UNIVERSITÉ DU QUÉBEC À MONTRÉAL

COMPORTEMENT DE MISE EN RÉSERVE DU RENARD ARCTIQUE DANS UNE COLONIE D'OIES DES NEIGES À L'ÎLE BYLOT, NUNAVUT

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AVANT-PROPOS

Ce mémoire comprend une introduction et une conclusion générale rédigées en français et trois articles scientifiques rédigés en anglais. Je suis premier auteur sur tous ces articles, avec mon directeur, Jean-François Giroux, et mon co-directeur, Dominique Berteaux. Pour le chapitre I, s'ajoutent Nicolas Lecomte, Joël Bêty et Gilles Gauthier, puisqu'ils ont fourni une partie des données utilisées pour ce chapitre. Le chapitre II est issu des données que j'ai récoltées à l'île Bylot durant les étés 2004 et 2005. Le chapitre III est présentement sous presse dans la revue *Journal of Ethology*. J'ai participé à la collecte de toutes les autres données et réalisé toutes les analyses et rédaction des manuscrits.

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RÉSUMÉ

Le comportement de mise en réserve de nourriture a évolué chez plusieurs espèces comme une adaptation pour faire face à des périodes de pénuries alimentaire. Les mammifères terrestres de l'Arctique sont sujets à des variations importantes en abondance de nourriture. Le renard arctique (*Alopex lagopus*) est reconnu pour son habitude à cacher de la nourriture, particulièrement dans les colonies d'oies où les œufs sont très abondants durant une période très brève (saison de nidification). L'hypothèse générale de ce projet est que le renard de l'île Bylot maximise son accès aux œufs de la grande oie des neiges (*Chen caerulescens atlantica*) via la mise en réserve de nourriture. Des observations comportementales ont été effectuées durant 8 saisons de nidification couvrant deux cycles complets de lemmings. Le taux d'acquisition en œufs des renards était très élevé durant la ponte et a diminué tout au long de la saison de nidification, tout comme le taux de cache, puisque les œufs ont été cachés en proportions de leur acquisition indépendamment de la variation saisonnière en abondance d'œufs. La proportion d'œufs cachés a plutôt varié annuellement en lien avec l'abondance de lemmings; les renards ont caché la majorité des œufs (>90%) durant les années de forte abondance de lemmings et durant les deux années suivantes. Cette proportion a diminué à 40% durant la troisième année après le pic de lemmings, probablement parce que les renards ont dû consommer une plus grande proportion des œufs qu'ils obtenaient. Le taux avec lequel les renards ont récupéré les œufs cachés a varié en fonction de l'abondance des œufs dans les nids et l'abondance de la réserve en œufs cachés. La périssabilité et le temps de consommation sont deux facteurs ayant un effet sur les décisions de cache du renard arctique. Parmi les proies les plus importantes (œuf, oison et lemming) pour les renards à Bylot, l'œuf est la moins périssable et est celle qui requiert le plus de temps à manger. La théorie prédit que les œufs devraient donc être cachés en plus grande proportion et c'est ce qui a été observé dans cette étude. Les deux facteurs pourraient être importants puisque la saison de nidification des oies est courte et que les renards doivent se faire une réserve potentiellement utile à long terme. Le comportement de mise en réserve des renards a été quantifié à un niveau inégalé à l'aide de l'utilisation d'une technique de suivis télémétriques des œufs cachés. L'hypothèse de la séquestration rapide a ainsi pu être testée pour expliquer pourquoi les renards recachent les œufs d'oies. Les renards utiliseraient une stratégie de mise en réserve en deux étapes; d'une part, pour maximiser la récolte d'une ressource abondante, mais éphémère et d'autre part, pour relocaliser les œufs dans des endroits plus sécuritaires. Cette étude fait aussi état d'une première mention à propos d'interactions interspécifiques entre le renard arctique et le grand corbeau (*Corvus corax*). Ce dernier peut prélever efficacement les réserves faites par les renards. Somme toute, en utilisant de simples données à long terme combinées à des observations plus détaillées et à une technique originale, ce projet nous informe sur les mécanismes comportementaux ayant évolué chez le renard arctique pour maximiser son accès aux œufs d'oies. Ceci peut potentiellement éclairer certains patrons observés à l'échelle de la population et de la communauté de l'île Bylot.

Mots-clés : Mise en réserve, décisions de cache, périssabilité, hypothèse de la séquestration rapide, *Alopex lagopus*, *Chen caerulescens atlantica*, *Corvus corax*, île Bylot.

INTRODUCTION GÉNÉRALE

Le comportement de mise en réserve

Le comportement de mise en réserve (CMR; du mot anglais *hoarding*) est synonyme de comportement de stockage (*storing*) et de dissimulation (*caching*). Deux points sont essentiels pour définir le CMR : la consommation de la nourriture doit être différée et la nourriture doit être manipulée de manière à réduire la probabilité qu'un autre organisme la consomme (Vander Wall 1990). Le CMR est commun à plusieurs animaux, particulièrement là où l'environnement est variable et où une saison froide aide à la conservation de la nourriture (Andersson et Krebs 1978; Smith et Reichman 1984). Le CMR permet aux animaux d'avoir un certain contrôle sur la répartition temporelle de l'apport en nourriture. Des périodes de pénurie alimentaire peuvent même être évitées si la quantité de nourriture stockée est suffisamment grande. L'utilisation de nourriture stockée permet aux animaux de demeurer en région familière sans avoir à emmagasiner des réserves de graisses. Le CMR est donc une stratégie alternative ou complémentaire à la migration, à la torpeur ou à l'hibernation (Smith et Reichman 1984; Vander Wall 1990). Le CMR peut aussi être avantageux lorsqu'il réduit le temps investi à la quête de nourriture alors que d'autres comportements sont plus importants, qu'il maximise la récolte de nourriture durant une courte période et qu'il permet de supplémenter le régime alimentaire des jeunes en croissance (Smith et Reichman 1984; Vander Wall 1990).

Décisions de cache

Les animaux emmagasinant de la nourriture doivent toujours choisir entre la nourriture à consommer et celle à entreposer. Les décisions de cache des animaux sont influencées par les bénéfices reliés à la consommation immédiate d'un aliment et les bénéfices futurs si l'aliment est entreposé (Kotler *et al.* 1999). Ces valeurs présente et future sont grandement déterminées par l'état physiologique de l'animal; un individu en déficit nutritionnel doit manger et un autre à satiété peut se permettre de cacher. Cependant, entre la famine et la satiété, les décisions de cache sont influencées par les propriétés intrinsèques des aliments. Parmi ces propriétés, le taux de décomposition et le temps requis pour consommer un item ont été identifiés comme étant des facteurs importants (Hadj-Chikh *et al.* 1996; Jacobs 1992). Puisque la décomposition peut diminuer considérablement la valeur future d'un item caché, les animaux, particulièrement les rongeurs, évitent de cacher des items périssables (Gendron et Reichman 1995; Smallwood et Peters 1986). Cependant, le temps de consommation pourrait aussi être important dans les décisions de cache. En assumant qu'il est plus rapide de cacher un item que de le manger, Jacobs (1992) suggéra que les animaux cachent préférentiellement les items qui nécessitent le plus de temps à consommer. Ces deux hypothèses ne sont pas exclusives. La périssabilité des aliments pourrait être moins importante pour les animaux vivant dans les environnements où la décomposition est lente ou qui entreposent la nourriture sur une courte période. Toutefois, pour un animal ayant recours à ses réserves pour survivre à une période prolongée de pénurie, les avantages reliés à une sensibilité aux différences de temps de consommation seraient perdus devant une réserve décomposée (Hadj-Chikh *et al.* 1996).

La récupération des items cachés

Le moment de la récupération d'un item caché dépend habituellement du rôle que joue le CMR pour l'individu. La survie durant les périodes de pénurie semble être, pour plusieurs espèces, la principale raison de la récupération de la nourriture entreposée (Vander Wall 1990). Pour que le CMR soit adaptatif et puisse ainsi évoluer, un individu qui cache doit avoir plus de chance de retrouver ses propres réserves qu'un autre voulant les prélever (Andersson et Krebs 1978; Vander Wall *et al.* 2006). Pourtant, le pillage des caches est un phénomène courant chez les animaux dont les domaines vitaux se chevauchent. Dans une situation où l'animal se faisant piller une de ses caches peut piller à son tour (pillage réciproque), Vander Wall et Jenkins (2003) ont démontré théoriquement que le CMR peut évoluer même avec des taux élevés de pillage. Le pillage est plus dommageable lorsqu'il n'est pas réciproque (e.g. caches pillées par des individus qui ne cachent pas ou qui recachent dans des endroits inaccessibles). Ainsi, le pillage interspécifique, qui a reçu peu d'attention jusqu'à maintenant, est probablement une contrainte plus importante que le pillage intraspécifique dans l'évolution du CMR. Cette contrainte a façonnée d'une part l'évolution des comportements de protection des caches et d'autre part les comportements visant à augmenter le succès de pillage (Dally *et al.* 2006).

L'hypothèse de la séquestration rapide de nourriture

Les animaux ne consomment pas toujours la nourriture au moment de la récupération des réserves (Vander Wall 1990). En effet, il a été largement rapporté que plusieurs animaux transfèrent les items cachés d'un site à un autre (Clarke et Kramer 1994; Jenkins *et al.* 1995; Vander Wall 1995; Vander Wall et Joyner 1998). Cependant, la valeur adaptative de ce comportement est peu comprise jusqu'à maintenant. L'hypothèse de la séquestration rapide offre une explication pour le comportement de recache. Selon cette hypothèse, les animaux adopteraient une stratégie de mise en réserve en deux étapes pour maximiser la récolte d'une source de nourriture abondante, mais éphémère. Cette hypothèse prédit que les animaux cachent la nourriture une première fois près de la source pour diminuer le temps de voyagement et maximiser la récolte. Puisque ces caches sont localisées près de la source, elles sont relativement concentrées et donc plus susceptibles d'être prélevées par d'autres individus, surtout si d'autres animaux fréquentent la source. L'hypothèse de la séquestration rapide implique donc que les animaux devraient recacher la nourriture à des endroits plus sécuritaires (Jenkins et Peters 1992).

Comportement de mise en réserve chez les canidés

Plusieurs membres de la famille des canidés (36 espèces) sont reconnus pour cacher de la nourriture, particulièrement les renards (Macdonald 1976; Macdonald et Sillerio-Zubiri 2004; Vander Wall 1990). Chez cette famille, le CMR implique une séquence de comportements stéréotypés aboutissant à une excellente dissimulation de l'item (Phillips *et al.* 1990; Phillips *et al.* 1991; Vander Wall 1990). Les corvidés, une autre famille dont plusieurs membres sont connus pour leur habitude à cacher, ont la capacité de piller les caches des canidés à l'aide d'indices visuels (Bugnyar et Kotrschal 2002; Henry 1986; Macdonald 1976). La dissimulation de l'item semble donc être un aspect important pour diminuer les chances de pillage interspécifique. Chez les canidés, il existe une importante variation intra et interspécifique dans la répartition spatiale des caches en réponse aux conditions environnementales (Sklepkovych et Montevecchi 1996). Comme pour les carnivores en général, l'intensité à laquelle les canidés cachent la nourriture semble être reliée à l’accessibilité des proies et/ou au statut nutritionnel du prédateur (Vander Wall 1990). Macdonald (1976) observa chez des renards roux (*Vulpex vulpes*) semi-apprivoisés que des caches temporaires pouvaient être créées afin de maximiser l’obtention de nourriture lorsque cette dernière n’était disponible que pour une période de temps limitée (séquestration rapide). En milieu naturel, le renard roux cache des œufs de tortues (*Caretta caretta*) dans le sable des plages de la Turquie (Macdonald *et al.* 1994). Le suivi des pistes laissées dans le sable a permis de démontrer que durant la nuit suivant la création des caches, les adultes récupéraient celles-ci habituellement accompagnés de leurs jeunes, suggérant que ces renards cachaient les œufs de tortues spécifiquement pour alimenter leurs jeunes.

