathrm{Wf}_{\mathrm{Ad.}}$				-18.11 ± 0.21	7.55 ±0.18	_	_	_	2.04 ±0.72	3.68 ±0.28

Wv	-20.15 ±0.09	7.91 ±0.14	_	_	_	2.12 ±0.23	3.05 ±0.28

a. Gb: Grizzly bear, Wf$_{Juv.}$: Wolf juvenile, Wf$_{Ad.}$: Wolf Adult, Wv: Wolverine, Pb: Polar bear

b. $\delta^{13}C_{LN}$ diet signatures were normalized for lipid content following the equations in Post, et al., (2007). See Table S3 for calculation details.

2.5.3 Diet-hair discrimination in carbon and nitrogen stable isotopes

At the individual level, $\Delta^{13}C$ ranged from 1.88 ±0.69‰ to 3.2 ±0.69‰ (the combined average of all individuals was 2.45 ±0.40‰, CI 95% [2.22: 2.68‰]) and $\Delta^{15}N$ ranged 1.58 ±0.17‰ to 3.81 ±0.22‰ (the combined average was 3.03 ±0.70‰, CI 95% [2.63: 3.43‰]) (Table 2.2). Although small sample sizes precluded statistical tests, average $\Delta^{13}C$ in adult wolves (2.03 ±0.7‰) appeared lower than in young wolves (2.60 ±0.8‰, CI 95% [1.56:3.64‰]) and any other species (combined average 2.59 ±0.28‰, CI 95% [2.24: 2.94‰]) except wolverine (2.12 ±0.23‰) (Table 2.2, Figure 2.1). However, overlapping variance among groups precludes any firm conclusion. On the other hand, variation in $\Delta^{15}N$ was more pronounced across species (and variance did not overlap), with wolves showing higher average values (juveniles: 3.51 ±0.34‰, adults: 3.68 ±0.28‰) than any other species (combined average of 2.5 ±0.58‰, CI 95% [1.96: 3.04‰]; Table 2.2, Figure 2.1). For polar bears, the variance in $\Delta^{15}N$ prevents clear patterns from emerging (adult female: 1.58 ±0.17‰, M cub: 2.74 ±0.21‰, F cub: 2.90 ±0.21‰) (Table 2.2, Figure 2.1).

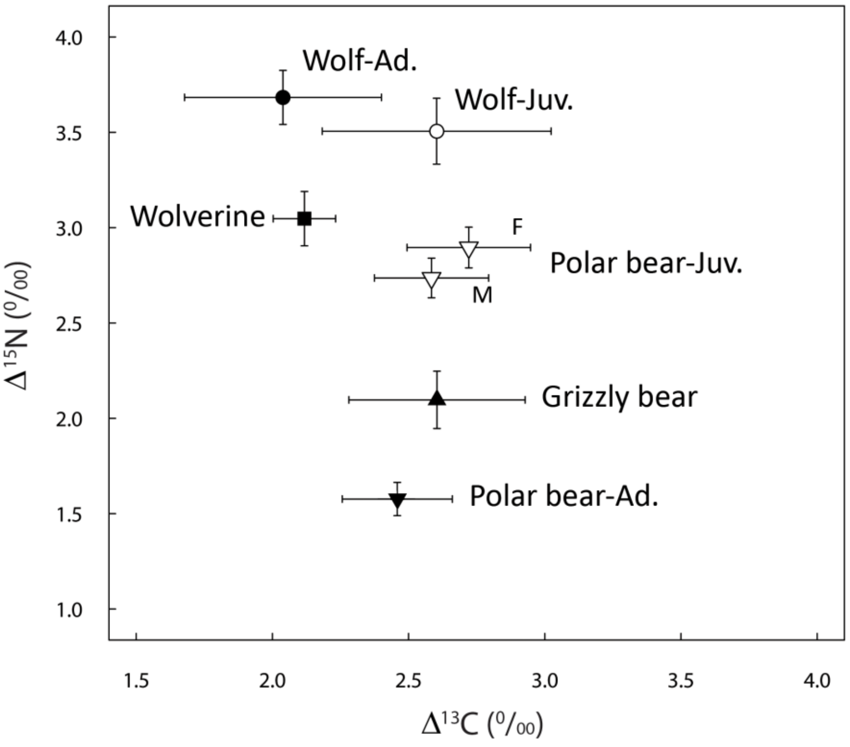

Figure 2.1 Mean and standard deviation of diet-hair discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) for four species of carnivores fed in captivity (open symbols: juveniles, closed symbols; adults). Discrimination factors for $\delta^{13}C$ were calculated on lipid-normalized values (see methods).

2.6 Discussion

Incomplete comprehension of the sources of variation in diet-consumer isotopic discrimination and the lack of experimental validation of discrimination factors of $\delta^{13}C$ and $\delta^{15}N$ is common in field wildlife studies (Lecomte *et al.* 2011). Our study provides experimentally derived diet-hair discrimination factors applicable to free-ranging Arctic carnivore species, with implication for conservation methodologies. Experimental diet-hair $\Delta^{13}C$ and $\Delta^{15}N$ values are provided for the first time in wolverines and can serve as a comparison basis in grizzly and polar bears (Hilderbrand *et al.* 1996; Rode *et al.* 2016) and in wolves (Derbridge *et al.* 2015; McLaren *et al.* 2015), for which published values are also available. Importantly, no discrimination values have yet been published for juvenile wolves, where our results suggest that age can generate as much variation in $\Delta^{13}C$ as does species (this needs confirmation, however, given that observed trends could not be statistically validated, Figure 2.1) (see also Lecomte *et al.* 2011).

2.6.1 Comparison with published discrimination factors

The overall average diet-hair discrimination factors for $\delta^{13}C$ (2.45 ±0.52‰) and $\delta^{15}N$ (3.03 ±0.22‰) observed in our study were higher than those reviewed by Caut et al. (2009) for mammals ($\Delta^{13}C$: 0.5 ±0.75‰, n=21 studies, $\Delta^{15}N$: 2.59 ±0.41, n=23 studies). This is not surprising given that carnivores typically show higher $\Delta^{13}C$ and $\Delta^{15}N$ values than species from other mammalian orders (Vanderklift & Ponsard 2003; Dalerum & Angerbjorn 2005). Recent experiments on carnivore isotopic discrimination provide further support to this trend (Parng *et al.* 2014; Montanari & Amato 2015).

$\Delta^{13}C$ values obtained in adult wolves (2.03 ±0.7‰) were very similar to those (1.97‰, n=10, calculated on lipid-extracted diet) provided by Derbridge et al. (2015) for guard hairs sampled in similar age class groups of wolves. However, $\Delta^{13}C$ values in adult wolves of our study were half those (4.25 ±0.36‰, n= 3) provided by McLaren et al. (2015) for the same tissue and age group. Wolf $\Delta^{15}N$ values (3.68 ±0.28‰) were higher in our study than in Derbridge et al. (2015) (3.04‰) and McLaren et al. (2015) (3.09 ±0.2‰). We suggest that differences in $\Delta^{13}C$ values across studies are explained by differences in the isotopic signatures of the diet fed to wolves. In our study and that of Derbridge et al. (2015), wolves were fed items encompassing a wide range of isotopic values (dry commercial dog food in our study versus deer, beaver, and goose in Derbridge et al. (2015), while McLaren et al. (2015) used horse meat exclusively. Horse meat is characterized by low and rather uniform $\delta^{13}C$ values (see Table B3, Appendix B). Differences in $\Delta^{15}N$ among the three studies were rather low given the similar trophic level of the food provided to wolves, yet the slightly higher $\Delta^{15}N$ reported in our study could be associated with the dry mixture provided. In juvenile wolves, mean $\Delta^{13}C$ (2.60 ±0.8‰) was higher than in adult wolves (2.03 ±0.7‰) as well as in Derbridge et al. (2015), suggesting that age is an important source of variation for this particular discrimination factor. This result is important since very few experimental studies have detected age effects on discrimination factors (but see Roth & Hobson 2000b; Matthews & Mazumder 2008), and most of them showed age effect on $\Delta^{15}N$ only. However, Lecomte et al. (2011) documented important variation in $\Delta^{13}C$ among age groups in captive Arctic foxes *Vulpes lagopus* fed a mixed diet. Contrary to our study, their results showed lower $\Delta^{13}C$ values in juveniles (M: 1.98 ±0.16‰, n=10; F: 1.89 ±0.13‰, n=10) than in adults (M: 2.16 ±0.32‰, n=10; F: 2.65 ±0.22 ‰, n=10) with the hypothesis that such an age effect could be related to different metabolic pathways or syntheses in yearlings compared to adults.

To our knowledge, only two studies (Hilderbrand *et al.* 1996; Rode *et al.* 2016) have experimentally determined discrimination factors in bears. Hilderbrand et al. (1996) did not document any diet-plasma and diet-red blood cells isotopic discrimination in black bears *Ursus americanus*. Rode et al. (2016) has addressed the effect of isotopic composition in diet on $\Delta^{13}C$ and $\Delta^{15}N$ in brown bears and polar bears' plasma tissue. Diet-hair $\Delta^{13}C$ values measured on captive adult grizzly bears in our study (2.60 ± 0.65‰, n=2) were higher than diet-plasma $\Delta^{13}C$ values (0.6 ± 0.1‰, n=4) measured on juvenile captive brown bears fed with a diet with similar proportions of lipids (~11%). On the other hand, our grizzly's diet-hair $\Delta^{15}N$ value (2.10 ±0.30‰) was lower than their diet-plasma values (3.4 ±0.1‰). The scale and the sign of the difference between diet-hair and diet-plasma Δ^{13}C and Δ^{15}N were nonetheless similar to those reported in other experimental studies (Lecomte *et al.* 2011). It is noteworthy that age and lipid extraction (not performed in Rode et al., 2016) are potential confounding effects in this comparison. Diet-hair Δ^{13}C and Δ^{15}N values of our adult polar bear (2.46 ±0.4‰ and 1.58 ±0.17‰, respectively) were similar (Δ^{13}C) and different (Δ^{15}N) to the diet-plasma results obtained in adult polar bears fed with a lipid-rich diet (2.0 ±0.6‰ and 2.5 ± 0.2‰, n=4, respectively). Such differences could be associated with tissue types and differences in lipid content. Δ^{15}N in polar bear cubs was higher (M: 2.74 ±0.21‰; F: 2.90 ±0.21‰) than in Rode et al. (2016) and in our adult female. The female polar bear that we studied was still providing milk to her two cubs. Mother-offspring δ^{15}N enrichment of about 1‰ is typical in both capital (Polischuk, Hobson & Ramsay 2001) and income (Dalerum, Bennett & Clutton-Brock 2007; Miller, Millar & Longstaffe 2011) mammalian breeders during lactation, with a fading trend during the weaning phase. The studied female was not in its prime lactating period (cubs of 1.5 years old are almost weaned in captivity), but the δ^{15}N enrichment observed in polar bears cub could still be partly explained by this factor. Aside from lactation, the observed variation in Δ^{15}N between mother and cubs could be associated with age and differences in the isotopic composition of diet, the proportion of herring with elevated δ^{15}N values being smaller in the diet of cubs than in the diet of the mother.

Finally, diet-hair Δ^{13}C in wolverines (2.12 ±0.23‰) was similar to that of adult wolves, while Δ^{15}N (3.05 ±0.28‰) was more comparable to that of polar bear cubs (Figure 1). Wolverines' discrimination factors were determined out of the most consistent diet fed in our experiment (CAZA meat for terrestrial carnivores) and thus contain less uncertainty. These results are the first published for this species.

2.6.2 Diet-dependent discrimination

Several studies insist that estimated discrimination factors depend on the diet's isotopic composition (Caut *et al.* 2008, 2009; Robbins *et al.* 2010; Lecomte *et al.* 2011). They also warn against using for free-ranging individuals the discrimination factors that were determined in controlled conditions from a single diet source, as this can blur results of diet reconstruction models. (Caut *et al.* 2009) showed an error of 2‰ in ca. 35% of the studies reviewed. Caut et al. (2009) henceforth recommend the use of their diet-dependent discrimination equations (derived from linear models between diet signature and discrimination values) for species without discrimination factors determined experimentally. Here, predicted estimates (0.86 ±0.41‰ and 3.29 ±0.17 for $\Delta^{13}C$ and $\Delta^{15}N$, respectively) from the hair models of Caut et al. (2009) were still lower than our experiment results for $\Delta^{13}C$ (2.45 ±0.52‰), but comparable for $\Delta^{15}N$ (3.03 ±0.22‰). Because our discrimination factors were calculated on an average diet made of items encompassing a wide range of isotopic signatures, we suggest that our results represent a more realistic approximation of discrimination factors for free-ranging carnivores than the equations for corrections, particularly for $\Delta^{13}C$. Henceforth, we recommend the use of Caut et al., (2009)'s equations with care, particularly in studies dealing with large carnivores with opportunistic foraging behaviours.

2.6.3 Effect of lipid normalization on isotopic discrimination

The presence of lipids in tissues depletes $\delta^{13}C$ values (thus decreasing $\delta^{13}C$) with a potential bias in the calculation of $\Delta^{13}C$. Yet some meta-analyses (Caut *et al.* 2009) and experimental studies (Montanari & Amato 2015) did not detect any differences in $\Delta^{13}C$ values between lipid-extracted and bulk diets. However the topic is still vigorously discussed and most recent studies still consistently address the effect of lipid extraction on their results (Parng *et al.* 2014; Rode *et al.* 2016). To cut the costs of isotopic laboratory analyses, we used mathematical lipid corrections (normalization) developed by Post et al. (2007) for animal muscle and vegetal tissue, a reliable alternative to chemical extraction (Logan *et al.* 2008). Lipid corrections ($\Delta\delta^{13}C$) applied to Total Diet Average's $\delta^{13}C_{bulk}$ were higher (in all species) than the uncertainty term (±SD) (Table 2.2). This was especially true in polar bears (fed with lipid-rich diet items) where Total Diet Average $\Delta\delta^{13}C$ (0.81‰ for adult female was twice the error term (0.46‰). In our study, the use of $\delta^{13}C_{bulk}$ in the calculation of $\Delta^{13}C$ would inflate results in all species, from 0.51‰ in wolverines to 0.85‰ in polar bear cubs. The lack of experiments on discrimination factors in large Arctic carnivores makes comparisons difficult and it is a challenge to determine which of $\delta^{13}C_{bulk}$ or $\delta^{13}C_{LN}$ should be applied. In wolves, for which diet-hair $\Delta^{13}C$ are published, both Derbridge et al. (2015) and McLaren et al. (2015) determined $\Delta^{13}C$ based on lipid-extracted diet, so no $\delta^{13}C_{bulk}$ diet-based carbon discrimination factors are available for further comparisons. Nevertheless, both our study and Derbridge et al. (2015)'s applied diet lipid correction upon the logic that in situations of heterogeneous lipid contents among several diet items, lipid correction is typically worthwhile to standardize the contribution of these items to total diet $\delta^{13}C$ of a consumer (Post et al., 2007). However, Newsome et al. (2010) recommends the use of $\delta^{13}C_{bulk}$ in determining discrimination factors of keratinous tissue such as animal hairs upon the argument that keratin structural carbon can originate from lipids.

2.6.4 Conclusion

The development of non-invasive research approaches is warranted to efficiently monitor and conserve large Arctic carnivores. The increasing use of inactive and easy to collect tissues such as hairs is promising despite the logistical challenges associated to low animal density (Mulders *et al.* 2007). Using stable isotopes, it is now possible to reconstruct diet of wild animals, yet the accuracy of models is sensitive to diet-consumer isotopic discrimination. The large Arctic carnivores' diet-hair discrimination factors provided in this study are directly applicable to wild animals but with caution. Although we characterized discrimination factors for several species, the conditions of our experiment did not allow extensive replications nor comparisons among age classes, sex classes, or diet types, except for wolves. Nevertheless, by documenting potential age effects on carbon isotope discrimination in wolves (so far, only reported in Lecomte et al. (2011), our study showed new evidence that population structure can alter isotopic discrimination. Experimental designs emphasizing population structure and discrimination factors are needed for these species, as well as those addressing what metabolic mechanisms are involved in the partitioning of carbon (and nitrogen) isotopes among age and sex classes. Future work should also address the effect of different diets (with distinct isotopic compositions) on isotopic discrimination of large carnivores (Caut *et al.* 2008). Meanwhile, we recommend the use of our wolf discrimination factors or those from other studies accounting for age and sex variation (Lecomte *et al.* 2011) in field studies of free-ranging large carnivores with heterogeneous population structure.

Acknowledgements

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CHAPITRE III

SUBSISTENCE SOCIAL-ECOLOGICAL SYSTEMS AND DEVELOPMENT: HUNTING PRESSURE AFFECTS TUNDRA WOLVES' CONDITION, BEHAVIOUR AND SOCIAL STRUCTURE

Vincent L'Hérault, Nicolas Lecomte, Malik Awan, Guillaume Szor, and Dominique Berteaux

Manuscrit en préparation pour soumission à *Ecology and Society*

Contributions des auteurs (initiales)
Mise en place du design de l'étude (VLH)
Récolte des données (VLH, MA, GS)
Analyse des données (VLH)
Interprétation des résultats (VLH, NL, DB)
Rédaction du manuscrit (VLH)
Commentaires et correction du manuscrit (VLH, NL, MA, GS, DB)
Financement (DB, MA)

3.1 Résumé

Les changements globaux peuvent pousser les systèmes socioécologiques (SES) de subsistance vers des états non durables. La recherche empirique sur ces transitions est nécessaire afin d'éviter leurs conséquences négatives. Dans un contexte de développement minier près de la communauté inuit de Qamani'tuaq, au Nunavut, nous avons évalué une hypothèse formulée localement et qui concernait l'impact de la chasse de subsistance sur les loups toundriques.

En nous basant sur des observations locales et des données biologiques issues d'un programme multiannuel de récolte de carcasses, nous avons testé quatre prédictions à propos de la condition corporelle, du comportement, de la structure sociale, et du régime alimentaire des loups. Nous avons comparé une zone d'impact située près de la communauté et incluant la route d'accès à une mine à une zone contrôle située loin de la communauté et des activités minières. Nous avons également utilisé le modèle de SES de subsistance de Fauchald et al. (2017) pour évaluer les perceptions des chasseurs locaux et aînés quant aux changements globaux susceptibles d'influencer la pression de chasse. Pour distinguer l'importance relative sur la pression de chasse du développement industriel et d'autres facteurs, nous avons comparé la condition corporelle des loups de la zone d'impact avec celle de loups récoltés dans d'autres communautés inuit non exposées au développement minier.

Les loups de la zone contrôle étaient en moyenne 4,1kg (IC 95% [0,1 :8,3]) plus lourds (indice de condition majoré pour la masse) et 56,6g (IC 95% [-6,8 :119,8], *p*=0,08) plus gras (indice de gras sternal) que les loups de la zone d'impact, ce qui était conséquent avec les observations locales. Les observateurs locaux ont également rapporté des signes de stress individuel face aux humains (évitement et peur) et des structures sociales perturbées (plus petits groupes de 2-3 individus en moyenne, individus alpha parfois absents) dans la zone d'impact. Nous n'avons observé aucun effet du traitement sur la qualité et la quantité de la nourriture utilisée par les loups, bien que les observateurs locaux suggèrent une diminution de l'utilisation de la viande de caribou et une augmentation de l’utilisation des restes de caribou laissés par les chasseurs dans la zone d’impact. Les différences dans l’état des loups étaient attribuées à une plus grande pression de chasse (également perçue comme étant plus élevée de nos jours qu’avant la présence de la mine) dans la zone d’impact que dans la zone contrôle. La pression de chasse était déterminée par i) un plus grand accès au territoire dû à la route d’accès à la mine et aux meilleurs salaires favorisant l’accès aux nouvelles technologies (motoneiges), ii) un plus grand besoin de revenus entrainant une plus grande demande de fourrures de loups dans la communauté et iii) l’émergence de nouvelles pratiques de chasse incluant la chasse sur de courtes distances surtout pratiquée les weekends. Deux facteurs, les activités industrielles dérangeant les animaux et dégradant les habitats d’une part, et les changements climatiques d’autre part, ont été identifiés comme les principales influences sur la condition des loups. Cette influence semblait due à des effets négatifs sur l’abondance et la qualité des caribous. Toutefois, la condition et les réserves corporelles des loups ne variaient pas entre la zone d’impact et d’autres communautés inuit, suggérant que des pressions de chasse élevées peuvent survenir même en absence du développement industriel.

Notre étude représente une première étape pour mieux comprendre la complexité des interactions humains-ressources influencées par des facteurs globaux. Elle suggère la possibilité d’une surchasse des loups dans un contexte de développement économique accéléré. Étant donné leur niveau trophique élevé, les loups peuvent être de bons indicateurs de la santé du milieu et nous pouvons donc appréhender d’autres impacts écologiques non identifiés dans notre aire d’étude. Afin de promouvoir la durabilité de ce SES de subsistance dans un contexte de développement industriel croissant, nous recommandons la mise en place d’une initiative de conservation communautaire, plutôt qu’une régulation par le gouvernement.

Mots-clés: Systèmes socioécologiques, chasse de subsistance, développement industriel, loup arctique, savoir local

3.2 Abstract

Global drivers can force subsistence social-ecological systems into unsustainable states. Empirical research is needed to investigate these transitions and help avoid their most negative effects. In the context of mining development near the Inuit community of Qamani’tuaq, Nunavut, we addressed a community-generated research hypothesis stating that subsistence hunting negatively impacts tundra wolves.

Using local observations and monitoring data from a multi-year wolf carcass recovery program, we tested four predictions dealing with the body condition, behaviour, social structure, and feeding patterns of wolves. We compared an impact area located near the community and encompassing a mine access road to a control area located away from the mine and community. We also used a subsistence SES model (Fauchald *et al.* 2017) to examine the perceptions of local hunters and Elders with regards to the main drivers influencing local hunting pressure. To discriminate the relative importance of industrial and other drivers on hunting pressure, we compared the body condition of wolves living in the impact area to that of wolves from other Inuit settlements exempt from industrial activity.

Wolves in the control area were 4.1 kg (95% CI [0.1:8.3g] heavier (scaled mass condition index) and 56.6g (95% CI [-6.8:119.8g], p=0.08) fatter (sternal fat) than those in the impact area, which was congruent with local observations. Local observers also reported signs of individual stress (fear of humans, frequent escape behaviour) and disturbed packs (small groups of 2-3 individuals, alpha individuals sometimes absent) in the impact area. We found no effect of treatment on the quality or quantity of food used by wolves, yet local observers suggested a decreased use of caribou meat but increased use of caribou leftovers in the impact area. Differences in wolves’ state were attributed to higher hunting pressure (also perceived as being higher than before the mine) in the impact than in the control area. Increased hunting was due to i) facilitated access to the land due to a new mine access road and access to the newest transportation technologies (performance snowmobiles) acquired through better cash income, ii) higher interest in wolf pelts in the community to satisfy increased need for cash income, and iii) emergence of new harvest practices such as short-distance and weekend hunting. Two drivers (industrial activity causing direct disturbance and habitat degradation, and climate change) were pointed as main influences on the state of wolves, mostly through effects on caribou availability and quality. However, the condition and body reserves of wolves did not differ among the impact area and other settlements, suggesting that elevated hunting pressure can happen even without industrial development.

Our study provides a first step into disentangling the complex human-resource interactions coupled to global drivers, as it suggests overharvest of wolves in the context of rapid economic development. Wolves may represent an integrative indicator of tundra health due to their high trophic position in the ecosystem, hence we suggest that other, unknown ecological impacts of development may also exist in our study system. To promote the sustainability of the studied subsistence SES in a context of rapid industrial development, we recommend the implementation of community-based conservation, rather than increased government regulation.

Key words: Social-ecological systems, subsistence hunting, industrial development, tundra wolves, local knowledge

3.3 Introduction

Cumulative impacts on the environment are a worldwide concern (*e.g.* Festa-Bianchet *et al.* 2011; Lewis, Edwards & Galbraith 2015) and investigating the dynamic interactions between societies and natural systems is critical to address them (Kates *et al.* 2001; Chapin *et al.* 2010). Maintaining balanced interactions within social-ecological systems (or SES) (Berkes, 2011; Berkes et al., 2003) is indeed key to the well-being and resiliency of humans and their natural environment (King & Hood 1999; Ommer 2007; Berkes, Doubleday & Cumming 2012). Such interactions are particularly at play in aboriginal (or local) communities based on a subsistence economy, where the harvest of living resources for food and supply is daily practice and embeds several layers of cultural values and beliefs. In these systems, the harvest of wildlife is traditionally conducted as a provisioning action; it adapts to and has no control on the natural fluctuations of resources, and it is performed at a small scale with little impact on resources (Fauchald et al., 2017; Gutierrez et al., 2011). For example, traditional subsistence hunt on large migratory herbivores, such as caribou in the Arctic, was performed in spatially restricted areas by family clans widely dispersed with respect to the distribution of the resource (Kulchyski and Tester, 2007; Mannik, 1998; Parlee and Manseau, 2005). Traditional principles of environmental stewardship encoded in local systems of knowledge, such as Inuit Qaujimajatuqangit (*e.g.* Mannik 1998; Tester & Irniq 2008; Clark & Slocombe 2009) were also key to minimize impacts on resources and thus promoting survival and resilience of both resources and resource users. Following a relatively recent history of colonization (Mannik, 1998; Tester and Kulchyski, 1994), modernization, globalization, and industrialization of the North (Bernauer, 2011; Lertzman and Vredenburg, 2005; Tester, 2016), arctic communities became exposed to new social, economic, and cultural realities (*e.g.* job-based wage economy and sedentary- and technology-based lifestyle) and departed from traditional lifestyles with consequences on subsistence SESs.

