TABLE DES MATIÈRES

CHAPITRE 1

INTRODUCTION GÉNÉRALE

LES INTERACTIONS ENTRE ÉCOSYSTÈMES

De nombreux écologistes ont étudié les facteurs influençant la structure et la dynamique des réseaux trophiques (Hairston et al. 1960, Oksanen et al. 1981, Schoener 1989, McLaren et Peterson 1994, Polis 1999). Une avenue récente en écologie est d'inclure les interactions entre les écosystèmes dans l'étude des réseaux trophiques, puisque ce type d'interaction peut modifier la structure et la dynamique de ces réseaux (Polis et al. 1997). Des écosystèmes adjacents ou éloignés peuvent effectivement interagir entre eux par le biais d'un flux de ressources d'un écosystème à l'autre. Ce type de flux peut résulter de l'action de vecteurs physiques (vent, eau) et/ou biologique (mouvement de proies ou de prédateurs) (Polis et al. 1997). Les mouvements biologiques peuvent être le fruit d'un transport passif par les vecteurs physiques, d'un mouvement migratoire ou d'un mouvement de dispersion des individus d'un écosystème à l'autre au cours de leur développement (Polis et al. 1997). Ils peuvent donc se faire à une échelle globale, continentale, régionale ou locale (Jefferies 2000).

Les flux de ressources entre les écosystèmes peuvent avoir des impacts importants sur les populations incluses dans ces systèmes. Par exemple, la productivité d'une population d'un écosystème A (autochtone) peut augmenter suite à la consommation de ressources provenant d'un écosystème B (allochtones), ce qui peut provoquer des cascades trophiques dans l'écosystème A. Ce type d'impact a été décrit par Polis et al. (1997) dans la définition suivante d'un subside allochtone : 1- ressource (proie, détritus ou nutriments) provenant d'un premier écosystème, 2- étant utilisée par une plante ou un consommateur provenant d'un second écosystème, 3- permettant à l'utilisateur de la ressource d'accroître la productivité de sa population et 4- altérant ainsi potentiellement la dynamique de l'interaction utilisateur/ressource dans le second écosystème (Polis et al. 1997). Les effets des subsides allochtones peuvent être ascendants (*Bottom-up forces*), par exemple quand des nutriments allochtones sont utilisés par les végétaux pour accroître leur productivité, provoquant alors des effets sur les herbivores puis sur les prédateurs. Les effets peuvent aussi être descendants (*Top-down forces*), par exemple quand la productivité des prédateurs augmente suite à une consommation de proies allochtones, suivi d'un effet sur les proies puis sur les végétaux autochtones (Polis et al. 1997). Il a été proposé que ce type de flux de ressources entre écosystèmes existe partout où deux écosystèmes se distinguant par leur productivité sont juxtaposés (Polis et Hurd 1996).

Pour donner un cadre théorique à ce type d'interactions entre écosystèmes, Loreau et al. (2003) ont proposé l'adoption d'une nouvelle échelle d'organisation écologique : le méta-écosystème. Un méta-écosystème est défini comme un ensemble d'écosystèmes liés par des flux d'énergie, de nutriments ou d'organismes (Loreau et al. 2003). Le modèle théorique élaboré à partir de ce concept met en évidence les propriétés des écosystèmes qui émergent des interactions locales, régionales et globales.

L'INTÉRÊT DE L'ÉCHELLE DU MÉTA-ÉCOSYSTÈME DANS CETTE ÉTUDE

L'utilisation de l'échelle du méta-écosystème est primordiale pour mieux comprendre la structure et la dynamique d'un réseau trophique chevauchant plus d'un écosystème (Polis et Hurd 1996, Polis et al. 1997). Cette échelle a été recommandée pour étudier le réseau trophique terrestre arctique de notre aire d'étude, l'île Bylot (Gauthier et al. 2004). En effet, une hypothèse assumant l'absence d'interactions entre écosystèmes, soit l'hypothèse d'exploitation des écosystèmes (HEE, Oksanen et al. 1981, Oksanen et Oksanen 2000), a été réfutée sur notre aire d'étude. L'HEE prédit que la longueur des chaînes trophiques terrestres varie directement avec la productivité primaire de l'écosystème qui supporte la chaîne trophique (Oksanen et al. 1981). Pour un écosystème peu productif comme celui de l'île Bylot (productivité primaire < 0,70 kg/m^2/an : Gauthier et al. 1995), l'HEE prédit que l'écosystème peut supporter une communauté d'herbivores endothermes, mais non une communauté de prédateurs endothermes (Oksanen et Oksanen 2000). Dans ces écosystèmes relativement pauvres, l'HEE suggère aussi que ce serait l'interaction plante/herbivore qui structurerait la chaîne trophique plutôt que l'interaction prédateur/proie (Oksanen et Oksanen 2000).

Les interactions plante/herbivore et prédateur/proie sont toutes deux importantes dans le réseau trophique de l'île Bylot malgré sa faible productivité (Gauthier et al. 2004). Une hypothèse alternative proposée pour expliquer cette réfutation de l'HEE est que l'utilisation de subsides allochtones par le renard arctique accroît l'abondance de sa population, lui permettant d'avoir un impact important sur les populations locales d'herbivores malgré la faible productivité de l'écosystème (Gauthier et al. 2004). Pour évaluer cette hypothèse, la première étape est la quantification de l'importance des ressources allochtones dans le régime alimentaire du renard arctique. La deuxième étape est celle d'estimer l'impact de ces ressources sur la productivité du renard arctique. Ces deux étapes constitueront donc le cadre de la présente étude. Nous poursuivrons cette revue de littérature en présentant l'état des connaissances concernant l'utilisation des ressources allochtones par le renard arctique, la quantification de l'utilisation de ces ressources ainsi que l'influence de l'abondance de nourriture sur la productivité du renard arctique.

LE RENARD ARCTIQUE, UN UTILISATEUR OPPORTUNISTE DE RESSOURCES ALLOCHTONES

Le renard arctique est un bel exemple d'utilisateur de ressources allochtones. En effet, les ressources marines (invertébrés, oiseaux et mammifères), les oiseaux migrateurs nichant en Arctique et les œufs de ces oiseaux font fréquemment partie du régime alimentaire de ce prédateur terrestre (Chesemore 1968b, Macpherson 1969, Fay et Stephenson 1989, Prestrud 1992, Angerbjörn et al. 1994, Roth 2002). L'utilisation de ces ressources peut permettre l'augmentation de l'abondance de populations de renard arctique

(Roth 2003) et même en assurer le maintien (Angerbjörn et al. 1994, Hersteinsson et Macdonald 1996). Cette utilisation peut aussi modifier la dynamique trophique du réseau dont fait partie le renard arctique. Par exemple, le renard arctique peut réduire le transport de nutriments marins vers la terre en se nourrissant d'oiseaux marins dont les fèces riches en nutriments fertilisent le sol. L'écosystème dominant d'une île, par exemple une prairie, peut alors être transformé en toundra (Croll et al. 2005).

Deux stratégies décrivent l'utilisation des ressources allochtones par le renard arctique. Premièrement, ces ressources peuvent dominer le régime alimentaire du renard arctique, du moins de façon saisonnière. Par exemple, les ressources allochtones forment l'essentiel du régime alimentaire estival de ce prédateur à l'intérieur d'une très dense colonie d'oiseaux migrateurs (Stickney 1991, Bantle et Alisauskas 1998). Dans certaines zones de son aire de répartition circumpolaire où les petits rongeurs sont absents ou très faiblement abondants, le régime alimentaire du renard arctique est dominé par des ressources marines (invertébrés, mammifères et oiseaux) et/ou des oiseaux migrateurs terrestres (Svalbard: Prestrud 1992, Islande et Groenland: Angerbjörn et al. 1994, Hersteinsson et Macdonald 1996).

Deuxièmement, les ressources allochtones peuvent être utilisées alternativement aux petits rongeurs, les proies préférées du renard arctique lorsqu'ils sont présents (Amérique du Nord: Chesemore 1968b, Macpherson 1969, Garrott et al. 1983, Fay et Stephenson 1989, Anthony et al. 2000, Roth 2002, Scandinavie: Angerbjörn et al. 1994, Russie:

Angerbjörn et al. 1999, Roth 2002). Dans ce cas, l'importance des ressources allochtones dans le régime alimentaire du renard arctique est déterminée par l'abondance cyclique (3-5 ans: Hansson et Henttonen 1985, Hanski et al. 1993, Stenseth et Ims 1993) des petits rongeurs arctiques (Macpherson 1969, Fay et Stephenson 1989, Elmhagen et al. 2000, Bêty et al. 2002, Roth 2002, Roth 2003). Par exemple, les oiseaux migrateurs, leurs œufs et les carcasses de phoques peuvent être utilisés en plus grande proportion durant les années de faible abondance de petits rongeurs que durant les années de forte abondance.

L'UTILISATION DES RESSOURCES ALLOCHTONES SUR L'ÎLE BYLOT

En été, la proie préférée du renard arctique à l'île Bylot est une proie autochtone, soit le lemming (lemming variable, *Lemmus sibiricus* et lemming brun, *Discrotonyx groenlandicus*) (Bêty et al. 2002). Cette proie utilise strictement des nutriments d'origine terrestre arctique (Negus et Berger 1998). La principale proie alternative du renard est la grande oie des neiges (*Chen caerulescens atlantica*) (Bêty et al. 2002), une proie allochtone (Gauthier et al. 2003). Cette proie migratrice forme chaque été une colonie d'environ 20 000 paires d'adultes reproducteurs sur l'île Bylot (Reed et al. 2002). Les œufs et les oisons sont principalement consommés (Gauthier et al. 2004), mais les adultes peuvent aussi être consommés par le renard arctique. En effet, des carcasses fraîches d'oies adultes sont trouvées sur les tanières de reproduction de renard arctique durant l'été (observations personnelles). Toutefois, les observations comportementales effectuées dans la colonie d'oies de 2002 à 2005 mettent en évidence que les renards peuvent attaquer les oies adultes, malgré qu'aucune observation d'attaque d'adultes ne se soit soldée par un succès (Lecomte et Careau, communication personnelle). Ainsi, les adultes sont potentiellement beaucoup moins importants dans le régime alimentaire du renard arctique à l'île Bylot que les œufs et les oisons. Les tissus des adultes sont constitués de nutriments provenant d'une part d'écosystèmes tempérées (accumulation de réserves dans les champs de maïs et les marais bordant le fleuve St-Laurent lors de la migration printanière : Gauthier et al. 1992), et d'autre part de la toundra arctique (consommation de graminées et d'herbacées sur l'île Bylot: Gauthier 1993). Les femelles investissent dans leurs œufs des nutriments allochtones provenant de leurs réserves endogènes et des nutriments autochtones provenant des plantes consommées sur le site de nidification (Gauthier et al. 2003). Après l'éclosion, les oisons consomment des plantes arctiques et ces nutriments autochtones sont intégrés dans les tissus en croissance des oisons. Tout au long de ce mémoire, nous identifierons les oies comme une ressource, une proie ou un organisme allochtone (relativement à l'écosystème arctique terrestre que nous identifions comme autochtone). Cette appellation est sujette à débat, puisque les oies contiennent à la fois des nutriments allochtones et autochtones. Nous avons basé cette appellation sur deux faits : 1- les oies sont des vecteurs de nutriments allochtones et 2- durant les dernières décennies, l'accroissement de la population d'oies était fortement corrélé aux variations environnementales sur les haltes migratoires et les aires d'hivernage (Gauthier et al. 2005). Cela suggère que cette population était principalement limitée par la disponibilité de nourriture dans les écosystèmes tempérés.