Le renard arctique

Le renard arctique est présent sur la plupart des terres arctiques situées au nord de la limite des arbres, incluant des îles éloignées des continents telles que l’Islande, Svalbard, Commander, et Wrangel (Tannerfeldt 1997). Le renard arctique possède de nombreuses adaptations physiologiques et physiques pour survivre dans l’environnement arctique. Il conserve sa chaleur corporelle avec la fourrure la plus isolante de tous les mammifères, des poils sous ses pieds, de petites oreilles, un nez court et une habileté à réduire le flux sanguin dans les régions périphériques de son corps (Klir et Heath 1992; Prestrud 1991; Scholander *et al.* 1950). Le renard arctique peut entrer en dépression métabolique pour diminuer ses dépenses d’énergie lors des périodes de pénurie alimentaire (Fuglei 2000). Malgré toutes ces adaptations, le manque de nourriture durant l’hiver semble être un facteur déterminant dans la régulation des populations de renards arctiques. En effet, la mortalité hivernale des juvéniles se situe habituellement entre 50 et 80% (Hiruki et Stirling 1989; Macpherson 1969; Prestrud 1992a; Tannerfeldt *et al.* 1994) et peut être aussi élevée que 95% (Angerbjörn *et al.* 1991).

L’importance de la mise en réserve chez le renard arctique

Pour le renard arctique, les deux seules façons de stocker de l’énergie pour l’hiver sont le dépôt de gras et le CMR (Prestrud 1992a). Selon Prestrud (1991), une cache de 10 Mergules nains (*Alle alle*) et de 4 Guillemots de Brünnich (*Uria lomvia*) contient autant d’énergie que la moyenne de dépôt de gras chez un renard arctique à la fin de l’automne. Il a été rapporté que certaines caches de renard arctique contenaient plus d'une trentaine d'oiseaux marins et de petits mammifères (voir Sklepkovych et Montevecchi 1996) et qu'un seul renard pouvait cacher plus de 1000 œufs d'oies au cours d'un été (Samelius et Alisauskas 2000). Ainsi, le CMR peut être plus avantageux que le dépôt de gras pour assurer la survie en hiver puisque l'énergie peut être stockée en plus grande quantité et plus rapidement (Prestrud 1991). De toute évidence, le renard arctique vit dans des conditions favorisant le CMR (climat froid et fluctuations des ressources), ce qui explique probablement pourquoi il est le plus assidu dans ce comportement parmi tous les carnivores (Frafjord 1992).

Fluctuation annuelle et saisonnière des ressources

La productivité secondaire du milieu est généralement basse dans l'aire de répartition du renard arctique. Cependant, certaines ressources alimentaires peuvent être extrêmement abondantes à des endroits localisés et durant de courtes périodes. Le renard arctique est opportuniste et s'adapte rapidement aux variations en abondance de nourriture et ceci se reflète dans sa diète (Angerbjörn *et al.* 1994; Dalerum et Angerbjorn 2000; Frafjord 1993; Hersteinsson et Macdonald 1996). Le patron dominant de fluctuation des ressources est déterminé par le cycle des populations de rongeurs tels que les lemmings (*Lemmus* et *Dicrostonys spp*) et campagnols (*Microtus* et *Clethrionomys spp*). Le renard arctique montre de très fortes réponses fonctionnelle et numérique à l'abondance des rongeurs, mais doit exploiter d'autres ressources alimentaires lors des périodes où ils sont rares ou inaccessibles (Angerbjörn *et al.* 1995; Elmhagen *et al.* 2000; Macpherson 1969). Durant ces périodes, certains items comme les oiseaux et leurs œufs ainsi que les carcasses d'animaux marins peuvent former une portion considérable du régime alimentaire du renard arctique (Anthony *et al.* 2000; Bantle et Alisauskas 1998; Chesemore 1968b; Fay et Stephensen 1989; Kapel 1999; Roth 2002). De toutes les proies du renard arctique, les œufs sont probablement les moins périssables une fois entreposés puisqu'ils possèdent des barrières physiques et chimiques contre l'invasion bactérienne (Board 1966; Board et Fuller 1974). Le CMR du renard arctique est particulièrement intense dans les colonies d'oies où 80-97% des œufs acquis sont cachés (Samelius et Alisauskas 2000; Stickney 1991).

Système à l'étude

Située dans le Haut Arctique Canadien, l'île Bylot est le plus important site de nidification de la grande oie des neiges (*Chen caerulescens atlantica*). Depuis 1989, les oies commencent habituellement à pondre vers le 12 juin et le font de manière très synchronisée, puisque 70 et 90% des nids sont initiés en 4 et 8 jours, respectivement (Gauthier et Tardif 1991; Lepage *et al.* 2000). L'incubation ne dure qu'environ 24 ± 1 jours et l'éclosion survient habituellement le 8 juillet, de façon aussi synchronisée que la ponte. La période durant laquelle les œufs sont disponible est donc très brève (max 40 jours). Ceci suggère que le renard arctique s'approvisionne sous une contrainte de temps durant la saison de nidification des oies. Durant l'incubation, la femelle est présente au nid ~94% du temps et le couple défend activement ses œufs contre les prédateurs. L'île Bylot abrite aussi une population cyclique de lemmings bruns (*Lemmus sibiricus*) et une population non-cyclique de lemmings variables (*Dicrostonyx groenlandicus*). Quatre pics d'abondance de lemmings y ont été documentés, soit en 1993, 1996, 2000 et 2004 (Fig. 1).

Le renard arctique ne peut habituellement pas capturer une grande oie des neiges adulte, mais peut efficacement prélever des œufs ou des oisons. En effet, le renard arctique est le prédateur qui a le plus d'influence sur la reproduction des oies de l'île Bylot (Bêty *et al.* 2001; Lepage *et al.* 2000). Sur cette île, le succès reproducteur des oies varie entre 22 et 91% selon les années de faible et de haute abondance de lemmings, respectivement (Bêty *et al.* 2001). Le taux d'activité des renards dans la colonie d'oies de l'île Bylot est 3,5 fois plus élevé lors d'un creux de lemmings que lors d'un pic de lemmings (Bêty *et al.* 2002). La consommation d'œufs d'oies par les renards peut varier d'un facteur trois selon le cycle des lemmings. Il existe donc un effet indirect entre l'abondance des lemmings et le succès reproducteur des oies causé par le partage de prédateurs (mutualisme apparent, Abrams et Matsuda 1996; Bêty *et al.* 2002; Holt 1987).

La présence des oies à l'île Bylot pourrait permettre à la population de renards arctiques de subsister à une densité plus élevée durant les creux de lemmings. Ainsi, le renard arctique pourrait avoir un impact plus important sur la population de lemmings. Ceci expliquerait possiblement pourquoi, contrairement à la théorie d'exploitation des écosystèmes d'Oksanen *et al.* (1981), les lemmings n'endommagent pas la végétation de l'île Bylot (Gauthier *et al.* 2004). Cependant, l'importance des oies pour les renards pourrait être surestimée puisque les oies n'habitent l'Arctique que pour la saison estivale et que les œufs ne sont disponibles que durant une courte période. Cette période est d'autant plus brève que l'abondance d'œufs peut diminuer considérablement lors de la période d'incubation à cause de la prédation (certaines années avec seulement 22% de succès reproducteur, Bêty *et al.* 2001). C'est ici que le CMR du renard arctique prend son importance puisqu'il lui permet de prolonger le subside alimentaire fourni par les oies bien au-delà de la période d'incubation. La contribution des réserves d'œufs au régime alimentaire du renard (et possiblement à d'autres espèces de prédateurs aviaires) pourrait constituer un des éléments-clés des relations prédateurs/proies dans la communauté de l'île Bylot (Gauthier et al. 2004).

Objectif de l'étude

Cette étude s'insère dans un programme de suivi environnemental à long terme de la dynamique des interactions trophiques de l'écosystème de l'île Bylot (Tableau 1). Pour pouvoir évaluer l'effet du CMR au niveau de la communauté de ce système (estimer l'énergie relative que les renards arctiques retirent des réserves d'œufs), il est important de comprendre les mécanismes comportementaux qui agissent au niveau des individus (Schmidt 1999; Sutherland 1996). L'hypothèse générale de ce projet de maîtrise est que le renard arctique maximise le subside alimentaire fourni par les oies via le CMR.

En premier lieu, nous examinons comment le CMR des renards est affecté par 1) la variation saisonnière en abondance d'œufs (proie secondaire) durant un même été et 2) la variation annuelle en abondance de lemmings (proie primaire). Pour répondre à cet objectif, nous utilisons des données comportementales récoltées sur les renards durant 8 périodes de nidification d'oies réparties sur deux cycles de lemmings complets. Nous examinons si l'abondance des œufs et l'abondance des lemmings affectent l'intensité de cache ou la proportion d'œufs cachés et mangés. Lors de la période de ponte, l'abondance des œufs augmente rapidement et atteint son maximum, alors que les œufs sont facilement accessibles pour le renard puisque que les oies ne défendent pas encore leur nid. Puisque l'abondance et l'accessibilité diminuent au cours de la saison, les renards devraient cacher les œufs en plus grande intensité durant la période de ponte et cette intensité devrait diminuer au cours de la saison. À mesure que leur proie primaire diminue en abondance, les renards doivent en principe consommer une plus grande proportion de leur proie secondaire. Ainsi, ils devraient cacher les œufs en moins grande proportion durant les années de faible abondance de lemmings.

En deuxième lieu, nous voulons identifier les facteurs qui influencent les décisions de cache chez le renard arctique et expliquer le comportement de recache. L'œuf, l'oison et le lemming sont les principales proies des renards et possèdent des caractéristiques différentes. Étant donné que les œufs possèdent des protections mécaniques et physiques contre l'invasion microbienne (Board 1966; Board et Fuller 1974), ils sont supposément moins périssables que les lemmings et oisons. La coquille de l'œuf pourrait aussi augmenter le temps de consommation. Ainsi, les renards devraient cacher les œufs des oies en plus grande proportion que les oisons et les lemmings. L'hypothèse de la séquestration rapide pourrait expliquer pourquoi le renard arctique recache les œufs d'oies. Pour tester cette hypothèse, nous combinons des observations comportementales à une technique innovatrice permettant de suivre les œufs cachés par les renards.

Au cours de l'étude, il a été observé que le grand corbeau (*Corvus corax*) pouvait récupérer des caches de nourriture créées par des renards arctiques. En réponse, le renard arctique défend parfois ses caches contre le corbeau lorsqu'il en aperçoit un à proximité d'une cache. Le dernier objectif de ce mémoire a donc été de décrire le comportement du renard et du corbeau lorsque ce dernier pratique le pillage interspécifique.