Fauchald *et al.* (2017) proposed a conceptual model for SES transitions in subsistence-based communities. According to this model, the subsistence hunt can transition from a traditional provisioning into complex new sets of action where the resources and the resource users are influenced by various drivers determining the state of the resource, the efficiency of hunters, and the demand on the resource (Figure 3.1). These drivers can include industrial activity, climate change, globalization, population and economic growth, and resource commercialization. They can have both positive and negative impacts on subsistence SESs (Young et al., 2006). Taken together, these interacting drivers determine the magnitude of the hunting pressure exerted on resources, which can eventually shift the balance from a provisioning local action towards an unsustainable resource use that necessitates collective effort and management measures to prevent overexploitation (Fauchald et al., 2017).

Empirical studies addressing the transition of subsistence SESs, that is the linkages between drivers of change and SESs components, are largely lacking (but see Fleischman *et al.* 2014). Yet such studies are needed to identify potential unsustainable interactions that can affect human and natural system well-being (Young et al., 2006). It is therefore critical to investigate potential sources of ecological, social and cultural knowledge and understanding. In this context, using knowledge and perspectives from local land users is important to build a complete information base (Berkes, Colding & Folke 2000; Kendrick & Manseau 2008; Gagnon & Berteaux 2009; Huntington 2011; Ford *et al.* 2016), and involving local land users in the research process is paramount (Brook & McLachlan 2008; Adams *et al.* 2014; Ford *et al.* 2016).

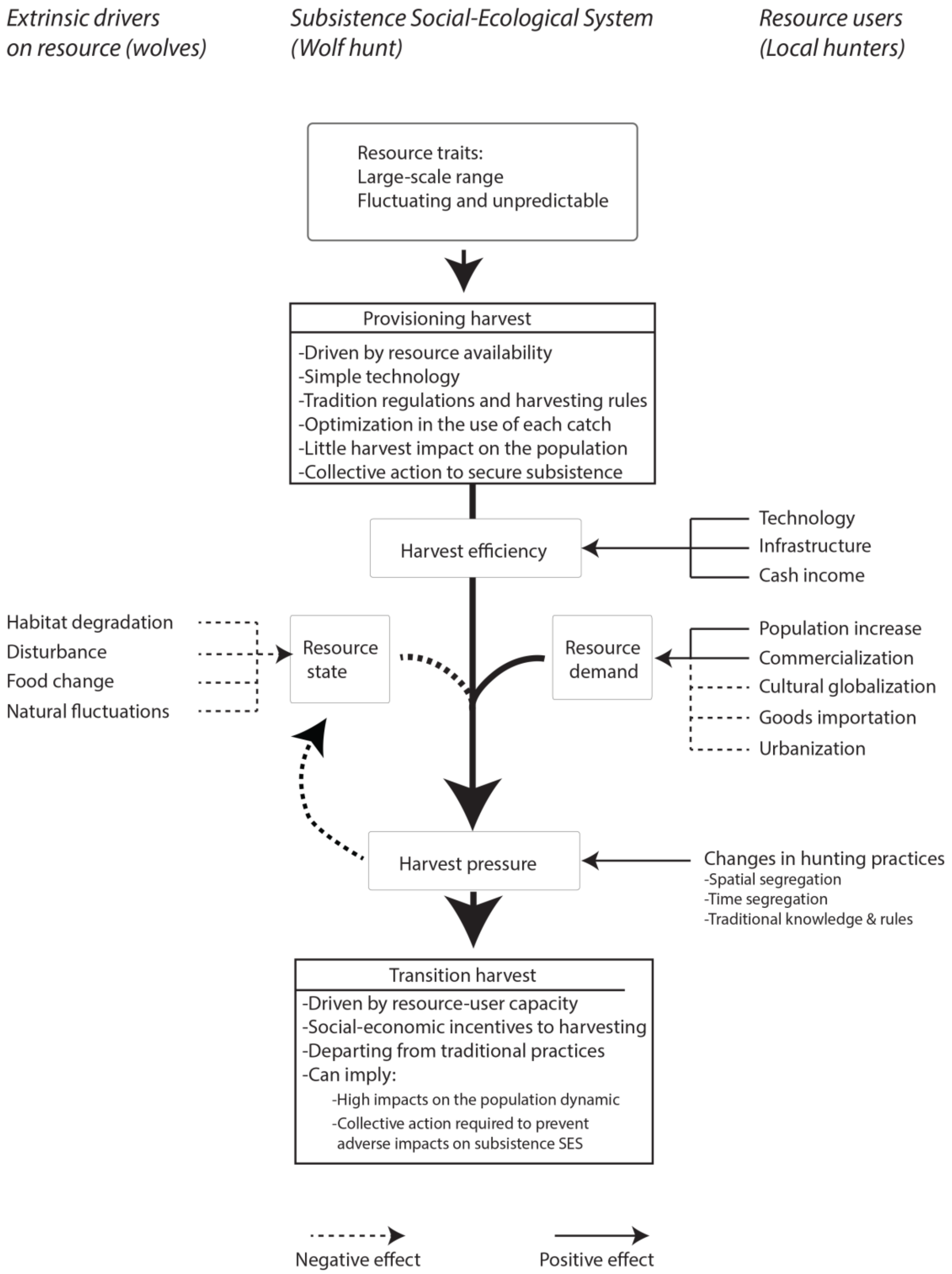
Extrinsic drivers
on resource (wolves)
Subsistence Social-Ecological System
(Wolf hunt)
Resource users
(Local hunters)
Resource traits:
Large-scale range
Fluctuating and unpredictable
Provisioning harvest
-Driven by resource availability
-Simple technology
-Tradition regulations and harvesting rules
-Optimization in the use of each catch
-Little harvest impact on the population
-Collective action to secure subsistence
Harvest efficiency
Technology
Infrastructure
Cash income
Habitat degradation
Disturbance
Food change
Natural fluctuations
Resource state
Resource demand
Population increase
Commercialization
Cultural globalization
Goods importation
Urbanization
Harvest pressure
Changes in hunting practices
-Spatial segregation
-Time segregation
-Traditional knowledge & rules
Transition harvest
-Driven by resource-user capacity
-Social-economic incentives to harvesting
-Departing from traditional practices
-Can imply:
-High impacts on the population dynamic
-Collective action required to prevent adverse impacts on subsistence SES
Negative effect
Positive effect

Figure 3.1 Conceptual framework of subsistence Social-Ecological System (SES) in transition adapted from Fauchald et al., (2017) to the case study of wolf hunting in Qamani'tuaq, Nunauvt, Canada. From an initial situation where the harvesting is driven by resource availability and limited by hunting efficiency (with a limited impact on the resource), the impact of extrinsic drivers (which can ultimately be influenced by industrial development and climate change) on the main SES components can force the provisioning harvest to transition into a new dynamic, with a potential risk to overexploitation and adverse consequences on the resource and the resource users. In this model, increased harvest efficiency and resource demand, and changes in hunting habits can increase hunting pressure on wolves. Elevated hunting pressure can impact the resource state (population size and/or social structure, behaviours, body conditions, physiological stress, genetic) which could in turn contribute to decreasing the hunting pressure as the population decreases or individuals become of less quality. Extrinsic drivers can, too, impact resource state.

Here, we use Fauchald et al. (2017)'s model as a tool to integrate various sources of local observations, perceptions, and biological data and provide a case study of the subsistence SES of Qamani'tuaq (Baker Lake), Nunavut. In the last few decades, this predominantly Inuit community experienced a rapid transition from a mostly subsistence economy based on the provisioning on live resources (caribou, fish, and furbearers) to a mixed economy involving wage-opportunities related to mining exploitation (Figure 3.2). In 2010, a medium-size gold mine opened about 85 km north of the community and an access road was built from Qamani'tuaq and across an important habitat and hunting ground for caribou, wolves and wolverines. The mine was and still remains a source of concern for land users, including the local Hunters and Trappers Organization (HTO), because the mine site, the road, and the socio-cultural changes associated with the transformation of a subsistence economy into an industrial-based wage economy may affect both humans and wildlife (Figure 3.1).

We examine a research hypothesis formulated by Qamani'tuaq hunters and suggesting that local development contributed to modifying hunting pressure on wolves, with consequences on the state of the local wolf population. Wolves are often harvested for trade in the vicinity of Qamani'tuaq (Bryan et al., 2015) and increasing use of technologies such as snowmobiles and firearms have likely increased the efficiency of wolf hunting (Figure 3.2, Cluff *et al.* 2010). In addition, the average market price for wolf fur has markedly increased in the 2000s (Figure 3.2, Fur Harvesters Auction Inc., 2017), although the trend in fur demand is hard to assess given that pelt sells are often unreported. On the other hand, both local observers and wildlife biologists (Bryan et al., 2015; Paquet and Carbyn, 2003) suggest that wolves are resilient predators who adjust their reproduction to changing conditions. Wolves are opportunistic predators but they largely depend on caribou, which are declining through most of their range (Festa-Bianchet et al., 2011; Vors and Boyce, 2009). Despite apparent stability in wolf numbers, local hunters report that body condition, behaviour, social structure, and diet have changed in the wolf population living north of the community, where is located the access road to the mine (hereafter, the impact area). These changes might have a broad ecological relevance since the state of arctic wolf populations integrates many aspects of regional ecosystem functioning (Cluff and Paquet, 2003).

We thus predicted that wolves from the impact area should show a lower body condition (P1), an increased fear of humans (P2), a disrupted social structure (P3), and a changed diet and feeding behaviour (P4) compared to wolves from a control area located further from industrial activities. We tested P1 and P4 by examining simultaneously local observations and monitoring data from a regional, multi-year wolf carcass monitoring program providing body condition, body reserve indices, and dietary data. We tested P2 and P3 using observations shared by local hunters. We use (Fauchald *et al.* 2017)'s SES model to examine the perception of local hunters and Elders with regards to the main drivers influencing wolf hunting pressure in Qamani'tuaq (Figure 3.1).

3.4 Material and methods

3.4.1 Study area

Qamani’tuaq (Baker Lake; $64^{o}19'$N, $96^{o}01'$W) is the Canadian Arctic’s sole inland community and is located 320 km west of the Hudson Bay in the Kivalliq district of Nunavut (Figure 3.3). The local subsistence economy is based on the harvest of several migratory caribou herds present near the community in summer (Festa-Bianchet *et al.* 2011) and of a resident herd (Nagy et al. 2009). Wolves, wolverines, grizzly bears and Arctic foxes are harvested for trade and local traditional uses, and represent the most important subsistence-based sources of income for local hunters and their families. The Qamani’tuaq settlement was formed in the late 1950s when, following an episode of starvation due to scarce caribou, the Canadian government moved people belonging to six traditional groups from their inland camps to Qamani’tuaq (Figure 3.2). These people originated from places sometimes located far away from Qamani’tuaq, thus assembling in one place a rich and diverse heritage of place-specific traditional knowledge and practices. Their traditional lifestyle then underwent a rapid transformation triggered by factors such as schooling (Figure 3.2). Despite these important changes, subsistence hunting remained a vital part of the local economy (Figure 3.2) until the 1990s when new economic and cultural shifts occurred due to mining development in the region (Figure 3.2). In particular, the construction and exploitation of the Meadow Bank gold mine in the late 2000s started a new economic and cultural era. The project annually employs ca. 150 local workers, or 15% of the Qamani’tuaq population (Bernauer 2011). Given the high turnover rate in the Inuit labour force, almost all of the ca. 580 households (Statistics Canada, 2016) of Qamani’tuaq has now been influenced by the presence of the mining company.

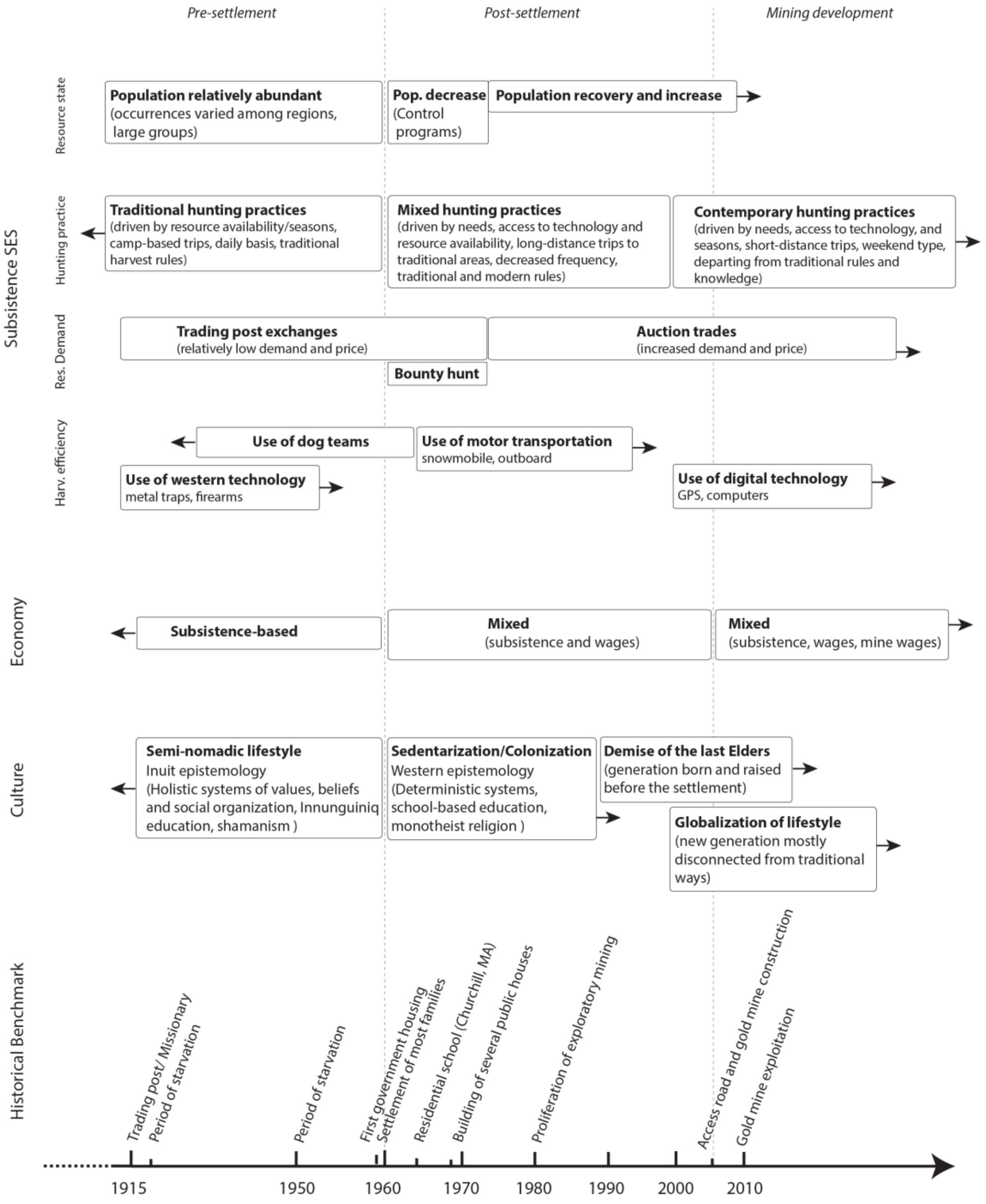

Figure 3.2 Timeline of the main events that have contributed to reframing Inuit culture and socio-economy in the last century while impacting local livelihoods and the wolf-human subsistence social-ecological system (SES) in Qamani'tuaq, Nunavut, Canada. Vertical lines delineate the pre-settlement, post settlement and

mining development periods. Boxes indicate important characteristics of the SES, economy and culture. Arrows indicate continuation in the past or future.

3.4.2 Initiation of the research project

In 2011, we held initial discussions with the community about industrial impacts on wildlife (Table C1 in Appendix C). These were conducted between Vincent L'Hérault, the manager of the Qamani'tuaq Hunters and Trappers Organization, and few local hunters participating in the collection program of wolf carcasses sponsored by the Government of Nunavut's Department of Environment. Discussions shed light on several concerns about the state of wolves observed and harvested in a broad region north to the community that encompassed the mine access road (hereafter called the impact area, see study design below). It was also established that some wolves were now regularly seen within or near the community, which was less frequent in the past. Local informants also reported differences in condition and behaviour between wolves from the impact and the control areas, and related these differences to increased hunting pressure in the impact area.

A digest of these informal discussions was discussed with the HTO board members in winter 2012 (Table C1 in Appendix C). Board members then actively participated in the design of a research project addressing the issue of industrial development, wolf hunting, and wolves' state. They also requested to look at scientific evidence of changes in condition and behaviour of wolves.

3.4.3 Study design

Impact studies typically use a Before–After Control-Impact design (Smith, 2013). Here, no biological data were available from before the impact of the mine, but local observations allowed us to infer some of the temporal changes that occurred since the construction phase of the mine and the access road (2007) up to the time of full-mining operations (2010) and onward. Based on the wolves harvested by long-range hunters in Qamani’tuaq (Figure 3.3), we had access to biological samples and ecological observations from remote hunting grounds, *i.e.* a control area without industrial exploitation and with limited hunting activities. However, we could not control for potential habitat differences in the impact and the control areas. We acknowledge this caveat in our study design, and we rely on the knowledge of local hunters to help characterize the differences between these two habitats. To discriminate the relative importance of industrial drivers and other drivers on the hunting pressure, we compared the condition of wolves in the impact area to that of wolves from other Inuit settlements of the Kivalliq region, where no industrial activity occurred but wolf hunting was common.

3.4.4 Gathering local observations and perspectives

We expanded the initial discussions held with HTO board members and local hunters in order to document more formally, and with distinct informants, observations related to wolves’ state and perspectives on the role of various drivers on the subsistence SES (Figure 3.1). We conducted interviews with eight long-range hunters, for whom most wolf harvest takes place away from mine-related activities, to contrast the observations and perspectives among the impact and the control areas (Figure 3.3). These hunters represented almost every of the few families still actively travelling to remote areas for wolf hunt.

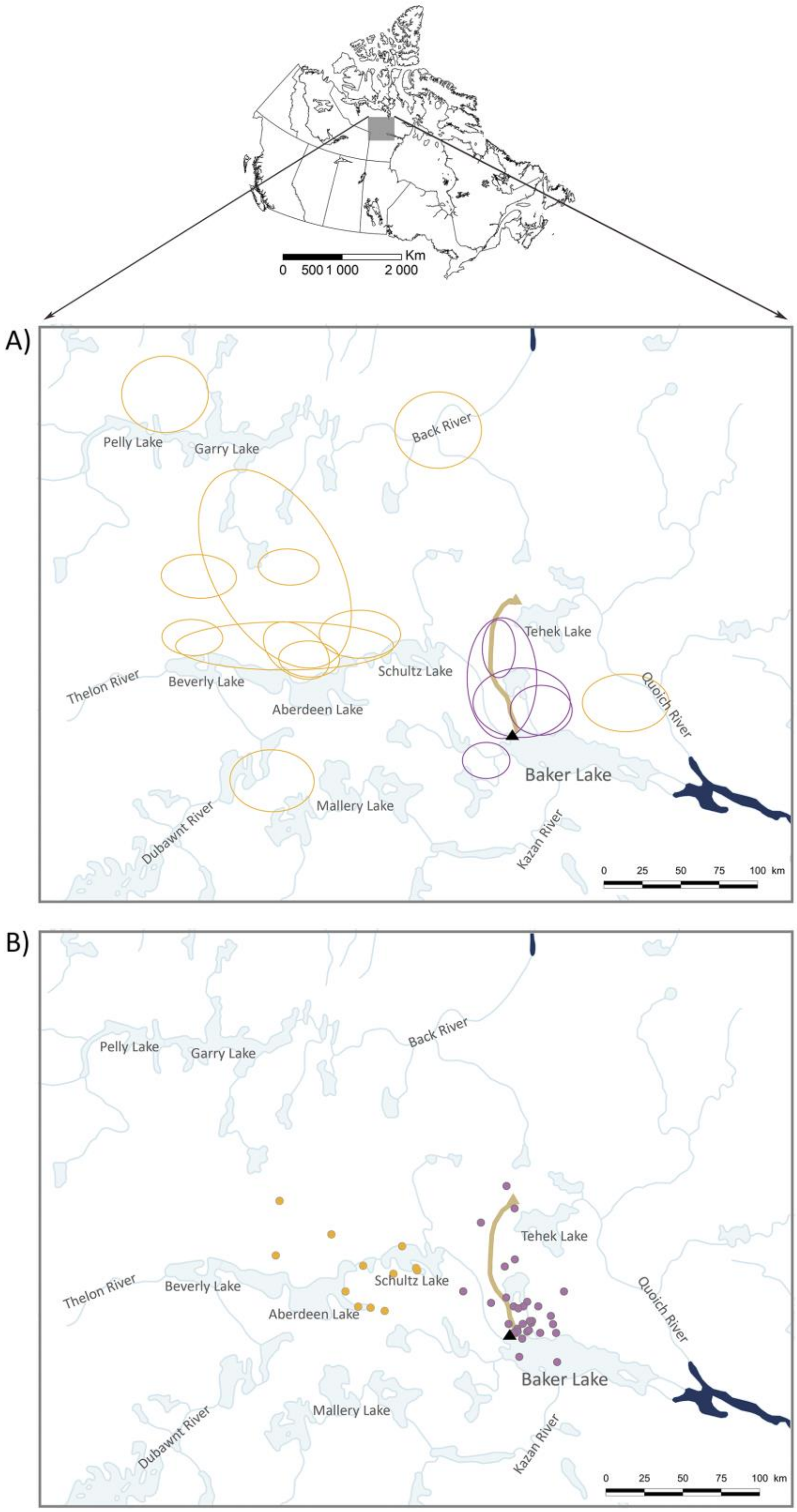
Km
0 500 1 000 2 000
A)
Pelly Lake
Garry Lake
Back River
Tehek Lake
Schultz Lake
Thelon River
Beverly Lake
Aberdeen Lake
Quoich River
Baker Lake
Mallery Lake
Dubawnt River
Kazan River
0 25 50 75 100 km
B)
Pelly Lake
Garry Lake
Back River
Tehek Lake
Schultz Lake
Thelon River
Beverly Lake
Aberdeen Lake
Quoich River
Baker Lake
Mallery Lake
Dubawnt River
Kazan River
0 25 50 75 100 km

Figure 3.3 Map of the study area with A) main wolf hunting areas used by eight long-range hunters and B) locations of the wolves harvested from 2011 to 2013 as part of a monitoring program conducted in Qamani'tuaq, Nunavut, Canada. Purple and orange ellipses (A) and dots (B) show the impact and control areas, respectively. The brown line shows the mine access road linking the mining site (brown triangle) to the community of Qamani'tuaq (black triangle).

We also met with ten Elders to learn more about the history of Qamani'tuaq, including changes in socio-cultural aspects, hunting culture, and wildlife. We also furthered specific elements of wolf biology (*e.g.* diet, social behaviour). With both long-range hunters and Elders, we discussed perspectives on the wolf hunting SES. We conducted interviews in the form of discussions and mapping sessions based on semi-structured questionnaires adapted to each participant upon their life experience and interest (see Appendix C). Consequently, questions and answers covered with each participant overlapped but greatly varied in nature. The sum of all information exchanges and stories contributed to a collective body of knowledge. Before each interview, we presented to each participant a consent form on which we defined the origin and objectives of the research, presented participants with their rights in regards to the interview and the future use and diffusion of the data, and requested the authorization to audio and videotape the conversation. We obtained ethics approval from the Université du Québec à Rimouski and a research licence from the Nunavut Research Institute (licence numbers are available in the permit section).

3.4.5 Biological data collection

From fall to spring in 2010-2013, the Government of Nunavut ran a large carnivore (wolves and wolverines) carcass recovery program across 13 Inuit communities including Qamani'tuaq. Hunters were compensated with cash subsidies to provide whole animal carcasses to their local conservation office or HTO, but they kept the pelt for trade. Such a method is common in other studies (Agarwala *et al.* 2010) and the subsidies provided are largely inferior to the incomes obtained from the trade of the pelt to avoid increasing hunting pressure. For each animal reported to the program, GPS coordinates of the harvest location, date of the harvest, and number of wolves observed (social structure) were recorded. We used the data and samples of wolf necropsies to examine wolves' body conditions and diet. We determined body condition by three Condition Indices (CIs), the Fulton's index, the Residuals index, and the Scaled Mass index (reviewed in Peig & Green 2010). The CIs employ different formulas based on the relationship between individual body mass and a linear body measure (*i.e.* body length, femur length, and condylobasal length) (see Appendix C). We used fat indices (FIs) (*i.e.* wet weight of sternal fat and omental fat, and thickness of back fat) as direct attributes of body reserves which typically correlate to individual fitness (Wilder et al., 2016).

Diet was determined in two ways. First we examined the content of wolf stomachs (wet weight of each diet item), picturing the average last meal ingested by wolves (Killengreen et al., 2011). Second, we used carbon and nitrogen stable isotopes (Kelly, 2000; Peterson and Fry, 1987) to determine the assimilated diet of wolves. We used two tissues, liver and muscle, to depict the diet assimilated during the last week and the last month, respectively (Killengreen *et al.* 2011). We also obtained demographic parameters (age and sex) from the necropsies. We determined the age of individuals by counting the number of cement annuli in a canine tooth (Jensen & Nielsen 1968). Although demographic parameters were not part of the tested predictions, they influence body weight and fat reserves and must therefore be accounted for as co-variables (Peig and Green, 2009).

3.4.6 Data analyses

Interviews (predictions 1, 2, 3, 4):

We translated audio and video records from Inuktitut to English with the help of a local interpreter. Records and transcripts were analyzed and information was classified in subcategories addressing research predictions (P1, P2, P3, P4), as well as each component of the social-ecological framework. For each category, we assigned each observation to a specific level in order to simplify our analyses. For example, we classified information relating to the ‘wolf condition’ category into three levels (‘poorer’, ‘same’, ‘better’) after comparing among areas or years. We performed frequency analyses on the occurrence of each level of observation for each category (Creswell, 1998).