Sur certains sites d'étude, le renard arctique met en réserve de la nourriture durant les périodes de forte abondance de ressources alimentaires (Fay et Stephenson 1989, Stickney 1991, Frafjord 1993, Bantle et Alisauskas 1998, Samelius et Alisauskas 2000). À l'île Bylot, les renards cachent près de 90% des œufs qu'ils acquièrent des nids d'oies (Careau, données non publiées). Ainsi, les renards allongent la période de disponibilité de cette ressource abondante mais éphémère. Cette ressource pourra alors être utilisée durant l'automne et le printemps suivant la mise en réserve (Careau, données non publiées).

En dehors de l'été, l'écologie de la population de renard arctique se reproduisant sur l'île Bylot est peu connue. Des études réalisées sur d'autres sites d'études de toundra côtière nous indiquent que ce prédateur peut utiliser la banquise en hiver et au printemps (Chesemore 1968a), mais qu'il peut aussi demeurer sur terre si les ressources alimentaires sont suffisantes (Wrigley et Hatch 1976, Eberhardt et al. 1983b). Les proies qu'utilise le renard arctique sur la banquise arctique sont les carcasses de mammifères marins et les phoques naissants (Chesemore 1968b, Macpherson 1969, Andriashek et al. 1985, Fay et Stephenson 1989, Prestrud 1992, Frafjord 1993, Angerbjörn et al. 1994, Hersteinsson et Macdonald 1996, Roth 2002, Roth 2003). C'est en suivant l'ours polaire que le renard arctique peut profiter des carcasses de mammifères marins abandonnées par ce prédateur (Elton 1949, Chesemore 1967, Lydersen et Gjertz 1986). Au printemps, le renard arctique est un prédateur de phoques naissants (Andriashek et al. 1985). Dans l'est de l'Arctique canadien, l'ours polaire consomme quasi-exclusivement des phoques annelés (*Phoca hispida*) (Stirling et Archibald 1977, Smith 1980). Sur terre, les petits rongeurs, les carcasses de caribous et les oiseaux (mis en réserve ou résidents) constitueraient l'essentiel de son régime alimentaire en dehors de l'été (Chesemore 1968b, Macpherson 1969, Fay et Stephenson 1989, Prestrud 1992, Frafjord 1993, Angerbjörn et al. 1994, Roth 2002, Roth 2003). Dans notre région d'étude, les renards arctiques consomment également en hiver les restes de phoques et de caribous laissés par les chasseurs inuits (Gagnon, communication personnelle), mais l'importance de cette source de nourriture pour la population de renards étudiée est inconnue.

Les périodes de disponibilité des différentes proies potentielles du renard arctique sur l'île Bylot sont résumées dans le tableau 1.

LA QUANTIFICATION DE L'UTILISATION DES RESSOURCES ALLOCHTONES

Différentes techniques sont utilisées pour qualifier et quantifier le régime alimentaire d'un prédateur : les observations comportementales, l'analyse de contenus stomacaux, de fèces et de sites d'alimentation (Litvaitis et al. 1994) ainsi que l'analyse d'isotopes stables (Kelly 2000). L'analyse d'isotopes stables, utilisée en combinaison avec les autres techniques, est pour notre étude la méthode idéale pour quantifier la proportion des différentes proies dans le régime alimentaire du renard arctique.

Le traçage isotopique est une technique de plus en plus utilisée en écologie, notamment pour qualifier et quantifier les nutriments assimilés par un consommateur (Kelly 2000, Dalerum et Angerbjörn 2005). Deux principes sont à la base de cette technique, soit 1- la différence dans la signature isotopique de différentes sources de nourriture (Smith et Epstein 1971, DeNiro et Epstein 1981) et 2- l'intégration de la signature isotopique d'une source de nourriture dans les tissus du consommateur (DeNiro et Epstein 1978, 1981). Les différences dans les proportions isotopiques du carbone ($^{13}C/^{12}C$) entre des sources de nourriture proviennent des différences dans la fixation des isotopes stables du carbone par les plantes terrestres en C_3, C_4 et la végétation marine en C_3 (Smith et Epstein 1971, Ehleringer 1991). En effet, les signatures isotopiques ($\delta^{13}C$, calculées à partir de $^{13}C/^{12}C$) de ces végétaux sont différentes ($\delta^{13}C_{C3\ Terrestre} < \delta^{13}C_{C3\ Marin} < \delta^{13}C_{C4}$). Les différences dans les proportions isotopiques de l'azote ($^{15}N/^{14}N$) proviennent quant à elles d'une proportion plus importante de ^{14}N que de ^{15}N dans les déchets azotés des consommateurs (Steele et Daniel 1978). Ainsi, un consommateur aura une proportion isotopique ($^{15}N/^{14}N$) plus élevée que sa proie. Les signatures isotopiques d'azote ($\delta^{15}N$) varient en moyenne de 2.5 $^{o}/_{oo}$ entre les niveaux trophiques (Vanderklift et Ponsard 2003).

Les signatures isotopiques du carbone et de l'azote d'un consommateur permettent de reconstruire son régime alimentaire (DeNiro et Epstein 1978, DeNiro et Epstein 1981, Tieszen et al. 1983, Hobson et Clark 1992b, Roth et Hobson 2000, Nardoto et al. 2006b, Stowasser et al. 2006). La signature isotopique du régime alimentaire d'un consommateur équivaut à la signature isotopique des tissus prélevés sur le consommateur, à laquelle on soustrait un facteur de fractionnement. Le facteur de fractionnement représente le changement dans les proportions isotopiques entre le régime alimentaire et les tissus, dû à la perte de certains isotopes durant les processus métaboliques se déroulant entre l'ingestion de la nourriture et l'assimilation des nutriments dans les tissus (Tieszen et al. 1983, Nardoto et al. 2006a). Les isotopes stables de l'azote et du carbone constituent des marqueurs naturels qui permettent de suivre le devenir de la matière organique dans un réseau trophique depuis les sources jusqu'aux échelons supérieurs.

Un avantage majeur de l'analyse d'isotopes stables est qu'elle permet de quantifier les nutriments assimilés, plutôt que ceux ingérés (Kelly 2000). De plus, cette quantification s'applique à une période variant en fonction du taux métabolique du tissu utilisé pour l'analyse (Tieszen et al. 1983, Hobson et Clark 1992a). Ainsi, un tissu ayant un taux métabolique rapide comme le foie permet de quantifier le régime alimentaire récent (moins d'une semaine) tandis que le collagène permet de quantifier le régime alimentaire à plus long terme (la dernière année) (Tieszen et al. 1983, Hobson et Clark 1992a).

Le régime alimentaire du renard arctique sur l'île Bylot comprend potentiellement trois proies principales ayant des signatures isotopiques du carbone distinctes les unes des autres puisque ces proies utilisent des nutriments provenant de différents réseaux trophiques. En effet, le phoque fait partie d'un écosystème basé sur les algues marines, les lemmings s'alimentent uniquement sur des plantes arctiques en C_3 et les oies s'alimentent de plantes tempérées en C_3 et en C_4 (sur leurs aires d'hivernage) et de plantes arctiques en C_3 (sur les aires de nidification). De plus, puisque ces proies ne sont pas toutes situées sur le même niveau trophique, des différences dans les signatures isotopiques de l'azote pourraient être observées (lemming : $\delta^{15}N_{Herbivore}$; oie : $\delta^{15}N_{Herbivore}$; phoque : $\delta^{15}N_{Carnivore}$).

Ces différences potentielles rendent possible l'utilisation de l'analyse d'isotopes stables. Dans notre étude, cette technique est particulièrement avantageuse puisque des ressources alimentaires potentielles du renard arctique (œufs d'oiseaux) ne contiennent que très peu de matériel non digestible, ce qui peut conduire à une sous-estimation de leur proportion dans le régime alimentaire lorsque les fèces ou les contenus stomacaux sont analysés. Cette technique sera utilisée en combinaison avec les autres techniques de quantification du régime alimentaire. En effet, une proie sera incluse dans l'analyse isotopique seulement si sa présence dans le régime alimentaire est supportée par des analyses complémentaires de fèces, de restes de proies sur les tanières et des observations comportementales.

INFLUENCE DE L'ABONDANCE DE NOURRITURE SUR LA PRODUCTIVITÉ DU RENARD ARCTIQUE

Chez le renard arctique (vivant en moyenne 3-4 ans et élevant de grandes portées, Audet et al. 2002), les indices de succès reproducteur (pourcentage de tanières occupées, pourcentage de tanières de reproduction, taille de portée) sont généralement utilisés pour décrire la dynamique de population (Angerbjörn et al. 1999, Elmhagen et al. 2000, Bêty et al. 2002, Roth 2003). Sur l'île Bylot, le pourcentage de tanières de reproduction est influencé par la phase du cycle de lemming (Gauthier et al. 2004). Ce résultat est similaire à ceux obtenus sur d'autres aires d'études, où il a été maintes fois démontré que les indices de succès reproducteur variaient avec l'abondance de lemmings (Eberhardt et al. 1983a, Angerbjörn et al. 1995, Kaikusalo et Angerbjörn 1995, Landa et al. 1999, Elmhagen et al. 2000). Sur les aires d'études où le lemming est la proie préférée du renard arctique, les scientifiques se sont surtout penchés sur l'influence de cette proie sur la reproduction de ce prédateur. Toutefois, des expériences d'ajout de nourriture ont également démontré que les indices de succès reproducteur variaient avec l'abondance de ressources alimentaires autres que les lemmings. En effet, le pourcentage de tanières occupées était influencé positivement par l'abondance de carcasses de grand mammifères en hiver et au printemps (Angerbjörn et al. 1991). De plus, l'abondance estivale de nourriture pour chien influençait la survie des jeunes (Tannerfeldt et al. 1994).

Ces expériences d'ajout de nourriture constituent un premier pas vers la compréhension des mécanismes sous-jacents à l'effet de la nourriture sur la reproduction du renard arctique. À partir des résultats de ces expériences, le patron suivant a été suggéré pour expliquer l'effet de l'abondance de nourriture sur la reproduction du renard arctique (Angerbjörn et al. 1995) : 1- toutes les femelles s'accouplent chaque année et 2- les variations dans le succès reproducteur résultent de l'effet de l'abondance de nourriture sur la condition corporelle des femelles et la survie des jeunes, de l'ovulation à la fin de l'élevage. Ainsi, le nombre de portées ou de jeunes perdus par les femelles tout au long d'un cycle de reproduction varierait avec l'abondance de nourriture durant les différentes étapes de ce cycle (voir tableau 1 pour la chronologie d'un cycle de reproduction chez le renard arctique).