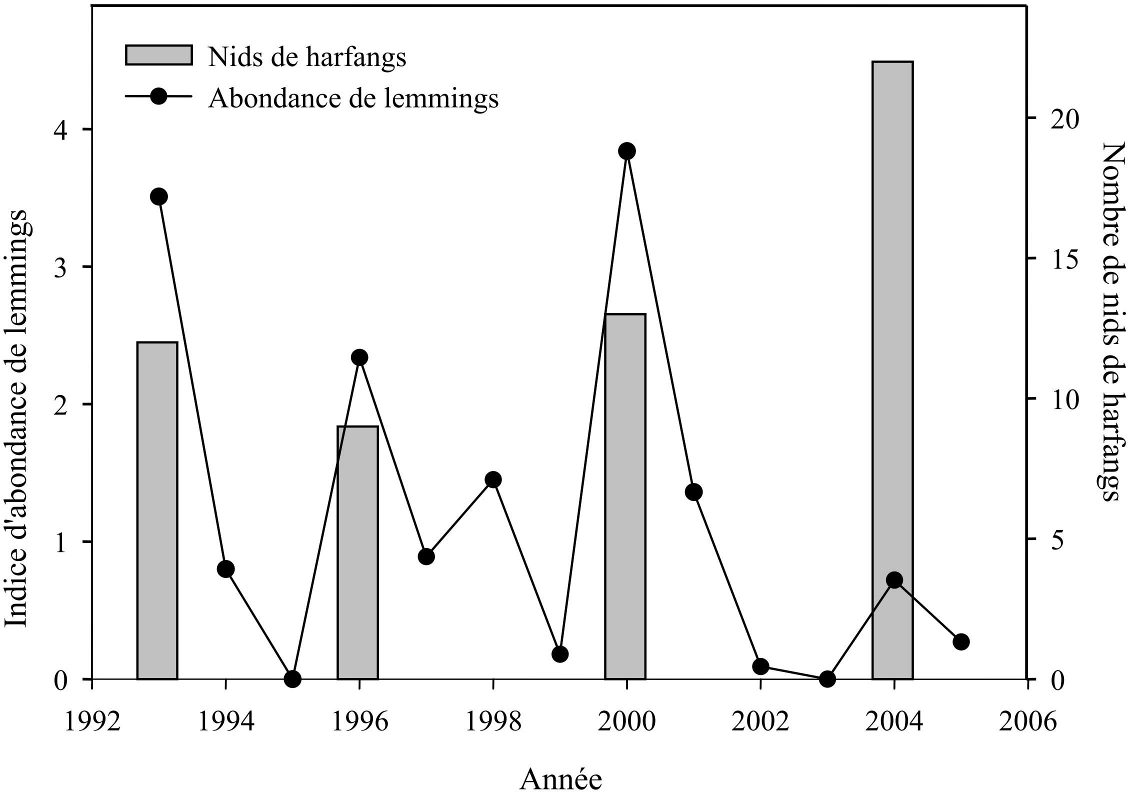

Figure 1 Indice d'abondance de lemmings (quantité capturée par 100 nuits-trappes) et nombre de nids de harfangs des neiges recensés à l'île Bylot, Nunavut, 1993-2005. En dépit d'un faible indice d'abondance en 2004, cette année est considérée comme un pic de lemmings puisque les harfangs étaient en présence record durant cette année.

Tableau 1

Mise en contexte du projet de maîtrise dans le cadre d'une étude à long terme du système de l'île Bylot et les effets de la relation prédateur-proie (renard-oie) au niveau des individus, de la population et de la communauté.

EFFETS	RELATION	
	Prédateur (Renard) ↔	Proie (Oie)
	Maximisation gains	Minimisation pertes
Conséquences comportementales (niveau individu)	**Vincent Careau (cette étude)**	Bêty *et al.* 2001 Nicolas Lecomte (PhD)
Conséquences écologiques (niveau population)	Guillaume Szor (MSc) Marie-Andrée Giroux (MSc)	Bêty *et al.* 2002 Nicolas Lecomte (PhD)
Conséquences écologiques (niveau communauté)	Marie-Andrée Giroux (MSc)	Gauthier *et al.* 2004

CHAPITRE I

PREDATOR MANAGEMENT OF A PULSED RESOURCE: SEASONAL AND ANNUAL VARIATIONS IN CACHING BEHAVIOUR OF THE ARCTIC FOX

Vincent Careau, Nicolas Lecomte, Joël Bêty, Jean-François Giroux, Gilles Gauthier, and Dominique Berteaux

Abstract

Resource pulses are common in several systems and have large impacts on trophic dynamics. Many animals hoard food during resource pulses, yet how this behaviour affects pulse diffusion trough trophic levels is poorly known. Our objective was to examine how the caching behaviour of arctic foxes (*Alopex lagopus*) preying on a seasonally abundant pulsed resource (goose eggs) was affected by annual and seasonal changes in resource availability. We monitored the foraging behaviour of foxes in a greater snow goose (*Anser caerulescens atlanticus*) colony during 8 nesting seasons that covered two lemming cycles. Egg acquisition rate and caching intensity declined from laying to hatching while egg caching proportion remained constant. In contrast, egg caching proportion fluctuated according to the annual lemming pulse independently of the seasonal pulse of goose eggs. Foxes cached the majority of goose eggs (>90%) at relatively high or moderate lemming abundance but this proportion decreased to 40% during the low phase of the lemming cycle. This likely occurred because foxes needed to consume a greater proportion of goose eggs to fulfill their energy requirement at low lemming abundance. This study reveals a behavioural mechanism of resource management that might extend the effects of resource pulses in arctic ecosystems. The allochthonous input brought by geese from the south into the arctic system is enhanced by hoarding behaviour.

Keywords

Alopex lagopus, arctic, Bylot Island, hoarding, lemming cycle, resource pulse.

INTRODUCTION

Temporal changes in resource availability exist in all natural systems and have major impacts on the functioning of ecosystems (Ostfeld & Keesing 2000; Sears *et al.* 2004). Resource pulses are events of ephemeral resource superabundance that occur in wide-ranging ecosystems, such as mast fruiting by trees, hurricane-mediated green falls, insect outbreaks, and storm-induced transport of marine resources to terrestrial ecosystems (Lodge *et al.* 1994; Rose & Polis 1998; Yang 2004). Some general patterns of community response to diverse resource pulses have recently been described (Schwinning & Sala 2004; Paetzold *et al.* 2006; Yang 2006). For example, consumers able to respond to resource pulses are usually generalist species that can sustain themselves on alternative resources between pulses (Ostfeld & Keesing 2000). Little is known, however, on the behavioural adaptations of consumer in regard to the management of the energy provided by resource pulses. As a result, the effects of pulsed resources on ecosystems remain unclear and studies focusing on mechanisms involved at the individual level are needed (Schoener 1986).

No consumer can control the timing or intensity of a resource pulse. On the other hand, consumers may use behavioural strategies to maximise the exploitation of resource pulses, such as tracking pulses over time and caching large amounts of resources (Wilmers *et al.* 2003). In that way, hoarding behaviour can be an effective strategy for capitalizing on brief periods of resource abundance (Humphries *et al.* 2002). Indeed, many birds and mammals are known to hoard large amount of seeds during masting events, which have consequence on trophic dynamics (i.e. seed germination, Vander Wall 1990; Schmidt & Ostfeld 2003). Yet the impact of hoarding from resource pulses remains unexplored in many other systems.

Most arctic tundra ecosystems are characterized by a cyclic resource pulse that greatly influences the functioning of the whole ecosystem (Ims & Fuglei 2005). Lemming populations usually exhibit strong fluctuations with a periodicity of 3-5 years (Gilg *et al.* 2003), which affect life history traits of their main terrestrial predator, the arctic fox (*Alopex lagopus* L., Tannerfeldt & Angerbjörn 1996). During peak lemming years (pulse), arctic fox populations show high pregnancy rates and large litter sizes, resulting in a numerical response with a 1-year time lag (Angerbjörn *et al.* 1999). Conversely, productivity is generally low during low lemming years (inter-pulse period, Gauthier *et al.* 2004). Arctic foxes rely opportunistically on several seasonal pulsed resources such as seal and reindeer carcasses as well as eggs of ground- and cliff-nesting birds (Bantle & Alisauskas 1998; Roth 2002; Eide *et al.* 2005).

The high nesting synchrony and the colonial habit of several goose species provide arctic foxes with a clumped, superabundant pulsed resource (Fig.1). The abundance of this resource increases rapidly and reaches its maximum during laying, decreases gradually throughout incubation because of egg predation and then abruptly during the synchronous hatching. Because arctic foxes forage primarily on lemmings when abundant (main prey) and switch to goose eggs (alternative prey) when lemmings are scarce, annual nest predation rate can vary from 10 to 80 % (Bêty *et al.* 2001; Bêty *et al.* 2002). Hoarding behaviour of arctic foxes is especially prominent in goose colonies and extends considerably the period during which they have access to goose eggs (>80% of eggs can be cached, Stickney 1991; Samelius & Alisauskas 2000). Prey caching and recovery can be related to food availability and/or the nutritional status of the predator in several carnivore species including arctic and red foxes (*Vulpes vulpes* L., Macdonald 1976; Sklepkovych & Montevecchi 1996). A better knowledge of the effects of seasonal and annual fluctuations in food abundance on caching intensity (number of cached items/h), cache recovery intensity (number of recovered caches/h), and caching decisions (% of items cached vs. consumed) will clearly improve our understanding of the mechanisms underlying hoarding from resource pulses (Vander Wall 1990).

The objective of our study was to examine how the caching behaviour of a carnivore (arctic fox) preying on a seasonally abundant pulsed resource (goose eggs) was affected by annual changes in resource availability. We monitored the lemming population, the goose nesting phenology and egg abundance, the rate at which foxes acquired goose eggs, recovered cached eggs, and their fate (eaten, cached, or recached) over two complete lemming cycles. We examined whether caching intensity, cache recovery intensity, and caching proportion was primarily related to the availability of goose eggs or to variations in lemming abundance. Goose egg abundance reaches its maximum during the laying period, while eggs are undefended (easily available) because geese are feeding away from their nest most of the time (Gauthier & Tardif 1991). Therefore, we predicted that foxes should cache eggs at a higher rate during this period. As lemmings become scarce, arctic foxes should consume a greater proportion of goose eggs (the alternative prey) to fulfill their immediate energy requirement. Therefore, we predicted that they should be caching a higher proportion of eggs during lemming peaks than during the low phases of the lemming cycle.

MATERIALS AND METHODS

Study area

The study was conducted on Bylot Island, Nunavut, Canada (72°53'N, 79°54'W), during 8 summers from 1996 to 1999 and 2002 to 2005. This island is part of the Sirmilik National Park of Canada and is the most important breeding site for the greater snow goose population with over 20,000 nesting pairs (*Anser caerulescens atlanticus* L., Gauthier *et al.* 2004). Compared to snow geese, the density of other terrestrial birds is relatively low. We conducted fieldwork in the highest nest density area of the colony located in a mosaic of wet polygon fens and dry upland surrounded by extensive upland habitats (see Tremblay *et al.* 1997 for a detailed description).

Annual variation in lemming abundance

Brown (*Lemmus sibiricus* Kerr) and collared (*Dicrostonyx groenlandicus* Traill) lemmings coexist on the study area (Gauthier *et al.* 2004). Since 1997, an index of lemming abundance is obtained in mid/late-July from snap trap censuses at the observation site (site 1) and at another site 30 km away (site 2). In 1996, the lemming index was only available at site 2. We took the mean of both sites (except for 1996) to have a better estimate of the general lemming abundance (Gauthier *et al.* 2004). Trapping was done in one study plot at site 1 (mesic upland) and in two plots at site 2 (wet polygon fens and mesic upland). In each plot, 50 baited traps were set for 10-11 days in order to achieve 500 night-traps (see Bêty *et al.* 2001). Snowy owls (*Bubo scandiacus* L.) are nomadic and specialist lemming predators that only breed when lemmings are abundant in spring (Wiklund *et al.* 1998). We therefore searched the study area for owl nests every year and used their presence as an additional indication of peak lemming years. Owl nests were found by spotting flying owls from a distance during goose nest searches or during helicopter surveys. Years were classified according to number of years after the occurrence of a lemming peak (time lag).

Seasonal variation in goose egg abundance

Each year, goose nests were searched during laying or early-incubation in portions of the colony (Bêty *et al.* 2001). For nests found after the laying period, laying date (day of the first laid egg) was determined by estimating incubation stage or by backdating from hatching date (Lepage *et al.* 2000). Nest initiation usually occurs in June and is highly synchronized (about 70% and 90% of nests are initiated within 4 and 8 days, respectively, Gauthier & Tardif 1991; Lepage *et al.* 2000). Nest attentiveness by the female increases as laying progresses (Poussart *et al.* 2000). Incubation last ~23 days and hatching occurs in early June. Arctic fox is the main predator of goose eggs and can account for up to 45% of successful nest attacks during which one egg or more is taken (Bêty *et al.* 2001). Because egg abundance (number of eggs in the colony) and availability (degree of nest attendance and defence) change during the goose nesting season, we divided it into 4 periods: laying, early-incubation, late-incubation, and hatching (Fig 1). Laying and hatching periods span from -5 to +5 days from the respective median dates. Early-incubation period ranged from day 6 to 15 after the median laying date whereas late-incubation ranged from -11 to -6 days from hatching date. Finally, goose nest density has been estimated since 1996 by searching nests in a sample area (9.6 ha) located in the observation area and in the center of the colony. This area is known to be representative of the whole colony (Bêty *et al.* 2001; Reed *et al.* 2005).