Condition indices and diet (predictions 1 and 4):

We conducted statistical analyses using the open-source software R, version 3.1.1 (R Development Core Team 2014). We used linear mixed models (LMM) to examine Condition and Fat Indices. We first checked for correlation between indices and used only one index when two or more indices were correlated (see Table C2 in Appendix C). We tested the contribution to CIs and FIs of the area (impact vs control vs other settlements), age, sex, season, diet ($\delta^{13}C$, caribou wet weight in stomach, and alternate prey), pack size (data collected as part of the carcass program), and latitude. We tested for co-linearity between the tested variables and used only one variable when two or more were correlated. We treated the year as random effect in the model. Details on the candidate models tested are available in Table C3 (Appendix C).

3.4.7 Validation workshop

Results obtained in interviews and biological data analyses were presented to a validation committee comprising HTO representatives, Elders, young hunters, and a local Member of the Legislative Assembly of Nunavut (MLA). This committee reviewed a summary document, attended an informal presentation where they asked questions, provided reviews and corrections and made recommendations with regards to the communication of the results back to the community (see Table C1 in Appendix C).

3.5 Results

We obtained local observations from eight long-ranging hunters and ten Elders. A total of 12, 45, and 25 wolf carcasses from the Control area, the Impact area, and other Kivalliq communities, respectively, were reported to the program.

3.5.1 Changes in wolves' condition (P1)

Observations from long-range hunters and Elders suggested no difference in the frequency of wolves encountered in the impact versus control areas (Table 3.1-1). However, four of 8 informants reported that it was now frequent to observe wolves coming into the community (Quote # 01 in Appendix C). Observations on colour patterns suggest no clear differences among areas. Supporting P1, four of 4 informants reported that wolves from the impact area are smaller than wolves from the control areas (6/7 reported such a difference; Table 3.1-1). Also supporting P1, seven of 10 informants reported a decrease in the condition of wolves compared to ca. 4-5 years ago (Quote # 02 in Appendix C) within the impact area. On the other hand, and also supporting P1, four of 4 informants reported that wolves from the control area were healthier and fatter than wolves from the impact area (Table 3.1-1).

Table 3.1 Summary of the observations, reported by eight long-range hunters and ten Elders, about the differences in wolves’ state (1), behaviour (2), social structure (3) and diet and feeding behaviour (4) between the impact and control areas near Qamani’tuaq, Nunavut, Canada. The numbers of informants reporting each observation is indicated. Observations related to changes through time are indicated by one star when changes occurred over 4-5 years and two stars when they occurred over a decade.

	Impact area	No.	Control area	No.
1) State				
Occurrence	You'll catch one for sure	1	Lots of wolves there	2
	I see one almost every time I go	3	Almost every time I go	1
	More are coming to town*	4		
Population trend	Same	2	Increasing	4
	Increasing	1	Same	1
Colours	Greyer and darker	1	Pure/even colours	2
	All blacks are rare	1	Whiter	2
	Same colours everywhere	2		
Size	They are smaller size	2	They are bigger size	3
	Alphas are smaller	1	Alphas are bigger	1
	Younglings much smaller	1	Younglings are bigger	2
			Some are small some are big	1
Body condition	Yearling in poorer health*	3	Healthier	1

	Skinnier, skin and bones *	3	Fatter	3
	Less fat on them*	1		
	Poor fur not healthy	3		
2) Behaviour	Scared easily/run away	2	They are not scared/don't run	4
	Run as soon they see a snowmobile	1	They are tamed	3
	Run as soon they see a riffle	1	Wilder	1
	Hungry/starving	7		
3) Social structure				
Age/Social status	Mostly yearlings seen in town	4	More alpha out there	4
	I see alphas but they are harder to catch	1	All family together in pack	1
	Quite a few alpha around	1		
	Never saw an alpha close to town	1		
	Adults are coming now	1		
Pack size	2-3/pack	5	7-8, up to 16/pack	3
	More common alone	2	15-20, up to 25/pack	1
	8-10	1	Bigger pack	2
	4-6	2	8-12/pack	3
	Rarer to see in pack	1		
	Always in pack	1		
	Come alone in town	6		
4) Diet and feeding behaviour				
Observations on prey	Caribou are gone by winter	1	Lots of caribou year-long	4

availability *and state*	Less caribou now (but good area)*	5	Muskoxen are everywhere	3
	Hardly any caribou around town now	3	There is more caribou now	4
	There is caribou all year long	2		
	Caribou walk East during winter	1		
	Caribou taste isn't the same	1		
	More caribou leftovers (from hunters)*	3		
	Muskox everywhere now	2		
	Muskox by the shore of Baker Lake**	4		
Hypotheses on changes in feeding behaviour	Disruption: parents shot, young unable	5	Hunt in packs more dominants	4
	Disturbance: less feeding time	2	No disturbance/ more feeding time	1
	Scavenging on hunter's leftovers*	2	Eat whole caribou	1
	Prey switch on small prey	1	They do their traditional hunt	1
	Feeding on garbage, food, or dogs in town	5		
	Coldness	2		
	Less caribou meat to eat	4		

Monitoring data also suggest that wolves from the impact area were in poorer condition than wolves from control areas, thus supporting P1. The best linear mixed model (LMM) for the scaled $\text{mass}_{\text{Condylobasal}}$ condition index indicates an increase of 14.8% (95% CI [0.4:29.1%]) in the body mass of wolves from control areas compared with the impact area (intercept), whereas no difference was found in wolves from other regions of the Kivalliq exempted from mining development (Table 3.2a). Yearlings were also 11.0% (95% CI [18.9:3.0%]) lighter than adults, which was expected in this species (Table 3.2a). The interaction between area and age was not significant, meaning that yearlings from the impact area were not significantly smaller than yearlings from the control areas and from elsewhere in the Kivalliq. Sex, seasons, $\delta^{13}C$, caribou wet weight in stomach, and social structure were not selected in the best LMM model for the scaled $\text{mass}_{\text{Condylobasal}}$ index (Table C3 in Appendix C). Supporting P1, best LMM for sternal fat index indicates an increase of 60.0% (95% CI [7.2:127.2%]) in wolves from the control areas compared with those from the impact area (intercept), whereas wolves from elsewhere in the Kivalliq were not significantly different (Table 3.2b). Yearlings had 43.9% (95% CI [81.5: 21.4%]) less sternal fat than adults. The interaction between area and age was not significant, suggesting that yearlings from control areas were not fatter than yearlings from the impact area. Sex, seasons, $\delta^{13}C$, caribou wet weight in stomach, occurrence of alternate prey, and social structure were not selected in the best LMM model for the sternal fat index.

Table 3.2 Results from the selected linear mixed models (LMM) relating wolves' condition and fat indices to spatial, seasonal, diet, and demographic drivers near Qamani'tuaq, Nunavut, Canada. Intercepts in a) and b) are the impact area, season fall, and age adult. See Table S4 in Supporting Information for a complete description of the candidate models tested. Stars indicate binary (presence/absence) variables. Significant coefficients are in bold.

	Estimate	95% CI (-/+)		d.f.	*P*	Estimate	95% CI (-/+)		d.f.	*p*
a) Condition Index best model						**b) Fat index best model**				
Scaled Mass$_{Condylobasal}$ *fixed effects:*						*Sternal fat fixed effects:*				
(Intercept)	27.95	25.34	30.55	68	0.0001	94.27	47.26	141.27	68	0.0002
Kivalliq	-0.68	-3.31	1.96	68	0.62	-2.43	-43.98	39.13	68	0.91
Control	4.13	0.12	8.13	68	**0.05**	56.57	-6.76	119.91	68	0.08
Yearling	-3.07	-5.29	-0.85	68	**0.009**	-41.39	-76.80	-5.98	68	**0.03**
Winter	1.35	-1.21	3.90	68	0.31	13.80	-26.74	54.35	68	0.51
Spring	-0.06	-2.74	2.62	68	0.96	1.69	-40.82	44.20	68	0.94
Alternate prey*	-2.98	-5.94	-0.02	68	**0.05**	-19.65	-66.25	26.95	68	0.41
Kivalliq: Yearling	0.74	-3.05	4.54	68	0.70	-23.18	-83.31	36.96	68	0.45
Control: Yearling	-2.37	-7.34	2.60	68	0.35	-31.23	-109.72	47.26	68	0.44
Kivalliq: Alternate prey*	0.56	-5.86	6.98	68	0.86	68.22	-33.59	170.03	68	0.19
Control: Alternate prey*	-3.17	-11.60	5.26	68	0.46	-107.33	-240.13	25.47	68	0.12
Random effect:						*Random effect*:				
Year	0.8					Year	23.9			
Residual	3.6					Residual	56.6			

3.5.2 Changes in behaviour of wolves (P2)

Five of 12 informants reported that wolves seen within the community exhibited abnormal ‘starving’ behaviour. Two of 12 informants also reported starving behaviour in wolves from the impact area. Supporting P2, four of 12 informants reported that wolves from the impact area were easily scared of humans travelling by snowmobile and carrying rifles and ran away (Quote # 03 in Appendix C), whereas 7/8 informants reported that wolves from control areas were not scared of, did not run, and could even come close to humans, exhibiting a ‘tame’ behaviour (Table 3.1-2).

3.5.3 Changes in wolves’ social structure (P3)

Supporting P3, four of 7 informants reported that yearlings were the most often seen in the community, 1/7 that ‘alpha’ individuals are never seen around town, and 2/7 that alphas were still in the impact area but harder to find and catch. Four of 5 reported more alphas in the control area (Table 3.1-3), supporting P3. Six of 17 informants reported that wolves were seen alone in the community. Supporting prediction 3, three of 17 informants reported that wolves from the impact area were more commonly seen alone and more rarely in packs than wolves from the control area. Also supporting P3, seven of 17 informants reported wolf packs size of between 2-3 to 4-6 ind./pack in the impact area, which was smaller than the number reported in the control area (between 7-8 to 8-12 ind./pack) by nine of the same 17 informants who commented on the social structure topic (Table 3.1-3, Quote # 04 in Appendix C).

3.5.4 Changes in diet and feeding behaviours (P4)

Contradicting P4, the best LMM on δ^{13}C and δ^{15}N indicated no effect of the area on isotopic variation (Table C4 in Appendix C). Also contradicting P4, the best LMM on stomach contents indicated no effect of the area on caribou wet weight and on the presence of alternate prey (Table C4 in Appendix C).

Local hunters and Elders did not report any difference in use of prey by wolves among the impact and control areas. Yet they provided valuable observations on temporal changes in prey abundance observed in the impact area. Eleven of 16 informants reported that caribou abundance has decreased and/or distribution has changed (in ca. the last 4-5 years) in the impact area (Quote # 05a in Appendix C), whereas 2/16 estimated that it has not changed (Table 3.1-4). In addition, three of 16 informants reported that more caribou remains were left on the tundra by local hunters (than ca. 4-5 years ago, Quote #05b in Appendix C). Six of 6 informants reported an overall increase in muskox abundance compared to the 80s or 90s (Quote # 06 in Appendix C). These observations led the informants to five food-related (and non-exclusive) hypotheses that can provide some support to P4 (Table 3.1-4). Five of 16 informants suggested that the social disruption caused by the harvest of parents (alphas) can prevent hunting of caribou by wolves, resulting in low food intake in yearlings (Quote # 07 in Appendix C). Two of 16 informants suggested that the perpetual disturbance of wolves by snowmobile traffic and noise can lead to less feeding time (Quote # 08 in Appendix C). Two of 16 informants suggested that increased scavenging behaviour by wolves on caribou leftovers from hunters can lead to less food intake when compared to caribou hunted by wolves (Table 3.1-4). Four of 16 informants suggested that the decreased caribou abundance affects food intake in wolves, and 1/16 suggested that wolves can switch to smaller prey (such as lemmings), which decreases the food intake. Finally, two of 16 suggested that coldness, rather than food, can decrease wolf condition.

Interestingly, monitoring results revealed some similar trends linking the use of caribou to the body condition of wolves. We found a positive (and near significant) correlation between $\delta^{13}C_{Liver}$ and the scaled $mass_{Condylobasal}$ index, (1.16, 95% CI [-0.09:2.42], p=0.07) as well as between $\delta^{13}C_{Muscle}$ and the scaled $mass_{Condylobasal}$ index (1.77, 95% CI [-0.24:3.78], p=0.09). This suggests a positive association between the assimilation of caribou (caribou show the highest $\delta^{13}C$ ratio among tundra herbivores) and the body condition of wolves. In addition, the presence of alternate prey (muskox and small mammals) in wolf stomachs was negatively correlated (-2.97, 95% CI [-5.94:-0.02], *p*=0.05) to the scaled $mass_{Condylobasal}$ index (Table 3.2).

3.5.5 Hunters' perception of the drivers affecting hunting pressure (Table 3.3)

Wolf state

Four of 13 informants reported that wolves are sensitive to industrial activities (3 of them reported on the loss of breeding habitat, Quote # 09 in Appendix C), 8/13 reported that wolves have already adapted their behaviour to industrial activity and are not likely affected (Quote # 10 in Appendix C), and 1/13 reported that wolves can be affected by industrial activities through impacts on caribou (Table 3). Fourteen of 21 informants reported direct industrial impacts on caribou (migratory pattern (4/21), road as a barrier (3/21), pollution (2/21), disturbance and avoidance (4/21), taste (1/21), Quote #11a,b in Appendix C). On the other hand, seven of 21 informants reported that caribou are not disturbed by industrial activities or that changes in caribou distribution nearby the community are not due to industrial activities (Quote # 11c in Appendix C).

Table 3.3 Summary of the perceptions reported by eight long-range hunters and ten elders on the potential impact of exogenous drivers on resource state (1), hunting efficiency (2), resource demand (3), hunting practices (4) and hunting pressure (5), which are the main components of the wolves-human subsistence social-ecological system at play in Qamani'tuaq, Nunavut (see Figure 1). The numbers of informants reporting each observation is indicated. Observations related to changes through time are indicated by one star when changes occurred over 4-5 years and two stars when they occurred over a decade.

	Observations	No.
1) Resource state		
Industrial activities on wolves	Wolves or any animal will never have a den near a road or camp, near human	3
	They are sensitive to human constructions/activities	1
	That's the only threat I see for wolves, through caribou though not directly	1
	They are changed now, not bothered by camp and road	6
	Mining activities do not affect them as they do for caribou	1
	They seem attracted to the noise	1
Climate Change on wolves	Snow period is shrinking; wolves need snow and ice to catch caribou easier	4
	Snow is harder like cement now, no good for igloo building	5
	Weather seems a little cooler now, late spring	1
	The warming benefit wolves because it's less cold, but it impacts caribou	1
Industrial activities on main food source	Caribou change migration route because there are too many explorations	4
	Road affects the caribou behaviour they are reluctant to cross	3
	Dust and fume pollution affect caribou	2
	We are surrounded by mining activities…it makes the caribou go away	2
	The mining companies make the caribou taste different	1
	Even the experienced hunters come back empty-handed, need to go further	2

	Caribou are not bothered by the road and camp, they come close by	5
	Caribou moved away because of other factors (vegetation, rain)	2
	It's hard to say	2
Climate Change on main food source	Drier summer can bring micro cuts on hooves and swollen hoof disease	2
	Summer rain is less, rain makes the plants grow for caribou, for meat and fur	3
	Extreme mild in the winter: rain makes caribou food icy and they move away	4
	Caribou migration routes are impacted by warmer spring with no ice	1
	More mosquitoes at summer for caribou	2
	Too hot in summer: used to be areas with snow patches where caribou cool down	3
	The weather is changing a lot, the meat tastes different	1
2) Hunting efficiency		
*Mine access road**	After they built the road to the mine wolves became skinnier and skinnier	2
	More people go to the land now because there is a road	3
	It's much easier now to go hunting by the road (for caribou and wolves)	3
	It's even easier in the winter using the road as guidance	1
	Road makes it easier to spot wolves	1
	It's rocky there we used to travel slow, travel time is faster with a road	3
Cash income and technology	You can travel faster and further now with newest machines (skidoos)	6
	Hunters have money and technology, if they don't catch, they'll just go back	1
	We have better technology, but it is regardless when you're in remote areas	1
	People are getting more wolves now that there are fast snowmobiles	3
	There are too many skidoos now they bother animals	1
3) Resource demand	I hunt wolves for incomes mainly	11

Community harvest for fur trade	I hunt wolves for clothing when needed	6
	There are more people hunting wolves now, more need for incomes for families	3
	A lot of new people are catching wolves now, people I've never seen hunting**	1
4) Hunting practices		
Spatial scale	Only a handful of people/families know remote areas now	3
	From Baker to Whitehills (North)	8
	The mine site it was hunting area but now it's regulated, it affects hunters	2
Timing	Only day trip now	8
	Nobody is doing it full time now, even healthy people	1
	We work week and hunt weekend now	1
Knowledge loss	I'm not hunting as far as before, once a month when I'm off from mine	3
	in 20 years from now the guys are going to know less but they will have GPS	1
	You have to maintain your way of life when you go far to remote areas	3
	Traditionally we followed animal cycles hunting caribou, wolves and others	1
	20 years ago just about everyone would be considered as hunter	1
	Big brothers and parents used to teach the youth, it's changed now	2
5) Hunting pressure	More disturbed and overhunted North to the community than in remote areas	5
	Too many hunters North to the community*	4

Climate change was also mentioned as a driver of wolf state, either directly or indirectly through its food sources. Nine of 11 informants suggested that climate change could potentially impact wolves by hardening the snow cover and thus decreasing hunting efficiency, whereas 2/11 believe that weather is only slightly changed and this is not likely to affect wolves, or could benefit them. Eight of 16 informants reported that drier summer (3/8) and extreme events of milder temperature during winter (4/8) can affect the caribou food quality and impact caribou energy and fat intake. One of 8 informants reported changes in caribou meat taste. Two of 16 informants believed that drier summer cause the spreading of hoof disease in caribou. Six of 16 informants believed that the warmer summer is adverse to caribou condition, either by increasing mosquito harassment on calves and adults (2/6) or by decreasing the availability of cool areas (river sides, snow and ice patches) causing them to overheat (3/6). One of 6 informants also mentioned that warmer spring temperature and the early melt of water bodies can impose potential barriers to caribou migration. Informants generally believed that caribou hunting pressure is higher nowadays in the impact area (mainly because of the access road) which decreases their numbers and the amount of food available to wolves. However, two Elders believed that the hunting pressure on caribou is less overall (Quote # 12 in Appendix C).

Harvest efficiency

Informants generally perceived that their hunting of both wolves and caribou has become more efficient nowadays. Two of 13 informants perceived that the presence of the access road directly relates to a decrease in wolf condition due to the increased number of hunters (Quotes # 13 in Appendix C), and 11/13 perceived that the road greatly increased hunting efficiency (more people are going hunting now (3/11), it is easier to go hunting (4/11) and spot wolves from the road (1/11), travel is faster (3/11)). Six of 12 informants reported that use of snowmobiles enable hunters to travel faster and further to track animals, and 3/12 reported that people catch more wolves nowadays. One of 12 informants reported that technology does not influence harvest efficiency in the most remote areas.

Demand for wolves

Informants perceived that the growing need for income contributes to increasing hunting pressure on wolves. Eleven of 17 informants mentioned that they hunt wolves solely for incomes, and 6/17 that they hunt for income and for clothing material. Three of 4 informants reported that more people are hunting wolves nowadays, and 1/4 reported that new wolf hunters are seen nowadays (Quote # 14 in Appendix C).

Hunting practices

Eight of 13 informants reported that traditional hunting areas are less frequented than areas closer to the community, 3/13 that fewer people have knowledge of remote areas, and 2/13 that the mine site was an actual traditional hunting ground and was lost due to mining regulations. Eight of 13 informants reported that most people go hunting on day trips nowadays, and 5/13 that they go hunting less frequently than before giving their work obligations at the mine (Quote # 15a in Appendix C). Eight informants commented on the loss of hunting practices and knowledge due to the modern way of life (Quote # 15 b,c in Appendix C).

Hunting pressure

Five of 9 informants reported that the wolves are more impacted and overhunted in the impact than the control area, and 4/9 believed that there are too many ‘day-trip’ hunters nowadays (Quote # 16 in Appendix C).

3.6 Discussion

We used local observations and monitoring data to examine, in an industrial development context, the impacts of subsistence hunting on a wolf population near Qamani'tuaq, Nunavut, Canada. Our results suggest that wolves from an area impacted by industrial activities had lower body condition and fat reserves, showed individual stress in the presence of humans, and had disrupted social structures compared with wolves from a control area (supporting our predictions 1 and 3). On the other hand, the diet of wolves likely did not vary among areas (contradicting prediction 4). Yet local observers perceived that feeding behaviours changed in the impact area in reaction to the elevated hunting pressure. Using a subsistence SES conceptual model (Fauchald *et al.* 2017), we provided a first step into the disentangling of complex human-resource interactions coupled to extrinsic drivers. Local hunters and Elders generally perceived a higher hunting pressure in the impact than the control area due to increased harvest efficiency (caused by use of a mine access road and a greater access to modern transportation and hunting technologies), a higher demand for wolf pelts, and some changes in hunting practices (such as more short-distance and weekend hunting). Local observers also believe that industrial activities and climate change can influence the state of wolves by affecting the availability and quality of caribou, both through direct disturbance and habitat degradation.

3.6.1 Effects of hunting pressure and prey availability on wolves' state

Local hunters hypothesized that elevated harvest could disrupt wolf social structure by reducing pack size and removing alpha individuals, thus leaving the juveniles unable to kill caribou. They also hypothesized that persistent hunting decreased feeding time and caused stress (Table 3.1-4). Several empirical studies have demonstrated that wildlife can experience physiological stress from heavy hunt (Bryan et al., 2015), hunting pursuit (Bateson and Bradshaw, 1997), snowmobile activity (Creel *et al.* 2002; Cluff *et al.* 2010), anthropogenic activities (Llaneza *et al.*

2016), and social disruption caused by hunting (Gobush et al., 2008). Other studies (*e.g.* Hayes *et al.* 2000; Wydeven *et al.* 2004; Zimmermann 2014) also suggest that hunting can decrease wolf pack size, thus altering hunting and foraging patterns, increasing time spent to defend kills from competitor species, and increasing likelihood of conflict with humans because wolves from small packs are more likely to visit communities, local dumps, and mine sites Table 3.1-3).

On the other hand, some other hunters related the decrease in wolves' condition to a decline in local caribou abundance and quality in the impact area, suggesting that alternate resources are insufficient for wolves to thrive (Table 3.1-4). Klaczek et al. (2016) recently demonstrated a relatively strong numerical response of tundra wolves preying on a declining caribou herd, suggesting that wolves can be impacted by the decrease of a single prey base. Here, our diet analyses could not detect any significant association between caribou use and wolf conditions and fat indices, yet some results indicated positive trends between caribou assimilated and condition index (see results section for prediction 4). Our results nonetheless highlighted a significant and negative correlation between the use of alternate prey such as muskox and small mammals, and body condition of wolves (Table 3.2). This result aligns with the findings of Klaczek et al. (2016), and suggests that alternative prey can not fully sustain a good body condition in wolves, at least in our study area.

3.6.2 Effects of industrial development

We found no significant differences in wolves' condition and fat indices between the impact area and the other settlements in the Kivalliq region of Nunavut (Table 3.2), suggesting that hunting pressure can be elevated enough to impact conditions even in contexts where the industrial development is not in play. Similarly, Bryan et al. (2015) reported higher levels of physiological and social stresses and increased reproductive activity in hunted tundra wolves compared with unexploited boreal wolves (after controlling for habitat effects). Moreover, this study collected ca. one third of its tundra/taiga wolf sample nearby Qamani’tuaq during winters 2007 and 2008, *i.e.* at the very beginning of the construction of the access road and the mining exploitation (Bryan *et al.* 2015).

Alternatively, based on our SES framework (Figure 3.1), it is likely that industrial activities do influence some components of the subsistence SES (positively or negatively), but that the sum of these effects does not increase the harvest pressure. For example, the positive influence of mining development on harvest efficiency (access road and access to technology) can be counterbalanced by its negative influence on wolf demand, for example by providing more lucrative sources of incomes to hunters (see Fauchald *et al.* 2017). Mine-employed hunters depend less on subsistence harvesting for living and hence diminish their personal wolf harvest, whereas non-employed hunters may behave conversely and increase wolf harvest. The influence of development on hunting pressure can thus depend on the socio-economic situation of the hunters themselves, which in turn determines the demand. In addition, development can promote cultural globalization and modernization of lifestyle which can lead hunters to depart from, or to conduct less often, traditional hunting practices which can also diminish hunting pressure (Table 3.3-4, see also Fauchald *et al.* 2017). Mine wages can also, for long-range hunters, subsidize equipment and costs for the maintenance of traditional hunting practices, thus contributing to lowering the harvest in the impact area (Quote # 18 in Appendix C). A closer characterization of hunters’ socio-economic situation (including employment at the mine), cultural and family values, and hunting habits would help to further test these hypotheses.