OBJECTIFS DE L'ÉTUDE ET HYPOTHÈSES DE TRAVAIL

Les interactions entre écosystèmes peuvent influencer la structure et la dynamique des réseaux trophiques. L'échelle du méta-écosystème inclut ce type d'interactions. Il est donc fortement suggéré d'adopter cette échelle lorsque le système à l'étude est lié à d'autres écosystèmes. Par le biais du régime alimentaire du renard arctique, notre système d'étude est lié à d'autres écosystèmes et ne fonctionne donc pas de manière isolée. Il a été suggéré que ce lien entre écosystèmes pouvait expliquer pourquoi l'interaction prédateur/proie est importante dans la structure du réseau trophique de notre aire d'étude, contrairement à la prédiction de l'HEE. L'objectif de notre étude était donc d'étudier le régime alimentaire estival et le succès reproducteur d'une population de renard arctique en adoptant l'échelle du méta-écosystème. Nous avons testé l'hypothèse selon laquelle l'utilisation de ressources allochtones par le renard arctique sur l'île Bylot influence son succès reproducteur. Pour vérifier cette hypothèse, nous avons formulé les prédictions suivantes : 1- la contribution de l'oie dans le régime alimentaire estival du renard arctique (jeunes et adultes reproducteurs) est plus grande dans le secteur à proximité de la colonie d'oies que dans le secteur qui en est éloigné (où les oies sont presque absentes) et 2- le succès reproducteur du renard arctique, que l'on sait être partiellement influencé par l'abondance de lemming (Gauthier et al. 2004), est également plus grand à proximité de la colonie d'oies.

Tableau 1 : Superposition temporelle, d'après la littérature et des observations personnelles, du cycle de reproduction du renard arctique (R), de la disponibilité des proies fraîches et cachées (P), de la disponibilité des habitats (H) et du régime alimentaire décrit par l'analyse isotopique de tissus (T) dans le cadre particulier de notre étude à l'île Bylot, Nunavut, Canada.

	Saison	*Hiver*										*Printemps*				*Été*						*Automne*				
	Mois	Nov		Déc		Jan		Fév		Mar		Avr		Mai		Jun		Jui		Aoû		Sep		Oct		**Références**
R	Accouplement										▨	▨	▨													Macpherson 1969
	Gestation										▨	▨	▨	▨	▨	▨	▨									Macpherson 1969
	Mise bas														▨	▨	▨									Macpherson 1969
	Allaitement														▨	▨	▨	▨	▨	▨						Garrott et al. 1984
	Élevage														▨	▨	▨	▨	▨	▨	▨	▨	▨			Macpherson 1969
P	Phoque annelé	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨							National Ice Center 1998
	Lemming	Frais	▨	▨	▨	▨	▨	▨	▨	▨	▨	Frais/Caché	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Roth 2002
	Oie (adulte)															Frais	▨	▨	▨	▨	▨					Observations personnelles
	Oie (œuf)											Caché	▨	▨	▨	Frais/Caché	▨	▨	Caché	▨	▨	▨	▨	▨	▨	Lepage et al. 1998, Samelius 2004
	Oie (oison)											Caché	▨	▨	▨	▨	▨	▨	Frais/Caché	▨	▨	Caché	▨	▨	▨	Lepage et al. 1998, Gauthier et al. 2004,
H	Banquise	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨							National Ice Center 1998
	Toundra	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Eberhardt et al. 1983a
T	Sang														▨	▨	▨	▨	▨							Hobson et Clark 1992a

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CHAPITRE 2

BENEFITING FROM A CONTINENTAL META-ECOSYSTEM: EFFECTS OF ALLOCHTHONOUS RESOURCES ON AN ARCTIC FOX POPULATION

Manuscrit en préparation pour une publication

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M.-A. GIROUX, D. BERTEAUX, J. BÊTY, G. GAUTHIER, N. LECOMTE AND G. SZOR.

Benefiting from a continental meta-ecosystem: effects of allochthonous resources on an arctic fox population.

Flows of nutrients and organisms across ecosystem boundaries can substantially modify the dynamics of populations included in these systems. We studied the effect of consumption of allochthonous organisms (migrating birds) on the productivity of an arctic fox population (*Alopex lagopus*) on Bylot Island, Nunavut, Canada. This arctic fox population is included in a meta-ecosystem spanning the North American continent. In fact, it feeds on greater snow geese (*Chen caerulescens atlantica*) that migrate annually from the east coast of the United States to the Canadian Arctic. We compared the summer diet (2004-2005) and the reproductive output (1996-2005) of arctic foxes between two sectors of our study area (the goose and the non-goose sector), characterized by contrasting abundances of geese (high vs. negligible). The preferential prey of the arctic fox (lemmings) is known to influence its reproduction. Hence, we also compared arctic fox reproductive output across the different phases of the lemming cycle (peak, decline, crash). Using stable isotope analysis, we showed that the proportion of goose in the diet of foxes was larger for individuals breeding in the goose sector. The annual percentage of breeding dens was also larger in the goose sector. The annual percentage of breeding dens varied across the lemming cycle and was at its lowest during the crash phase. Litter size was similar between sectors and across lemming phases. This study thus suggests that flow of organisms (geese) within a continental meta-ecosystem can subsidize a predator (arctic fox) population living in an ecosystem of low primary productivity. Further studies should aim at estimating

potential cascading effects of this allochthonous subsidization on the structure and functioning of the tundra ecosystem.

M.-A. GIROUX, D. BERTEAUX, J. BÊTY, G. GAUTHIER, N. LECOMTE ET G. SZOR. Effets des ressources allochtones sur une population de renards arctiques à l'île Bylot, Nunavut, Canada

Les flux de nutriments et d'organismes entre les écosystèmes peuvent modifier la dynamique des populations incluses dans ces systèmes. Nous avons étudié l'effet de la consommation d'organismes allochtones (oiseaux migrateurs) sur la productivité d'une population de renard arctique (*Alopex lagopus*) à l'île Bylot, Nunavut, Canada. Cette population est incluse dans un méta-écosystème englobant le continent nord américain. En effet, le renard arctique se nourrit de la grande oie des neiges (*Chen caerulescens atlantica*), qui migre annuellement de la côte est des États-Unis à l'Arctique canadien. Nous avons comparé le régime alimentaire estival (2004-2005) et le succès reproducteur (1996-2005) du renard arctique entre deux secteurs de notre aire d'étude : le secteur à proximité de la colonie d'oies et un autre qui en est éloigné (où les oies sont presque absentes). La proie préférée du renard arctique (le lemming) est reconnue pour influencer la reproduction de ce prédateur. Nous avons donc comparé le succès reproducteur du renard arctique entre les différentes phases du cycle de lemming (pic, déclin, creux). Par l'analyse d'isotopes stables, nous avons démontré que la contribution de l'oie dans le régime alimentaire du renard arctique était supérieure dans le secteur à proximité de la colonie d'oies que dans celui éloigné de la colonie. Le pourcentage de tanières de reproduction était également supérieur dans le secteur proche de la colonie d'oies, mais plus faible durant les creux de lemming. La taille de portée était similaire entre les secteurs et les phases du cycle

de lemming. Cette étude suggère qu'un flux d'organismes transportant des nutriments à l'échelle d'un continent (oies) peut provoquer l'augmentation de la productivité d'une population de prédateur (renard arctique) vivant dans un écosystème peu productif. Il serait maintenant intéressant d'estimer les cascades trophiques pouvant résulter de cet effet des ressources allochtones sur la productivité du renard arctique.

INTRODUCTION

Spatial coupling of ecosystems, generated by flows of nutrients and organisms across ecosystem boundaries, are ubiquitous (Polis et al. 1996, Polis and Hurd 1996, Loreau and Holt 2004). The effects of these flows need to be incorporated into food web studies because they can substantially modify dynamics of local populations (Polis et al. 1997). For example, use of allochthonous resources can subsidize a consumer, i.e. increase the productivity of its population, and thereby modify its interactions with local resources (Polis et al. 1997). Effects of such allochthonous subsidies often characterize the structure and dynamics of food webs when two ecosystems differing in productivity are juxtaposed (Polis and Hurd 1996).

To promote the inclusion of spatial coupling of ecosystems into ecological studies, Loreau et al. (2003) proposed a theoretical framework based on the meta-ecosystem concept defined as "a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries". This framework emphasizes the properties of ecosystems emerging from spatial coupling at various scales. Interactions between allochthonous and autochthonous populations, arising from the foraging behavior of a consumer, are among the properties highlighted by this framework. This property closely links the scale of a meta-ecosystem to the concept of allochthonous subsidy.

The association between the meta-ecosystem and the allochthonous subsidy offers a theoretical addition to the food chain models that have dominated food web studies during the last decades (Van de Koppel et al. 2005). A well known example of such food chain models is the exploitation ecosystem hypothesis (EEH, Oksanen et al. 1981, Oksanen and Oksanen 2000). According to this model, the primary productivity of an ecosystem influences the length of the food chain that it can sustain, and hence determines whether plant-herbivore or predator-prey interactions will drive the system. The EEH had stimulated fruitful debates in food web theory (bottom-up and top-down forces: Power 1992; trophic cascades: Polis et al. 2000). However, it has failed to predict the trophic structure of many food webs (Polis and Strong 1996, Gauthier et al. 2004), because it assumed closed systems (Oksanen and Oksanen 2000). The empirical demonstration of allochthonous subsidization within a meta-ecosystem, resulting from the openness of ecosystems, may be the starting point to explain the limited predictive power of the EEH.

The effect of allochthonous resources on the productivity of aquatic and terrestrial autochthonous populations has often been addressed (Durbin et al. 1979, Polis et al. 1997, Roth 2003, Carpenter et al. 2005). Some studies have empirically demonstrated allochthonous subsidization by linking direct use of allochthonous resources by a consumer to the productivity of its population (Art et al. 1974, Anderson and Polis 1999, Barrett et al. 2005). When this has been done, ecosystems were located within a local or regional scale. To our knowledge, no study has associated use of allochthonous resources to productivity of a population when resources flow within a meta-ecosystem spanning a continent.