Behavioural observations

In most years, behavioural observations took place from 23 June to 8 July during the laying, incubation, and hatching periods of geese. In 2004 and 2005, observations began earlier in the season (8 June) and stopped later (14 July) to sample the laying and hatching periods more intensively. Each year, observations were conducted by two observers and averaged 145 ± 34 (SE) hours/yr (Table 1). Three observers (JB, NL, and VC) collected 73% of the data while the rest was done by three other observers. During the first lemming cycle (1996-1999), 24 observation periods of 4 h were systematically conducted in rotation throughout the 24-h daylight cycle. During the second lemming cycle (2002-2005), 61% of the observation effort was spent between 20:00 and 04:00 h to maximise our chance to observe foraging foxes. Although fox activity is usually higher at night (VC and JB, unpublished data), there was no difference in egg acquisition rate ($F_{(1,95)} = 1.45$, $P > 0.05$) and caching rate ($F_{(1,95)} = 0.46$, $P > 0.05$) between this period and the rest of the day.

We observed foxes foraging in the goose colony using 20-60x spotting scope from a single blind in 1996-1999, two in 2002-2004 and three in 2005. An observer could monitor approximately 2 km² from a blind, depending on the visibility and topography. We monitored focal foxes as long as they were actively foraging within the observation limits. Foxes were identified on a daily basis by the distinctive patterns of their fur (shedding from winter to summer pelage). Multiple sightings of an individual during an observation period were pooled and treated as a single foraging period (the sample unit). When two foxes were observable, the closest one was sampled except if it was not actively foraging.

Each time a fox acquired a goose egg, we noted the source (nest or cache) and subsequent fate (eaten or cached). The source or the fate of an egg were considered unknown when a fox appeared or disappeared with an egg in its mouth. Eggs were considered recovered from a cache when the fox dug the ground before it retrieved it (Vander Wall 1990). Acquisition, recovery, and caching rates were calculated by dividing the number of eggs acquired, recovered, and cached by the duration of the foraging period, respectively. Because we focused on actively foraging and caching foxes, we restricted our analyses only to successful foraging periods (with the acquisition or recovery of at least one egg).

Statistical analyses

Short observation periods may give poor estimates of acquisition rates (Stickney 1991). Therefore, we used Spearman correlations (r_s) (data were not normally distributed) to explore the effect of the duration of the foraging period on the acquisition, recovery and caching rates. We progressively deleted short foraging periods until correlation between observation length and acquisition rate became non significant. We then performed ANOVAs on rank-transformed data to test the effects of nesting period, time lag since lemming peak, and nest density on acquisition, recovery, and caching rates. We searched for differences using *post hoc* Tukey's honestly significant difference (HSD) tests.

We used a logistic regression model to predict the fate of eggs (cached = 1, eaten = 0) according to the seasonal and annual variation in food abundance. There were potential sources of non independence in our data set. First, we were not always able to identify all foxes from one day to the next; therefore we could not calculate the true (i.e. inter-individual) variances of our measures of caching behaviour. Second, the fate of multiple eggs acquired by an individual during a foraging period is a repeated measure. We thus used generalized estimating equation (GEE) with the logit link function implemented in SAS (procedure GENMOD using the statement REPEATED, SAS Institute Inc. 2005) to model caching behaviour. The GEE method estimates the within-cluster similarity of residuals and uses this estimated correlation to re-estimate the regression parameters and to calculate standard errors (Hanley *et al.* 2003). We modeled the working correlation matrix with exchangeable correlation structure (one correlation coefficient for all individuals and repeated measures, Horton & Lipsitz 1999). The GEE method thus considers each foraging period as independent. We used a type 3 GEE analysis to test for significance of a variable in the model with other variables already included (nesting period and density, time lag after peak lemming year, and egg source). Another correlation structure exists in our data because some eggs were acquired from the same nest. To overcome the potential problem of a spatial correlation structure, we weighted each egg according to the nest where it came from. Unbalanced sampling design precluded the inclusion of second-order interaction terms in the ANOVA and the GEE models. All probabilities are two-tailed, significance level was set at $\alpha = 0.05$, and means are reported with ± SE.

RESULTS

Annual variation in lemming abundance

The snap-trap census indicated lemming peaks in 1996 and 2000, which was corroborated by the finding of several snowy owl nests in the study area in those years (Fig. 2). In 2004, a record number of owl nests were located in June despite a moderate index of lemmings measured in mid/late-July. The reason for this discrepancy in 2004 is unknown but may result from either a sampling bias in the lemming index (record rainfall occurred during trapping in July 2004) or that the abundance of predators like foxes and owls considerably reduced the number of lemmings before trapping took place. We thus considered the 2004 goose nesting season as a peak lemming year and our study therefore spans two complete lemming cycles of 4 years.

Seasonal variation in goose egg abundance

Median dates of goose laying and hatching ranged from 7-17 June and 4-12 July, respectively. The difference between these two events was relatively constant among years (range 25-27 days; Table 1). This means that the duration of the period during which goose eggs were available to foxes was constant each year although the timing of the nesting season slightly differed annually (Fig 1). Nest density in the observation area varied 14-fold among seasons (0.8 to 11 nests/ha; Table 1).

Egg acquisition and recovery

Foxes obtained 228 eggs from 209 nests and 69 eggs from as many caches during 141 successful foraging periods. When all these periods were considered, the duration of the foraging period was significantly correlated with acquisition rate ($r_s = -0.44$, $P < 0.01$, $n = 141$) and recovery rate ($r_s = 0.18$, $P < 0.05$, $n = 141$). These relationships became non significant when only foraging periods lasting >10 min were retained in the analyses (egg acquisition rate: $r_s = -0.17$, $P = 0.10$, egg recovery rate: $r_s = 0.03$, $P = 0.80$, $n = 96$). We therefore restricted the analyses to these 96 foraging periods.

Overall, the mean egg acquisition rate from nests was 3.8 ± 0.4 eggs/h (range 0-16). Acquisition rate differed among nesting periods but not according to the phases of the lemming cycle nor to nest density (Fig. 3a; nesting periods: $F_{(3,88)} = 9.44$, $P < 0.0001$; time lag effect: $F_{(3,88)} = 2.04$, $P = 0.11$; nest density effect: $F_{(1,88)} = 1.98$, $P = 0.16$). Egg acquisition rate declined linearly from laying to hatching. Overall, the egg recovery rate from caches averaged 1.3 ± 0.2 eggs/h (range 0-13) and varied among phases of the lemming cycle (Fig. 3b; time lag effect: $F_{(3,88)} = 4.20$, $P < 0.0001$). Lowest recovery rates occurred during the second and third year after the lemming peak. Egg recovery rate was not related to nest density ($F_{(1,88)} = 0.17$, $P = 0.68$) but tended to increase in the later goose nesting stages ($F_{(3,88)}$

= 2.54, P = 0.06). Overall, acquisition and recovery rates were negatively correlated (r_s = -0.59, $P < 0.001$, n = 96).

Egg caching

Overall, the mean caching rate was also 3.8 ± 0.4 eggs/h (range 0-17). Caching rate was positively correlated with acquisition rate (r_s = 0.69, $P < 0.001$, n = 96), but negatively correlated with recovery rate (r_s = -0.21, P = 0.044, n = 96). Caching varied seasonally but not with the lemming cycle (nesting periods: $F_{(3,88)}$ = 5.65, $P < 0.01$; time lag effect: $F_{(3,88)}$ = 2.37, P = 0.076). On a seasonal basis, caching rate followed the same trend as the acquisition rate (Fig. 3c). On an annual basis, caching rate followed a trend opposite to acquisition rate, with the lowest caching rate occurring during the year with the highest acquisition rate (Fig. 3c).

There were no annual or seasonal differences in the proportion of eggs with unknown fate (n = 20) when accounting for the source ($\chi^2 < 6.02$, d.f. = 3, $P > 0.05$). We thus discarded eggs with unknown fate to calculate the proportion of cached eggs during 135 foraging periods. We found no seasonal nor nest density effects on egg caching proportion (nesting period: χ^2 = 3.26, d.f. = 3, P = 0.33; nest density; χ^2 = 0.04, d.f. = 1, P = 0.84). Overall, foxes cached 87% of the eggs acquired from nests (n = 219) and recached 64% of the eggs recovered from caches (n = 58; source effect: χ^2 = 14.2, d.f. = 1, $P < 0.001$; Fig. 4). Time lag after peak lemming year affected egg caching (χ^2 = 14.2, d.f. = 3, $P < 0.01$). Foxes cached a lower proportion of eggs during the third year after lemming peak than during any other years (Fig. 4; $\chi^2 \geq 20.2$, d.f. = 1, $P < 0.001$ for all comparisons between time lag 3 vs. time lag 0, 1, and 2). Thus, foxes ate a higher proportion of acquired eggs in the low phase of the lemming population cycle.

DISCUSSION

The natural experimental setting of the Bylot Island terrestrial ecosystem allowed us to show how foraging and caching behaviour of an arctic carnivore varied with seasonal and annual fluctuations in resource abundance. Arctic foxes cached the same proportion of goose eggs throughout the nesting season, yet their caching intensity decreased from laying to hatching as a consequence of a decreasing acquisition rate. Arctic foxes cached a much lower proportion of eggs when lemmings were scarce (i.e. third year after the peak) even if their acquisition rate did not change with the lemming cycle phases. This means that the proportion of alternative prey items cached is related to the abundance of the predator primary prey. The annual variation in the management of a seasonal resource pulse (goose eggs) according to variation of another resource (lemmings) is likely part of a behavioural mechanism that optimizes the use of the pulse by delaying its consumption through hoarding.

Acquisition rate of a seasonal resource pulse

Active nest defence by snow geese is the primary factor limiting foraging success of arctic foxes (Samelius & Alisauskas 2001; Bêty *et al.* 2002) and this likely explains most of the seasonal pattern in egg acquisition rate. During laying, geese are feeding away from their nests most of the time (Gauthier & Tardif 1991), so egg acquisition rate of foraging foxes should be limited mostly by travelling time between undefended nests and time spent hoarding. When incubation begins, nest defence behaviour lowers the acquisition rate of the predator (Samelius & Alisauskas 2001). Foraging theory on nest predation also predicts a reduction in acquisition rate through the nesting season because predation increases the ratio of inactive vs. active nests, which in turn increases missed opportunities and travelling time between active nests (Schmidt 1999).

Acquisition rate should increase with density, as travelling time decrease from nest to nest (Schmidt 1999). Surprisingly, nest density had no effect on acquisition rate (when accounting for successful foraging periods only) despite its large annual variation. Because geese breed in complex habitat refugees (e.g. polygon fens), preventing terrestrial predators to run directly from nest to nest, nest density itself does not reflect the actual travelling distance that foxes need to complete between nests (Tremblay *et al.* 1997). Therefore, travelling time might be more influenced by habitat characteristics than nest density per se. This habitat effect, coupled with the active nest defence behaviour by geese, probably explain why the range of nest density observed during our study does not influence acquisition rate.

Cache recovery rate

The seasonal abundance and accessibility of goose eggs decrease as the nesting season progresses while the abundance of cached eggs increases because foxes cached a substantial proportion of eggs acquired both from nests and caches. As observed in other goose colonies (Stickney 1991; Samelius & Alisauskas 2000), arctic foxes tended to increase their recovery rate late in the nesting season, presumably in response to declining egg availability. Cache recovery rate was the lowest in years when caching intensity, and thus abundance of cached eggs, was also the lowest. This suggests that cache recovery rate depends on a combination of prey availability and cache abundance.