3.6.3 Unsustainable wolf hunting and local collective efforts

Did the in Qamani’tuaq subsistence SES transition into an unsustainable stage? The perception of the local hunters and Elders on that issue was controversial. Most Elders perceived that the wolf population was increasing and thus encouraged younger hunters to harvest wolves, whether wolves were in good condition or not, because they can reproduce and recover quickly (Quote # 19a,b in Appendix C). On the other hand, most hunters perceived the changes in wolf condition, behaviour and pack size (Table 3.1) as a problem that may affect the populations on the long-term (Quote # 20 in Appendix C). Interestingly, conservation biologists also disagree on how wolf populations can cope with hunting pressure (Orians 1997). Most of them assume that northern wolves, through adjustment in recruitment, can sustain moderate harvest pressure, up to an annual harvest of 25-50%, without significant changes in population size (reviewed in Haber 1996). However, emphasis on the numerical status of wolves may overlook the long-term implications of exploitation on social group composition and genetic structure (Haber 1996; Sidorovich *et al.* 2007; Rutledge *et al.* 2010; Bryan *et al.* 2015). Wolves may be particularly sensitive to social disruption because their complex social structure influences many aspects of their population dynamics (Haber 1996). Genetic studies also documented high levels of inbreeding (Moura *et al.* 2014) or decreased genetic diversity (Leonard, Vilá & Wayne 2005) in wolves responding to unregulated harvest, with consequences on the long-term viability of populations. In our study, local observations suggest evidence of reduced pack sizes. This requires further investigation, including quantitative measurements of the social composition and genetic structure of wolves in the impact area (Rutledge *et al.* 2010). Such research should also include information on the persistence of socially important and reproductive individuals within packs, as the large population turnover in overharvested populations can bear ecological and evolutionary implications (Rutledge *et al.* 2010).

What local strategies should be privileged to diminish the hunting pressure on wolves? Due to the colonial history of game management in Qamani’tuaq (Kulchyski

& Tester 2007), local hunters were reticent to the implementation of quotas by government in the impact area (Quote # 21 in Appendix C). One local hunter with experience in wildlife co-management suggested that, if quota regulation is to be implemented, it would need to come with compensatory measures for wolf hunters and their families, because they would suffer from subsistence-based income loss (Quote #22 in Appendix C). Compensatory programs have been employed with relative success in farmlands to support wolf conservation efforts (e.g. Naughton-Treves *et al.* 2003; Agarwala *et al.* 2010). Yet, this incentive may not be an appropriate option in Qamani'tuaq as it would not include hunters' perspectives, knowledge and capacity to engage with the management of their own resources, perpetuating colonial game management practices (Kulchyski & Tester 2007). Instead, a community-based conservation initiative, including local wolf monitoring programs as used in this study (see also Johnson *et al.* 2015a), may be more appropriate. Such conservation initiatives are employed in a number of social-ecological systems worldwide (Hackel 1999; Armitage *et al.* 2009; Gutierrez, Hilborn & Defeo 2011; Cinner *et al.* 2012) including in the Arctic (Kendrick 2013). In Qamani'tuaq, such a program could help to better incorporate local socio-economic and cultural priorities, and enhance local leadership and collective ownership by local hunters in decision-making. In addition, it would increase compliance with local-made regulations, and increase monitoring and surveillance capacity for a more efficient and ethical collective effort to avoid over-harvest of wolves and potential impacts on natural and human systems (Gutierrez *et al.* 2011; Fauchald *et al.* 2017).

3.6.4 Methods caveats

By combining biological data with local observations, we were able to address various aspects of the state of wolves (Table 3.1), and converging results (prediction 1: body condition) strengthened our conclusions. The knowledge of long-range hunters and the animal samples they provided from remote (control) areas to the monitoring program were key to determine the impact effects in our study. Yet biological sample size in the control area remained modest (n=12) and we could not retrieve data from the remotest hunting grounds (Figure 3.3a *vs* Figure 3.3b). The local observations provided could nevertheless compensate this limitation. In future research, increasing the sample size, for instance by adjusting the cash subsidy to compensate for the additional costs of long-range hunting, could help to validate our conclusions (prediction 1: body condition) and to further evaluate other questions (prediction 4: diet and feeding behaviours).

Our study design did not allow testing of potentially confounding habitat effects between the impact and the control areas (see Bryan *et al.* 2015). Yet the biophysical and ecological features of both the impact and control areas were typical of the arctic tundra (Kivalliq Ecological Land Classification Map Atlas 2015), and local observers (including Elders) confirmed that these two areas were traditional 'hotspots' for caribou, and therefore good habitats for wolves. With the ongoing industrial activities and elevated hunting pressure taking place in the impact area, many hunters believed that the habitat of wolves was degraded there, mainly via impacts on caribou (Table 3.3-1 and 3.3-2). Consequently, the perspective of long-range hunters was that, at the time the study was conducted, the control area provided a higher quality habitat for wolves because caribou were more abundant (Table 3.1-4, Quote #17 in Appendix C). In summary, differences in habitat quality between the two areas were likely attributed to the impact effect itself, rather than to naturally occurring differences in habitats that could influence the state of wolves. Clearly, more quantitative and qualitative information is needed to better understand the implication of habitat bias in our study.

3.6.5 Conclusion and recommendations for future research

The community of Qamani’tuaq is in the midst of a long-term and large-scale mining development, including the current expansion of the Meadowbank gold mine project into the new Amaruq project and the development of the large-impact Kiggavik uranium mine project West of Qamani’tuaq (Bernauer 2011). In this context, continued monitoring of wolf populations should help to depict a more complete portrait of the potential for wolf over-harvest, and to provide a good integrative index of ecosystem health (Cluff & Paquet 2003; Sergio *et al.* 2005). To do so, we recommend the following key research areas. Our suggestions stem from our results, take into account the most sensitive SES components (Figure 1), and rely on research methods available elsewhere.

1) In the impact area, the total annual harvest and its demographic structure (sex ratio, age, occurrence of alpha individuals) should be quantified;
2) In the impact area, the annual size of the population (Mulders *et al.* 2007), the physiological stress and reproductive activity of individuals (Bryan *et al.* 2015), and the social composition and genetic structure of packs (Rutledge *et al.* 2010) should be determined. Results should be compared with those from the control area or with data from other unexploited tundra wolf populations;
3) How wolf hunters relate to the various drivers of change (socio-economic situation, livelihood, cultural values, access to technology, use of infrastructure, etc.) and how they can exert a positive or negative influence on the harvest pressure should be examined, with a special attention on how mining development can affect the SES components;
4) The state of the caribou population (population size, indicators of physiological stress, etc.) should be estimated in the impact area, and how this state relates to industrial activities (Boulanger *et al.* 2012) and other drivers such as climate change (Wenzel 2009) should be researched.

Finally, our study illustrates the complementary nature of local knowledge and scientific knowledge, as was found in other systems (Huntington, Suydam & Rosenberg 2004; Gagnon & Berteaux 2009; Polfus, Heinemeyer & Hebblewhite 2014). Importantly, we also suggest the importance of involving local observers in the design of the research to ensure a better fit between local priorities and research objectives.

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Research permits

The collection of biological data on wildlife was approved by the Government of Nunavut’s Department of Environment under Wildlife Research permit # WL-2012-018. The documentation of local observations, perceptions and knowledge with wolf hunters and elders was approved by the Université du Québec à Rimouski under the Certificat Éthique en Recherche # CÉR-67-385 complying with the principles of Canada’s Tri-Council policy for working with human subjects, and by the Nunavut Research Institute under the Scientific Research Licence #03-006-12N-A.

CHAPITRE IV

CONCLUSION

4.1 Originalité et importance de l'étude

L'étude de l'utilisation des ressources alimentaires (la niche alimentaire) par les prédateurs est indispensable pour mieux comprendre la nature et la force des interactions trophiques qui influencent la structure et le fonctionnement des écosystèmes (Legagneux *et al.* 2014). L'utilisation des ressources par les grands carnivores est particulièrement mal connue puisqu'elle peut survenir sur de grandes échelles spatiales, ce qui pose d'importantes contraintes logistiques pour les études de terrain. Ainsi, la majorité des études ayant déterminé la niche alimentaire des grands carnivores se sont déroulées à des échelles locales ou régionales impliquant souvent l'échantillonnage d'un nombre d'individus relativement restreint (p. ex. Urton & Hobson 2005; Darimont *et al.* 2009; Adams *et al.* 2010). En revanche, dans notre système d'étude, la toundra arctique est un milieu très ouvert permettant aux chasseurs de parcourir de grandes distances dans le cadre de leurs activités de subsistance. Au chapitre I, grâce à la mise en place d'une collaboration avec les communautés inuit et les biologistes et gardes-chasse du gouvernement du Nunavut, nous avons été en mesure d'étudier deux espèces sympatriques de grands carnivores sur une aire représentant la quasi-totalité du Nunavut continental (ainsi que l'île Victoria située au nord du continent), soit environ 900 000 km^2. Nous avons également amassé des quantités d'échantillons inégalées chez ces espèces, soit 287 loups et 376 carcajous, ce qui a permis une grande puissance d'analyse et l'examen de plusieurs variables indépendantes. Les deux prédateurs, bien qu'exposés aux mêmes conditions environnementales et aux mêmes ressources, présentaient des contraintes biologiques fort différentes, le loup chassant en groupe et le carcajou étant surtout un charognard solitaire. Ceci nous a permis d'étudier l'effet des contraintes biologiques sur la variation des niches alimentaires. Notre aire d'étude était également un lieu privilégié pour évaluer l'influence de la disponibilité des ressources sur la niche alimentaire des grands carnivores, étant donné sa forte saisonnalité et son hétérogénéité spatiale. Ces deux facteurs déterminaient des patrons très nets dans la disponibilité et la distribution des grands herbivores et dans les opportunités écologiques comme l'accès aux ressources allochtones marines, aux proies locales et aux proies migratrices. À notre connaissance, notre étude est la seule à avoir étudié simultanément la niche alimentaire de plusieurs grands carnivores terrestres à une échelle continentale.

L'analyse des isotopes stables représente un atout pour l'étude de la niche alimentaire d'espèces vivant à faible densité, comme les grands carnivores (Newsome, Clementz & Koch 2010), puisqu'elle peut se faire à partir de tissus (comme les poils) pouvant être récoltés de manière non invasive. Au chapitre II, nous avons développé un partenariat avec le Zoo sauvage de Saint-Félicien (Québec, Canada) afin de déterminer expérimentalement les taux de fractionnement isotopique (carbone et azote) entre les poils et les sources de nourriture de grands carnivores de l'Arctique. Malgré la simplicité conceptuelle de ce genre d'étude, les taux de fractionnement disponibles pour ces prédateurs sont très rares dans la littérature et notre étude vient ainsi répondre à un important besoin méthodologique. Elle est en fait la première à fournir des taux de fractionnement pour le carcajou, pour les loups juvéniles, et pour les poils d'ours blancs et grizzlys. Nos résultats peuvent être utiles dans le cadre d'études appliquées à la conservation des grands carnivores.

En plus de leur importance pour les écosystèmes, les grands prédateurs revêtent une importante composante culturelle et économique pour les communautés autochtones (Clark & Slocombe 2009). Les interactions humains-prédateurs peuvent influencer les populations de prédateurs et l'ensemble de l'écosystème, et le contexte de développement industriel peut quant à lui influencer la durabilité des pratiques de prélèvement. Au chapitre III, nous avons tenté de répondre à une hypothèse générée localement concernant l'impact de la chasse de subsistance sur l'état d'une population de loups près d'une communauté inuit en pleine transformation socio-économique et culturelle. Nous avons utilisé le modèle récent de Fauchald et al. (2017) afin de structurer l'analyse des observations et perceptions locales et des données biologiques. Les études empiriques de ce genre sont très rares dans la littérature (mais voir Fleischman *et al.* 2014; Fauchald *et al.* 2017) et ont permis de mieux comprendre les interactions possibles entre les facteurs de changement tels que les activités industrielles et différentes composantes des systèmes socioécologiques de subsistance (c.-à-d. l'état de la population de loups, l'efficacité de la chasse, la demande de fourrures et les pratiques de chasse). Nos résultats révèlent un potentiel de surchasse du loup, c.-à-d. de pratiques non durables, et peuvent aiguiller la mise en place de mesures pour la protection de l'espèce et de la chasse de subsistance en général. Notre étude se démarque, entre autres, par le haut niveau d'éthique de nos interactions avec la communauté de Qamani'tuaq et par l'intégration de différents savoirs tels que les connaissances locales et les connaissances scientifiques (discutées plus en détail à la section 4.3.4).

4.2 Discussion des principaux résultats

4.2.1 Chapitre I

Nous avons étudié comment l'interaction entre les contraintes biologiques, les opportunités écologiques et la disponibilité de la proie principale (le caribou) influençaient la niche alimentaire du loup et du carcajou de la toundra arctique. Nos résultats indiquent que ces deux prédateurs utilisaient les ressources allochtones marines au cours des mois froids environ de décembre à mai, ce qui causait l’élargissement de la niche isotopique et l’augmentation de la variation interindividuelle chez les deux espèces (Table 1.2, Figure 1.1, Figure 1.2). Bien que l’utilisation des ressources marines par les grands carnivores terrestres soit relativement bien connue (Rose & Polis 1998; Ben-David *et al.* 2004; Adams *et al.* 2010), très peu d’études l’ont documenté chez ceux de l’Arctique (mais voir Rausch & Pearson 1972; Parker & Luttich 1986; Mulders 2001). Pourtant, ce phénomène semble bien connu des chasseurs inuit. L’utilisation de phoques (vivants ou sous forme de restes) serait particulièrement commune durant les mois froids étant donnée leur accessibilité sur la banquise (voir aussi Lai *et al.* 2015).

L’utilisation des opportunités écologiques variait fortement en fonction de la disponibilité des proies préférées. Le carcajou avait une plus grande niche isotopique (et variation interindividuelle) dans les régions les plus nordiques (et moins productives) de notre aire d’étude où le caribou était rare (Table 1.2, Figure 1.1). Ces résultats sont similaires à ceux de Darimont et al. (2009) qui ont démontré que les opportunités écologiques, comprenant des ressources allochtones marines (dans ce cas des saumons), peuvent élargir la niche alimentaire et augmenter la spécialisation individuelle chez les loups côtiers ayant un accès limité aux cerfs-mulets (Figure 0.3). Par contre, dans notre système, le loup avait la plus grande niche isotopique (et variation interindividuelle) dans une région plus productive située au nord-ouest de notre aire d’étude (Table 1.2, 1.4, Figure 1.1), un résultat inattendu puisque cette région offrait un accès aux caribous tout au long de l’année. Toutefois, il est possible que la disponibilité du caribou fût amoindrie dans cette région si la compétition intraspécifique et interspécifique était plus élevée (voir Araujo *et al.* 2011 pour les causes écologiques de variation de la niche alimentaire). L’analyse de la densité des loups et carcajous (deux espèces en compétition) dans cette région pourrait aider à tester cette hypothèse. La niche isotopique du loup était aussi plus grande au nord qu’au sud de notre aire d’étude (Figure 1.1) bien que cette variation n’était vraisemblablement pas associée à l’utilisation de ressources marines, mais plutôt à l’utilisation de proies terrestres telle que les lemmings, les lièvres arctiques, ou encore les renards arctiques qui ont des signatures isotopiques différentes du caribou, mais largement différentes des ressources marines. L’utilisation de ces ressources alternatives par le loup semble commune dans l’Arctique en général (Marquard-Petersen 1998; Mech 2007; Dalerum *et al.* 2017).

De manière intéressante, nos résultats indiquent que les loups et les carcajous peuvent utiliser une grande partie des opportunités écologiques à l’été, c.-à.d. les proies locales et les proies allochtones migratrices (Table 1.2, Figure 1.1) et ce, même si la disponibilité du caribou est maximale au cours de cette période (Nagy *et al.* 2011). L’utilisation de ces proies, facilement accessibles et profitables, par les grands carnivores arctiques est relativement bien connue (Marquard-Petersen 1998; Samelius *et al.* 2002; Wiebe *et al.* 2009).

Finalement, nos résultats suggèrent que la niche alimentaire des prédateurs était influencée par les contraintes biologiques spécifiques à l’espèce, au sexe (carcajou), au statut reproducteur (carcajou), et à l’individu (Table 1.2, 1.3). Le carcajou était plus prompt que le loup à utiliser les ressources marines lorsque la disponibilité du caribou était moindre. Les variations phénotypiques dans la capacité à détecter, capturer, ou digérer les ressources marines peuvent expliquer la plus grande variation interindividuelle de niche isotopique observée chez ce prédateur (Table 1.4, Figure 1.2, revu par Araujo *et al.* 2011). À l’opposé, le loup ignorait largement les ressources marines, et ce même lorsque le caribou était rare (à l’exception de la région du nord-ouest où les signatures isotopiques indiquent une utilisation répandue des ressources marines). Ceci était vraisemblablement dû à la faible profitabilité des ressources marines par rapport au caribou chez cette espèce, qui est grandement adaptée à la chasse aux ongulés (Peterson & Ciucci 2003; Musiani *et al.* 2007; Klaczek *et al.* 2016). En absence du caribou, le loup utilisait préférablement le bœuf musqué comme ressource alternative.

De manière générale, nos résultats supportent l'hypothèse selon laquelle les opportunités écologiques peuvent déterminer la niche alimentaire et la variation interindividuelle des grands carnivores, tel qu'il a été démontré chez d'autres prédateurs généralistes (Layman *et al.* 2007b; Costa *et al.* 2008; Darimont *et al.* 2009; L'Hérault *et al.* 2013; Horswill *et al.* 2016). Toutefois, en supplément à ces études, la nôtre révèle que l'utilisation des opportunités écologiques peut varier grandement entre deux prédateurs sympatriques en vertu des contraintes biologiques qui les distinguent (voir aussi Kernaléguen *et al.* 2015; Yurkowski *et al.* 2016), et selon l'abondance de la proie préférée. Pour de futures études, nous recommandons de déterminer et comparer les densités des populations de prédateurs puisque la compétition peut affecter la disponibilité des proies principales et peut causer la diversification de la niche alimentaire.

4.2.2 Chapitre II

Nous avons déterminé expérimentalement les taux de fractionnement isotopique (carbone et azote) entre les poils et les sources de nourriture de quatre grands carnivores arctiques. Nos résultats indiquent que les taux de fractionnement moyens, pour δ^{13}C et δ^{15}N, de tous les individus (les quatre espèces confondues) étaient plus élevés que les taux moyens mesurés chez 21 espèces de mammifères (Caut et al. 2009). Ce résultat n'est pas surprenant puisque les carnivores ont typiquement des facteurs de discrimination plus élevés que les autres mammifères (Vanderklift & Ponsard 2003; Dalerum & Angerbjorn 2005). Dans notre étude, les taux de fractionnement isotopique variaient entre les espèces et les groupes d'âge (déterminés chez le loup et l'ours blanc seulement). Chez le loup, le fractionnement de δ^{15}N était comparable entre les adultes et les juvéniles, mais le fractionnement de δ^{13}C était plus élevé chez les juvéniles (Table 2.2, Figure 2.1). Nous n'avons pu comparer la différence entre groupes d'âge avec d'autres études puisque notre expérience est la première à fournir des résultats chez les jeunes loups. Cependant, Lecomte et al. (2011) ont obtenu un résultat différent chez le renard arctique où le fractionnement de $\delta^{13}C$ était plus faible chez les juvéniles que chez les adultes. Le fractionnement de $\delta^{13}C$ chez les loups adultes que nous avons étudiés était toutefois comparable aux valeurs fournies par Derbridge et al. (2015), mais deux fois plus faible que celles fournies par McLaren et al. (2015) pour le même tissu. Ceci était probablement attribuable à des différences dans la nourriture donnée aux loups. En effet, dans notre étude et dans celle de Derbridge et al. (2015), plusieurs nourritures avec des signatures isotopiques différentes étaient fournies, alors que McLaren et al. (2015) donnaient une seule nourriture, qui avait donc une signature isotopique fixe. Par contre, le fractionnement de $\delta^{15}N$ était légèrement plus élevé dans notre étude et que dans les deux autres études. Notre expérience est la première à déterminer les taux de fractionnement chez le carcajou, lesquels étaient comparables à ceux des loups adultes. Finalement, notre expérience était également la première à déterminer les taux de fractionnement pour le poil de grizzly et d'ours blanc. Conséquemment, nos résultats ne sont pas comparables à ceux déterminés sur d'autres tissus chez ces espèces (Hilderbrand *et al.* 1996; Rode *et al.* 2016). Le fractionnement de $\delta^{13}C$ était plus élevé chez les ours que chez les loups et carcajous, alors que le fractionnement de $\delta^{15}N$ était plus faible chez les ours que chez les loups et carcajous. Chez l'ours blanc, les jeunes avaient un taux de fractionnement de $\delta^{15}N$ plus élevé que celui de leur mère, ce qui est typique chez les jeunes mammifères non sevrés (Polischuk *et al.* 2001; Dalerum *et al.* 2007; Miller *et al.* 2011).

De manière générale, les taux de fractionnement calculés dans notre étude peuvent être utilisés dans les études écologiques menées en nature. Tout comme les autres études du genre, nous recommandons toutefois d'utiliser ces valeurs avec précaution lorsque la structure d'âge ou de sexe des populations est très hétérogène. Nous soulignons ainsi qu'il est nécessaire de mener de plus amples études expérimentales sur l'effet des différents groupes d'âge (et de sexe) et des variations de sources de nourriture (p. ex. terrestre vs marine) sur les taux de fractionnement des carnivores.

4.2.3 Chapitre III

Nous avons utilisé des observations locales et des données biologiques pour mieux comprendre comment la chasse de subsistance, pratiquée dans une nouvelle réalité socio-économique causée par le développement industriel, aurait un impact sur l'état d'une population de loups près de Qamani'tuaq au Nunavut. Nos résultats indiquent que les loups vivant dans la zone d'impact (près de la communauté inuit et le long de la route menant à la mine) avaient une condition corporelle et des réserves énergétiques diminuées par rapport aux loups vivant dans une zone contrôle éloignée de la communauté (Table 3.2). De plus, les observateurs locaux ont rapporté, chez les loups de la zone d'impact, des comportements apeurés ou d'évitement face aux humains, de même que des structures sociales perturbées (petites meutes, absence d'individus alpha plus fréquente). Dans la zone contrôle, les loups étaient au contraire sans crainte et semblaient même apprivoisés, et ils étaient observés en grands groupes (Table 3.1). De manière similaire, des études ont démontré que les activités humaines en général (Llaneza *et al.* 2016), la chasse de subsistance (Bryan *et al.* 2015), et le dérangement et la poursuite en motoneige (Creel *et al.* 2002; Cluff *et al.* 2010) peuvent affecter les niveaux de stress physiologique des loups. D'autres études (Hayes & Harestad 2000; Wydeven *et al.* 2004; Zimmermann 2014) suggèrent également que la pression de chasse peut contribuer à diminuer la taille des groupes sociaux, ce qui peut affecter l'efficacité à la chasse et donc l'approvisionnement des loups, et ainsi augmenter les risques de conflits avec les activités humaines, puisque les loups s'approchent alors davantage des communautés ou des camps à la recherche de restes de nourriture. De manière intéressante, les chasseurs de notre aire d'étude pensaient aussi que la pression de chasse dans la zone d'impact causait la diminution de la taille des groupes de loups et, conséquemment, affectait la capacité des loups à se nourrir (Table 3.1). Cependant, nos résultats issus des analyses des isotopes stables du carbone et de l'azote et des contenus stomacaux n'ont pas révélé de différence dans l'utilisation du caribou entre les loups de la zone d'impact et ceux de la zone contrôle. Certains chasseurs ont suggéré que les loups de la zone d'impact chassaient moins, mais se nourrissaient davantage de carcasses de caribou laissées par les chasseurs de la communauté, ce qui peut passer inaperçu dans l'analyse des isotopes et des contenus stomacaux (table 3.1). En comparaison aux proies fraîches, les carcasses seraient de moindre qualité nutritionnelle. Cette hypothèse nécessite néanmoins plus d'attention.

De manière générale, les chasseurs et aînés pensaient que le développement industriel pouvait influencer la pression de chasse sur les loups de la zone d'impact en augmentant l'efficacité des chasseurs, qui avaient accès au territoire par la route minière et pouvaient profiter de nouvelles technologies grâce à de meilleurs salaires. De plus, la pression de chasse aurait aussi été intensifiée par la modernisation des pratiques, entrainant notamment une augmentation de la chasse sur de courtes distances et durant les weekends (Table 3.3). Toutefois, l'étude de Fauchald et al. (2017), menée sur des systèmes socioécologiques de subsistance arctiques, suggère aussi que la modernisation pourrait faire diminuer la pression de chasse puisque les chasseurs bénéficiant de meilleurs salaires auraient moins besoin de vendre des fourrures. Les activités industrielles étaient également associées au dérangement et à la dégradation des habitats du loup et du caribou, ce qui a été observé dans différents contextes de développement dans l'Arctique (Johnson *et al.* 2005; Vistnes & Nellemann 2008; Boulanger *et al.* 2012; Kuemmerle *et al.* 2014). Nous recommandons plus de recherche sur les effets cumulatifs du développement industriel et d'autres facteurs comme les changements climatiques sur la chasse au loup à Qamani'tuaq. En particulier, il serait pertinent d'approfondir les liens entre le développement, les conséquences socio-économiques pour les chasseurs, leurs habitudes de chasse et leur récolte annuelle.

L’Arctique, dont la communauté de Qamani’tuaq, est au cœur de développements industriels en pleine expansion. Nos résultats indiquent que certains impacts de l’industrie sur les systèmes socioécologiques peuvent être difficiles à détecter par des mesures scientifiques uniquement et nécessitent l’utilisation des observations et connaissances locales. Dans ce contexte, nous recommandons également les suivis écologiques et communautaires des espèces de haut niveau trophique telles que le loup, puisque ceux-ci sont de bons indicateurs de la santé des écosystèmes (Sergio *et al.* 2005).