Using long-term data (10 years), we studied the diet and productivity of a population of arctic fox (*Alopex lagopus)* included in a meta-ecosystem spanning the North American continent. Our study population lives in a typical tundra habitat of the Canadian High Arctic, preys on cyclic lemmings and on migrating geese (Gauthier et al. 2004). Geese nesting in the Arctic overwinter and accumulate endogenous reserves in temperate areas, more than 4000 kilometers south of their breeding grounds (Gauthier et al. 1992, Bêty et al. 2003; see Figure 1a for areas involved in migration and Figure 2 for the phenology of migration and reproduction). Hence, the migratory behavior of geese connects temperate and arctic ecosystems at a continental scale. This link between ecosystems differing in productivity could allow arctic fox populations to reach abundance levels not predicted solely by the primary productivity of the arctic tundra (Oksanen and Oksanen 2000, Gauthier et al. 2004).

The distribution of breeding geese relative to fox dens in our study area offered a unique opportunity to investigate the effect of goose consumption on arctic fox productivity. The goose nesting colony is established at the same location every year, and its distribution is highly clumped relative to that of arctic fox dens (Figure 1b). Moreover, the location of breeding dens relative to resources during the summer rearing period is a spatial constraint in the foraging activities of breeding arctic fox, because cubs stay at dens and are supplied in food by adults. The clumped distribution of the goose colony and the spatial constraints in foraging activities of adult foxes could generate spatial heterogeneity in arctic fox breeding output. Indeed, productivity is generally estimated with reproductive output (Angerbjörn et al. 1999, Elmhagen et al. 2000) in this short-lived species raising large litters (Audet et al. 2002), and food abundance during summer is known to affect cub survival (Tannerfeldt et al. 1994).

Our main objective was to test the hypothesis that arctic foxes denning close to the goose colony are provided with an allochthonous subsidy, which leads to an increase in their reproductive output. We formulated the following two predictions: 1- the contribution of goose to the diet of arctic foxes (cubs and breeding adults) is higher close to the goose colony than far from it and 2- the reproductive output of arctic fox, which is already known to be partially driven by the lemming abundance (Gauthier et al. 2004), is also higher around the goose colony.

METHODS

Study area

We worked from 1996-2005 on the south plain of Bylot Island (Figure 1b), Sirmilik National Park of Canada (72°53'N, 78°54'W). Our 425 km^2 study area mostly consists of dry upland plateau (mesic tundra) intersected by lowland valleys filled with wetlands (Massé et al. 2001). About 20,000 pairs of greater snow geese (*Chen caerulescens atlantica*) breed on Bylot Island (Reed et al. 2002). Density of other migrating birds is small compared to that of geese (Lepage et al. 1998b). Two lemming species coexist on Bylot. The brown lemming (*Lemmus sibiricus*) prefers wetland habitats and the collared lemming *(Dicrostonyx groenlandicus)* prefers mesic tundra (Rodgers and Lewis 1986). Other herbivores are found at low density on the island (Gauthier et al. 1996). The arctic fox is the main terrestrial predator of the food web (Bêty et al. 2002). Geese (adults, eggs and goslings) and lemmings were the main prey included in summer fox diet on Bylot Island in 2004-2005 (based on fecal analyses, prey remains on dens and direct behavioral observations, unpublished data).

Study design

Our study was designed in two parts. First, we compared the importance of geese in the summer diet of arctic foxes (cubs and breeding adults) in 2004-2005 between two sectors of the study area (Figure 1b): the goose sector (within 10 km from the periphery of the colony) and the non-goose sector. We set the 10 km threshold based on the maximum home range size of adult arctic foxes (62 km^2: Landa et al. 1998, Eide et al. 2004), which corresponds to a circular home range of 9 km in diameter (see Tannerfeldt et al. 2002 for a similar assumption). The contribution of geese to the summer diet of arctic foxes was measured with stable isotope analysis of carbon (C) and nitrogen (N) of blood samples of cubs and breeding adults. Isotopic quantification of the diet of a consumer is possible when food sources are isotopically distinct (Phillips et al. 2005). In our study, we anticipated differences in carbon isotopic signatures ($\delta^{13}C$) between lemmings and geese, resulting from their use of nutrients from different food webs (reviewed in Kelly 2000). Lemmings feed exclusively on arctic C_3 plants and geese feed on both temperate C_3 and C_4 plants (in farmlands and marshes of wintering and staging areas) and arctic C_3 plants (on breeding ground). Heterogeneity in lemming abundance between the goose and the non-goose sectors could also explain variations in fox diet. We thus monitored summer distribution of lemmings. For this purpose, we built an index of lemming activity based on counts of active lemming burrows and we compared that index between sectors in 2004-2005.

Secondly, we contrasted the reproductive output of arctic fox (litter size and annual percentage of breeding dens) between the goose and the non-goose sectors over a 10-year period (1996-2005). Because the lemming cycle is known to drive variations in arctic fox reproductive output (Eberhardt et al. 1983a, Angerbjörn et al. 1999, Gauthier et al. 2004), we always included the annual phase of the lemming cycles in our analyses.

In our study, we focused on the effects of the flow of nutrients on the tundra ecosystem. Therefore, we considered the tundra as the autochthonous ecosystem and the temperate farmlands and marshes as the allochthonous ecosystems. Because geese feed in both autochthonous and allochthonous ecosystems, they are a mixed source of nutrients for arctic foxes. At arrival on arctic breeding grounds, digestible tissues of adult geese are essentially composed of allochthonous nutrients accumulated on wintering and staging areas (Gauthier et al. 2003). Thereafter, geese start to feed on arctic plants and these autochthonous nutrients are gradually incorporated into their tissues (Gauthier et al. 2003). During egg formation, geese invest 30% and 70% of allochthonous and autochthonous nutrients in eggs, respectively (Gauthier et al. 2003). After hatching, goslings feed on arctic plants and the proportion of autochthonous nutrients in their tissues increases. Although geese are a mixed source of nutrients, we considered them as allochthonous organisms because 1- they are vectors of allochthonous nutrients (Gauthier et al. 2003) and 2- the increasing trend in the goose population during the last decades (from 25,400 in 1965 to more than 600,000 in 2003, Reed et al. 1998) closely matched environmental variations on temperate wintering and staging areas (especially the increase in the extent of corn fields, Gauthier et al. 2005). This suggests that resources available in temperate ecosystems strongly influence the size of this population and its presence on arctic breeding grounds.

Arctic fox monitoring

In 2004-2005, we monitored diet of cubs and breeding adults from the beginning of the rearing season (around mid May: Macpherson 1969, Audet et al. 2002) until cubs leave dens (around late July: Giroux, personal observation). We ended the study period when cubs leave dens because at this time, the spatial constraint on foraging activities (imposed by den location relative to resources) may be relaxed. Blood $\delta^{13}C$ and $\delta^{15}N$ represent nutrients assimilated over a period of around 1 month (reviewed in Dalerum and Angerbjörn 2005). Therefore, to describe the diet of foxes at the beginning of the rearing season, we started to collect blood from June 19 in 2004 and from June 28 in 2005. To cover the whole rearing period, we collected blood until July 28 in 2004 and July 27 in 2005. Blood was collected from the cephalic vein of 52 cubs trapped on 14 breeding dens (8 dens in 2004 and 6 in 2005) and on 9 adults trapped on 8 breeding dens (6 adults in 2004 and 3 in 2005). Foxes were trapped using collapsible live traps (Tomahawk cage traps #205, Tomahawk Live Trap Company, Tomakawk, WI, USA) placed directly on the den, or padded leghold traps (Softcatch #1, Oneida Victor Inc. Ltd. Cleveland, OH, USA) positioned within 100 m of the den. Traps were baited with sardines, dead lemmings or goose eggs, and were kept under continuous surveillance or visited at least every 12 hours, depending on the site. We anesthetized adults by injecting 15 mg Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA) into the upper rear leg muscle. Juveniles were manipulated without chemical immobilization using a large fabric bag. Each individual was measured, weighed, sexed and tagged on both ears using a unique set of colored and numbered plastic tags, allowing individual recognition (Dalton Rototags).

From 1996-2005, we monitored arctic fox dens to estimate reproductive output. From 1996-2002, we searched fox dens in both sectors of the study area. We found new dens every year, because the size of the surveyed area increased during the study. In 2003, we conducted an extensive and systematic den survey to find all dens in the 425 km^2 study area. We determined the position of each fox den using a Global Positioning System (GPS) receiver. From 1996 to 2005, dens were visited during summer as explained in Bêty et al. (2002). These visits allowed identification of breeding dens (with cubs) and estimation of minimum litter size, i.e. the highest number of cubs observed at any visit (see Bêty et al. 2002 for details). The annual percentage of breeding dens (number of breeding dens*100/number of dens visited) was estimated in each sector between 1996 and 2005.

Prey monitoring

To identify the goose and the non-goose sector, we mapped the average extent of the goose colony from 1996-2005. From 1991-2005, 9305 female geese were fitted with an individually numbered plastic neck band (see Menu et al. 2001 for methods of capture). Each year, we performed a systematic survey of nests of collared females throughout the colony, and we determined the position of each nest with a GPS receiver. We assumed that collared females were randomly distributed in the goose colony that we mapped with a 95% kernel of all collared goose nests found between 1996-2005. We used nests positions from all years because at the scale of the study area, there are relatively small variations in the extent of the colony between years.

To compare the activity of lemmings between the goose and the non-goose sectors, we built an index of lemming activity from counts of active burrows performed in 2004-2005 (for details, see appendix 1). To determine the phase of the lemming cycle (peak, decline, crash), we calculated an annual index of lemming abundance from snap-trap censuses performed each July from 1996-2005 (see Bêty et al. 2001 for details). To identify the phase of the lemming cycle in any given year, we used this index in combination with the occurrence of nesting snowy owls (*Bubo scandiacus*), which are nomadic specialist predators of microtines that breed essentially where prey are highly abundant (Wiklund et al. 1998). We searched owl nests every year on the study area. Crashes were identified when the index of lemming abundance was equal or nearly equal to zero. Otherwise, we discriminated between peak and decline phase with the presence of owl nests, which indicated a peak.

For stable isotope analysis, we collected muscle from fresh carcasses of lemmings and geese (adults and goslings), as well as egg content from broken eggs. These samples were opportunistically collected on the study area throughout summers of 2004-2005.