The inverse association between egg acquisition and recovery rates could have several causes. First, arctic foxes could rely more on cached eggs when their acquisition rate is low, as red foxes and seed-caching rodents do (Reichman & Fay 1983; Henry 1986). This is supported by the larger proportion of recovered eggs that were eaten by arctic foxes compared to those obtained in nests. Second, the time spent by foxes eating or recaching recovered eggs may reduce the time they could spend acquiring additional eggs from nests. The relatively high proportion of recovered eggs that were recached (64%) implies that this activity is important and could possibly limit the time available to acquire new eggs. Third, what we interpret as recaching could alternatively be cache pilfering, a common phenomenon in solitary, long-term hoarding animals (Vander Wall & Jenkins 2003). Because foxes cache eggs in the goose colony where several home ranges overlap (Anthony 1997; Eide *et al.* 2004), there are many eggs cached by different foxes in the same area. The cache pilfering strategy may become more advantageous as the nesting season progresses towards hatching because the abundance of cached eggs increases while the abundance of eggs in nests decreases. This could result in more time spent by foxes searching for cached eggs and moving eggs from existing caches at the expense of egg acquisition in goose nests. These non-exclusive possibilities may explain why egg acquisition and recovery rates were negatively correlated.

Annual variation in resource availability

In the goose colony of Bylot Island, Bêty *et al.* (2002) showed that foraging decisions by arctic foxes were influenced by the lemming cycle. Lemming is a profitable prey for arctic fox because it represents a valuable trade-off between energy reward and foraging costs such as handling time and injury risk (Stein 1977; Bêty *et al.* 2002). In contrast, because snow geese actively defend their nests, foraging on eggs may require a longer handling time and may be risky (Gilchrist *et al.* 1998; Samelius & Alisauskas 2006). Lemming abundance influences fitness reward of goose eggs and this is reflected in the foraging decisions, as foxes switch from lemmings to goose eggs in years with low lemming abundance (Bêty *et al.* 2002). Our study shows that lemming abundance also influences hoarding decisions.

Arctic foxes feed primarily on lemmings when abundant, but still acquire goose eggs and cache a high proportion of them for later use. As their preferred item (lemming) became scarce, foxes needed to consume a greater proportion of the alternative item (goose egg) to fulfill their daily energy requirement. Hence, optimal foraging theory (Pyke *et al.* 1977) likely explains why eggs were cached in a lower proportion in the third year after the lemming peak. The abundance of a primary prey determines the proportion of an alternative prey that is consumed immediately rather than stored for later use. This study reveals a behavioural mechanism of resource management that might extend the effects of resource pulses in arctic systems.

Implications on arctic trophic dynamics

Because it is faster to cache than to consume food, food-storing consumers have the capacity to rapidly acquire energy from pulsed resources. For instance, ants are efficient users of locally pulsed resources because they can inform each other where food is abundant and they can rapidly transport the food into their nests (Paetzold *et al.* 2006). During mast years, eastern chipmunks (*Tamias striatus* L.) can hoard a winter's worth of energy requirement in a single day (Humphries *et al.* 2002). Similarly, foxes can accumulate important energy reserves during a single nesting season (~30 days). Indeed, the relatively high rate of acquisition by foxes (3.8 eggs/hour) and the high amount of energy contained in a single goose egg (mean of 900 ± 9 kJ/egg, Choinière & Gauthier 1995) make hoarding behaviour highly profitable. According to Prestrud (1991), a resting fox having an average weight of 3.5 kg and an average fat content of 22% will survive on a basal metabolic rate for about 30 days. Such an energy reserve (~15 640 kJ) can be stored by an arctic fox in only ~5 hours of actively foraging and caching during the nesting season. The use of a reserve during periods of food scarcity (winter) probably enhances arctic fox survival and the number of pups born in the following year (Angerbjörn *et al.* 1991). Hoarding behaviour, by increasing the reproductive numerical response of arctic fox to the seasonal pulse in egg abundance, may thus increase the negative-negative long-term apparent competition between lemmings and geese described by Bêty *et al.* (2002).

Like most other arctic breeding goose species, the greater snow goose population increased 14-fold in the last 40 years, in part due to the food subsidy that they receive while feeding in southern agricultural lands during winter and spring (Gauthier *et al.* 2005). For the low-productive arctic terrestrial ecosystems, breeding geese represent an allochthonous energy input. By storing large numbers of eggs in the arctic ground, arctic foxes increase their own access to eggs, but also for other predators such as common ravens (*Corvus corax* L.) that can raid foxes' food caches (Gauthier *et al.* 2004). Hence, the hoarding behaviour of arctic fox should enhance the effects of this allochthonous resource pulse across several trophic levels.

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REFERENCES

Angerbjörn A., Arvidson B., Norén E. & Strömgren L. (1991). The effect of winter food on reproduction in the arctic fox, *Alopex lagopus*: a field experiment. *J. Anim. Ecol.*, 60, 705-714

Angerbjörn A., Tannerfeldt M. & Erlinge S. (1999). Predator-prey relationships: arctic foxes and lemmings. *J. Anim. Ecol.*, 68, 34-49

Anthony R.M. (1997). Home ranges and movements of arctic fox (*Alopex lagopus*) in western Alaska. *Arctic*, 50, 147-157

Bantle J.L. & Alisauskas R.T. (1998). Spatial and temporal patterns in arctic fox diets at a large goose colony. *Arctic*, 51, 231-236

Bêty J., Gauthier G., Giroux J.-F. & Korpimäki E. (2001). Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos*, 93, 388-400

Bêty J., Gauthier G., Korpimäki E. & Giroux J.-F. (2002). Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *J. Anim. Ecol.*, 71, 88-98

Choinière L. & Gauthier G. (1995). Energetics of reproduction in female and male greater snow geese. *Oecologia*, 103, 379-389

Eide N.E., Eid P.M., Prestrud P. & Swenson J.E. (2005). Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. *Wildlife Biol.*, 11, 109-121

Eide N.E., Jepsen J.U. & Prestrud P. (2004). Spatial organization of reproductive Arctic foxes *Alopex lagopus*: response to changes in spatial and temporal availability of prey. *J. Anim. Ecol.*, 73, 1056-1068

Gauthier G., Bêty J., Giroux J.F. & Rochefort L. (2004). Trophic interactions in a high arctic goose colony. *Integ. Comp. Biol.*, 44, 119-129

Gauthier G., Giroux J.F. & Reed A. (2005). Interactions between land use, habitat use and population increase in greater snow geese: what are the consequences for natural wetlands? *Glob. Chang. Biol.*, 11, 856-868

Gauthier G. & Tardif J. (1991). Female feeding and male vigilance during nesting in greater snow geese. *Condor*, 93, 701-707

Gilchrist H.G., Gaston A.J. & Smith J.N.M. (1998). Wind and prey nest sites as foraging constraints on an avian predator, the Glaucous Gull. *Ecology*, 79, 2403-2414

Gilg O., Hanski I. & Sittler B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science*, 302, 866-868

Hanley J.A., Negassa A., Edwardes M.D.D. & Forrester J.E. (2003). Statistical analysis of correlated data using generalized estimating equations: An orientation. *Am. J. Epidemiol.*, 157, 364-375

Henry J.D. (1986) *Red fox: The catlike canine*. Smithsonian Institution Press, Washington.

Horton N.J. & Lipsitz S.R. (1999). Review of software to fit generalized estimating equation regression models. *Am. Stat.*, 53, 160-169

Humphries M.M., Thomas D.W., Hall C.L., Speakman J.R. & Kramer D.L. (2002). The energetics of autumn mast hoarding in eastern chipmunks. *Oecologia*, 133, 30-37

Ims R.A. & Fuglei E. (2005). Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience*, 55, 311-322

Lepage D., Gauthier G. & Menu S. (2000). Reproductive consequences of egg-laying decisions in snow geese. *J. Anim. Ecol.*, 69, 414-427

Lodge D.J., Mcdowell W.H. & Mcswiney C.P. (1994). The importance of nutrient pulses in tropical forests. *Trend. Ecol. Evol.*, 9, 384-387

Macdonald D.W. (1976). Food caching by red foxes and some other carnivores. *Z. Tierpsychol.*, 42, 170-185

Ostfeld R.S. & Keesing F. (2000). Pulsed ressources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.*, 16, 232-237

Paetzold A., Bernet J.F. & Tockner K. (2006). Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage. *Freshwater Biol.*, 51, 1103-1115

Poussart C., Larochelle J. & Gauthier G. (2000). The thermal regime of eggs during laying and incubation in Greater Snow Geese. *Condor*, 102, 292-300

Prestrud P. (1991). Adaptations by the arctic fox *(Alopex lagopus)* to the polar winter. *Arctic,*, 44, 132-138

Pyke G., Pulliam H.R. & Charnov E.L. (1977). Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.*, 52, 137-154

Reed E.T., Gauthier G. & Pradel R. (2005). Effects of neck bands on reproduction and survival of female greater snow geese. *J Wildlife Manage*, 69, 91-100

Reichman O.J. & Fay F.H. (1983). Comparison of the diets of a caching and a noncaching rodent. *Am. Nat.*, 122, 576-581

Rose M.D. & Polis G.A. (1998). The distribution and abundance of coyotes: The effects of allochthonous food subsidies from the sea. *Ecology*, 79, 998-1007

Roth J.D. (2002). Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, 133, 70-77

Samelius G. & Alisauskas R. (2006). Sex-biaised costs in nest defence behaviours by lesser snow geese (*Chen caerulescens*): consequences of parental roles? *Behav. Ecol. Sociobiol.*, in press

Samelius G. & Alisauskas R.T. (2000). Foraging patterns of arctic foxes at a large arctic goose colony. *Arctic*, 53, 279-288

Samelius G. & Alisauskas R.T. (2001). Deterring arctic fox predation: the role of parental nest attendance by lesser snow geese. *Can. J. Zool.*, 79, 861-866

Schmidt K.A. (1999). Foraging theory as a conceptual framework for studying nest predation. *Oikos*, 85, 151-160

Schmidt K.A. & Ostfeld R.S. (2003). Songbird populations in fluctuating environments: Predator responses to pulsed resources. *Ecology*, 84, 406-415

Schoener T.W. (1986). Mechanistic approaches to community ecology: a new reductionism? *Am. Zool.*, 26, 81-106

Schwinning S. & Sala O.E. (2004). Hierarchy of responses to ressources pulses in arid and semi-arid ecosystems. *Oecologia*, 141, 211-220

Sears A., Holt R. & Polis G. (2004) Feast and famine in food webs: the effects of pulsed productivity. In: *Food webs at the landscape level* (eds. Polis G, Power M & Huxel G). University of Chicago, Chicago

Sklepkovych B.O. & Montevecchi W.A. (1996). Food availability and food hoarding behaviour by red and arctic foxes. *Arctic*, 49, 228-234

Stein R.A. (1977). Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology*, 58, 1237-1253

Stickney A. (1991). Seasonal pattern of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. *Can. J. Zool.*, 69, 2853-2859

Tannerfeldt M. & Angerbjörn A. (1996). Life history startegies in a fluctuating environment: establishment and reproductive success in the arctic fox. *Ecography*, 19, 209-220

Tremblay J.P., Gauthier G., Lepage D. & Desrochers A. (1997). Factors affecting nesting success in greater snow geese - effects of habitat and association with snowy owls. *Wilson Bull.*, 109, 449-461

Vander Wall S.B. (1990) *Food hoarding in animals*. University of Chicago Press, Chicago.

Vander Wall S.B. & Jenkins S.H. (2003). Reciprocal pilferage and the evolution of food-hoarding behavior. *Behav. Ecol.*, 14, 656-667

Wiklund C.G., Kjellen N. & Isakson E. (1998). Mechanisms determining the spatial distribution of microtine predators on the arctic tundra. *J. Anim. Ecol.*, 67, 91-98

Wilmers C.C., Stahler D.R., Crabtree R.L., Smith D.W. & Getz W.M. (2003). Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecol. Lett.*, 6, 996-1003

Yang L.H. (2004). Periodical cicadas as resource pulses in North American forests. *Science*, 306, 1565-1567

Yang L.H. (2006). Interactions between a detrital ressource pulse and a detritivore comunity. *Oecologia*, 147, 522-532

Table 1

Stage of the lemming cycle, nesting parameters of greater snow geese, and details of the behavioural observations of foraging foxes on Bylot Island, Nunavut, 1996-2005.