4.3 Implications et avenues de recherche

4.3.1 Théorie des niches

Des études récentes (Bolnick *et al.* 2003; Araujo *et al.* 2011) suggèrent que la variation au sein des espèces et des populations de la niche alimentaire est commune chez les vertébrés. Toutefois, on connait encore assez mal quel mécanisme, de la variation interindividuelle (spécialisation) ou la variation intra-individuelle (généralisation), détermine la variation de la niche au sein des populations (Figure 0.2). La théorie de la variation des niches (NVH; Van Valen 1965) stipule que la variation au sein des populations est causée par la spécialisation individuelle (voir Bolnick *et al.* 2007). Toutefois, cette hypothèse a rarement été démontrée chez les carnivores terrestres (Meiri *et al.* 2005). Au chapitre I, nos résultats indiquent que la diversification de la niche alimentaire des loups et carcajous était révélée par une augmentation des distances isotopiques moyennes entre les individus (Table 1.4, Figure 1.2), ce qui tend à supporter la NVH. Toutefois, nos données ne permettent pas de mesurer la composante de variation intra-individuelle qui nécessite une réplication de l'échantillonnage individuel (voir Newsome *et al.* 2012). La spécialisation individuelle peut avoir d'importantes implications sur l'écologie des populations et des communautés, sur l'évolution des espèces, et pour la conservation des espèces en général (Bolnick *et al.* 2011). Nous abordons la première et troisième implication dans les deux sections qui suivent.

4.3.2 Écologie des populations et des communautés

Plusieurs études ont démontré que les ressources allochtones peuvent agir comme subsides pour les consommateurs lorsqu'ils permettent à ces derniers de maintenir des densités plus élevées que ce que permet le milieu (l'hypothèse des subsides; Polis & Hurd 1996, voir aussi Rose & Polis 1998; Legagneux *et al.* 2012). Au chapitre I, nos résultats indiquent que les carcajous et les loups pouvaient utiliser les ressources allochtones en provenance de l'écosystème marin (principalement des phoques vivants ou sous forme de restes) et d'écosystèmes tempérés (oiseaux migrateurs). Selon l'hypothèse des subsides, il est probable que l'utilisation de ces ressources contribuait à maintenir des densités plus élevées de prédateurs (surtout de carcajous), en particulier dans le nord de notre aire d'étude où le caribou est le plus rare. Ceci est d'autant plus plausible que l'utilisation des ressources allochtones par les prédateurs était plus importante à l'hiver et à l'été, les deux périodes les plus exigeantes énergétiquement. L'utilisation de ces ressources peut contribuer à augmenter la survie (à l'hiver) et la reproduction (à l'été) des individus (Persson 2005; Giroux *et al.* 2012). Pour tester ces prédictions émanant de l'hypothèse des subsides, nous recommandons de quantifier la survie et la reproduction d'individus et de comparer ces paramètres selon la niche alimentaire de ces individus. Par exemple, des individus utilisateurs de ressources marines pourraient être comparés à d'autres qui n'utilisent que des ressources terrestres. Les densités de populations allopatriques ayant des niches différentes pourraient aussi être comparées.

L’utilisation de subsides allochtones par les organismes de haut niveau trophique peut avoir des conséquences importantes sur l’ensemble des écosystèmes, à cause de cascades trophiques (Leroux & Loreau 2008). Dans le système que nous avons étudié, de plus hautes densités de grands carnivores pourraient influencer la nature et la force des interactions prédateurs-proies terrestres (Bety *et al.* 2002; Legagneux *et al.* 2014). Dans le nord de notre aire d’étude où la productivité primaire et les densités de grands herbivores sont les plus faibles, de plus hautes densités de prédateurs pourraient même changer la contribution relative des forces de régulation ascendantes et descendantes (Legagneux *et al.* 2014). De plus, nos résultats indiquent que certains individus peuvent se spécialiser sur les ressources terrestres comme le caribou ou sur les ressources marines, ce qui peut limiter la connectivité entre les écosystèmes (Quevedo *et al.* 2009; Matich, Heithaus & Layman 2011b). Pour approfondir ces questions, il serait important de comparer les interactions trophiques entre les grands carnivores et leurs proies terrestres dans des contextes où les ressources marines sont utilisées et dans des contextes où elles ne le sont pas.

4.3.3 Gestion et conservation des grands carnivores

Conservation de la diversité des niches alimentaires

La conservation est communément basée sur la niche alimentaire de l’espèce et ne tient pas compte de la variation au sein de l’espèce ou de la population, ni de la spécialisation individuelle (Bolnick *et al.* 2003). Au chapitre I, nos résultats démontrent que la niche alimentaire des grands carnivores de la toundra arctique peut-être très variable dans le temps et l’espace, même chez le loup pour lequel les mesures de conservation sont typiquement basées sur la prémisse d’une utilisation presque exclusive des grands herbivores (Peterson & Ciucci 2003; Adams *et al.* 2010). Historiquement (mais encore de nos jours, voir Boertje, Valkenburg & Mcnay 1996; Hayes & Harestad 2000), les campagnes d’abattage et d’empoisonnement des loups et d’autres prédateurs reposaient sur la conception d’une niche alimentaire unique et d'un impact nuisible des prédateurs sur les populations de grands herbivores. Nos résultats révèlent que ces mesures peuvent à tort décimer des individus dont la niche alimentaire dévie considérablement de celle de la population, avec le risque de réduire la diversité naturelle (phénotypique et génétique) des niches alimentaires. Ces mesures tendent aussi à sous-estimer l'utilisation (et donc la protection) des ressources alternatives telles que les ressources allochtones, qui peuvent jouer un rôle important dans la dynamique des populations et des écosystèmes (Rose & Polis 1998; Darimont & Reimchen 2002; Mech 2007; Adams *et al.* 2010; Dalerum *et al.* 2017). Conséquemment, nous recommandons plus de recherche sur la variation des niches alimentaires chez les grands carnivores arctiques, afin de développer des mesures de conservation de la diversité des niches alimentaires. Les recherches devraient aussi s'intéresser aux effets de la dégradation et de la perte d'habitats fauniques causés par exemple par le développement ou les changements climatiques(Johnson *et al.* 2005; Post *et al.* 2009; Vors & Boyce 2009) sur les communautés de proies, surtout les grands herbivores.

Chasse de subsistance et pratiques durables

Au chapitre III, nous avons vu que la condition corporelle, les réserves de gras, les comportements, et la structure sociale des loups étaient négativement influencés par la pression de chasse dans une zone située à proximité de la communauté de Qamani'tuaq et des activités industrielles. Ces résultats ont des implications importantes pour la conservation de l'espèce et de l'activité de chasse de subsistance de la communauté. Les perceptions locales sur l'état des populations de loups et la nécessité d'agir pour les préserver étaient très hétéroclites au sein même de la communauté de Qamani'tuaq. Les aînés étaient d'avis qu'il est inutile de protéger les loups puisqu'ils peuvent ajuster leur reproduction en réponse à la pression de chasse. Toutefois, les chasseurs étaient beaucoup plus inquiets et craignaient qu'une pression de chasse excessive puisse affecter les populations de loups. De manière très intéressante, ce désaccord local existe aussi chez les biologistes de la conservation, qui ont des idées contrastées sur la chasse et la capacité d'adaptation des loups (Haber 1996; Orians 1997). Selon Haber (1996), une majorité de biologistes considère que les loups nordiques peuvent subir des taux de récolte annuels de 25 à 50% sans diminution de la taille des populations. Cependant, le même auteur met en garde contre cette idée, car elle ne tient pas compte des conséquences à long terme de la chasse sur la structure et la génétique des populations (voir aussi Sidorovich *et al.* 2007; Rutledge *et al.* 2010; Moura *et al.* 2014). Ainsi, plus de recherche quantitative à long terme serait nécessaire afin de mieux comprendre l'impact de la chasse sur les structures et la génétique des populations de loups arctiques (Moura *et al.* 2014). Dans le cas spécifique de Qamani'tuaq cependant, nos résultats suggèrent une surchasse selon la définition de Haber (1996). Afin d'atténuer ce problème, nous recommandons l'instauration d'un programme de conservation mené par la communauté (voir aussi Hackel 1999; Gutierrez *et al.* 2011 dans d'autres systèmes socioécologiques). Ce programme, par opposition à un système de quotas, aurait l'avantage de prendre en compte les priorités socio-économiques et culturelles de la communauté, de promouvoir le leadership local, d'augmenter la capacité de surveillance des populations de loups et de manière importante, d'augmenter le respect par les chasseurs des règles de récolte définies par la communauté.

4.3.4 Importance des connaissances locales et éthique de recherche

Bien que l'utilisation des connaissances locales dans les études écologiques soit reconnue et promue (Huntington 2011; Diaz *et al.* 2015), les exemples d'études intégrant les connaissances locales aux données scientifiques écologiques sont encore rares (Brook & McLachlan 2008). Au chapitre III, l'analyse combinée des connaissances locales et de données biologiques nous a permis de mieux répondre à nos objectifs de recherche. Spécifiquement, nous avons évalué un plus grand éventail de questions que ce qui aurait été possible en n'utilisant que des données biologiques, puisque les données biologiques ne permettaient de répondre qu'à deux prédictions sur quatre. De plus, les connaissances locales nous ont dans certains cas apporté des réponses plus détaillées. La convergence des résultats provenant des deux approches, comme ce fut le cas pour la condition corporelle des loups, a également permis de renforcer la validité de nos interprétations (Polfus *et al.* 2014). De plus, la prise en compte des perceptions des chasseurs et aînés sur les facteurs influençant la pression de chasse nous a également permis d'explorer les liens entre les facteurs environnementaux, les communautés humaines et la faune, qui sont très difficile à documenter avec des approches de recherche plus traditionnelles. Bien que les perceptions des chasseurs et aînés ne sont pas des observations, mais plutôt des prédictions et des associations basées sur des observations et des connaissances, elles sont pourtant très utiles pour identifier les priorités locales et des pistes de recherche et de conservation. Notre étude souligne donc la complémentarité entre la connaissance scientifique et le savoir local et l'importance d'utiliser ces types de savoir simultanément (voir aussi Huntington *et al.* 2004; Gagnon & Berteaux 2009).

De manière importante, notre éthique de recherche reposait d'abord sur une relation de confiance entre moi-même, chercheur non autochtone, et les chasseurs de la communauté. Cette relation s'est progressivement installée au fil d'expériences et d'une intégration culturelle vécue lors de séjours prolongés dans la communauté au sein de familles inuit. La qualité de ma relation avec la communauté a grandement facilité la profondeur des discussions lors des entrevues, la participation d'acteurs locaux dans le processus de recherche, de même que la validation des résultats. Nous soulignons que la mise en place d'une telle approche est nécessaire pour favoriser le partage de connaissances entre chercheurs et acteurs locaux et assurer que les priorités locales sont bien représentées dans les recherches.

4.4 Limites de l'étude

4.4.1 Niche isotopique et niche alimentaire

Les analyses isotopiques sont très utiles pour étudier la niche alimentaire réalisée par les organismes, c.-à-d. l'ensemble des ressources qu'ils assimilent au cours d'une certaine période de temps. Par contre, la niche isotopique ne renseigne pas exactement sur la diversité des ressources assimilées, mais dépend plutôt de la diversité isotopique de ces ressources (Newsome *et al.* 2015). Les signatures isotopiques des proies sont essentiellement déterminées par les signatures isotopiques des plantes à la base des chaînes trophiques (pour $\delta^{13}C$; voir Tieszen *et al.* 1983) et du niveau trophique des proies elles-mêmes (pour $\delta^{15}N$; voir Deniro & Epstein 1981). Ainsi, la niche isotopique de prédateurs se nourrissant de proies provenant de différents écosystèmes et de différents niveaux trophiques est plus grande que la niche isotopique de prédateurs se nourrissant de proies provenant d'un même écosystème et appartenant toutes au même niveau trophique. Au chapitre 1, nos résultats indiquent un élargissement de la niche isotopique au niveau populationnel, et l'augmentation de la variation interindividuelle des niches isotopiques chez les carcajous vivant au nord de notre aire d'étude, là où le caribou était le plus rare. À l'opposé, la niche isotopique variait relativement peu chez les carcajous et les loups vivant au sud de notre aire d'étude, là où le caribou était plus disponible. Ainsi, il est possible que nos résultats isotopiques sous-estiment la variation de la niche alimentaire des carnivores vivant au sud si ces derniers utilisaient diverses proies ayant des signatures isotopiques similaires. Pour nous affranchir de ce biais, nous avons également analysé les contenus stomacaux des prédateurs pour confirmer l'identité et la proportion des proies consommées. De manière générale, nos résultats indiquent que la variabilité des proies consommées par les prédateurs était plutôt faible dans l'ensemble de notre aire d'étude, hormis dans le nord où la proportion de caribous dans les estomacs diminuait d'environ 30% par rapport au sud. Ce résultat confirme que la faible variation de la niche isotopique des prédateurs vivant au sud de notre aire d'étude était associée à l'utilisation presque exclusive du caribou, ce qui correspond à nos prédictions. Dans les régions du nord, la présence dans les estomacs d’une variété de proies alternatives, dont le lemming, le lièvre arctique, le renard arctique, le poisson et le phoque, a été confirmée. Toutefois, la détection de ces proies était compromise par leur digestibilité plus grande que celle des ongulés (Afik & Karasov 1995). Conséquemment nous recommandons, pour de futures études sur la niche alimentaire de ces prédateurs, de combiner l’utilisation des isotopes et des contenus stomacaux avec de nouvelles méthodes telles que le séquençage génétique des contenus stomacaux et des fèces (Valentini, Pompanon & Taberlet 2009). De plus, l’étude des déplacements des prédateurs et de leur utilisation de la banquise comme habitat hivernal pourrait grandement aider à mieux comprendre les comportements d’approvisionnement et le temps passé à la recherche de proies marines, tel qu’observé chez d’autres prédateurs terrestres arctiques (Tarroux *et al.* 2010; Therrien *et al.* 2011; Lai *et al.* 2015).

4.4.2 Design expérimental

Les études d’impact utilisent typiquement un design d’étude Avant-Après et Contrôle-Impact (Smith 2013). Au chapitre III, nous nous sommes intéressés à l’effet de la pression de chasse sur les loups dans un contexte de développement industriel près de Qamani’tuaq. Pour ce faire, nous avons comparé l’état de deux « populations » de loups, une située dans une zone d’impact et l’autre dans une zone éloignée servant de contrôle. Toutefois, nous ne pouvions avoir accès à des données biologiques sur l’état de la population dans la zone d’impact avant le projet minier. L’analyse de l’effet Avant-Après était impossible. Nous avons partiellement résolu ce problème grâce aux observations des chasseurs, qui ont commenté l’état des loups et des caribous avant et après le développement minier, même si leurs observations étaient assez vagues dans le cas des loups. Les observations concernant la dégradation de l’habitat et la diminution des caribous dans la zone d’impact allaient généralement dans le même sens. Une autre limite associée à notre design est que nos zones contrôle et impact étaient différentes en termes d’habitats, une variable confondante dans notre analyse de l’impact. Toutefois, les caractéristiques biophysiques et écologiques des deux zones étaient typiques de la toundra arctique (Kivalliq Ecological Land Classification Map Atlas 2015) et les chasseurs et aînés considéraient généralement ces deux zones comme étant de bonnes aires de chasse pour le loup et le caribou. Plusieurs chasseurs ont tout de même mentionné qu’ils préféraient chasser dans la zone contrôle, loin de la communauté, là où la pression de chasse était moindre et les loups en meilleure condition. Pour de futures études, il serait important de travailler davantage avec les chasseurs pour tenter de mieux comprendre le biais potentiel dû aux différences d’habitats entre les deux zones et, éventuellement, d’étudier une zone contrôle alternative dont les habitats seraient plus semblables à ceux de la zone d’impact. Pour élaborer un design Avant-Après, il serait important de prendre un nouveau cas d’étude avec une communauté pour laquelle un projet de développement est annoncé, mais pas encore débuté.

4.5 Bilan

En résumé, cette étude apporte une contribution empirique (chapitre I), méthodologique (chapitre II) et appliquée (Chapitre III) à l’écologie des grands carnivores. Ces contributions sont importantes étant donné le manque de connaissances pointues sur ces organismes, et en particulier à de grandes échelles spatiales. L’étude démontre comment deux espèces de grands carnivores toundriques peuvent avoir des niches alimentaires très contrastées, incluant au niveau des variations interindividuelles, en réponse aux patrons régionaux et saisonniers de disponibilité des ressources. Ces résultats permettent de mieux comprendre la théorie des niches et sont utiles à l’écologie des populations et des communautés et à la conservation des grands carnivores. Les flux d’énergie et d’éléments nutritifs entre l’écosystème marin ou d’autres écosystèmes éloignés et la toundra arctique pourraient augmenter les densités de prédateurs et ainsi influencer les interactions prédateurs-proies et le fonctionnement de la toundra, naturellement peu productive. Ces interactions peuvent également être influencées par des facteurs d'origine anthropique tels que les changements climatiques et le développement socio-économique. Notre étude démontre comment le développement industriel peut affecter les interactions entre les écosystèmes et les communautés humaines, dont la chasse de subsistance. De manière importante, cette étude impliquait la contribution des communautés inuit du Nunavut et souligne l'importance de la collaboration entre les chercheurs et les communautés locales afin d'approfondir nos connaissances en écologie tout en respectant l'identité et les priorités des cultures holistiques.

APPENDICE A

All tissue samples were frozen at -20°C until preparation for isotopic analyses. Muscle samples were rinsed in ethanol 70% and cut into small pieces, dried through vacuum lyophilization, and reduced to powder using a grindmill (Cryomill, Retsch ©) (for details see Ehrich *et al*. (2010)). Liver samples were treated as muscle samples. Fur samples were brushed and cleaned in ethanol 70% and then clipped to small particles. All samples were weighed into tin capsules (precision ± 0.01 mg).

Samples were combusted in either a CarloErba NC2500 or a Costech 4010 elemental analyzer (EA) connected via continuous flow to a Finnigan Mat Delta Plus isotope-ratio mass spectrometer. Isotope ratios are represented as permil (‰) ratios referenced against Peedee belemnite carbonate (PDB) for δ13C and atmospheric nitrogen (AIR) for δ15N, according to: $[(^{13}C/^{12}C_{sample})/(^{13}C/^{12}C_{PDB})-1] \times 1000$ and $[(^{15}N/^{14}N_{sample})/(^{15}N/^{14}N_{AIR})-1] \times 1000$, respectively.

Obtaining measures of precision and accuracy is essential for estimating analytical error (Jardine and Cunjak 2005). First, the overall precision was obtained by randomly duplicating a subset of our samples (about one every 15 samples loaded for each tissue). This includes both errors of precision inherent in the mass spectrometer and within-sample variations due to lack of homogeneity of powdered samples. Average absolute difference between duplicates was as follows for the various predator tissue samples: $\delta^{13}C$ = 0.12± 0.21‰ SD and $\delta^{15}N$ = 0.08± 0.06‰ SD (n =51) (liver), $\delta^{13}C$ = 0.13± ‰ 0.16 SD and $\delta^{15}N$ = 0.17± 0.32 ‰ SD (n =55) (muscle), and $\delta^{13}C$ = 0.22± 0.52‰ SD and $\delta^{15}N$ = 0.09 ± 0.08‰ SD (n =22) (fur). Average absolute difference between duplicates was $\delta^{13}C$ = 0.07± 0.06‰ SD and $\delta^{15}N$ = 0.03± 0.03‰ SD (n =15) for prey muscle samples. Precision across spectrometer runs was measured at the Stable Isotope in Nature Laboratory (SINLAB), University of New Brunswick (http://www.unb.ca/research/institutes/cri/labs/sinlab/index.html), using an internal smallmouth bass muscle standard. Obtained measures estimates were -23.4 ± 0.1‰ SD for $\delta^{13}C$ and 12.3 ± 0.1‰ SD for $\delta^{15}N$ (n =101). Finally, accuracy was estimated at SINLAB using a commercially available standard (Nicotinamide, Elemental Microanalysis Ltd.) with the following target ratios: $\delta^{13}C$ = -34.5‰ ± 0.1‰ and $\delta^{15}N$ = -1.7 ± 0.07‰ SD (n = 56).

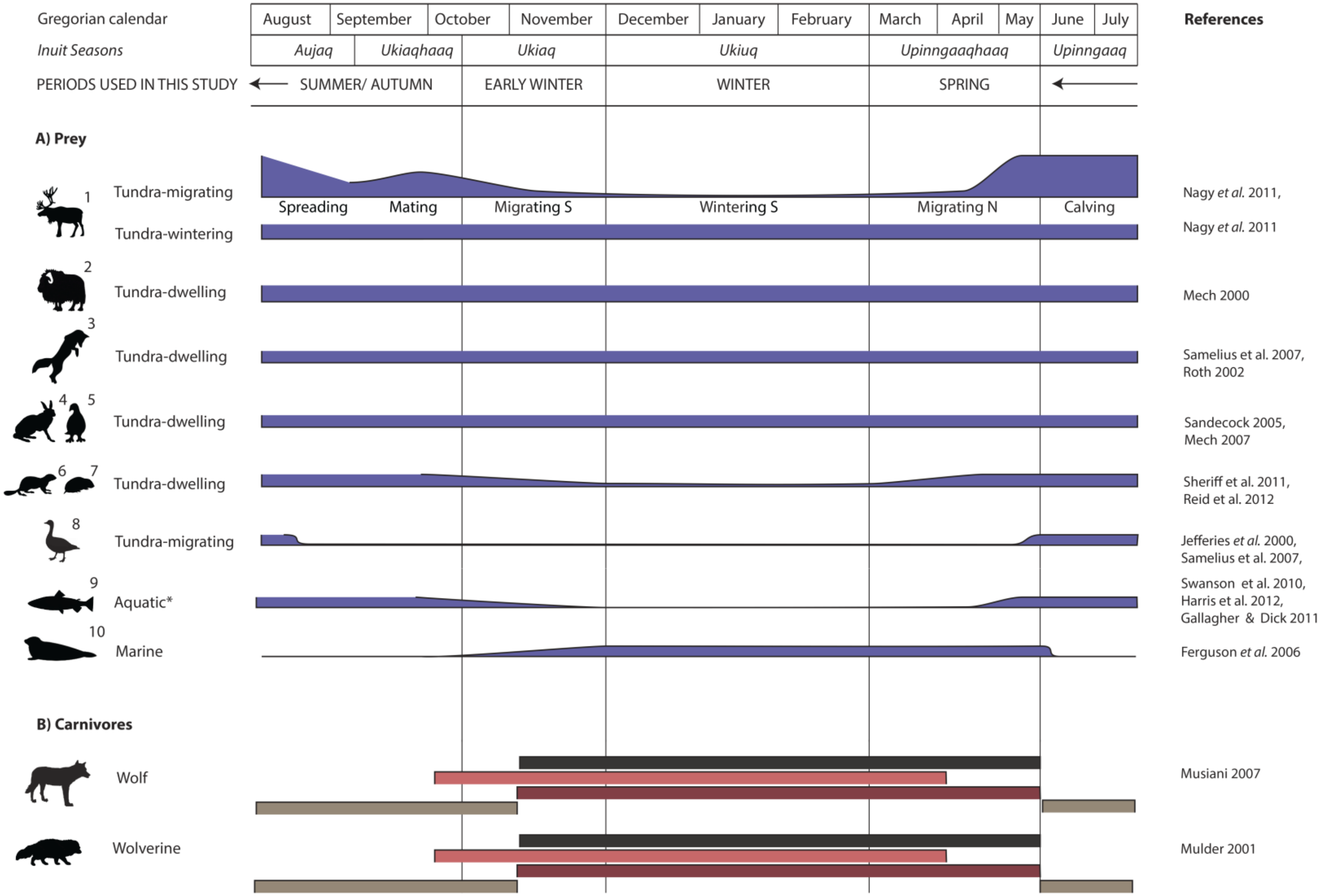
The lipid normalization model derived by Ehrich *et al.* (2010) for terrestrial mammals and birds was applied to correct $\delta^{13}C$ values on muscle samples with C/N ratios above 3.5 for lipid content (for both top predators and prey). We applied the same lipid correction model (Ehrich et al. 2010) to liver samples because they were all enriched in lipids (C:N> 3.5). We have not applied normalization to $\delta^{13}C$ values on fur samples given their very low lipid content (only 10 out of 146 samples had a C:N ratio above 4).

$\delta^{13}C$ and $\delta^{15}N$ ratios were corrected for tissue-specific discrimination (ΔX) based on population average ratios of Arctic foxes *Vulpes lagopus* fed of a known terrestrial diet (Lecomte *et al*. 2011): $\Delta^{13}C$ = +0.51‰ and $\Delta^{15}N$ = +2.68‰ for liver, $\Delta^{13}C$ = +0.95‰ and $\Delta^{15}N$ = +2.51‰ for muscle and $\Delta^{15}N$ = +3.34‰ for fur. For $\Delta^{13}C$ (fur), we used a discrimination ratio of +2.6‰ from red foxes *Vulpes vulpes* fed on a terrestrial diet provided by (Roth & Hobson 2000a). These average ratios were calculated on balanced sex and age ratios. However, sex and age ratio in both predator species were in biased toward males and adults in our study area (1.3 male for 1 female and 1.9 male for 1 female in wolves and wolverines, respectively, and 2.7 adults for 1 juvenile in both species combined). Lecomte et al. (2011) reported that discrimination for $\delta^{13}C$ and $\delta^{15}N$ can vary among sex and age in muscle (from 0 to 0.4‰ and 0.1 to 0.3‰, respectively), and fur (from 0.2 to 0.7‰ and 0.3 to 1.2‰, respectively). Assuming that these results apply to our predator species, we may have overcorrected isotopic ratios (δ^{13}C and δ^{15}N) for sex-specific discrimination (discrimination is typically higher in females than in males), yet we under corrected for age (discrimination is typically higher in adults than in juveniles). Yet sex and age ratio patterns were generally consistent among regions in both species and it is thus unlikely that this bias affected result interpretation. However, age ratios were greater in the spring (7.3 adults for 1 juvenile in both species combined) than in winter and fall (ca. 1.5 adult for 1 juvenile in each species). Discrimination bias was thus considerably reduced in winter, when most isotopic niche variation arose in predators. Overall, the bias associated with intra-population variability in isotopic discrimination was therefore relatively moderate in muscle and likely not much different than the precision and accuracy errors associated with the mass spectrometer (see above). However, we expect the bias to be more elevated in fur tissues (the summer diet), yet the use of population discrimination averages might have contributed to lowering the residual differences between sex and age groups. No data source was available on sex and age discrimination for liver tissue, but population discrimination average is typically lower in this tissue for δ^{13}C, and comparable for δ^{15}N, compared to muscle (Lecomte *et al.* 2011).