Stable isotope analysis

To estimate the percentage of goose in summer diet of arctic fox, we first measured the $\delta^{13}C$ and $\delta^{15}N$ of arctic fox blood and prey tissues. Laboratory methods used for these measurements are explained in appendix 2. We corrected isotopic signatures of arctic foxes for isotopic fractionation (i.e. difference between diet and tissues) by using factors calculated for adult and subadult red foxes (Roth and Hobson 2000, see appendix 3 for details). We then analyzed these corrected arctic fox signatures with the IsoSource mixing model (Phillips and Gregg 2003). This model is well suited when n isotopic tracers are used to estimate contribution of more than $n + 1$ different sources. We estimated the contribution to arctic fox diet of the two prey types (lemmings and geese) for which we had non-isotopic evidence of consumption during the summer (fecal analysis, prey remains on dens and direct behavioral observations). Although we worked with two isotopes, we used IsoSource because goose items (adults, eggs and goslings) and lemming species were not clustered enough to respectively pool their signatures into two different groups (Figure 4a). Using a

MANOVA, we compared $\delta^{13}C$ and $\delta^{15}N$ (both log transformed) between prey types (collared lemming, brown lemming, goose adults, eggs and goslings), years (2004-2005) and both variables in interaction. Isotopic signatures of prey types were significantly different (Wilks Lamba: $F_{8,96}=84.5$ $P<0.001$, $n=59$). Isotopic signatures in 2004 and 2005 were similar (Wilks Lamba: $F_{2,48}=0.5$ $P=0.6$, $n=59$), except for lemmings (interaction between year and prey, Wilks Lamba: $F_{8,96}=3.3$ $P=0.003$, $n=59$). In fact, signatures of brown and collared lemmings were similar in 2004 but different in 2005 (Tukey pairwise comparisons, 2004: $P>0.5$, $n=15$ and 2005: $P=0.002$, $n=13$). Consequently, we pooled prey signatures by year, except signatures of lemming species in 2005 (Figure 4a). To avoid pseudoreplication, we pooled signatures of cubs from the same den because diet of cubs is not independent at the den level. Indeed, their diet depends on food brought back to the den by the same adults. However, we considered that diet of adults was independent at the den level, because they usually hunt separately. Mean signatures of prey for each year are shown in appendix 4 and we explain in appendix 5 when we included goslings in analyses of diet (median date of hatching: 8 July). To estimate the contribution of geese items and lemmings species to fox diet, we used $\delta^{13}C$ and $\delta^{15}N$ of arctic foxes (one signature per den and per adult), lemmings and geese in the IsoSource model. For each den and each adult, we respectively combined the contributions of geese and of lemmings species (2005 only) *a posteriori*, as recommended by Phillips et al. (2005) when prey from the same food web are not clustered enough.

Data analysis

Our first prediction was that the percentage of goose in diet of arctic foxes (cubs and breeding adults) is greater in the goose sector than in the non-goose sector. Because it is recommended to use raw isotopic data rather than results of mixing models in statistical analyses of isotopic diet data (Ben-David and Schell 2001), and because mean percentage of goose in diet obtained from IsoSource and $\delta^{15}N$ were positively correlated (Pearson's correlation, see results), we used $\delta^{15}N$ as an index of mean percentage of goose in diet obtained from IsoSource to test this prediction. We analyzed $\delta^{15}N$ of cubs and adults separately. We investigated the source of variation in $\delta^{15}N$ of cubs by comparing models including sector (goose and non-goose) and year as predictors. Date of capture was included as a covariate to take into account intra-seasonal variation in foraging behavior of adults (Careau et al., unpublished results). We excluded index of lemming activity from analyses because it was similar between sectors (see appendix 1). We used the Akaike information criterion corrected for small sample size (AICc) to select the general linear models (GLM) that best fit our data. The model with the smallest AICc value and those within 2 AICc units from this model (ΔAICc < 2) were considered as having substantial empirical support (Burnham and Anderson 2002). For $\delta^{15}N$ of adults, we compared GLM including sector and year as predictors, and date of capture as covariate. We also selected models with the information theoretic approach, using AICc.

Our second prediction was that the reproductive output of arctic fox, which is known to be driven by the lemming abundance, is greater in the goose sector than in the non-goose sector. To test this prediction, we also used the information theoretic approach. For each index of reproductive output (litter size and annual percentage of breeding dens), we compared GLM including sector, phase of the lemming cycle and their interactions as predictors. Non breeding dens (litter size equal to zero) were not included in litter size analysis. We identified the GLM that best supports the data using AICc.

For both predictions, we also provide the percentage of variation (r^2) explained by the best GLM. When conditions of normality and heterogeneity of residuals were not met with untransformed or log transformed data, we rank transformed data. Because rank transformation is robust for the analysis of additive factors, but has low power for testing interactions (Seaman et al. 1994), we removed interactions from analyses of rank transformed data. We performed all statistical analyses with SAS, V.9 (SAS Institute Inc. 2002). Unless mentioned, values are reported as mean ± 1 SE.

RESULTS

Phase of the lemming cycle

From 1996 to 2005, the annual index of lemming abundance varied strongly (Figure 3). Crashes occur in 1999, 2002 and 2003. The index of lemming abundance was fairly low in 2005, but demographic analyses showed that the lemming population was in its declining phase (Gruyer and Gauthier, unpublished results). Whether we considered 2005 as a crash or declining year did not change results of analyses of arctic fox reproductive output. The presence of nesting snowy owls in 1996, 2000 and 2004 indicated lemming peaks.

Arctic fox diet

The mean percentage of goose in diet of cubs and breeding adults ranged respectively from 2-72% and 36-91%, and was positively correlated with $\delta^{15}N$ (r=0.92, P<0.001, Figure 4b). Sector was the best predictor of variation in $\delta^{15}N$ of cubs (Table 1) and explained 45% of this variation. In the goose sector, $\delta^{15}N$ of cubs (3.7 ± 0.3, n=10 dens) was 1.8-fold greater than in the non-goose sector (2.1 ± 0.4, n=4 dens; Figure 4a). Sector was also a plausible predictor of variation in $\delta^{15}N$ of adults (log transformed, Table 2), with 50% of the variation explained. In the goose sector, $\delta^{15}N$ of adults (5.0 ± 0.3, n=7 adults) was 1.4-fold greater than in the non-goose sector (3.6 ± 0.4, n=2 adults; Figure 4a). For adults, the null model was within 2 AICc units from the best model. Therefore, other variables may also account for variation in $\delta^{15}N$ of adults.

Arctic fox reproductive output

None of our variables explained variations in litter size (Figure 5) because the null model was the most plausible one (Table 3). Because there were no breeding dens in the non-goose sector during lemming crashes, no data from this sector and phase were included in litter size analysis (see methods). Variation in the annual percentage of breeding dens (rank transformed) was best explained by the additive effect of the sector and the phase of the lemming cycle (Table 3). This model accounted for 55% of variation in the annual percentage of breeding dens. The annual percentage of breeding dens (23.4 ± 6.5%, *n*=10) was 3.5-fold larger within than outside the goose sector (6.7 ± 2.4%, *n*=10; Figure 5). The effect of the phase of the lemming cycle on the annual percentage of breeding dens was mainly observed when contrasting crashes to other phases of the cycle. The annual percentage of breeding dens was 4.1 and 5.6-fold higher during declines (17.0 ± 5.0%, *n*=8) and peaks (23.3 ± 9.8%, *n*=6), respectively, than during lemming crashes (4.1 ± 2.6%, *n*=6; Figure 5).

DISCUSSION

As anticipated (prediction 1), arctic foxes increased the proportion of goose in diet when breeding close to the goose colony. In accordance with our second prediction, the presence of the goose colony and the phase of the lemming cycle both influenced arctic fox reproductive output; the annual percentage of breeding dens was lowest in the non-goose sector and during lemming crashes, and there were no breeding dens in the non-goose sector during lemming crashes. However, litter size was similar between sectors and phases. This study thus highly suggests that flow of organisms (geese) within a continental meta-ecosystem can subsidize a predator (arctic fox) population.

Flow of allochthonous resources

In the literature, input of allochthonous resources within an ecosystem is typically discussed when flowing resources are purely constituted of allochthonous nutrients (Polis et al. 1997). However, when spatial coupling occurs through movement of prey, nutrients from more than one ecosystem can be mixed within tissues of these prey. Indeed, there are many examples of migrating prey feeding in more than one ecosystem (Dockx et al. 2004, Jardine et al. 2005). Species migrating at a continental scale are good candidates to become mixed sources of nutrients because of the relatively high costs of migrating long distances. Predation upon this type of prey could lead to a transfer of allochthonous nutrients along with autochthonous nutrients.

Our study exemplifies this type of transfer. We found that geese constituted between 2-72% and 36-91% of nutrients assimilated respectively by arctic fox cubs and breeding adults during the cub rearing period. However, not all goose nutrients assimilated by arctic fox are allochthonous. Consequently, consumption of geese by arctic fox induced both a direct input of allochthonous nutrients into the arctic ecosystem, and a transfer of arctic primary production to the predator trophic level. This latter transfer can also occur through consumption of lemmings. However, the presence of geese appears essential to the transfer of autochthonous nutrients to arctic foxes during lemming crashes, when most attacks by arctic foxes in the colony are directed toward goose nests (Bêty et al. 2002).

Effect of resources on diet and reproduction

Abundance of goose was higher in the goose sector (1996-2005) and the index of lemming activity was similar between sectors (2004-2005, see appendix 1). Although the index of lemming activity was not calibrated against abundance and was not estimated from 1996-2003, our results indicate a relative homogeneity in abundance of lemmings across the study area. Therefore, total food abundance was probably higher in the goose sector, because of the presence of allochthonous organisms.

Food abundance is known to influence the diet of arctic fox, since this predator is opportunistic and uses resources in relation to their availability (Bantle and Alisauskas 1998, Dalerum and Angerbjörn 2000, Roth 2002, Eide et al. 2005). We showed that $\delta^{15}N$ (index of percentage of goose in diet) of cubs and breeding adults was greater around the goose colony. This result suggested an opportunistic foraging behavior. At the scale of the meta-ecosystem, this opportunistic foraging behavior would spatially modulate the transfer of allochthonous nutrients into the tundra. For adults, these conclusions are limited by our small sample size (*n*=9) and by the relatively small proportion of breeding adults sampled in both sectors (19% and 20% in goose and non-goose sectors, respectively). For cubs, our sample size was also relatively low (*n*=14), but we sampled a substantial proportion of breeding dens, i.e. 55% and 80% in goose and non-goose sectors, respectively. We are therefore confident that our results described well patterns in diet of cubs from our population.

Observational studies showed that food abundance influenced positively the reproductive output in the arctic fox (Macpherson 1969, Eberhardt et al. 1983a, Kaikusalo and Angerbjörn 1995). Moreover, two feeding experiments demonstrated that food abundance during winter-spring and summer influenced respectively percent of occupied dens (Angerbjörn et al. 1991) and cub survival (Tannerfeldt et al. 1994). Angerbjörn et al. (1995) suggested that variations in reproductive output in the arctic fox result from the effect of food abundance on females body condition and cub survival, occurring at any steps from the ovulation to the end of the rearing season.

We showed that the phase of the lemming cycle influenced the annual percentage of breeding dens. The influence of microtine abundance on the arctic fox reproduction is well known and has been thoroughly discussed (Eberhardt et al. 1983a, Kaikusalo and Angerbjörn 1995, Landa et al. 1999, Elmhagen et al. 2000). On the other hand, the influence of the presence of the goose colony on the annual percentage of breeding dens is a less classical result. In fact, it involves the effect of spatial (rather than annual) variations in abundance of an alternative (rather than a preferential) prey. This result suggests that variations in abundance of allochthonous resources (geese) on our study area induce a numerical response in the arctic fox population, through an increase in the proportion of breeding attempts or of successful breeding attempts where geese are present.