Year	Number of years after lemming peak	Goose nests/ha	Number of nests monitored	Median laying date	Median hatching date	Observation season	Observation effort (h)
1996	0	1.3	367	14 June	11 July	22 June-6 July	96
1997	1	3.3	326	10 June	7 July	23 June-6 July	96
1998	2	4.5	349	7 June	4 July	23 June-1 July	96
1999	3	1.4	185	17 June	12 July	24 June-8 July	96
2002	2	7.4	470	16 June	11 July	23 June-10 July	111
2003	3	11.0	585	9 June	6 July	13 June-2 July	92
2004	0	0.8	676	11 June	7 July	15 June-12 July	198
2005	1	3.8	346	12 June	8 July	8 June-14 July	363

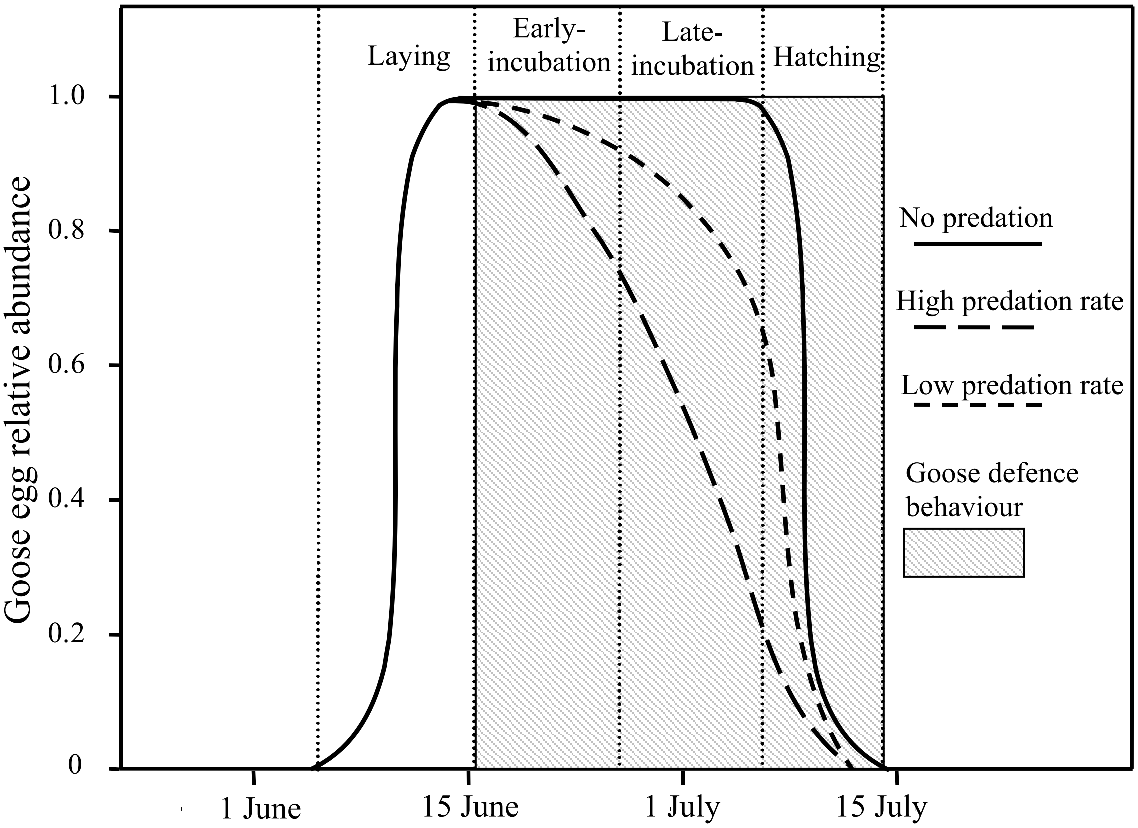

Figure 1 Relative abundance and timing of the seasonal pulse of greater snow goose eggs on Bylot Island, Nunavut. The nesting season was divided into 4 periods (laying, early- and late-incubation and hatching). Nest abandonment is generally rare in greater snow geese (Bêty *et al.* 2001). Predation by arctic fox is the main cause of decrease in egg abundance during incubation and can vary from ~20% (low predation years) to 80% (high predation years) (Bêty *et al.* 2002). The shaded portion of the graph represents the period where geese attend their nest most of the time (~95%, for incubation) and actively defend their eggs against predators (Choinière & Gauthier 1995).

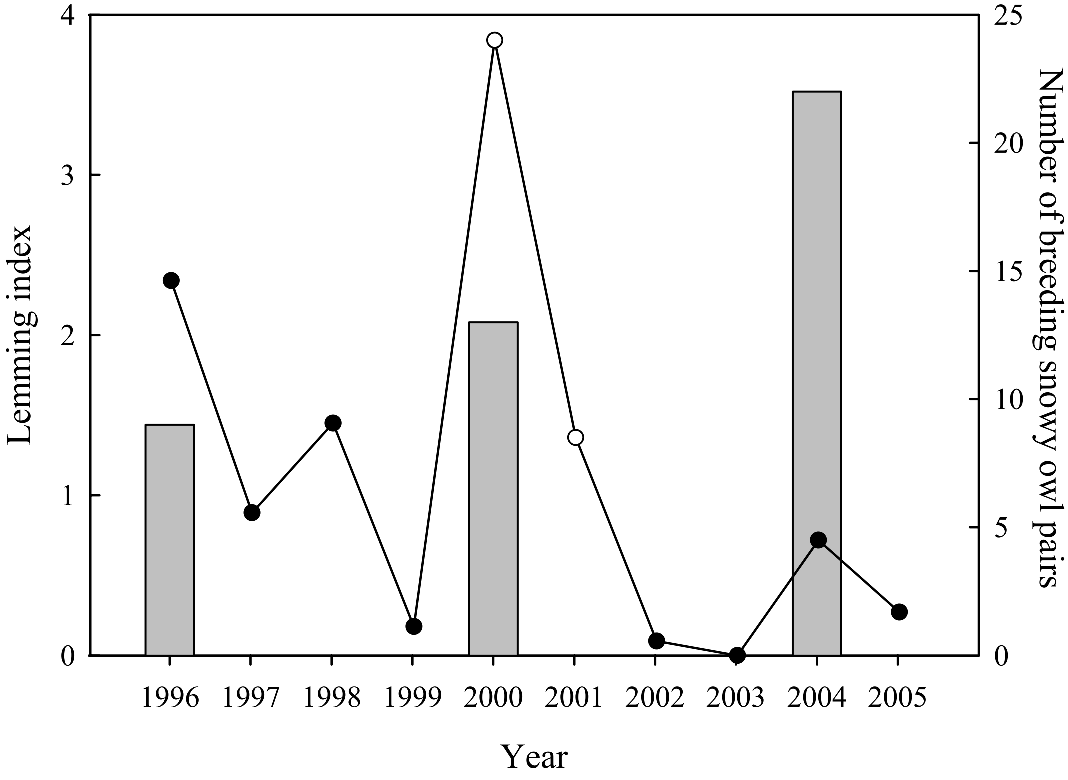

Figure 2 Index of lemming abundance (line, pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights) and number of breeding snowy owl pairs (bars) recorded on Bylot Island, Nunavut. Lemming abundance is averaged from two sites during 1997-2005 whereas only one site was sampled in 1996 (see methods for details). Closed circles indicate years with observations of arctic fox behaviour.

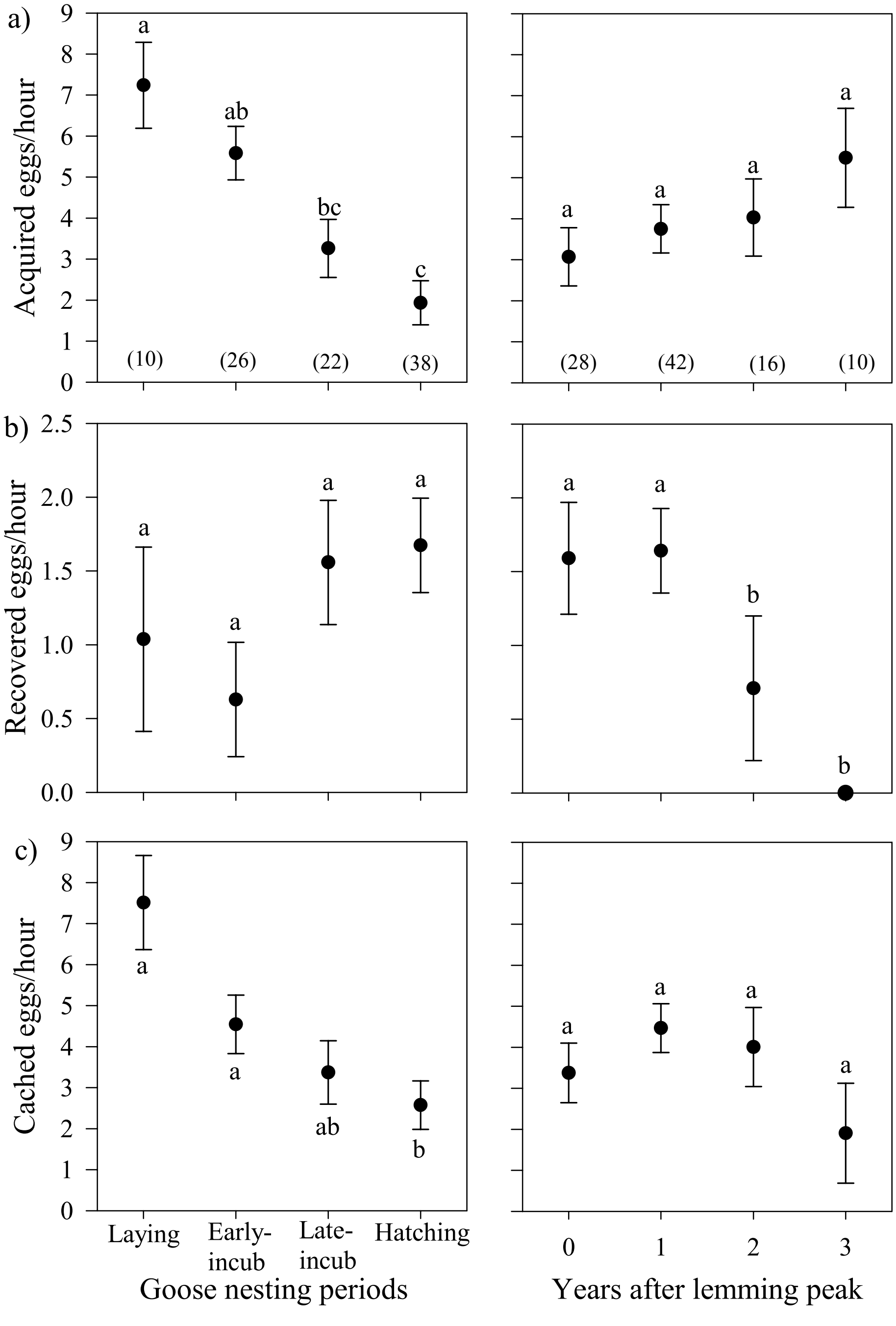

Figure 3 Seasonal and annual variations in a) acquisition rate (eggs from nests), b) recovery rate (eggs from caches), and c) caching rate of arctic fox on Bylot Island, Nunavut, 1996-1999 and 2002-2005. Mean are presented with ± SE, numbers in parentheses represent sample size (number of foraging periods), and different letters indicate significant differences (*post hoc* Tukey HSD tests).