Stomach content analysis, preparation and identification

Stomach contents can give an accurate description of the diet recently ingested by an animal ((Killengreen *et al.* 2011), although they underestimate highly digestible food (Afik & Karasov 1995). Stomach contents of 261 wolves and 340 wolverines were analyzed, of which 214 (82%) and 269 (79%) contained food items in wolves and wolverines, respectively. All stomachs were stored at -20^{o}C until analyzed in the laboratory. Defrost stomach contents were washed out and rinsed in water using 0.5 mm mesh sieves and sorted into identifiable prey species or categories using a reference collection of hairs, bones, skulls, and teeth. Items were divided into 10 categories: caribou, muskoxen, Arctic foxes, small herbivores (arctic ground squirrels, arctic hares, muskrats), microtines (lemmings and voles), ptarmigan, waterfowls (geese and ducks), passerine birds, fishes and seals. Wet weight was determined for each item found (±0.01g).

Table A.1 A) Seasonal prey availability to top predators in continental Nunavut; the height of the purple bars is proportional to prey availability. B) Diet periods represented by muscle (pink), liver (dark red), and fur (grey) isotopic signatures as compared with the period during which the carcass collection program took place (black), for each predator species.


Gregorian calendar
August
September
October
November
December
January
February
March
April
May
June
July
References
Inuit Seasons
Aujaq
Ukiaqhaaq
Ukiaq
Ukiuq
Upinngaaqhaaq
Upinngaaq
PERIODS USED IN THIS STUDY
SUMMER/ AUTUMN
EARLY WINTER
WINTER
SPRING
A) Prey
1
Tundra-migrating
Spreading
Mating
Migrating S
Wintering S
Migrating N
Calving
Nagy *et al.* 2011,
Tundra-wintering
Nagy *et al.* 2011
2
Tundra-dwelling
Mech 2000
3
Tundra-dwelling
Samelius et al. 2007,
Roth 2002
4
5
Tundra-dwelling
Sandecock 2005,
Mech 2007
6
7
Tundra-dwelling
Sheriff et al. 2011,
Reid et al. 2012
8
Tundra-migrating
Jefferies *et al.* 2000,
Samelius et al. 2007,
9
Aquatic*
Swanson et al. 2010,
Harris et al. 2012,
Gallagher & Dick 2011
10
Marine
Ferguson *et al.* 2006
B) Carnivores
Wolf
Musiani 2007
Wolverine
Mulder 2001

1- Barren-ground caribou *Rangifer tarandus*, Linnaeus 1758;
2- Muskox *Ovibos moschatus*, Zimmermann 1780;
3- Arctic fox *Vulpes lagopus*, Linnaeus 1758;
4- Arctic hare *Lepus arcticus*, Ross 1819;
5- Rock Ptarmigan *Lagopus muta*, Montin 1781;
6- Arctic ground squirrel *Spermophyllus parryii*, Richardson 1825
7- Collared lemming *Discrostonyx groenlandicus*, Traill 1823, & Brown lemming Lemmus trimucronatus, Richardson 1825
8- Waterfowls: Brant sp., Chen sp.,
9- Freshwater fishes: Salvelinus sp., Coregonus sp.
10- Seal: phoca sp., marine fishes: Salvelinus sp.

Table A.2 Isotopic ratios of the prey groups obtained from prey muscle sampled in the field (lipid-normalized, see Ehrich *et al.* 2010) and from the literature.

	Prey groups[b]	$\delta^{13}C$	$SD\delta^{13}C$	$\delta^{15}N$	$SD\delta^{15}N$	n	Location[i]	Year	Source
1.Main ungulate prey: *(per region[a])*									
SET	Caribou-Summer	-22.86	0.76	4.58	1.07	2	AR	2011-13	1
	Caribou-cold months	-22.06	0.60	4.74	1.13	8	AR	2011-13	1
	Muskox-Summer	-23.45	0.54	3.15	0.61	5	AR	2011-13	1
	Muskox-cold months	-23.45	0.54	3.15	0.61	5	AR	2011-13	1
EB[c]	Caribou-Summer	-22.62	0.59	3.43	0.97	7	RI/BL	2011-13	1
	Caribou-cold months	-21.88	0.70	5.00	1.17	9	RI/BL	2011-13	1
	Muskox-Summer	-22.86	0.14	4.53	0.42	3	RI/BL	2011-13	1
	Muskox-cold months	-22.25	0.70	4.20	0.46	8	RI/BL	2011-13	1
NB	Caribou-Summer	-21.47	0.20	4.13	0.83	29	KL	2011-13	2
	Caribou-cold months	-21.88	0.70	5.00	1.17	9	KL	2011-13	1
	Muskox-Summer	-21.5	1	5.2	0.5	2	KL	2011-13	2
NWT	Caribou-Summer	-24.29	0.51	4.05	0.59	7	KU	2011-13	1
	Caribou-cold months	-23.16	0.51	3.95	0.65	19	KU	2011-13	1
	Muskox-Summer	-24.94	0.26	4.80	1.07	6	CB	2011-13	1
	Muskox-cold months	-23.68	0.58	3.96	1.11	7	KU	2011-13	1

BI	Caribou-Summer	-24.29	0.51	4.05	0.59	7	KU	2011-13	1
	Caribou-cold months	-23.16	0.51	3.95	0.65	19	KU	2011-13	1
	Muskox-Summer	-24.94	0.26	4.80	1.07	6	CB	2011-13	1
	Muskox-cold months	-23.68	0.58	4.80	1.07	7	KU	2011-13	1
2.Alternative preys: (all regions)	Arctic fox-cold months	-24.46	0.41	6.83	0.54	5	BL	2011-13	1
3.Alternative preys: (SET-EB-NEB)	Caribou fawn-Summer	-22.28	0.34	7.15	0.89	9	Bev.L	2012	1
	Passerine-Summer	-22.92	1.02	6.43	1.30	27	RI	2008	3
	Freshwater fish-Summer	-26.29	1.16	10.27	1.02	6	AR	2011-13	1
	Tundra herbivores[d]	-25.65	1.43	2.21	1.08	18	RI/AR	2008/2011-13	1,3
	Marine sources[e]-Summer	-20.63	0.43	15.59	0.58	5	AR	1999-2006/2011-13	1,4
	Waterfowl+Egg[f]-Summer	-23.09	1.63	7.54	0.64	10	AR	2011-13	1
	Seal-cold months	-20.39	0.1	15.8	0.15	3	AR	1999-2006	4
4.Alternative preys: (NB)	Tundra herbivores	-25.29	1.29	2.80	1.09	15	KL/RI	2000-2004/2008	2,3
	Waterfowl+Eggs-Summer	-23.90	1.17	6.85	0.61	154	KL	2000-2004	2
	Marine sources-Summer	-20.64	1.41	16.98	1.85	5	KL/AR	2000-2004/2011-13	1,2
	Seal-/Spring	-20.4	1.9	18.1	1.3	3	KL	2000-2004	2
5.Alternative preys:	Caribou fawn-Summer	-23.95	0.34	7.15	0.89	9	Bev.L[g]	2012	1

NWT-BI	Passerine-Summer	-24.59	1.02	6.43	1.30	27	RI[g]	2008	3
	Freshwater fish-Summer	-26.75	1.18	10.20	1.30	4	KU	2011-2013	1
	Tundra herbivores[h]	-25.48	1.22	1.71	1.23	26	KU/CB	2011-2013	1
	Marine sources-Summer	-23.02	0.75	15.41	1.17	19	KU	2011-2013	1
	Waterfowl+Eggs-Summer	-23.23	1.37	7.61	1.13	9	KU	2011-2013	1
	Seal-Winter/Spring	-22.30	0.20	16.48	0.15	4	KU	2011-2013	1

a. SET: South Eastern Transition, EB: Eastern Barren, NEB: North Eastern Barren, NB: North Barren, NWT: North Western Transition, BI: Barren Island

b. summer: June-Oct., Cold months: Nov.-May

c. caribou and muskox data from the Eastern Barren were used for the North Eastern Barren region

d. Arctic Ground squirrel, collared lemming, rock ptarmigan, and Arctic hare

e. Arctic char and ringed seal

f. Canada goose and snow goose

g. Data from the Eastern Barren region -1.67 (a correction based on the average difference calculated on caribou from EB and NWT)

h. same as d, but includes moose

i. AR: Arviat, RI: Rankin Inlet, BL: Baker Lake, KU: Kugluktuk, CB: Cambridge Bay, KL: Karak Lake, Bev.L: Beverly Lake

Sources- 1: this study, 2: Samelius et al. 2007, 3: L'Hérault et al. 2013, 4: Young, Lesoto &Ferguson, 2010.

Additional information on Table S2: prey clustering

Prey samples were balanced across study regions and seasons, along the 3-year period during which the top predators were sampled. Caribou (tundra dwelling and migratory) and muskoxen were sampled more often than other prey given their importance in the diet of predators and their isotopic similarity. Using a MANOVA, we determined whether the signatures of different prey items were clustered enough to pool their signatures (Phillips & Koch 2002). In addition, preys were grouped according to functional groups (e.g. tundra dwelling herbivores). The prey clusters per region/season are shown in Figure 1 (core article). Variation in the isotopic signatures of prey sources were mostly driven by trophic level differences (*e.g.* large herbivores showed lowest δ^{15}N values than carnivores freshwater fishes) and the source of carbon across ecosystems (*e.g.* δ^{13}C in freshwater fishes <waterfowls < marine sources). We found important variation in large herbivores sources among study regions: mean δ^{13}C difference between Eastern (SET-EB-NEB, and NB) and Western regions (BI and NWT) was -1.60±0.57 SD and -1.34±0.53 SD in caribou and muskox, respectively, while the δ^{15}N difference among Western and Eastern was -0.48±0.87 SD and -0.02±0.84 SD. Caribou and muskox isotopic signatures also varied among seasons: mean δ^{13}C difference between summer and winter (including spring) was 0.68±0.82 SD and -0.08 ±0.76 SD, and mean δ^{15}N difference was 0.48± 1.29 SD and -0.26± 1.15 SD in caribou and muskox, respectively.

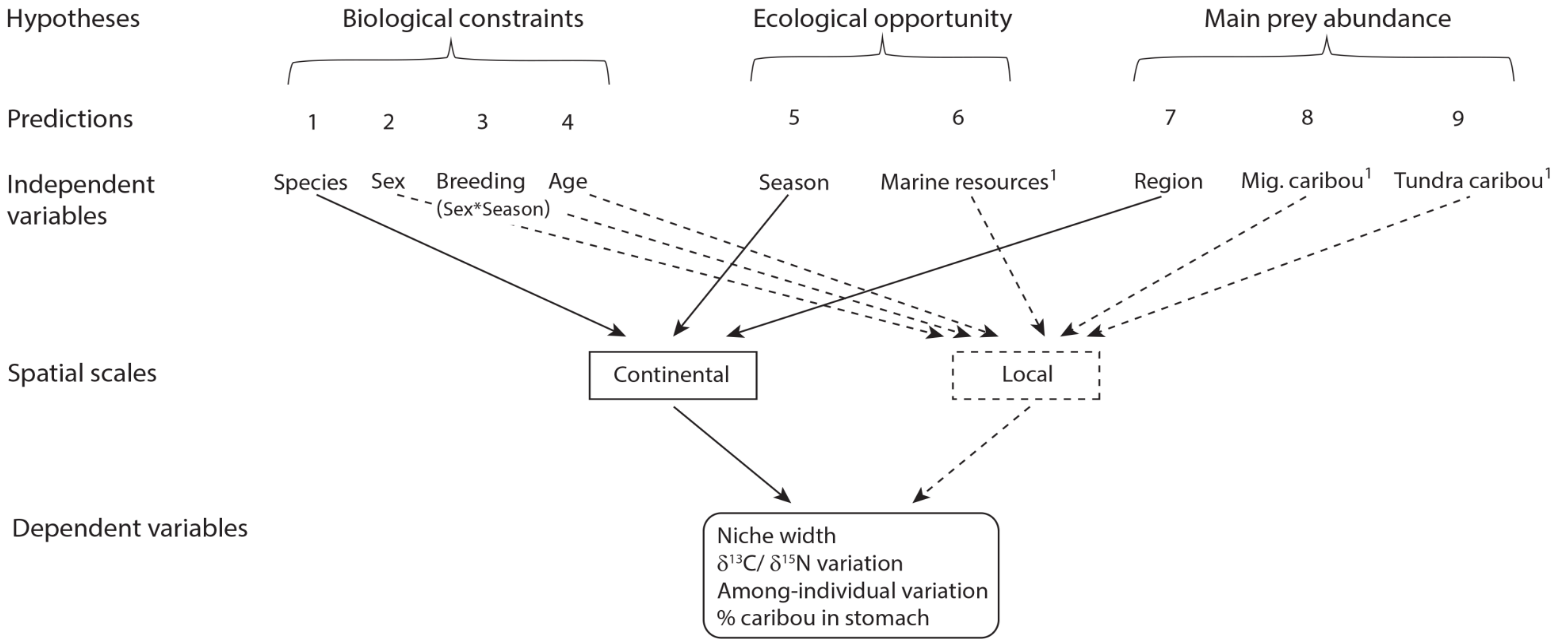


Figure A.1 Summary of the study design illustrating the two complementary spatial scales under which the predictions were tested for the three research hypotheses. Plain and dashed arrows refer to large-scale and local-scale models, respectively. Predictions 6 and 8-9 (superscript 1) refer to the distance between predators' harvest location and marine resources and main prey (see Methods for more details)

Table A.3 Candidate models of linear mixed effect regression (LMEM) tested in this study. A) presents independent variables tested in large-scale models and the results of model selection (AICc) for each dependent variable tested (the three components of niche variation and among-individual variation, see Table 1 in the core article). B) presents the independent variables tested in local-scale models and the results of model selection (AICc) for each dependent variable tested. Intercepts are indicated with an asterisk. In b), the superscripts 1 and 2 indicate when a model was run for wolves only, or for wolverines only, respectively. Selected models appear in bold.

a) *Large-scale models of niche variation in large tundra predators:*

Independent variable	Levels		M1	M2	M3	M4	M5	M6	M7	M8
Species	WF*-WV		X			X	X	X	X	X
Season	Fall*-Winter-Spring-Summer			X		X	X		X	X
Region	SET*-EB-NB-NEB-NWT-BI				X	X		X	X	X
Species:Region								X	X	X
Species:Season							X		X	X
Region:Season										X
Dependent variable										
$\delta^{13}C$		AICc	2961.2	2494.1	2934.7	2469.8	2499.8	2909.2	**2427.5**	2435.6
		ΔAICc	533.7	66.5	507.2	42.2	72.2	481.7	**0.0**	8.0
$\delta^{15}N$		AICc	3672.7	3274.9	3657.1	3262.9	3285.8	3640.5	**3222.1**	3233.3
		ΔAICc	450.5	52.8	434.9	40.8	63.7	418.3	**0.0**	11.3
AIV		AICc	1457.9	1504.6	1501.3	1462.6	1472.6	**1381.5**	1396.2	1396.2
		ΔAICc	76.4	123.1	119.8	81.1	91.1	**0.0**	14.6	14.6

% caribou in stomach	AICc	4250	4250	4196	4179	4232	4160	**4141.3**	na
	DAICc	108.6	108.7	55.1	37.75	90.6	18.7	**0**	na
% muskox in stomach	AICc	3920	3913	3865	3855	3902	3835.6	**3818.7**	na
	ΔAICc	100.9	94.6	46.7	36	82.9	16.9	**0**	na

b) *Local-scale models of niche variation in large tundra predators:*

Independent variable(s)	Levels	M1^2	M2^2	M3^1	M4	M5^2	M6^1	M7	M8	M9
Sex	F*-M	X	X			X				
Age	Adult*-juvenile, young adult, old			X			X			
Season	Fall*-Winter-Spring		X			X				
tEd_Coastline	continue				X	X	X	X	X	
tEd_Migratory caribou	continue				X	X	X	X		X
tEd_Tundra caribou	continue				X	X	X		X	X
Sex:Season			X			X				
tEd_Coastline:tEd_Tun.cbou									X	
tEd_Mig. Cbou:tEd_Tun.cbou										X
tEd_Mig. Cbou:tEd_Coastline								X		
Dependent variable										
1) Wolves:										
δ^{13}C	AICc			1148.4	1149.3		1152.5	1145.4	**1145.9**	1150.1

	ΔAICc			3.0	3.8		7.0	0.0	**0.4**	4.7
$\delta^{15}N$	AICc			1031.4	1027.0		1031.3	1026.5	1025.7	**1009.2**
	ΔAICc			22.2	18.1		22.1	17.3	16.6	**0.0**
AIV	AICc			396.2	357.4		367.2	**354.8**	360.3	379.1
	ΔAICc			41.4	2.6		12.4	**0**	5.5	24.3
% caribou in stomach	AICc			1888	1871		**1856**	1869.8	1877	1860.2
	ΔAICc			31.7	14.9		**0**	13.6	20.9	4.1
% muskox in stomach	AICc			1722	1706		**1693**	1708.1	1707.9	1706.9
	ΔAICc			29.3	13.6		**0**	15.4	15.2	14.2
2) Wolverines:										
$\delta^{13}C$	AICc	1133.5	**1026.7**		1146.2	1033.7		1145.6	1146.2	1145.2
	ΔAICc	106.8	**0.0**		119.5	6.92		118.9	119.5	118.4
$\delta^{15}N$	AICc	1482.4	1494.5		1473.1	1484.4		**1465.1**	1471.2	1477.4
	ΔAICc	16.3	28.4		7.0	18.3		**0**	5.1	11.3
AIV	AICc	668.7	676.8		614.8	624.3		**608.3**	616.1	636.8
	ΔAICc	60.4	68.5		6.4	16		**0**	7.8	28.5
% caribou in stomach	AICc	2335	na		2327	**2317.5**[1]		2322.7	2325.5	2329.1
	ΔAICc	17.4	na		9.9	**0**[1]		5.2	8.1	11.6
% muskox in stomach	AICc	2172	na		2166	**2155.8**[1]		2167.2	2163.8	2165
	ΔAICc	15.8	na		10.7	**0**[1]		11.5	8	9.2

1- Sex:Season interaction could not be tested due to limited sampling size

Table A.4 Results from the selected large scale (a) and local scale (b) linear mixed models relating caribou (and muskox) proportion (%) in the stomachs of wolves and wolverines to species, seasons and regions (a) (predictions 1, 5 and 7 in Table 1), and to sex (wolverine, prediction 2), age (wolf, prediction 4), and the distance to marine resources (prediction 6) and to main prey (predictions 8 and 9)(b). Intercept in a) is species wolf, region SET, and season fall. Intercept in b) is sex male (wolverine), age adult (wolf), and distance 0. In b), distances are transformed Euclidean distances. See Table S3 for the list of candidate models tested. Significant coefficients (p<0.05) appear in bold whereas coefficients with p<0.1 appear in italics.

	Value	%95 CI (-/+)		d.f.	*p*	Value	%95 CI (-/+)		d.f.	*p*
a) Large-scale model										
% Caribou fixed effects						*% Muskox fixed effects*				
(Intercept)	95.9	70.6	121.2	373	**0.0001**	-5.8	-24.6	12.9	373	0.54
Species_WV	-8.4	-41.2	24.5	373	0.62	6.0	-16.2	28.1	373	0.60
Region_EB	-4.4	-26.3	17.5	22	0.70	2.6	-15.0	20.1	22	0.78
Region_NEB	-3.7	-30.9	23.6	22	0.79	-4.0	-25.5	17.5	22	0.72
Region_NB	-36.5	-60.6	-12.4	22	**0.007**	6.5	-12.6	25.5	22	0.51
Region_NWT	-22.8	-46.6	1.1	22	*0.08*	15.5	-3.6	34.6	22	0.13
Region_BI	-78.7	-105.8	-51.5	22	**0.0001**	78.2	56.8	99.6	22	**0.0001**
Season_Winter	-14.9	-35.1	5.3	373	0.15	14.5	1.0	28.1	373	**0.04**
Season_Spring	-8.0	-26.1	10.2	373	0.39	7.6	-4.7	19.9	373	0.23
Species_WV:Region_EB	-3.9	-30.6	22.7	373	0.77	4.4	-13.9	22.7	373	0.64
Species_WV:Region_NEB	-12.7	-49.3	23.9	373	0.50	11.3	-13.4	36.1	373	0.37
Species_WV:Region_NB	-23.7	-57.7	10.2	373	*0.17*	2.5	-20.5	25.5	373	0.83
Species_WV:Region_NWT	-7.5	-33.9	19.0	373	0.58	-6.6	-24.5	11.3	373	0.47
Species_WV:Region_BI	-2.4	-37.7	32.8	373	0.89	-18.1	-41.9	5.7	373	0.14

Species_WV:Season_Winter	12.7	-15.6	41.1	373	0.38	-10.2	-29.1	8.7	373	0.29
Species_WV:Season_Spring	-0.7	-27.5	26.2	373	0.96	-4.9	-22.8	13.0	373	0.59
Random effects						*Random effects*				
Year/Settlement/Residual (SD):	0.005/ 6.8/ 38.8					2.4/ 8.6 / 25.5				

b) Local-scale models

Wolf

% Caribou fixed effects						*% Muskox fixed effects*				
(Intercept)	101.5	75.0	128.0	171	**0.0001**	0.6	-19.9	21.2	171	0.95
Age_juv	-5.9	-18.9	7.2	171	0.38	-4.8	-12.9	3.4	171	0.26
Age_catYA	-6.7	-19.6	6.2	171	0.31	-0.8	-8.8	7.3	171	0.85
Age_Old	16.8	-12.1	45.7	171	0.26	-18.2	-36.6	0.2	171	**0.05**
tEd_Coastline	20.1	-3.4	43.7	171	*0.10*	-21.4	-37.8	-5.1	171	**0.01**
tEd_Mig. caribou	-41.3	-65.9	-16.6	171	**0.001**	17.9	0.7	35.0	171	**0.04**
tEd_Tund. Caribou	-25.1	-45.9	-4.3	171	**0.02**	19.1	3.8	34.5	171	**0.02**
Random effects						*Random effects*				
Year/Settlement/Residual (SD):	1.4/18.6/33.5					0.003/21.5/20.4				

Wolverine

% Caribou fixed effects						*% Muskox fixed effects*				
(Intercept)	41.6	12.7	70.5	209	**0.005**	18.8292	-2.15	39.81	209	*0.08*
Sex_female	-3.3	-15.5	9.0	209	0.60	2.8296	-5.64	11.3	209	0.51
tEd_Coastline	24.9	-3.2	53.1	209	*0.08*	-14.542	-34.3	5.167	209	0.15
tEd_Mig. caribou	10.3	-15.9	36.5	209	0.44	-5.3347	-23.6	12.95	209	0.57
tEd_Tund. caribou	-3.4	-23.6	16.7	209	0.74	13.1896	-0.83	27.21	209	*0.07*
Random effects						*Random effects*				

Year/Settlement/Residual (SD):	9.5/22.7/41.2	0.9/18.9/28.4

APPENDICE B

Table B.1 Guaranteed analyses and main ingredients used in dry commercial dog food fed to captive Arctic carnivores

		Mix #1[a]	Mix#2[b]	Mix #3-4[a,c]		Fox mix[d]
		Zooba	Champêtre	Pro-nature	1st Choice	Fox dev.
Guaranteed	% Lipid (min.)	8	7.5	13	13	11
analyses	% Protein (min.)	21	22	26	23	34
	% Fibre (max.)	6	5	4	4.5	5
Ingredients[e]	Chicken flour		X	X	X	
	Pork flour	X				X
	Fish flour					X
	Chicken fat in tocopherols	X	X	X	X	
	Fat					X
	Wheat flour	X	X	X		X

Grounded corn	X	X	X		X
Brewery rice			X	X	
Soybean meal		X			X
Dried beets		X	X	X	
Dried Yeast		X	X		
Barley				X	
Oat					
linen seeds			X	X	
alphalpha flour			X		
Cellulose					
Calcium carbonate	X	X	X		X
Choline chlorure	X	X	X	X	
Sodium chlorure		X			
Ammonium chlorure					X
Monosodic phosphate			X		
Potassium chlorure		X	X	X	

Vit. And min.	X	X	X	X	X

a. Zooba, Pro-nature and 1st choice are provided by PLB International inc.

b. Champêtre is provided by Tradition^{TM}

c. Dry mix #3 and #4 were 2 batches of bulk commercial dog food mixing the Pro-Nature and 1st Choice brands

d. Fox developer in provided by Purina inc.

e. List of ingredients is provided in decreasing order of importance

Table B.2 Standard meat recipe for terrestrial and marine carnivores from the Canadian Association of Zoos and Aquariums (CAZA) fed to captive Arctic carnivores.