Our study was not designed to investigate the detailed mechanisms linking the abundance of allochthonous resources to the annual percentage of breeding dens. However, we suggest three hypotheses that could be further tested to unravel those mechanisms. First, the proportion of successful breeding attempts could have been larger around the colony, because of the influence of summer food abundance on body condition of breeding adults. Secondly, variations in winter and spring food abundance could also have influenced the body condition of breeding adults. We did not sample resources during winter and spring, but we are aware of potential variation in abundance of resources during spring on our study area. Each summer in the goose colony of Bylot Island, over 133 goose eggs/fox are hoarded and around 14% of these eggs can be recovered during the following spring (Careau, unpublished data). Because arctic foxes often stay in their summer home range during winter and spring when resources are sufficient (Wrigley and Hatch 1976, Eberhardt et al. 1983b), this could have influenced body condition and breeding success of arctic foxes. Thirdly, the proportion of breeding attempts could have been higher around the goose colony, because a greater proportion of dens would have been selected for reproduction in this sector. The greater food abundance during summer (and potentially spring) would have induced an aggregative response in the arctic fox population.

Litter size did not vary in relation to food abundance. Indeed, litter size was similar between sectors and phases of the lemming cycle. We estimated minimum litter size by counting cubs on dens, but detection of variations in this variable could have been improved by using genetic analyses because plural breeding (breeding females sharing a den) may occur on Bylot Island (Carmichael et al. in press).

Our study was designed as an unreplicated observational comparison of two sites. A weakness of our study is thus that spatial confounding factors may account for observed spatial variations in both diet and reproductive output. Moreover, individual predators could not be assigned randomly to the two sectors of our study area. Nevertheless, our results may describe a potential widespread pattern throughout the arctic fox range because the productivity of arctic fox populations is food limited (Elmhagen et al. 2000) and migrating colonial birds are often arctic fox alternative prey during summer (Quinn et al. 2003).

CONCLUSION

Our study indicates that a predator population (arctic fox) is subsidized by flows of allochthonous organisms within a continental meta-ecosystem. This may result in this predator population reaching abundance levels higher than predicted solely from the primary productivity of the tundra (Oksanen and Oksanen 2000, Gauthier et al. 2004), and may induce top-down cascading effects through the subsidized food web (Polis et al. 1997). For instance, apparent competition could be observed between geese and other prey species (Bêty et al. 2002, Holt 1977). For instance, the presence of geese at high density could indirectly affect the abundance of lemmings or other bird species, through the numerical response of the arctic fox, a shared predator. Further work should aim at estimating such potential cascading effects in the arctic tundra.

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TABLES AND FIGURES

Table 1. Results of the model selection procedure for fitting the effect of the sector (goose vs. non-goose), year, and date of capture on $\delta^{15}N$ of cubs trapped on Bylot Island in 2004-2005 (n = 14 dens). For each model, we report the AICc value relative to the model with the lowest AICc (ΔAICc), as well as the AICc weight of the model (ωAICc). Models are ranked by their AICc values and the best model is shown in bold.

Model	AICc	ΔAICc	ωAICc
Sector	**38.1**	**0.0**	**0.39**
Sector + Date	38.9	0.8	0.27
Sector + Year	40.2	2.1	0.10
Sector + Date + Year	41.0	2.8	0.08
Sector + Date*Year	41.2	3.1	0.02

Subscripts: + = additive model, * = model with interaction (individual effects and interaction included in the model).

Table 2. Results of the model selection procedure for fitting the effect of the sector (goose vs. non-goose), year, and date of capture on $\delta^{15}N$ of adults (log transformed) on Bylot Island in 2004-2005 (n = 9). For each model, we report the AICc value relative to the model with the lowest AICc (ΔAICc), as well as the AICc weight of the model (ωAICc). Models are ranked by their AICc values and the best models are shown in bold.

Model	AICc	ΔAICc	ωAICc
Sector	**-12.2**	**0.0**	**0.41**
Null	**-10.9**	**1.3**	**0.21**
Sector + Year	-8.3	3.9	0.06
Year	-7.8	4.4	0.06
Sector + Date	-1.5	10.7	0.00

Subscripts: + = additive model

Table 3. Results of the procedure of model selection fitting the effect of the sector (goose vs. non-goose) and the phase of the lemming cycle (lemming) on the indexes of reproductive output on Bylot Island from 1996 to 2005. The annual percentage of breeding dens was ranked transformed. The sample size is shown for each index. For each model, we report the AICc value relative to the model with the lowest AICc (ΔAICc), as well as the AICc weight of the model (ωAICc). Models are ranked by their AICc values and the best models are shown in bold.

Index	Model	AICc	ΔAICc	ωAICc
Litter size n=54	**No effect**	**253.7**	**0.0**	**0.51**
	Lemming	255.1	1.4	0.26
	Sector	256.1	2.4	0.16
	Sector + Lemming	257.9	4.2	0.06
	Sector * Lemming	2601.0	7.2	0.01
Breeding dens (%) n=20	**Sector + Lemming**	**118.1**	**0.0**	**0.93**
	Lemming	124.1	6.0	0.05
	Sector	125.7	7.6	0.02
	No effect	128.9	10.8	0.00

Subscripts: + = additive model, * = model with interaction (individual effects and their interaction were included in the model).

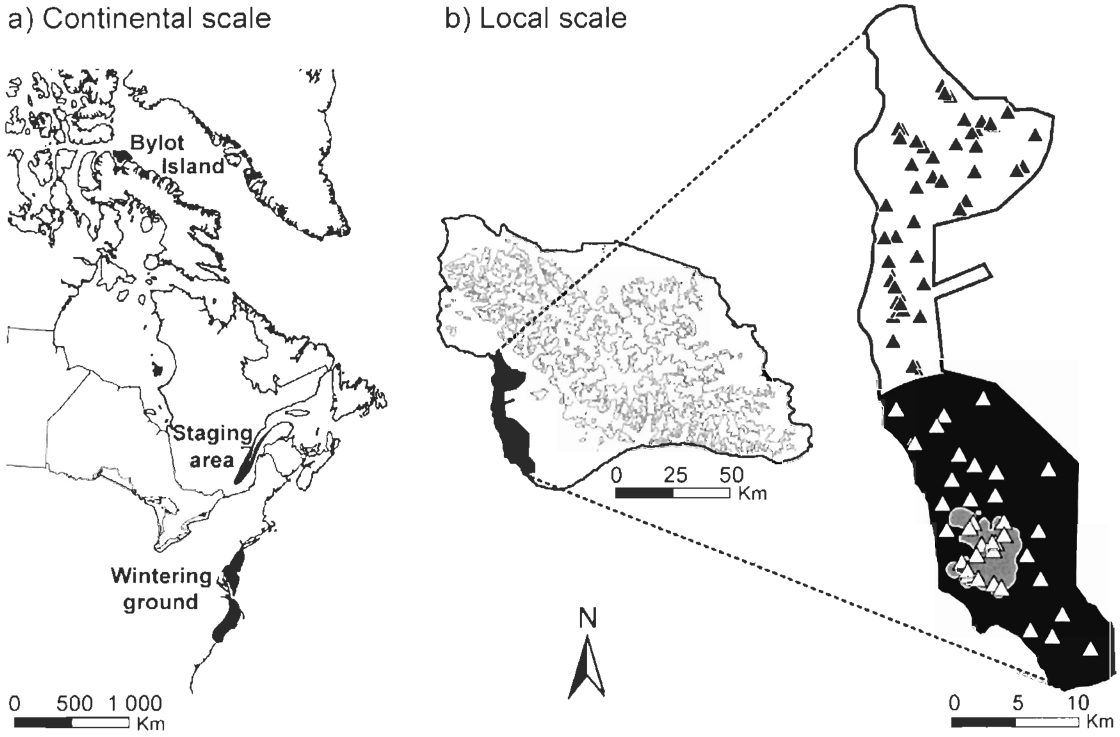
Fig.1. a) Map showing the main areas used by migrating greater snow geese during the annual cycle, from their temperate wintering grounds to their arctic breeding ground on Bylot Island. b) Map of Bylot Island showing the study area (south plain) in black. The enlargement shows the study area with the goose colony ( ), the goose sector (black) and the non-goose sector (white). Arctic fox dens in both sectors are represented by triangles.

Fig.2. The annual cycle of the greater snow geese (Bêty et al. 2003, Gauthier et al. 2005)

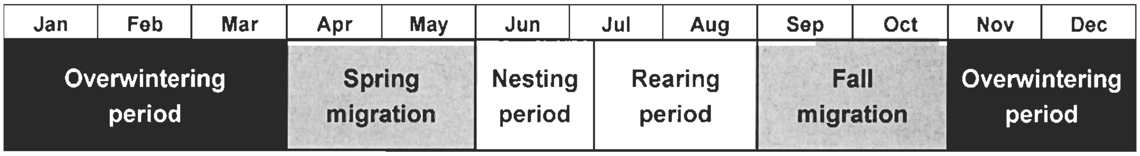
Fig.3. Index of annual lemming abundance and number of snowy owl nests recorded on Bylot Island from 1996-2005.

Fig.4. a) Carbon and nitrogen isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$, corrected for fractionation) of arctic fox cubs and breeding adults from the goose and the non-goose sectors. Also shown are mean signatures (± SE) and sample sizes for the following prey: goose (goslings, eggs and adults), lemming species pooled in 2004 (Lem. sp.), and collared and brown lemming in 2005 (C. lem. and B. lem.). b) Relation between $\delta^{15}N$ and the mean percentage of goose in arctic fox diet obtained with IsoSource. The Pearson's correlation coefficient (*r*) and the *p* value are shown.