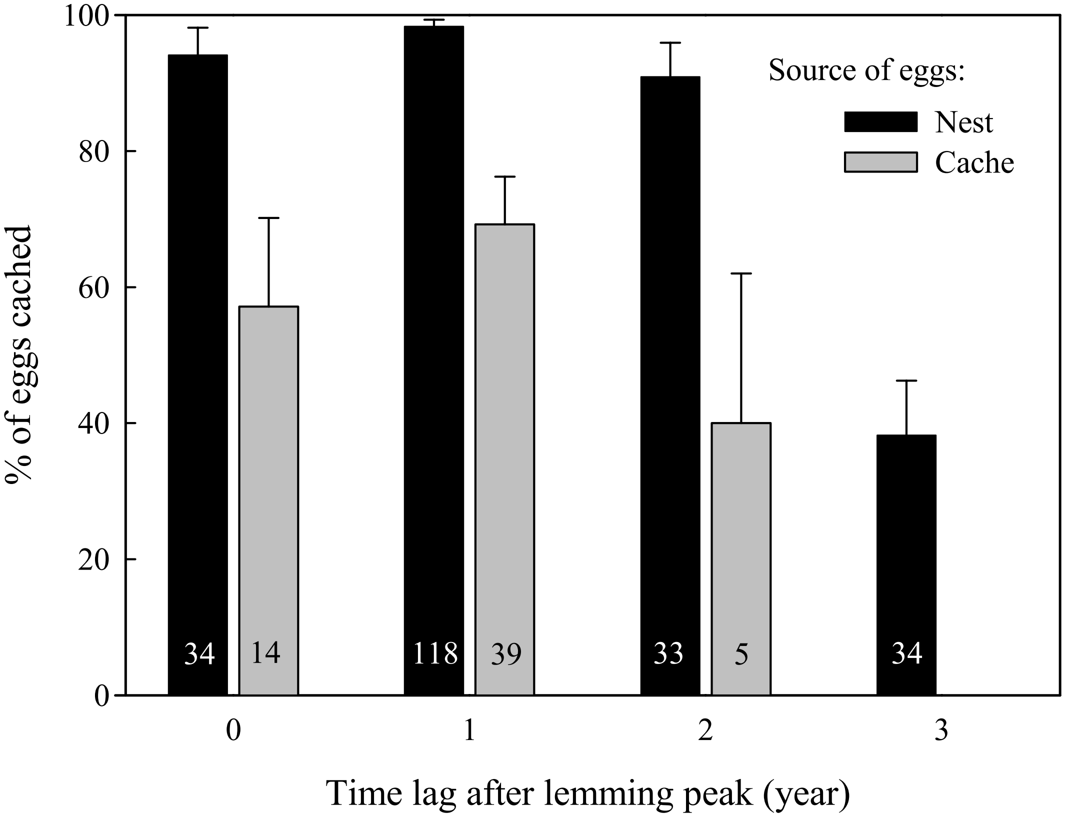

Figure 4 Annual variation in the percentage (+SE) of goose eggs cached by arctic foxes according to the source of eggs (nest or cache) and the time lag after the lemming peak on Bylot Island, Nunavut, 1996-1999 and 2002-2005. Sample size is shown within bars.

CHAPITRE II

FOOD CACHING BY ARCTIC FOXES FORAGING ON MULTIPLE PREY SPECIES

Vincent Careau, Jean-François Giroux, and Dominique Berteaux

Abstract Food-hoarding animals may be influenced by the perishability and consumption time of food items when making caching decisions. They are expected to preferentially cache items with the lower perishability and/or the higher consumption time. We observed arctic foxes (*Alopex lagopus*) foraging in a greater snow goose (*Anser caerulescens atlanticus*) colony where food available to foxes consisted mainly in goose eggs, goslings, and lemmings (*Lemmus* and *Dicrostonyx* ssp). We recorded the number of prey consumed and cached, and the time that foxes invested in these activities. Consumption time was longer for goose eggs than for goslings or lemmings. Foxes cached a greater proportion of goose eggs than goslings or lemmings. This may be caused by the eggshell, which presumably decreases egg perishability, but also increases egg consumption time. Arctic foxes recached goose eggs but not goslings or lemmings. We tested whether the rapid-sequestering hypothesis could explain this recaching behaviour. Foxes spent more time carrying an egg and travelled more distance when performing a secondary than a primary cache. To gain further information on the location and subsequent fate of cached eggs, we used experimental eggs containing radio-transmitters and tracked them using telemetry. Lifespan of primary caches increased with distance from the nest. Secondary caches were generally located farther from the nest and had a longer lifespan than primary caches. Behavioural observations and the radio-tagged egg technique gave consistent results that support the rapid-sequestering hypothesis. Arctic fox may adopt a two-stage strategy to maximize egg acquisition rate in an undefended nest and subsequently to secure eggs in potentially safer sites.

Keywords caching decisions, temporary cache, recaching, rapid-sequestering hypothesis

Introduction

The value of a food item for a food-hoarding animal has two components: its current value if consumed immediately and its future potential value if stored and consumed later (Kotler et al. 1999). Both current and future values influence the decision of what to eat and what to cache (caching decision). These values are largely determined by the food item characteristics, such as its perishability and the time needed for its consumption (Vander Wall 1990). Food perishability has been implicated as a primary determinant of caching decisions in many food-hoarding rodents (Smallwood and Peters 1986; Reichman 1988; Post and Reichman 1991; Gendron and Reichman 1995; Smallwood et al. 2001). Because perishability decreases the future value of stored items, animals should avoid caching perishable items. Alternatively, for food-hoarding animals constrained by time when foraging and caching, the time required to eat an item can override the effects of perishability (referred to as handling time hypothesis by Jacobs 1992). Given that caching items requires less time than consuming them, Jacobs (1992) showed that captive grey squirrels (*Sciurus carolinensis*) cache items with the higher consumption time in order to maximize both foraging and caching efficiency. Perishability and consumption time hypotheses are not mutually exclusive (Hadj-Chikh et al. 1996).

When food-hoarding animals recover a cached item, they do not always consume it immediately (Vander Wall 1990). Many animals rather transfer stored items from one cache to another (Clarke and Kramer 1994a; Jenkins et al. 1995; Vander Wall 1995; Vander Wall and Joyner 1998). Although this behaviour is well documented, its adaptive significance is still poorly understood. The rapid-sequestering hypothesis predicts that animals first cache food near the source to reduce travel costs and to maximize harvest rate of a temporarily abundant food resource (Jenkins and Peters 1992). However, if other foragers visit the food source, primary caches may be susceptible to raiding since they are relatively concentrated around the food source. In this context, recaching in more distant and potentially more secure sites may be a way of reducing pilferage (Vander Wall and Jenkins 2003).

Caching and recaching behaviour is common in arctic fox (*Alopex lagopus*, Frafjord 1993; Sklepkovych and Montevecchi 1996; Samelius and Alisauskas 2000). This small carnivore consumes a variety of food items such as lemmings, reindeer and seal carcasses as well as eggs and juveniles of many bird species (Elmhagen et al. 2000; Roth 2003; Eide et al.

2005). Food resources fluctuate greatly in the Arctic where a cold climate is predominant. These two factors make food-hoarding a potentially highly advantageous strategy (Smith and Reichman 1984). Low temperatures of permafrost provide a unique opportunity to extend in time the availability of protein- and energy-rich but highly ephemeral food resources.

Few detailed studies have been conducted on caching behaviour of free-ranging carnivores despite the substantial scientific attention that this behaviour has attracted. This is so because of the extreme difficulty and the vast effort required observing predatory behaviour in carnivores (Vander Wall 1990). We studied arctic fox behaviour in an open tundra habitat under continuous sun light during the Arctic summer where they forage on prey with different characteristics: goose eggs, goslings, and lemmings. Given that eggs possess physical and chemical mechanisms that protect them against microbial invasion (Board 1966b; Board and Fuller 1974), they should be less perishable than lemmings and goslings. However, the presence of an indigestible eggshell could also potentially increase consumption time of eggs relative to small vertebrates. Therefore, we submit that both hypotheses (perishability and consumption time) predict that arctic fox will cache goose eggs in higher proportion than goslings and lemmings. In addition, we tested whether the rapid-sequestering hypothesis could explain why arctic fox recache goose eggs. We predicted that arctic fox will spend more time and will travel longer distances when performing a secondary than a primary cache. Secondary caches should be located further away from the origin (nest) and have a longer lifespan than the primary cache. We also predicted that lifespan of primary caches increases with distance from the nest.

Materials and methods

Study site

We worked during the summers of 2004 and 2005 on Bylot Island, (72°53′N, 79°54′W), Nunavut, Canada, which contains one of the largest breeding sites of greater snow geese (*Anser caerulescens atlanticus*, Reed et al. 2002). Nest density was 0.8 and 3.8 nests/ha in 2004 and 2005, respectively. Density of other ground-nesting species was low relative to that of geese (Lepage et al. 1998). Geese began laying in early June and hatching occurred one month later in early July. Although most geese leave the nesting area after hatching, some geese stayed in the area for brood-rearing (Mainguy et al. 2006). The brown lemming

(*Lemmus sibiricus*) and the collared lemming (*Dicrostonyx groenlandicus*) coexist on Bylot Island (Gauthier et al. 2004). Lemming abundance was high (peak lemming year) in 2004 and low in 2005 (declining phase; snap-trap census, Careau et al. in prep).

Behavioural observations

Each year, we observed foraging behaviour of arctic foxes from June 8 to July 14. We standardized data collection among observers (three) at the beginning of each field season. Although we observed foxes during both day and night, we spent more time (60%) observing from 20:00-04:00, when fox activity is highest (Anthony 1997). We observed foraging foxes using a 20-60x spotting scope from two blinds in 2004 and three in 2005. An observer could monitor approximately 2 km^2 from a blind, depending on the visibility and topography. We identified individual foxes using 1) their distinctive fur patterns, due to variations in timing of spring molt and 2) ear tags fitted for a concurrent study. When two foxes were present in the observation area, we sampled the one closest to the observer unless it was not actively foraging. Multiple sightings of an individual during an observation session were pooled and considered as a single observation period.

We noted the time that foxes spent consuming, carrying, and caching food items using a digital voice recorder. *Carrying* was defined as the time taken by a fox transporting a prey until its consumption or caching. When a fox carrying a prey started to dig the ground, this behaviour was recorded as *caching* until the fox stopped packing the soil over the item with its snout and left the cache site. Alternatively, if the fox began masticating or licking the prey, this was recorded as the *consumption* time until it resumed travelling. All these activities include short periods where the fox temporarily stopped to scan its surroundings. We excluded all periods where foxes were lying down or performing maintenance behaviours such as grooming or resting. Hoarding behaviour is highly stereotyped among canids (Phillips et al. 1991), so *carrying* and *caching* phases were clearly distinguishable, and we considered the sum of the two phases as the *hoarding* time.

During observations, we noted the type of food items (goose egg, lemming, gosling) acquired by foxes, the source of these items (*new* or *cache*), and the fate (eaten, cached, unknown). Eggs acquired in goose nests were considered to be a *new* source. The same applied for live-captures of lemmings and goslings. We considered a lemming to be live-captured when a fox caught it after a pounce or a sprint, or after having aggressively dug the ground. Foxes captured live goslings by attacking goose families or by finding goslings left behind in abandoned nests. Items were considered to be acquired from a cache if the fox carefully dug the ground before retrieving the food (Vander Wall 1990). We assigned the distance over which the fox carried food items before caching them to one of two categories: less than 100 m or more than 100 m. We noted the location of the cache site so we could detect if foxes recovered caches that were previously made during the same observation period (*temporary caches*). In June and July of each year, we visited all dens surrounding the goose colony to check for signs of fox reproduction (fresh scats, tracks, prey remains or recent diggings). Dens with signs of activity were revisited to determine the presence of pups and to identify adults. When a reproducing fox carrying a prey left the observation area by moving directly towards its den, we assumed that this food was taken to the den. If it left the area in another direction (or if the fox was not reproducing), the fate of the food item was recorded as unknown.

Radio-tagged eggs

Contrary to most prey used by carnivores, goose eggs are rather inanimate objects that can be readily manipulated by observers. We took advantage of this characteristic and used dummy eggs containing radio-transmitters (hereafter called radio-tagged eggs) that we could substitute for real eggs. This created unique opportunities to quantify fox caching behaviour.