	CAZA-$_{\textit{terrestrial carnivores}}$		CAZA-$_{\text{marine carnivores}}$	
	kg[a]	% of total	kg[b]	% of total
Horse meat	20.00	0.56	5.68	0.71
Fox mix[c]	9.00	0.25	0.00	0.00
Fat	2.30	0.06	0.00	0.00
Liver	1.00	0.03	1.59	0.20
Wheat oil	0.67	0.02	0.00	0.00
Fish oil[d]	0.00	0.00	0.40	0.05
Vit.-Min plus	0.50	0.01	0.18	0.02
Mirra-Coat	0.17	0.005	0.00	0.00
Vit. E	0.04	0.001	0.01	0.001
Taurine	0.00	0.00	0.05	0.01
Thiamine	0.00	0.00	0.06	0.01
Solka-Floc	0.00	0.00	0.09	0.01
Water	2.00	0.06	0.00	0.00
Total	**35.67**	**1.00**	**8.06**	**1.00**

a. Base recipe for 30 feeding days/ 2 animals

b. Base recipe for 3 feeding days/ 3 animals

c. See table S1 for details

d. Fish oil was also supplemented to polar bears as treats

Table B.3 Values used to calculate lipid content (%) and lipid correction factor ($\Delta\delta^{13}C$) to determine lipid-normalized carbon signature ($\delta^{13}C_{LN}$) of diet items fed to captive Arctic carnivores. Value units are in $^{0}/_{00}$.

Diet Item	ID	$\delta^{13}C$	$\delta^{15}N$	%C	C/N	%lipid	$\Delta\delta^{13}C_{Ani.}$	$\Delta\delta^{13}C_{Veg.}$	$\delta^{13}C_{LN}$
Dry mix #1[a]	NL 5706	-19.78	3.06	48.04	9.91	8.00	0.07	0.76	-19.36
Dry mix #1	NL 5704	-19.23	3.28	47.24	9.50	8.00	0.07	0.76	-18.81
Dry mix #1	NL 5705	-20.11	3.12	42.99	9.36	8.00	0.07	0.76	-19.70
						X	**0.07**	**0.76**	**-19.29**
						SD	**0.00**	**0.00**	**0.45**
						n	**3**	**3**	**3**
Dry mix #2[a]	NL 5708	-19.35	2.61	46.45	11.16	7.50	0.01	0.73	-18.98
Dry mix #2	NL 5709	-19.66	2.28	44.93	10.25	7.50	0.01	0.73	-19.29
Dry mix #2	NL 5710	-19.76	2.94	45.15	12.78	7.50	0.01	0.73	-19.39
						X	**0.01**	**0.73**	**-19.22**
						SD	**0.00**	**0.00**	**0.21**
						n	**3**	**4**	**3**
Dry mix #3[a]	NL 5711	-21.22	3.89	50.39	9.01	13.00	0.62	1.11	-20.36
Dry mix #3	NL 5712	-20.75	3.49	49.60	10.58	13.00	0.62	1.11	-19.89
Dry mix #3	NL 5713	-20.91	3.97	51.08	10.35	13.00	0.62	1.11	-20.04
Dry mix #3	NL 5715	-21.77	3.44	49.79	12.06	13.00	0.62	1.11	-20.90
Dry mix #3	NL 5716	-20.38	3.46	50.99	9.49	13.00	0.62	1.11	-19.52
Dry mix #3	NL 5718	-18.79	3.58	48.85	9.06	13.00	0.62	1.11	-17.93
Dry mix #3	NL 5719	-18.70	3.70	51.50	9.02	13.00	0.62	1.11	-17.83
						X	**0.62**	**1.11**	**-19.50**

						SD	**0.00**	**0.00**	**1.18**
						n	**7**	**7**	**7**
Dry mix #4[a]	NL 5720	-24.06	5.52	47.08	9.20	13.00	0.62	1.11	-23.20
Dry mix #4	NL 5721	-22.77	4.81	46.95	9.86	13.00	0.62	1.11	-21.90
Dry mix #4	NL 5722	-22.23	4.88	48.10	8.94	13.00	0.62	1.11	-21.36
Dry mix #4	NL 5723	-20.91	4.02	48.57	7.07	13.00	0.62	1.11	-20.05
						X	**0.62**	**1.11**	**-21.63**
						SD	**0.00**	**0.00**	**1.30**
						n	**4**	**4**	**4**
CAZA meat-tc[b]	NL 5692	-22.61	4.96	52.90	7.12	11.00	0.40	0.97	-22.10
CAZA meat-tc	NL 5693	-22.80	5.23	54.48	7.57	11.00	0.40	0.97	-22.29
CAZA meat-tc	NL 5694	-22.53	4.79	51.48	7.26	11.00	0.40	0.97	-22.01
CAZA meat-tc	NL 5695	-22.85	4.47	54.05	7.44	11.00	0.40	0.97	-22.34
CAZA meat-tc	NL 5696	-22.93	4.60	43.79	7.47	11.00	0.40	0.97	-22.41
CAZA meat-tc	NL 5697	-22.80	4.77	46.87	6.96	11.00	0.40	0.97	-22.29
CAZA meat-tc	NL 5727	-22.94	4.83	53.03	6.66	11.00	0.40	0.97	-22.42
CAZA meat-tc	NL 5698	-22.53	5.07	47.82	6.85	11.00	0.40	0.97	-22.02
CAZA meat-tc	NL 5699	-22.74	5.21	48.21	6.85	11.00	0.40	0.97	-22.22
CAZA meat-tc	NL 5700	-22.94	5.04	52.34	7.69	11.00	0.40	0.97	-22.43
CAZA meat-tc	NL 5701	-23.22	4.69	50.49	7.41	11.00	0.40	0.97	-22.70
CAZA meat-tc	NL 5702	-22.76	4.56	49.43	7.52	11.00	0.40	0.97	-22.25
CAZA meat-tc	NL 5703	-22.49	5.07	52.12	7.69	11.00	0.40	0.97	-21.98
						X	**0.40**	**0.97**	**-22.27**
						SD	**0.00**	**0.00**	**0.21**
						n	**13**	**13**	**13**
CAZA meat-mc[c]	NL 5667	-25.01	5.41	53.28	5.37	27.13	2.17	_	-22.84

CAZA meat-mc	NL 5668	-24.76	5.72	51.97	5.32	26.58	2.11	_	-22.64
CAZA meat-mc	NL 5724	-24.71	5.41	53.22	5.36	26.96	2.16	_	-22.56
CAZA meat-mc	NL 5670	-23.17	5.74	57.41	6.47	38.93	3.47	_	-19.69
CAZA meat-mc	NL 5674	-23.97	6.01	54.30	4.98	22.93	1.71	_	-22.25
CAZA meat-mc	NL 5675	-23.80	6.01	52.48	5.01	23.23	1.75	_	-22.05
CAZA meat-mc	NL 5677	-24.01	5.01	52.12	4.93	22.40	1.65	_	-22.36
CAZA meat-mc	NL 5725	-23.94	4.95	51.13	4.79	20.89	1.49	_	-22.45
CAZA meat-mc	NL 5679	-23.08	5.01	52.00	5.41	27.50	2.21	_	-20.87
CAZA meat-mc	NL 5680	-23.13	5.01	54.96	5.60	29.61	2.45	_	-20.68
CAZA meat-mc	NL 5682	-24.62	5.28	51.90	5.21	25.36	1.98	_	-22.64
CAZA meat-mc	NL 5685	-23.92	5.66	51.55	5.53	28.78	2.36	_	-21.57
CAZA meat-mc	NL 5686	-23.87	5.61	51.86	5.53	28.86	2.36	_	-21.51
CAZA meat-mc	NL 5688	-23.48	6.19	52.97	5.64	30.02	2.49	_	-20.99
CAZA meat-mc	NL 5690	-24.70	5.78	51.65	4.87	21.68	1.57	_	-23.13
CAZA meat-mc	NL 5691	-24.61	5.81	50.97	4.83	21.32	1.53	_	-23.08
						X	**2.09**		**-21.96**
						SD	**0.50**		**0.98**
						n	**16**		**16**
Horsemeat[c]	NL 5669	-27.57	4.25	49.17	3.92	11.58	0.46	_	-27.10
Horsemeat	NL 5671	-25.98	5.41	51.02	3.99	12.29	0.54	_	-25.44
Horsemeat	NL 5676	-26.41	7.14	50.14	3.65	8.63	0.14	_	-26.27
Horsemeat	NL 5678	-24.55	5.73	48.49	3.99	12.32	0.55	_	-24.01
Horsemeat	NL 5681	-25.45	5.19	43.80	3.72	9.34	0.22	_	-25.23
Horsemeat	NL 5683	-24.58	6.43	44.58	3.55	7.60	0.03	_	-24.55
Horsemeat	NL 5687	-26.86	5.41	48.91	3.67	8.85	0.16	_	-26.69
Horsemeat	NL 5726	-26.81	5.32	47.72	3.62	8.33	0.11	_	-26.71

Horsemeat	NL 5689	-26.52	4.97	47.20	3.59	7.98	0.07	_	-26.45
Horsemeat	NL 5730	-23.31	4.65	49.44	3.66	8.69	0.15	_	-23.17
Horsemeat	NL 5707	-23.60	7.34	49.30	3.40	5.93	0.00	_	-23.60
Horsemeat	NL 5728	-23.72	7.42	48.13	3.40	5.96	0.00	_	-23.72
Horsemeat	NL 5714	-27.75	5.36	51.49	4.00	12.40	0.55	_	-27.20
Horsemeat	NL 5717	-24.41	6.76	49.82	3.63	8.44	0.12	_	-24.30
Horsemeat	NL 5729	-24.60	6.81	49.44	3.66	8.74	0.15	_	-24.45
						X	**0.22**		**-25.26**
						SD	**0.20**		**1.39**
						n	**15**		**15**
Herring[c]	NL 5731	-20.12	12.50	48.99	3.62	8.31	0.10	_	-20.02
Herring	NL 5732	-20.17	12.45	48.29	3.60	8.11	0.08	_	-20.09
Herring	NL 5733	-19.84	12.61	46.71	3.38	5.74	0.00	_	-19.84
Herring	NL 5734	-20.62	12.12	47.08	3.63	8.37	0.11	_	-20.51
Herring	NL 5735	-20.52	12.14	48.33	3.56	7.68	0.03	_	-20.48
Herring	NL 5736	-21.95	11.98	48.76	4.34	16.06	0.96	_	-20.99
Herring	NL 5737	-20.50	12.48	47.05	3.43	6.27	0.00	_	-20.50
Herring	NL 5739	-21.46	12.33	55.90	5.30	26.38	2.09	_	-19.37
Herring	NL 5740	-21.44	12.68	54.15	5.10	24.23	1.85	_	-19.58
						X	**0.58**		**-20.15**
						SD	**0.85**		**0.51**
						n	**9**		**9**
Bread[d]	NL 5744	-25.59	4.08	46.30	14.26	_		0.65	-24.93
Bread	NL 5747	-24.83	3.93	45.54	16.58	_		0.55	-24.28
Bread	NL 5751	-25.16	3.65	45.13	13.81	_		0.49	-24.68
Bread	NL 5770	-25.32	3.51	44.49	13.74	_		0.40	-24.92
Bread	NL 5754	-24.64	3.74	46.35	15.48	_		0.66	-23.98

Bread	NL 5757	-25.33	3.72	48.53	14.45	_		0.96	-24.37
Bread	NL 5760	-25.25	3.36	46.24	15.61	_		0.64	-24.61
Bread	NL 5763	-25.30	3.81	46.07	14.75	_		0.62	-24.68
Bread	NL 5766	-24.67	3.50	46.53	14.64	_		0.68	-23.99
Bread	NL 5768	-24.77	4.01	46.38	14.48	_		0.66	-24.10
						X	**0.63**	**0.63**	**-24.45**
						SD	**0.15**	**0.15**	**0.36**
						n	**10**	**10**	**10**
Apple[d]	NL 5755	-27.31	1.19	41.50	207.10	_	_	-0.02	-27.33
Apple	NL 5761	-26.47	0.63	41.21	260.11	_	_	-0.06	-26.53
Apple	NL 5771	-26.36	0.33	40.30	273.73	_	_	-0.19	-26.54
Apple	NL 5764	-25.31	1.01	40.24	209.54	_	_	-0.20	-25.51
Apple	NL 5767	-27.32	1.00	40.68	247.92	_	_	-0.13	-27.45
Apple	NL 5749	-27.04	1.87	41.46	160.29	_	_	-0.03	-27.06
Apple	NL 5752	-28.22	0.48	41.71	208.40	_	_	0.01	-28.22
Apple	NL 5742	-26.33	2.74	40.84	191.32	_	_	-0.11	-26.44
Apple	NL 5758	-27.17	3.71	40.69	103.03	_	_	-0.13	-27.30
Apple	NL 5745	-26.74	2.29	40.93	98.77	_	_	-0.10	-26.84
Apple	NL 5741	-26.43	2.97	41.33	184.66	_	_	-0.04	-26.48
Apple	NL 5769	-26.35	2.31	41.36	193.43	_	_	-0.04	-26.39
						X		**-0.09**	**-26.84**
						SD		**0.07**	**0.70**
						n		**11**	**11**
Carrot[d]	NL 5743	-26.67	5.21	40.07	98.09	_		-0.22	-26.88
Carrot	NL 5746	-25.65	4.27	41.21	66.32	_		-0.06	-25.71
Carrot	NL 5750	-25.41	0.43	40.86	55.09	_		-0.11	-25.52
Carrot	NL 5753	-27.89	8.23	39.61	32.76	_		-0.28	-28.17

Carrot	NL 5756	-27.35	1.52	40.19	30.61	_	-0.20	-27.55
Carrot	NL 5759	-28.07	0.43	39.73	30.49	_	-0.27	-28.34
Carrot	NL 5762	-28.58	4.79	40.98	56.09	_	-0.09	-28.68
Carrot	NL 5765	-28.38	4.42	40.35	36.14	_	-0.18	-28.56
						X	**-0.18**	**-27.43**
						SD	**0.08**	**1.26**
						n	**8**	**8**

a. Dry mix #1-2-3-4: % lipid was determined by Guaranteed Analyses provided by food suppliers (see Table S1). $\Delta\delta^{13}C$ was determined twice using Post et al. (2007)'s equations to account for the mixed content of animal vs vegetal sources in the dry mix. We used equation 4 in Post et al. (2007) ($\Delta\delta^{13}C_{Animal} = -0.81 + 0.11 * \%$ lipid) for animal sources and equation 7 ($\Delta\delta^{13}C_{Vegetal} = 0.20 + 0.07 * \%$ lipid) for vegetal sources. We used the average of animal and vegetal $\Delta\delta13C$ ratios ($\Delta\delta13C_{Mean}$) as correction ratio applied to $\delta^{13}C_{bulk}$.

b. CAZA-tc: %lipid was determined by summing the proportion of fatty items in the recipe (see Table S2) $\Delta\delta^{13}C$ was calculated as in a. above, we applied a proportion of 80% $\Delta\delta^{13}C_{Animal}$, and 20% $\Delta\delta^{13}C_{Vegetal}$ to $\delta^{13}C$

c. CAZA-mc, horsemeat,and herring: % lipid was calculated from equation 5 in Post et al., (2007): % lipid = –30.57 + 10.74 * C/N. $\Delta\delta^{13}C$ was calculated from equation 4 in Post et al., (2007): $\Delta\delta^{13}C$Animal = –0.81 + 0.11 * % lipid.

d. Bread, Apple and Carrot: lipid % was not available and so we calculated $\Delta\delta^{13}C$ from equation 13 in Post et al. (2007): $\Delta\delta^{13}C = -5.83 + 0.14 * \%$ carbon.

Table B.4 Values used to calculate the carbon and nitrogen signatures of the Total Average Diet fed to captive Arctic carnivores

A) For Grizzly bears, wolves and wolverines:

Species	Ind.	Diet item	Daily qte (kg/ind.)	Nb day	Total (kg)	% of diet	X $\delta^{13}C_{LN}$ ($^{0}/_{00}$)	SD $\delta^{13}C_{LN}$ ($^{0}/_{00}$)	X $\delta^{15}N$ ($^{0}/_{00}$)	SD $\delta^{15}N$ ($^{0}/_{00}$)	n
Gb	All	Mix #1	1.8	12	21.8	0.04	-19.29	0.45	3.16	0.12	3
		Mix #2	1.7	10	16.6	0.03	-19.22	0.21	2.61	0.33	3
		Mix #3	2.1	13	27.1	0.06	-19.50	1.18	3.65	0.21	7
		Mix #3	2.6	24	61.5	0.13	-19.50	1.18	3.65	0.21	7
		Mix #3	3.5	11	38.8	0.08	-19.50	1.18	3.65	0.21	7
		Mix #4	3.1	33	103.6	0.21	-21.63	1.30	4.81	0.61	4
		Herring	1.1	103	109.0	0.22	-20.19	0.52	12.38	0.23	10
		Bread	0.3	103	25.8	0.05	-24.45	0.36	3.73	0.23	10
		Apple	0.6	103	64.4	0.13	-26.80	0.70	1.84	1.05	11
		Carrot	0.2	103	18.2	0.04	-27.43	1.26	3.01	2.13	8
		Total			**486.8**						
Wf	All	Mix #1	2.6	12	30.8	0.12	-19.29	0.45	3.16	0.12	3
		Mix #2	2.6	10	25.7	0.10	-19.22	0.21	2.61	0.33	3
		Mix #3	2.6	48	123.4	0.46	-19.50	1.18	3.65	0.21	7
		Mix #4	2.6	33	84.8	0.32	-21.63	1.30	4.81	0.61	4
		Horse	0.1	11	0.7	0.00	-25.26	1.39	6.74	0.83	5
		Total			**265.4**						

Wv	All	CAZA-$_{tc}$	0.68	103	**70.04**	1	-22.27	0.21	4.87	0.25	13

% of diet * X $\delta^{13}C_{LN}$ ($^{0}/_{00}$)	% of diet * SD $\delta^{13}C_{LN}$ ($^{0}/_{00}$)	% of diet * X $\delta^{15}N$ ($^{0}/_{00}$)	% of diet * SD $\delta^{15}N$ ($^{0}/_{00}$)
-0.87	0.02	0.14	0.01
-0.66	0.01	0.09	0.01
-1.08	0.07	0.20	0.01
-2.46	0.15	0.46	0.03
-1.55	0.09	0.29	0.02
-4.60	0.28	1.02	0.13
-4.52	0.12	2.77	0.05
-1.29	0.02	0.20	0.01
-3.55	0.09	0.24	0.14
-1.03	0.05	0.11	0.08
-21.61	**0.37**	**5.53**	**0.22**
-2.24	0.05	0.37	0.01
-1.86	0.02	0.25	0.03
-9.06	0.55	1.70	0.10
-6.91	0.42	1.54	0.20
-0.07	0.00	0.02	0.00
-20.14	**0.69**	**3.87**	**0.22**
-22.27	**0.21**	**4.87**	**0.25**

B) For Polar bears:

Ind.	Diet item	Daily qte (cups/ind.^{1})	Daily qte (kg/ind.)	Nb day	Total (kg)	% of diet	X $\delta^{13}C_{LN}$ ($^0/_{00}$)	SD $\delta^{13}C_{LN}$ ($^0/_{00}$)	X $\delta^{15}N$ ($^0/_{00}$)	SD $\delta^{15}N$ ($^0/_{00}$)	n
Ad. F	CAZA-$_{mc}$		0.9	103	92.7	0.14	-21.96	0.98	5.54	0.40	16
	Horse	2 LBS	0.9	103	93.7	0.14	-25.26	1.39	5.45	0.84	10
	Herring	8	2.1	103	217.9	0.34	-20.19	0.52	12.38	0.23	10
	Mix #1	16 Cups	2.2	12	26.9	0.04	-19.29	0.45	3.16	0.12	3
	Mix #2	16 Cups	2.0	10	20.4	0.03	-19.22	0.21	2.61	0.33	3
	Mix #3	16 Cups	2.6	48	123.0	0.19	-19.50	1.18	3.65	0.21	7
	Mix #4	16 Cups	2.3	33	75.3	0.12	-21.63	1.30	4.81	0.61	4
	Total				**650.0**						
Juv. F	CAZA-$_{mc}$		0.8	103	82.4	0.18	-21.96	0.98	5.54	0.40	16
	Horse	2 LBS	0.9	103	93.7	0.21	-25.26	1.39	5.45	0.84	10
	Herring	4	1.1	103	109.0	0.24	-20.19	0.52	12.38	0.23	10
	Mix #1	8 Cups	1.1	12	13.4	0.03	-19.29	0.45	3.16	0.12	3
	Mix #2	8 Cups	1.0	2	2.0	0.00	-19.22	0.21	2.61	0.33	3
	Mix #2	11 Cups	1.4	8	11.2	0.03	-19.22	0.21	2.61	0.33	3
	Mix #3	11 Cups	1.8	48	84.6	0.19	-19.50	1.18	3.65	0.21	7
	Mix #4	11 Cups	1.6	33	51.8	0.12	-21.63	1.30	4.81	0.61	4
	Total				**448.2**						

Juv. M	CAZA-$_{mc}$		0.8	103	82.4	0.17	-21.96	0.98	5.54	0.40	16
	Horse	2 LBS	0.9	103	93.7	0.19	-25.26	1.39	5.45	0.84	10
	Herring	4	1.1	103	109.0	0.23	-20.19	0.52	12.38	0.23	10
	Mix #1	8 Cups	1.1	12	13.4	0.03	-19.29	0.45	3.16	0.12	3
	Mix #2	8 Cups	1.0	2	2.0	0.00	-19.22	0.21	2.61	0.33	3
	Mix #2	11 Cups	1.4	8	11.2	0.02	-19.22	0.21	2.61	0.33	3
	Mix #3	11 Cups	1.8	26	45.8	0.09	-19.50	1.18	3.65	0.21	7
	Mix #3	13 Cups	2.1	12	25.0	0.05	-19.50	1.18	3.65	0.21	7
	Mix #3	16 Cups	2.6	10	25.6	0.05	-19.50	1.18	3.65	0.21	7
	Mix #4	16 Cups	2.3	33	75.3	0.16	-21.63	1.30	4.81	0.61	4
	Total				**483.6**						

% of diet * X $\delta^{13}C_{LN}$ ($^{0}/_{00}$)	% of diet * SD $\delta^{13}C_{LN}$ ($^{0}/_{00}$)	% of diet * X $\delta^{15}N$ ($^{0}/_{00}$)	% of diet * SD $\delta^{15}N$ ($^{0}/_{00}$)
-3.13	0.14	0.79	0.06
-3.64	0.20	0.79	0.12
-6.77	0.17	4.15	0.08
-0.80	0.02	0.13	0.00
-0.60	0.01	0.08	0.01
-3.69	0.22	0.69	0.04
-2.51	0.15	0.56	0.07
-21.14	**0.40**	**7.19**	**0.17**

-4.04	0.18	1.02	0.07
-5.28	0.29	1.14	0.17
-4.91	0.13	3.01	0.06
-0.58	0.01	0.09	0.00
-0.09	0.00	0.01	0.00
-0.48	0.01	0.07	0.01
-3.68	0.22	0.69	0.04
-2.50	0.15	0.56	0.07
-21.56	**0.45**	**6.58**	**0.21**

-3.74	0.17	0.94	0.07
-4.90	0.27	1.06	0.16
-4.55	0.12	2.79	0.05
-0.54	0.01	0.09	0.00
-0.08	0.00	0.01	0.00
-0.45	0.00	0.06	0.01
-1.85	0.11	0.35	0.02
-1.01	0.06	0.19	0.01
-1.03	0.06	0.19	0.01
-3.37	0.20	0.75	0.10
-21.51	**0.42**	**6.42**	**0.21**

Table B.5 Results from linear mixed models relating changes in $\delta^{13}C$ and $\delta^{15}N$ in fur tissues of captive Arctic carnivores among species, age, sex and tissue types. Intercept is grizzly bear, adult, female, and guard hair.

	Estimate	SE	DF	t-value	*p*
$\delta^{13}C$ fixed effects					
(Intercept)	-19.09	0.24	8	-79.21	0.0000
SpeciesPolar bear	0.11	0.31	8	0.36	0.7268
SpeciesWolf	1.08	0.28	8	3.86	**0.0048**
SpeciesWolverine	-1.03	0.31	8	-3.31	**0.0107**
TissuUnderfur	-0.22	0.16	8	-1.39	0.2024
AgeJ	0.40	0.17	8	2.42	**0.0417**
SexM	0.16	0.15	8	1.08	0.3131
Random effect					
ID	0.00003				
Residual	0.32				
$\delta^{15}N$ fixed effects					
(Intercept)	7.56	0.18	8	41.16	0
TissuUnderfur	-0.10	0.09	8	-1.08	0.3137
SpeciesPolar bear	1.42	0.25	8	5.78	**0.0004**
SpeciesWolf	-0.34	0.22	8	-1.56	0.1578
SpeciesWolverine	0.29	0.24	8	1.22	0.2585
AgeJ	0.23	0.15	8	1.57	0.155
SexM	0.14	0.12	8	1.11	0.3008
Random effects:					
ID	0.17				
Residual	0.18				

APPENDICE C

Table C.1 Summary of the study stages, main activities and participants from Qamani’tuaq involved in the development of this study. Main research and interactions with participants were conducted by Vincent L’Hérault (VLH) as non-indigenous researcher

Study stage	**Timing (duration)**	**Purpose**	**Participants**	**Short description (activity conducted by VLH and participants)**
Preliminary	Spring 2011 (2 weeks)	-Identifying local concerns and priority	-Joan Scottie (HTO manager) -Local wolf hunters, Government of Nunavut’s biologists	-Informal discussions on local observations and perceptions reported to HTO -Informal discussions as part of a wolf carcass recovery program
Inception	Fall 2011	-Determining HTO interest for a formal study	-Joan Scottie (HTO manager)	-Email and phone correspondence, permit applications, etc.
Development	Winter 2012 (3 weeks)	-Defining study design and research hypothesis -Testing	-HTO board members	- Meeting in Qamani’tuaq

		questionnaire, recording observations -Cultural integration	-Long-range wolf hunters, Elders -Local family of subsistence hunters	-Formal Interviews -Home stay and help, trip on the land, attending local cultural activity
	Spring 2012 (2 weeks)	-Recording observations and perceptions -Cultural integration	-Elders -Local family of subsistence hunters	-Formal interviews -Home stay and help, trip on the land, attending cultural activity
	Spring 2013 (2 weeks)	-Presenting preliminary results, validation and next steps	-HTO board members	-Informal presentation at HTO meeting
Conclusion	Summer 2015 (2 weeks)	-Presenting the main results and validation	-Reviewing committee made of HTO board members, Elders rep., and Young	-Validation workshop including the review of a summary document, Q&A, -Recommendations

		-Presenting the main results to a large public	hunter rep. -Community members	-Photo exhibit, Q & A
	Fall 2017	-Reviewing poster and manuscript	-Hugh Nateela (HTO manager) and HTO board members	-Presentation of the manuscript and purpose, discussion on ethics.