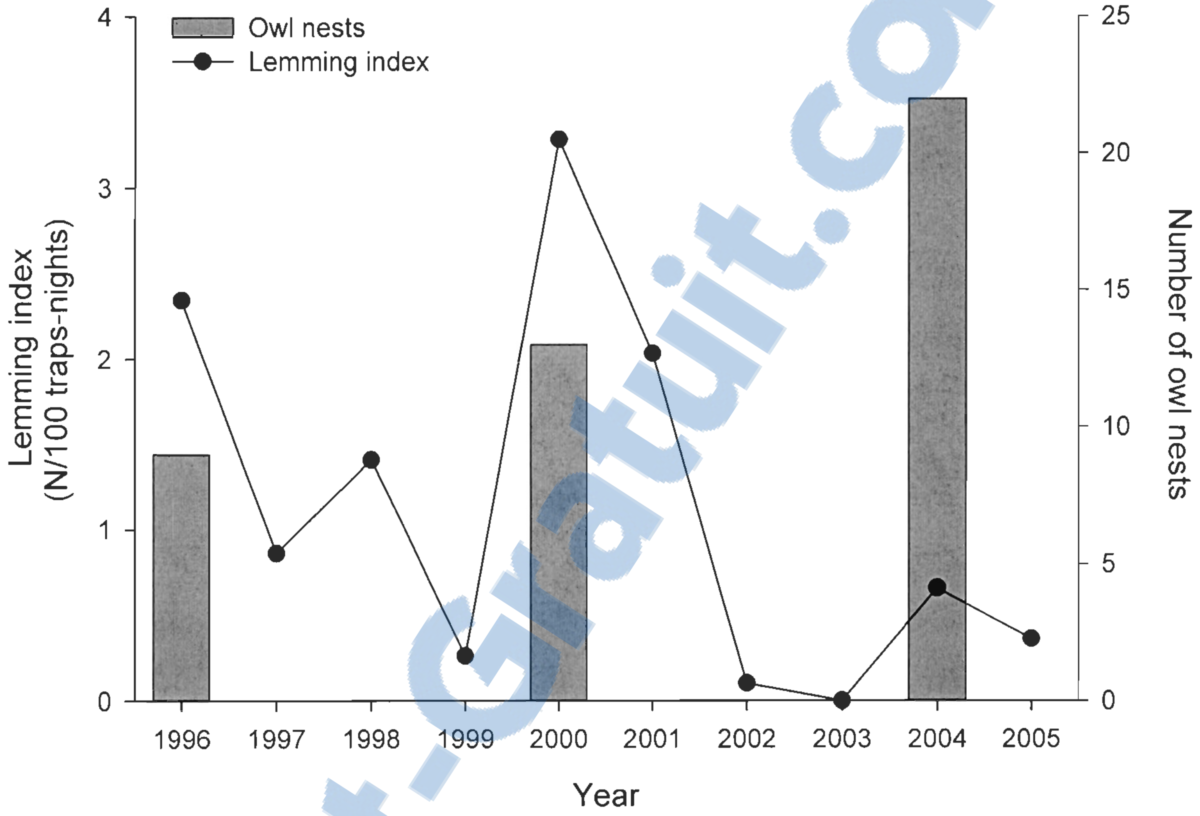
Fig.5. Litter size and annual percentage of breeding dens (mean ± SE) in both sectors (goose vs. non-goose) during the three phases of the lemming cycle. Sample sizes are shown above error bars.



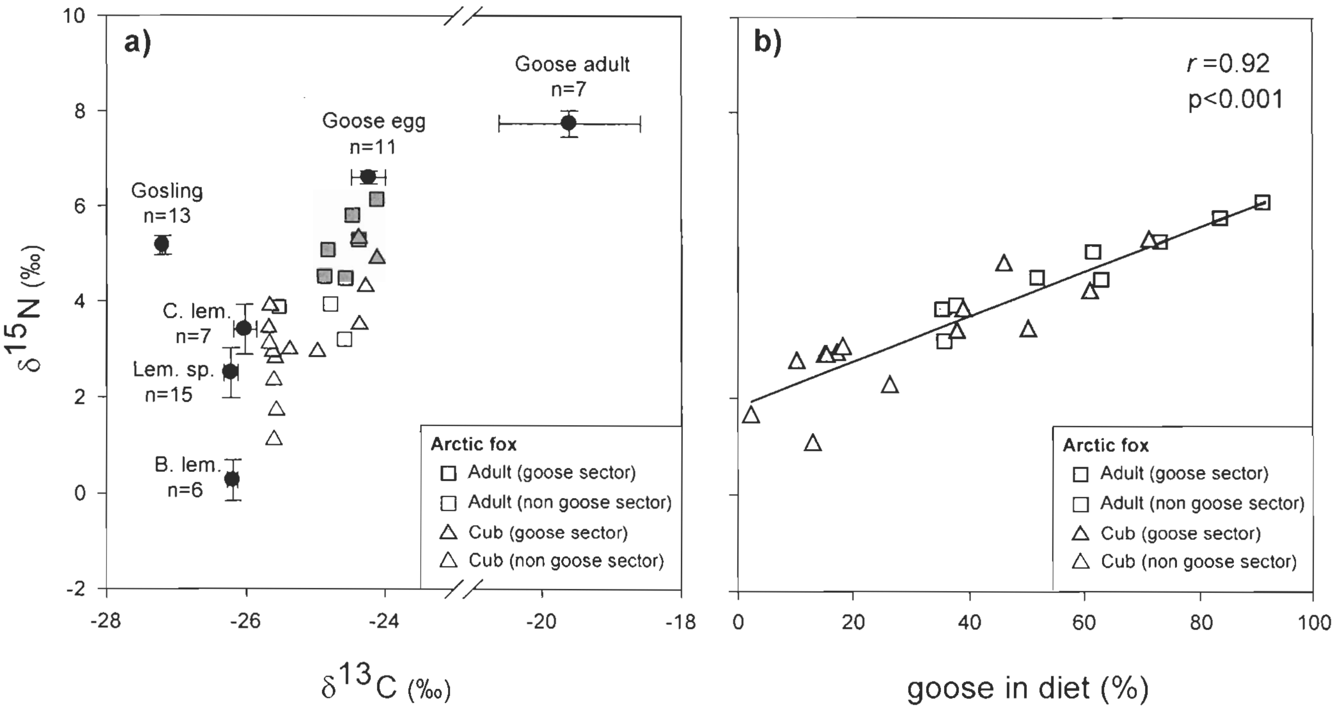
Giroux et al. Fig.1.



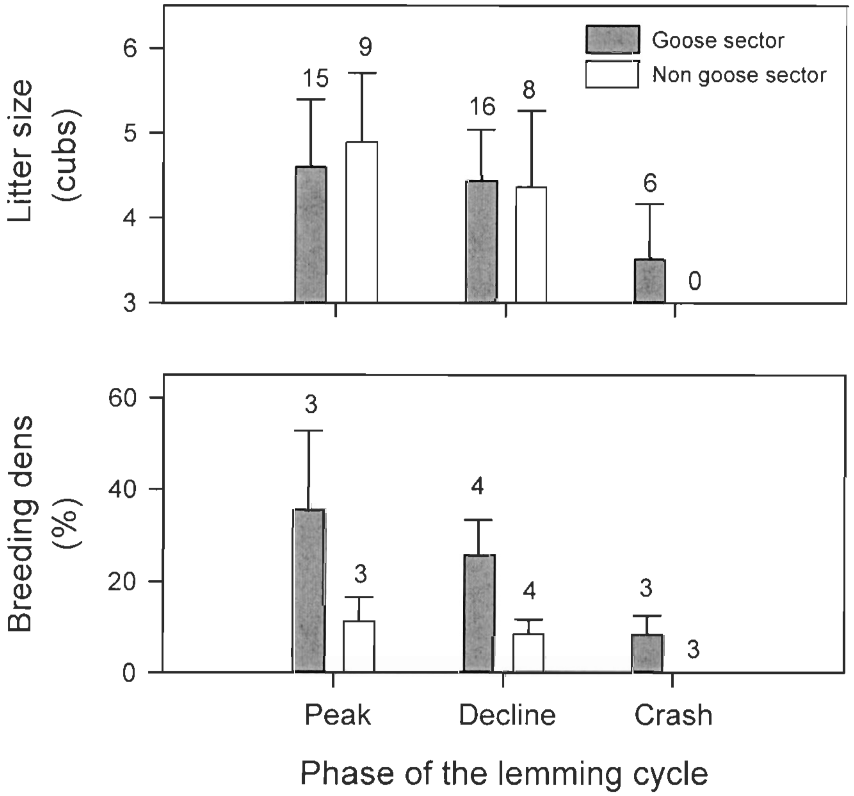
Giroux et al. Fig.2.



Giroux et al. Fig. 3.



Giroux et al. Fig. 4.



Giroux et al. Fig. 5.

APPENDIXES

Appendix 1: Index of lemming abundance (ILA)

Methods

Our objective in building the ILA was to include in analyses a variable representing spatial variations in lemming activity between the two sectors (goose vs. non goose). Because the index of lemming abundance varies with years (Gauthier et al. 2004) and habitat (Gauthier, unpublished results), we also included these variables to calculate the ILA. We built the ILA in two steps. First, we sampled from 3 to 37 stations in each combination of sectors, years (2004-2005) and habitats (wetlands and mesic tundra), for a total of 128 stations. At each station, we counted the number of active burrows in six transects (2 x 20 m) positioned on two parallel rows. We considered a burrow active when the entrance was not blocked by vegetation and we observed scats and trampled vegetation around burrows. We compared the effect of sector, year and habitat on average number of active burrows per sites with a three-way ANOVA for unbalanced design. In order to respect assumptions of ANOVA, we rank transformed data. This method is robust for the analysis of additive factors, but has low power for testing interactions (Seaman et al. 1994). We therefore tested interactions with the aligned rank test procedure (Salter and Fawcett 1993). Pairwise comparisons were performed with a Tukey-Kramer adjustment for multiple comparisons of least square means. In the next step, average number of burrow for each combination of sector, year and habitat were pooled when this analysis did not showed significative differences.

The second step was performed to include potential differences in proportions of habitats between sectors, because annual index of lemming abundance is generally lower in mesic tundra than in wetlands (Gauthier, unpublished results). This step consists of computing the ILA (within patches of land randomly selected in both sectors) by summing the product of the proportion occupied by both habitat by the average number of active burrow per habitat [ILA = Σ(%cover$_i$ * average number of active burrows$_i$), where i is the habitat]. We repeated this computation for both years in the two sectors. In this computation, we used average number of active burrows specific to sector, habitat and year only when they were statistically different (see the first step). Otherwise, we pooled average values across classes of effects being not statistically significant. We then tested the effect of sector, year and their interaction on ILA with a two-way ANOVA on ranked transformed data (with the aligned rank test procedure for interactions). The proportion of habitat in random patches was obtained as follow: 1) we generated 28 random points distributed in both sectors and 2) we measured the proportion of wetlands and mesic tundra in a 500m radius around each random point with a digital map of Bylot Island. To avoid spatial pseudo-replication, we set the minimal distance between each point at 3 km (the maximum distance traveled by a lemming is 100m, Gauthier, unpublished results).