Interview questionnaire

SECTION 1- PERSONAL QUESTION

Q1: What date were you born? Where were you born? Can you point it on a map?

Q2: Can you circle on the map the region you have lived in when you used to live on the land? For how long have you been living in this region? What year did you settle in Baker? After you settle in Baker, can you now circle on the map the region you have most often use for hunting? For how long have you been hunting in this region?

A. If you've never lived on the land, can you circle the region you know the most from having spent the most time?

Q3: Are you actively hunting/ fishing and camping on the land?

A. If yes, how often do you go and what time of the year?
B. If no, when did you stop going?

Q4: What animals do you hunt?

A. For how many years have you been hunting these species?
B. Do you hunt these animals on a regular basis (every weekend, once in a while, once a year)?

Q5: Can you point on the map the best place to find (winter + summer):

A. Caribou
    a. Are these places the same year after year?
B. Muskox
    a. Are these places the same year after year?
C. Wolf
D. Other predators (Wolverine, grizzly bear, foxes)?

Q6: When you go (or used to go) on the land what predator species do you most often see?

A. Before you settle in Baker (when you used to live on the land)?

B. After you settle in Baker (when you used to hunt on the land only)?
C. Can you tell me what time of year you see these animals?

Q7: Can you tell me what you use the wolves for?

Q8: Can you explain why the wolves are important to you and your community?

A. Have you ever heard any stories from your parents and grandparents about wolves?

Q9: Can you comment about how people behave towards wolves?

A. Do they show respect to them?
B. Are there any particular beliefs when it comes to wolves?

Q10: What local names do you use for wolves?

A. Is there different name given to male, female or young?
B. Do you have different names for different shape, colour or behaviour?

Q11: Do you think there are different kinds of wolves?

A. Do you think there are different kinds of wolves among the ones spending the winter on the tundra and the ones spending the winter beyond the tree line?
B. Can wolves move back and forth between the tree line and your area during winter?
C. Do you observe the wolves spending the winter on the tundra as lonely animal or they always come in packs?
D. Are wolves nearby the community different from the wolves living in remote areas?

SECTION 2-POPULATION TRENDS

Q11: Can you tell me how many wolves you harvest annually (or used to harvest)?

A. Is that number the same as it used to be?
B. If not, can you comment on what have changed?

Q12: From your lifetime experience, would you say that the number of wolves in your area is increasing, decreasing or remain stable?

A. Is there any difference today from when you were younger (before you settle)?

Q13: Can you show me on the map areas where the number of wolves have changed?

A. If yes, can you comment these changes

Q14: Have wolves state (condition/health) increased, decreased or remained the same as it used to be?

A. Did you ever hear your parents/ grandparents talking about the state of wolves?

SECTION 3- WOLVES DIET (and other predators)

Q15: Can you explain how wolves kill caribou?

A. How does the hunt happen?
B. What part of caribou do they eat first? What part do they eat after?
C. Are younger wolves eating the same part as dominant (alpha) wolves?
D. What period of the year do wolves eat the most caribou?

Q16: Is there a link between wolves' numbers and caribou numbers?

A. Do you think that caribou number change over years because of Wolves predation?
B. Do you think that wolves' predation on caribou is important for the ecosystem? Why so?

Q17: Do you know if wolves compete with other animals for caribou?

A. What kind of interaction have you witnessed between wolves and other predators?
B. Are wolves providing caribou to the other predators? Or can they kill caribou on their own?
C. Has it changed over time?

Q18: What do you know about wolves eating muskox and other smaller prey?

A. Can you describe what time of the year? And where? Is it frequent?

Q19: Does Wolves' food change between seasons?

Q20: Have you ever witnessed wolves feeding on animal leftovers?

A. Can they survive by eating only bones and skin?
B. Do you know if Wolves can hide away some food (like foxes do) during summer and use it during winter? What kind of food?

SECTION 4- ENVIRONMENTAL CHANGES

Q21: From your lifetime experience, do you consider that the environment is healthier, less healthy or just as healthy as it used to be when you were younger?

A. Did you ever hear your parents/ grandparents talking about the way the environment got healthier, less healthy or remain stable compared with the environment they used to live in?
B. What is the impact of mining activities (Agnico, Areva) on the environment? Do you know what happens when mining company build roads and buildings on the land? Do you have any concerns?
C. Do you think the climate is changing? What did you observe in your environment that makes you believe the climate is changing? Is CC good or not good for the environment? Can you explain why?

Q22: Are Wolves sensitive to mining activities?

A. Are Wolves avoiding community, mining camps, trails and roads?
B. Do you have any concern about industrial development regarding wolves? Do you believe they will adapt or be affected? Can you explain why you think so?

Q23: Do you think mining activities can affect/disturb caribou? What have you observed?

A. Is there less or more caribou around Qamani’tuaq since the meadow bank mine has gone under development and operation? Since the road has been constructed?
B. Along the road to Meadow bank, is there any particular place where you used to see caribou but you don’t see them anymore?
C. Prior to, or aside from mining activity, is mining exploration (plane, drilling, outfitting camp) affects caribou as well?
D. Do you think caribou can adapt to mining activities or they will be affected?
E. Do you know if muskoxen are impacted by mining activities?

Q25: Do you know if wolves are sensitive to climate change?

A. What observations or expectations do you have?
B. Do you know if wolves will adapt to it or be affected? Can you explain why you think so?

Q26: Do you know if caribou are sensitive to climate change?

A. Is CC affecting their food?
B. Is CC affecting their movement?
C. Do you think caribou can adapt to CC or they will be affected?

SECTION 5- EXTRA QUESTIONS

Q27: Do you know when wolves moult fur?

A. Do you know when wolves start growing fur?
B. Do you know when wolves stop growing fur?

Q28: Other than yourself, is there any other people in Qamani’tuaq that would be knowledgeable about wolves?

MA’NA!!!!

Quotes from wolf hunters and elders

Quote #01

“Not enough food on the land caribou moved somewhere…looking for food at the dump or near the houses….it's new from this year (2012)…didn't happen before… Avaala's dog eaten by a wolf…nearby John…just by the road to the airport…” ***Silas Kenalogak***

Quote #02a

“Much more skinny now..., no extra meat just bone under skin…back 3-4-5 years ago they were healthier back then than they are now…they are constantly running around Baker now…from snowmobiles…” ***Sam Qarliksak***

Quote #02b

"You'll see a lot of difference compared to these (the wild) when you get there and these (close to the community)…they are bigger and not afraid out there…that's good!” ***Brian Owkowt***

Quote #03

“A wolf knows when you have rifle on you or not from my own experience…I've seen a wolf with no gun (North to the community) and we stop together and watch to each other…but when I went back get my gun and came back to where I saw him he starts running right away...they know when you have a rifle...they can go right to you if you don't have a rifle...” ***Sam Qarliksak***

Quote #04

Bigger pack out there (Aberdeen), 8-10-12 average…nothing less than 5-6…cause they are less disturbed out there, less human activity…close to town more common to see 2-3, more rare to see packs…they have a tendency out there to come in pack…they survive better, they hunt better I guess... ***David Toolooktook***

Quote #05a

“Less than 10 years ago the caribou used to be here near the community all year round we would go by Honda to get them!…maybe 8 years ago…Airport called in at Hamlet if they could shoot them away cause they were dangerous on the run way…there were allover this area all winter...in the last 4 years especially they disappeared... the last 5 years or 4…I don't know what happened to the caribou…they went further...now you need to go 80 miles by snowmobile to get them... even experienced hunters come back empty-handed ...a lot and a lot of Inuit are being hungry coming at the HTO and I've seen it…there are people calling is there any more meat…people you think are healthy enough to go out hunting…” ***Joan Scottie***

Quote #05b

“Nowadays there are so many leftovers of caribou from hunters that the wolves and wolverines don’t have to hunt anymore…they can just eat what was left behind…people leave the guts…” ***Sam Qarliksaq***

Quote #06

“There is muskoxen now on the north shore of the Lake while they used to be nothing there few years ago…they were West and South west near the Princess Mary Lake…nobody, a handful of people hunt them so they don’t even move…they got more abundant from the Thelon Game Sanctuary where there was a quota...increasing because of the feeding on the ground...very close to town now too...when I was 14 we would go way further south...1980s they start to come closer...”

Simeon Mikkungwak

Quote # 07

"Too many hunters in this area are taking their parents so they end up being skinny and nobody to show them how to hunt…they end up skinny and bony…" 'That's why they end up right close to Baker Lake to get an easy thing to eat like garbage at the dump...that's why they end up pretty close…" ***Mark Tunguaq***

Quote #08

“When they are feeding they hear noise, then have a quick bite and they try to run off somewhere else…whereas up here (Aberdeen) I guess they have more feeding time…when they finally do catch maybe its limited time to consume the meat and…you got more traffic here close to Baker Lake.” ***Simeon Mikkungwak***

Quote #09

"In the switch back hills (halfway hills...there is a valley in there...)…there used to be a den area for wolves but since that Agnico Eagle project and road have started that den was left by wolves and got taken over by foxes…wolves or any sorts of carnivores animal will never have a den near a road area… even when we used to live on the land my family and I used to walk back and forth between the camp and the community, and just by walking by the wolves dens it would be enough to move them away...not even talking of heavy equipment or anything loud..."***Thomas Anirniq***

Quote #10

"Animals now, wolves, even caribou they can go on the road now…they changed a lot…they are changed…totally changed now…road doesn't bother them anymore…"
John Killulark

Quote #11a

"The tuktu are running away from them…even the meat is not the same it's not as great…the mining companies they don't taste the same as they used to be…too much plane going around and trucks and the caribou meat is tasting too different now…it's from the mining companies...they are not the same anymore...June to August the meat used to be real good...but now no more..." ***John Killulark***

Quote #11b

"I've seen them on few occasions that they seem to be reluctant to cross the road…which normally they would pass on through with no problem if the road was not there…they seem to hoard the road and come really close to the town before they cross…they still do eventually cross some places...They are not used to roads and look confused... " ***Peter Owingayak***

Quote #11c

"before they built that road the caribou would run away…ever since they built that road they don't run away anymore they are used to it…the road is not a problem at all for the caribou…" ***John Nukik***

Quote #11d

“it happened before in the 1980s and even 1970s that the caribou moved…it's just from the food…he went last year during ukiuq in an area where there was a lot of caribou food and there was lots of caribou there...it means that close to the community they're not enough now...they move around a lot with the seasons too...”

Thomas Iksiraq

Quote # 12

“Caribou I think there is more because people don't hunt them as we did years ago…we hunted a lot of them for dog food too…nowadays there are no dogs to feed so there is less caribou hunted I believe…we also used to prepare lots of cached meat and dry meat back then...” ***Thomas Qaqimat***

Quote #13

“After they built the road (3-4-5 years ago) wolves started to get skinnier and skinnier…most people go to the land by the road now…summer time…some people do shoot them in the summer too…” ***Sam Qarliksak***

Quote #14

“A lot of new people are catching wolves now…it's not mainly the same people that hunt wolves now…overhunted that's what I think…that's why I prefer to spend overnight in another area….much easier” ***Sam Qarliksak***

Quote #15a

“I go out there (Aberdeen) every two weeks break from the camp…when I'm off the job I go hunting maybe one week out of the two…4-5 days out there…so maybe I go once a month out there…” ***Roy Avaala***

Quote #15b

“Nowadays looks like there is only 5-6 wolves hunters making a living out of it now...which is relatively few on a community of 2000s people...there are weekend hunters yes...go for a day...I don't know them I don't look at them…but I know it is important for them to support their family though, that I know...” ***David Toolooktook***

<u>Quote #15c</u>

"A lot of people with full-time jobs they are able to go out, they take couple weeks to go wolves hunt…I don't think anybody is doing it full-time now…I don't understand why if they're in good health…they can bring a satellite phone VHF radio…my dad used to live out there with no contact to say he is sick when he was sick...!! Today we have satellite phones, spots…what's stopping them from being out there one month? Everything is too much I don't know...I don't know how to say it everything is stored bought everything is technology now people look more forward to watching TV going to the internet...Oh it would be good to go out this weekend...it became a sport!" ***Joan Scottie***

<u>Quote #16</u>

"The wolves they are overhunted along the road to many people going close by... that's why they are so skinny so unhealthy, that's because they're constantly hunted they don't finish their food…they are more afraid they are hardly eating they never know when the next hunters will come" ***Thomas Anirniq***

<u>Quote #17</u>

"There is caribou all year long even winter time…there is hardly any hunters going there…what I think it's for the best of the animals…it's much better going hunting [speaking of wolves] than eating the leftovers cause it's much bigger… Everything is much better near Aberdeen!" ***Sam Qarliksaq***

<u>Quote #18</u>

"It's a good habit too, a way of life as opposed to stay home and do nothing…good way to keep knowledge of the land and the country…keep busy…overnighting is a big step towards learning the land and stuff…community-wise the knowledge of the land….in 20 years from now the guys are going to know less but they will have GPS to go...but they will know less than Elders for sure...programs for youth would be important...I heard of few young people going out and doing well...it's a lot less now than just a few years ago...some families keep the traditions alive and going...it's a lot less now....10-20 families still do that...it's hard to tell..." ***Roy Avaala***

<u>Quote #19a</u>

“there seems to be more wolves…wolf population is increasing so I am encouraging people to shoot them whether they are finished eating or not or skinny I am encouraging shooting them…cause its increasing more than human population now…yeah they'll survive...if they eat one avingaq or two they'll survive longer so it doesn’t matter if they are healthy or not they are still going to survive...”

Thomas Iksiraq

Quote #19b

“The more you catch the more they make young, the less you catch the less they make young…they make 5 young and multiply fast…” ***Barnabas Osuaq***

Quote # 20

“I see that as a problem when they are being over hunted yeah…they need to get back to get healthy again to produce more for the future…like to get more than being unhealthy…over hunting that's what I think….over hunted…” ***Sam Qarliksak***

Quote #21

“If there is a quota I'm not going to stop hunting, I'm going to stop I'm a hunter”

Mark Tunguaq

Quote #22

“If Science is regulating then they should answer this, if people can’t hunt how they are going to feed people, how are they going to be responsible for that? Or do they have a compensation package… “ ***Simeon Mikkungwak***

Condition and fat indices

We followed Peig & Green (2009) where animal body condition is defined as the energy capital accumulated in the body as a result of feeding. Here body condition is assumed to be indicative of an animal's health and quality, and hence fitness. Most non-invasive studies calculate Condition Indices (CIs) based on the relationship between body mass (M) and body length (L) (Peig & Green 2010). A variety of formulas have been proposed to standardize body size and there is much debate about which ones are most suitable as CIs (Stevenson & Woods 2006). Conventional methods involve simple ratios between M and L where L is often raised to a specific power (*e.g.* Fulton's index 'K'= M/L^3). The most widely accepted CI in terrestrial ecology is currently the Residual index, 'R_i' which uses the residuals from an ordinary least squares regression of $\ln M$ against the ln of a linear morphometric measure (*e.g.* body length, femur length in mammals, or tarsus length in birds) representing body size (Jakob et al. 1996, Hayes and Shonkwiler 2001). An individual with a positive residual is considered to be in better condition than an individual with a negative residual. Recently, Peig & Green (2009) presented a novel CI called the Scaled Mass Index 'SM_i', which standardizes M at a fixed value of a linear morphometric measure based on the scaling relationship between mass and length, according to: $SM_i = M_i \, [L_0/L_i]^{bSMA}$, where M_i and L_i are the body mass and linear body measurement of individual 'i', respectively, L_0 is an arbitrary value of L (*e.g.* the arithmetic mean value for the study population), bSMA is the scaling exponent estimated by the standardized major axis regression of $\ln M$ on $\ln L$, and SM_i is the predicted body mass for individual 'i' when the linear body measure is standardized to L_0. Peig & Green (2010) suggests that SM_i is a better predictor of body reserve, compared with other CIs, because it successfully accounts for the changing relationship between M and L as body size changes and growth occurs (it standardizes all individuals to the same growth phase). On the other hand, Wilder et al. (2016) raises the importance of measuring actual lipid contents as direct estimate

of animal body reserves as most CIs are poorly correlated to lipids or fitness–related traits.
In our study, we calculated the Fulton's index, R*i*, and SM_i to allow comparison between the simplest and the most recent indices. We used three linear morphometric measures, the body length, the femur length, and the condylobasal length, and thus obtained nine CIs. Prior to calculation, we corrected animal body mass for animal carcasses lacking front and/or back limbs (tarsus), and/or feet that are occasionally removed by hunters to lower animal weight during transportation. To do so, we used the slope and intercept from linear regressions of limbs/feet mass against the total body mass of complete specimens (n=12) to infer total body mass in incomplete ones.

Carcass monitoring allowed us to measure, unlike non-invasive studies restricted to CIs, direct indices of body reserves, such as the mass of the sternal fat (lining against the front wall of the abdominal cavity), the mass of the omental fat (a net-like structure originating at the basis of the stomach and enveloping most of the intestines), and the thickness of the back fat (between the hips at the level of the spine) (Boertje & Stephenson 1992; Hillis & Mallory 1996). We performed Person's correlations on CIs and FIs to determine the best indices to use in statistical models (Table S2). Condylobasal and femur CIs (Fulton's, R_i, and SM_i) were all correlated (p>0.70), but not body length CIs. Body length CIs were correlated with each other. Only condylobasal CIs were correlated to fat indices (back fat thickness and mass of sternal fat). Back fat and sternal fat were correlated, and the correlation between sternal fat and omental fat (p=0.65) was near the 0.70 threshold. Based on these results, we used the $SMi_{Condylobasal}$ condition index in statistical modelling because of its association with the other Cis and FIs, and also based on the comparative study of Peig and Green (2010) who recommended the use of SMi over other indices because it better accounts for sex and age differences in body size (see discussion on SMi above). In terms of fat indices, we preferred the sternal fat index over the back fat index because we assumed that sternal fat's collection method was more consistent among individuals, and also because our measures were more precise (±0.1g on a scale, samples ranging from 0g to 317.4g) than those of the back fat (± 0.5mm on a ruler, samples ranging from 0mm to 9mm). In addition, back fat measurements could not be obtained on every individual carcass processed, while sternal fat measurements were obtained in ca. 100% of the carcasses.

Table C.2 Pearson’s correlation coefficients among condition indices (CIs: Fulton’s index, Residuals index, and Scaled Mass index) and fat indices (FIs: Back fat thickness, mass of sternal fat, mass of omental fat). N=45 wolves from Qamani’tuaq and other communities of the Kivalliq district of Nunavut, Canada. Correlations >0.70 are highlighted in bold. Note that 1) CIs$_{\text{Condylobasal}}$ and CIs$_{\text{Femur}}$ are all correlated, 2) CIs$_{\text{Body}}$ are correlated together but not to CIs$_{\text{Femur}}$ and CIs$_{\text{Condylobasal}}$, and 3) only CIs$_{\text{Condylobasal}}$ are correlated to FIs.

	Back Fat	Stern. Fat	Om. Fat	F$_{\text{Body}}$	F$_{\text{Femur}}$	F$_{\text{Condylo}}$	Ri$_{\text{Body}}$	Ri$_{\text{Femur}}$	Ri$_{\text{Condylo}}$	SMi$_{\text{Body}}$	SMi$_{\text{Femur}}$	SMi$_{\text{Condylo}}$
Back Fat	1.00											
Sternal Fat	**0.82**	1.00										
Omental Fat	0.56	0.65	1.00									
Fulton's$_{\text{Body}}$	0.56	0.41	0.53	1.00								
Fulton's$_{\text{Femur}}$	0.66	0.58	0.62	0.58	1.00							
Fulton's$_{\text{Condylo}}$	**0.81**	**0.76**	0.52	0.53	**0.79**	1.00						
Ri$_{\text{Body}}$	0.64	0.56	0.60	**0.96**	0.60	0.61	1.00					
Ri$_{\text{Femur}}$	**0.71**	0.65	0.65	0.62	**0.97**	**0.82**	0.67	1.00				
Ri$_{\text{Condylo}}$	**0.76**	0.69	0.44	0.52	**0.76**	**0.95**	0.59	**0.80**	1.00			
SMi$_{\text{Body}}$	0.62	0.50	0.60	**0.99**	0.63	0.61	**0.98**	0.67	0.57	1.00		
SMi$_{\text{Femur}}$	0.68	0.60	0.63	0.58	**1.00**	**0.81**	0.61	**0.98**	**0.77**	0.64	1.00	
SMi$_{\text{Condylo}}$	**0.75**	0.66	0.38	0.46	**0.75**	**0.96**	0.51	**0.74**	**0.97**	0.51	**0.75**	1.00

Table C.3 Candidate linear mixed models depicting the variables tested to explain variations in wolves' SMi condition index and sternal fat index near Qamani'tuaq, Nunavut, Canada. Candidate models included variables addressing spatial variation, age-sex classes, seasons, diet, social structure, and their interactions. Intercepts are indicated with a star. Pack size levels are 0 (single wolf), 1 (wolf pair), 2 (3-5 individuals), 3 (6-9 individuals) and 4 (>10 individuals). M11 (bold) was the selected model.

Independent variable(s)	Levels	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	**M11**	M12
Spatial:													
Area	Impact*- Control-Kivalliq	X		X	X	X	X	X	X	X	X	**X**	X
Age-sex classes:													
Sex	F*-M		X	X									
Age	Adult*-Yearling		X		X							**X**	X
Age:Area					X							**X**	X
Sex:Area				X									
Seasons:													
Season	Fall*-winter-spring					X						**X**	X
Season:Area						X							
Diet:													
$\delta^{13}C_{Liver}$	Continue						X						
$\delta^{13}C_{Liver}$:Area							X						
$\delta^{13}C_{Muscle}$	Continue							X					

$\delta^{13}C_{Muscle}$:Area								X					
Caribou wet weight	Continue								X				
Caribou wet weight:Area									X				
Alternate prey	Presence/absence									X		**X**	
Alternate prey:Area										X		**X**	
Social structure:													
Pack size	0*-1-2-3-4[1]										X		X
Pack size:Area											X		X
Dependent variable													
Scaled $Mass_{Condylobasal}$	AICc	458.5	449.9	455.4	444.1	456.9	453.5	451.1	500.2	447.4	454.7	**432.3**	440.2
	ΔAICc	26.2	17.6	23.1	11.8	24.6	21.2	18.8	67.9	15.1	22.5	**0.0**	7.9
Sternal fat	AICc	886.1	875.0	861.7	855.8	874.8	866.2	864.9	911.6	862.5	865.5	**819.7**	827.6
	ΔAICc	66.4	55.2	42.0	36.1	55.2	46.5	45.2	91.9	42.9	45.8	**0.0**	7.9

Table C.4 Results from the selected linear mixed models relating a) wolves' stable isotope ratios (δ^{13}C, δ^{15}N) and b) stomach contents (caribou wet weight and alternate prey) to spatial, seasonal, and demographic variables near Qamani'tuaq, Nunavut, Canada. Intercept in a) is season fall and in b) impact area, season fall, and sex female. Significant coefficients appear in bold.

	Estimate	95% CI (-/+)		d.f.	*p*		Estimate	95% CI (-/+)		d.f.	*p*
a) Stable isotopes model						**b) Stomach content model**					
δ^{13}C fixed effects:						*Caribou wet weight fixed effects:*					
Intercept	-22.31	-22.76	-21.87	179	**0.0001**	Intercept	1011.3	502.2	1520.3	113	**0.0002**
Winter	0.47	0.26	0.68	179	**0.0001**	Kivalliq	-46.2	-533.6	441.2	113	0.8529
Spring	1.33	1.08	1.57	179	**0.0001**	Control	-379.7	-1066.4	307.0	113	0.2808
						SexM	144.7	-321.8	611.2	113	0.5445
						Winter	-280.2	-797.4	237.0	113	**0.2906**
						Spring	-591.9	-1123.5	-60.3	113	0.0312
						Kivalliq:SexM	-178.5	-790.6	433.6	113	0.5687
						Control:SexM	1545.2	515.1	2575.2	113	**0.004**
Random effects:											
Year	5.48 e-06					Random effects:					
Settlement	0.4					Year	38.4				
id	0.6					Residual	790.3				
Residual	0.7										
δ^{15}N fixed effects:						*Alternate prey fixed effects:*					
Intercept	6.14	5.69	6.59	179	**0.0001**	Intercept	0.2	0.1	0.2	118	**0.0006**

Winter	-0.05	-0.27	0.16	179	0.5941	Kivalliq	-0.1	-0.2	0.0	118	0.1009
Spring	-0.29	-0.53	-0.04	179	**0.0165**	Control	-0.1	-0.3	0.1	118	0.4557
Random effect:						*Random effects:*					
Year	1.36E-04					Year	8.3 e-06				
Settlement	0.5					Residual	0.3				
id	0.2										
Residual	0.6										

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