Results

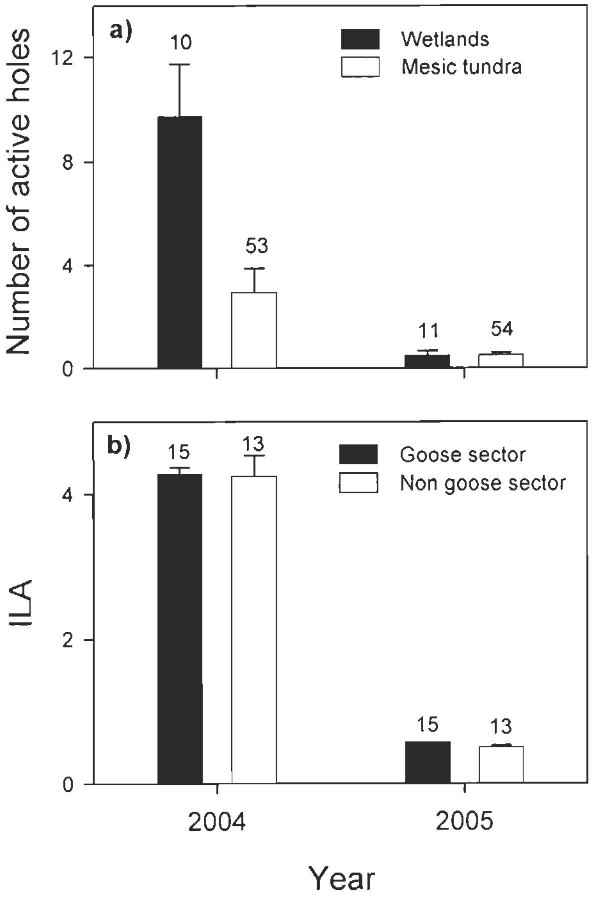
First step – Number of active burrows were influenced by year ($F_{1,121}$ = 58.37, P<0.001; Figure 1a) and by the interaction year and habitat ($F_{1,121}$ = 56.6, P<0.001; Figure

1a). Pairwise comparisons showed that there was a difference between wetlands and mesic tundra in 2004 ($t_{1,121}$=4.9, P<0.001), but not in 2005 ($t_{1,121}$=-1.7, P=0.3).

Second step – ILAs of 2004 were 8 times greater than those of 2005 ($F_{1,52}$=165.5, P<0.001; Figure 1b). Sector ($F_{1,52}$=1.7, P=0.2) and its interaction with year ($\mathrm{F}_{1,52}$=0.2, P>0.5) had no effect on ILAs.

Figure

Fig.1. a) Number of active holes in wetlands and mesic tundra in 2004-2005 (mean ± SE). Sample sizes are shown above error bars. b) Value of ILA in the goose and the non goose sectors in 2004-2005 (mean ± SE). Sample sizes (number of randomly selected patches) are shown above error bars.



Giroux et al. Fig.A1.1.

Appendix 2: Stable isotope analysis– Laboratory methods

Prior to laboratory analyses, we washed muscles samples in ethanol 70% (as recommended by Hobson et al. 1997) and dried both these samples under a fume-hood. We freeze-dried samples of blood, muscle and egg content. We removed lipids from muscles and egg contents with a 2:1 chloroform:methanol solution (a modification from Bligh and Dyer 1959). We powdered samples with a mortar and pestle. We loaded approximately 0.2 mg of each sample in tin capsules and combusted in a Carlo Erba NC2500 elemental analyzer. Resultants gases (CO_2 and N_2) were delivered via continuous flow to a Finnigan Mat Delta Plus isotope ratio mass spectrometer and analyzed for stable isotopes of carbon and nitrogen. Stable isotope ratios are expressed in δ-values as parts per thousand (‰) deviations from standards, namely Pee Dee Belemnite for C and atmospheric air for N, following $\delta^{13}C= [(^{13}C/^{12}C_{sample}-^{13}C/^{12}C_{standard})/\ ^{13}C/^{12}C_{standard}] \times 1000$ and $\delta^{15}N= [(^{15}N/^{14}N_{sample}-^{15}N/^{14}N_{standard})/\ ^{15}N/^{14}N_{standard}] \times 1000$. Analytical error is reported by providing measures of accuracy and precision (Jardine and Cunjak 2005). We estimated accuracy with measurements (mean ± SD) of a commercially available standard (acetanilide, Elemental Microanalysis Ltd.): $\delta^{13}C$= -33.6 ± 0.1‰ SD and $\delta^{15}N$ = -3.2 ± 0.3‰ SD (n = 58). Precision was measured across runs using an internal smallmouth bass muscle standard (SD): $\delta^{13}C$= ± 0.1‰ and $\delta^{15}N$= ± 0.2‰ (n = 23). Precision was also measured within analytical runs using duplicate samples. The average SD for duplicates was ± 0.1‰ for carbon and ± 0.2‰ for nitrogen.

Appendix 3: Stable isotope analysis– Fractionation factors

Fractionation factors ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) were calculated separately for blood cells and serum of captive subadult red foxes (Roth and Hobson 2000). In our isotopic analyses, we used samples of whole blood instead of separated blood fractions. To obtain $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ of whole blood samples, we measured the respective weights of both fractions of blood in dried samples of arctic fox blood and calculated a weighted average of whole blood $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ as follow (where w_{SERUM} and $w_{BLOODCELLS}$ is the weight of serum and blood cells in sample, respectively):

$$\Delta\delta^{13}C_{WHOLEBLOOD} =$$
$$\Delta\delta^{13}C_{SERUM} \times (w_{SERUM} / w_{WHOLEBLOOD}) + \Delta\delta^{13}C_{BLOODCELLS} \times (w_{BLOODCELLS} / w_{WHOLEBLOOD})$$

Because serum represents only 0.2% of whole blood dry weight in our samples, $\Delta\delta^{13}C_{Whole\ blood}$ and $\Delta\delta^{15}N_{Whole\ blood}$ were nearly equal to $\Delta\delta^{13}C_{Blood\ cells}$ and $\Delta\delta^{15}N_{Blood\ cells}$, respectively. We therefore subtracted blood cell fractionation values (Table 1) to signatures of cubs.

Blood fractionation values were not measured for adults. There were no difference in $\Delta\delta^{13}C$ between adults and subadults for all other tissues measured (Roth and Hobson 2000). Therefore, $\Delta\delta^{13}C$ of adult blood was assumed to be equal to subadult value. We estimated $\Delta\delta^{15}N$ of adults by subtracting to $\Delta\delta^{15}N$ of subadults the mean difference between subadults and adults values for other tissues (Table 1).

Table 1. Fractionation factors calculated for captive red foxes. In bold, factors used in our study to correct arctic fox signatures.

	ADULTS		**SUBADULTS**	
TISSUES	**$\Delta\delta^{13}C$**	**$\Delta\delta^{15}N$**	**$\Delta\delta^{13}C$**	**$\Delta\delta^{15}N$**
Fur	2.6	3.2	2.6	3.4
Muscle	1.1	3.3	1.1	3.6
Liver	0.4	3.4	0.4	3.6
Blood cells [a]	**0.6**	**2.4**	**0.6**	**2.6**
Mean difference of $\Delta\delta^{15}N$ subadults vs. adults				0.2

[a] For adults, these values were estimated, as explained above.

Appendix 4: Prey signatures

Table 2. Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$, mean ± SE) and sample size of prey of the arctic fox on Bylot Island in 2004 and 2005.

Prey type	**Year**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**n**
Brown lemming	2004	-26.3 ± 0.2	2.8 ± 0.6	8
Brown lemming	2005	-26.0 ± 0.2	3.4 ± 0.5	6
Collared lemming	2004	-26.1 ± 0.1	2.2 ± 0.9	7
Collared lemming	2005	-26.2 ± 0.1	0.3 ± 0.4	7
Goose adult	2004	-17.6 ± 0.5	7.8 ± 0.4	3
Goose adult	2005	-21.1 ± 1.2	7.7 ± 0.5	4
Goose egg	2004	-24.7 ± 0.1	6.9 ± 0.2	6
Goose egg	2005	-23.7 ± 0.4	6.3 ± 0.1	5
Goose gosling	2004	-27.2 ± 0.1	5.1 ± 0.2	7
Goose gosling	2005	-27.2 ± 0.1	5.3 ± 0.4	6

Appendix 5: Goslings in diet analyses

Estimation of sigmoid growth curve of goslings showed that the exponential increase in body mass starts around 10 days after hatching (Lesage and Gauthier 1997). We therefore assumed that before this sharp increase in body mass, isotopic signatures of goslings were similar to those of goose eggs. This threshold in isotopic value would correspond in 2004 and 2005 to July 17 and 18, respectively (Gauthier, unpublished results). Therefore, goslings were excluded from isotopic analyses (used to estimate the composition of arctic fox diet) for all foxes caught before these dates.

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CONCLUSION ET PERSPECTIVES

Nous avons démontré qu'une interaction entre deux écosystèmes séparés de milliers de kilomètres pouvait influencer la productivité du prédateur principal (renard arctique) d'un écosystème, *via* la consommation de proies provenant d'un autre écosystème (oies). Ce résultat constitue un pas important dans la compréhension de la structure du réseau trophique de l'île Bylot. Plus particulièrement, nos résultats suggèrent que l'importance de l'interaction prédateur/proie au sein de ce réseau trophique pourrait être le fruit d'une abondance de prédateurs plus grande que celle prédite uniquement par la productivité primaire de la toundra arctique. L'hypothèse d'exploitation des écosystèmes suggère en effet que la faible productivité primaire de la toundra arctique ne peut supporter une abondance de prédateurs suffisante pour que ceux-ci forment un niveau trophique fonctionnel, c'est-à-dire ayant un impact sur les herbivores.

La prochaine étape dans la compréhension des mécanismes à l'œuvre au sein du réseau trophique de l'île Bylot serait l'étude des cascades trophiques descendantes, découlant potentiellement de l'effet du subside allochtone sur la productivité du renard arctique. L'effet des subsides allochtones sur le prédateur pourrait entraîner une modification de la relation entre le prédateur et ses proies autochtones. Dans cette optique, une avenue à envisager serait la comparaison de la dynamique renard arctique/lemming entre les deux secteurs de l'aire d'étude.

Une autre avenue de recherche serait de mesurer l'impact de la consommation de ressources marines sur la productivité de la population de renard arctique. Les évidences non isotopiques (fèces, restes de proies sur les tanières et observations comportementales) ainsi que des analyses isotopiques préliminaires (données non publiées) ont démontré que les phoques annelés ne seraient par une ressource utilisée par les renards arctiques de l'île Bylot en été. Toutefois, les ressources marines pourraient constituer une partie importante du régime alimentaire hivernal et printanier du renard arctique, plus particulièrement durant les creux de lemmings. Cette consommation de ressources marines pourrait également affecter l'abondance de la population de renard arctique de l'île Bylot.

Pour clore cette étude, il est important de mentionner que d'un point de vue technique, cette étude n'aurait pas été possible il y a quelques décennies. Premièrement, l'utilisation des isotopes stables en écologie a émergé au cours des trois dernières décennies. Sans cette technique, nous aurions pu comparer le régime alimentaire des renards entre les deux secteurs avec d'autres techniques (fèces, contenus stomacaux, observations comportementales). Toutefois, l'effort aurait été beaucoup plus grand et nous n'aurions pu quantifier la proportion de nutriments réellement assimilés. Finalement, l'étude des processus globaux en écologie est également le fruit des développements technologiques récents qui ont permis des déplacements rapides à l'échelle planétaire. En effet, sans le développement du transport aérien et des technologies de télédétection, nous ne pourrions mesurer de façon aussi précise les déplacements globaux des espèces migratrices. Comme le mentionnait Gaston Badelard, philosophe français, la science n'aurait-elle pas l'âge de son outil de mesure?