We created artificial nests in the high-density goose nest area by restoring goose nests from the previous nesting season with dry goose down collected at the end of the previous summer. In each artificial nest, we included a natural egg collected from an active goose nest, and a radio-tagged egg (Advanced Telemetry Systems, Model# A2670). We did not put radio-tagged eggs into real goose nests because nest defence behaviour could have prevented foxes from acquiring them. Each radio-tagged egg was made of a plastic shell including a transmitter with an internal antenna and a minimum battery lifespan of 130 days. The width, length and weight of the radio-tagged eggs averaged (±SE) 56.8±0.2 mm, 80.9±0.3 mm, and 118±1 g (n = 30), respectively, which is within the range of greater snow goose eggs (width 48-58 mm; length 73-89 mm; weight 88-138 g; n = 50). To reduce odour contamination, we stored radio-eggs in goose down for at least one day before use and manipulated them with rubber gloves.

We visited each artificial nest daily until it was preyed upon. From the observation blinds, we watched the first 24-h exposure of a sample of artificial nests to observe how arctic foxes reacted to dummy eggs. We tracked radio-tagged eggs immediately after we detected a predator visit to a nest. We used nest remains to identify predators (birds or arctic fox) following Bêty et al. (2002) criteria. From the ground, radio-tagged eggs were detected through telemetry from distances ranging between 200-600 m, depending on topography and egg position. We used a helicopter on which we fixed two lateral antennas to locate radio-tagged eggs whose signals were lost. All the cached radio-tagged eggs were visited every second day during the goose nesting season in June and July and at 5-day intervals from 1-18 August. Time elapsed between the creation of a cache by a fox and its recovery (by the same or a different fox) is referred to as the cache lifespan. We marked caches using a flagged 0.5-cm diameter and 15-cm high stick located 10 m away from the cache, and another, unflagged similar stick located midway between the cache and the flagged stick. This marking was designed to reduce the chances that common ravens (*Corvus corax*) or other foxes cued on marks to locate and raid caches. We performed subsequent surveys of the cached radio-tagged eggs by checking the signal from a 10-m distance.

Statistical analysis

We used generalized linear mixed-effects models (mixed-GLM) implemented in the R 2.2.1 statistical program (lmer command in the Matrix library, Ihaka and Gentleman 1996; Bates and Maechler 2006) because we collected repeated behavioural observations of the same individuals over time. All mixed-GLM included fox identity as a random effect to avoid pseudoreplication (Hurlbert 1984; Machlis et al. 1985). Because year could have an effect on caching behaviour (Careau et al., in prep), we included it as fixed factor in all models. We rank-transformed the data when log-transformation did not approximate a normal distribution (Conover and Iman 1981). We used a mixed-GLM to test the prediction that a higher proportion of goose eggs were cached than lemmings or goslings. We also used a mixed-GLM for comparisons of consumption and hoarding times among and within food items. We used a mixed-GLM to test two predictions of the rapid-sequestering hypothesis: (1) foxes were more likely to transport eggs over 100 m when recaching than caching and (2) *carrying* and *caching* times were longer when recaching than caching.

We could not used mixed-GLM on data collected with radio-tagged eggs because we did not know the identity of foxes that cached and recached them. When the radio-tagged egg of a primary cache was recached in a secondary cache, we used a paired t-test on rank-transformed data to test the predictions that (1) distance between secondary and primary caches was greater than distance between the primary cache and the nest and (2) secondary caches were located further away from the artificial nest than primary caches. We analysed the lifespan of radio-tagged egg caches using survival time analysis (Nur et al. 2004) implemented in JMP 5.0.1 statistical package (SAS Institute, Inc., Cary, NC), with an exponential distribution and likelihood ratio tests. Radio-tagged eggs that were still cached on 18 August were right censored. We ran a parametric regression model to test the prediction that the lifespan of a primary cache increased with the distance from the nest. To test the prediction that secondary caches had a longer lifespan than the primary ones, we ran a parametric regression model including, as covariates, distance from the nest and date at which the cache was found. We used time quantile estimates to calculate the time span necessary for a group of caches to be recovered by one half (referred to as half life). Means are reported with ± SE, tests were two-tailed, and significance level was set at $\alpha = 0.05$.

Results

In 2004 and 2005, respectively, we sampled the behaviour of 6 and 8 individuals during 1454 and 2227 min on 39 and 59 successful foraging periods that lasted from 3 to 134 min (38±28, median=31). None of the 4 marked foxes observed in 2004 was seen in 2005. In 2004, we sampled 4 foxes whose reproduction was confirmed in 2 different dens located at 1380 and 550 m from the observation limits. In 2005, only one fox sampled was reproducing in another den located 600 m from the observation limit.

Source and fate of food items

Foxes acquired more lemmings in 2004 and more goose eggs in 2005 (Table 1). Goslings were preyed upon at about the same rate in both years. Foxes were observed carrying up to 5 lemmings and/or 5 goslings simultaneously, but never more than a single goose egg at a time. Foxes were more likely to cache goose eggs than lemmings (z=6.55, p < 0.001) or goslings (z=5.25, p<0.001; Fig. 1). We detected no difference in caching frequencies between goslings and lemmings (z=0.48, p=0.62). The fate of items also differed according to the source (z=5.06, p<0.001). Overall, foxes were more likely to eat eggs acquired from caches than those from nests (z=3.96, p<0.001). The proportion of lemmings and goslings carried by foxes outside the observation area (fate=unknown or den) was higher when these items were acquired from caches than when they were first captured (lemmings and goslings pooled: z=3.18, p<0.01).

Consumption and hoarding times of food items

Consumption time was significantly longer for goose eggs than for lemmings (t=8.14, df=56, p<0.001) or goslings (t=6.28, df=21, p<0.001), but was not significantly different between lemmings and goslings (t=1.54, df=50, p=0.13; Fig. 2). Hoarding time was also longer for goose eggs than for lemmings (t=5.49, df=168, p<0.001) or goslings (t=2.54, df=144, p=0.01), but was similar between lemmings and goslings (t=0.59, df=30, p=0.55; Fig. 2). Consumption time was significantly longer than hoarding time for goose eggs (t=3.85, df=153, p<0.001) but not for lemmings (t=1.38, df=70, p=0.17) or goslings (t=0.88, df=13, p=0.39; Fig. 2).

Temporary caches

None of the 148 eggs cached by foxes was recovered within a continuous observation period, whereas this occurred for 12 lemmings (35%) and 4 goslings (44%). These 16 cases of temporary caching were performed by 6 individuals, including 5 individuals whose reproduction was confirmed in one of the 3 dens surrounding the observation area. Time between creation and recovery of these temporary caches averaged 18±4 min (range 6-42). During this time, foxes acquired a mean of 1.4±0.2 (range 0-3) additional food items (all new lemmings or goslings). When foxes recovered these temporary caches, they always went out of sight while carrying the food (fate unknown: 4 cases; towards the den: 12 cases).

Recaching behaviour

Foxes recached 55% of eggs they recovered from caches (*n*=49; Fig. 1). They were more likely to move eggs more than 100 m away when recaching than when caching (73 vs. 10%; *z*=5.58, *p*<0.001). Foxes spent significantly less time hoarding eggs obtained from nests than from caches, and this difference was due to a longer carrying phase when recaching (carrying phase: *t*=6.77, *df*=136, *p*<0.001; caching phase: *t*=1.85, *df*=136, *p*=0.07; Fig. 3).

Radio-tagged eggs

We created 71 dummy nests and watched the first 24-h exposure for 29 of these. We observed 5 individual foxes acquiring 7 radio-tagged eggs in 7 dummy nests. They spent similar amounts of time hoarding radio-tagged eggs and real eggs (carrying phase: *t*=1.59, *df*=93, *p*=0.11; caching phase: *t*=0.22, *df*=93, *p*=0.83). We found 20 additional primary caches for a total of 27 cached radio-tagged eggs. Primary caches were located at a median distance of 82 m from the original artificial nests (range 5-985 m, *n*=27). The lifespan of a primary cache increased with the distance from the artificial nest (survival time analysis; χ^2=5.46; *df*=1; *p*=0.02). Time quantile estimates indicated that half life of primary caches located at 50 m from their nests was 3-fold lower than primary caches located at 500 m.

Foxes moved 11 radio-tagged eggs to secondary caches (Fig. 4). Generally, radio-tagged eggs were moved away from primary caches over a median distance of 256 m (range 36-1040 m) which is significantly greater than the distance between the primary cache and the artificial nest (paired t-test; *t*=2.67; *df*=10; *p*<0.05). Only one secondary cache was moved towards the source nest whereas all others were located further away (median distance from nest=358 m; paired t-test; *t*=3.58; *df*=10; *p*<0.01). Secondary caches had a longer lifespan than primary caches (survival time analysis; χ^2=7.02; *df*=1; *p*<0.01). Half life of primary and secondary caches was 9.2 and 38.5 days, respectively.

Tertiary and quaternary caches were few (5 and 1, respectively); they were moved away from their cache of origin over a median distance of 94 m (range 22-230 m). Foxes moved radio-tagged eggs away from the nest when moving them from secondary to tertiary and to quaternary caches (median distance from nest=534 m; range 121-979 m).

Discussion

Fate of food items according to their characteristics

Arctic fox allocated more time and travelled longer distance when hoarding goose eggs than lemmings or goslings. They also cached a greater proportion of eggs than the other two types of food. Since goose eggs are less likely to spoil than fleshy lemmings or goslings (Board 1966a; Board and Fuller 1974), our results support the perishability hypothesis. However, as expected, consumption time was longer for goose eggs than for lemmings or goslings. This is probably because a fox must cautiously crack the indigestible eggshell without loosing its semi-liquid content. Given that arctic foxes may be foraging under time constraints during the short goose nesting season, and that they cached goose eggs more quickly than they consumed them, the consumption time hypothesis may also explain why arctic fox cache goose eggs in greater proportion (Jacobs 1992). Although our data cannot be used to evaluate the relative effects of perishability and consumption time on caching decisions of arctic foxes, they may be acting simultaneously, which would result in a greater proportion of eggs being cached compared to other prey.

Our situation is comparable to the one described by James and Verbeek (1984) for northwestern crows (*Corvus caurinus*). Clams are the crow's favourite storage item because of the valves (shells) protecting the edible part against dehydration and arthropod invasions (James and Verbeek 1983). Moreover, crows must drop clams from the air to open them, which increases consumption time of clams (Richardson and Verbeek 1986). Because indigestible hard covers, such as valves or eggshells, influence both present and future values of food items, they may be an important attribute of food items in determining caching decisions in food-hoarding animals.

Temporary caches

On several occasions, arctic foxes recovered lemmings and goslings that had been previously captured and cached during the same observation period. Most individuals involved in temporary caching were associated with a breeding den where juveniles had to be fed. Arctic foxes behaved similarly when foraging on the ledge of a steep bird cliff in Svalbard (Prestrud 1992). This behaviour may thus play an important role in the hunting strategy of breeding arctic foxes.

When they are rearing juveniles, arctic foxes can be considered as central place foragers because they must bring back food to the den (central point) to sustain the development of their cubs (Tannerfeldt and Angerbjorn 1998). If we assume that a fox increases its fitness by maximizing the delivery rate of energy to its den, it should be advantageous to return to the den with more than one prey. Thus, a temporary caching strategy is likely favoured because holding one or more prey in the mouth could adversely affect a fox ability to capture additional prey (Orians and Pearson 1979). The short hoarding time of lemmings and goslings (~60 sec) reported in this study suggests that the time costs associated with finding a temporary cache location is relatively low. Temporary caching may minimize the risk of losing food to scroungers when attacking other prey, but does not eliminate this risk completely as raiding of temporary caches by avian predators like Common ravens and Glaucus gulls (*Larus hyperboreus*) has been reported (Prestrud 1992; Careau et al. 2006)

Recaching behaviour

We observed that arctic foxes invested more time carrying goose eggs and transported them over a longer distance when recaching them than when caching them for the first time. Tracking radio-tagged eggs showed that arctic foxes travelled longer distances when performing a secondary than a primary cache and that the former had a longer lifespan than the latter. Behavioural observations and telemetry gave consistent results that fit with the rapid-sequestering hypothesis. This hypothesis may be valid for two main reasons: egg accessibility and cache pilfering risk. First, the time window during which an arctic fox has easy access to a given goose nest is short because 1) geese are present at their nest for ~94% of the time during incubation, 2) they usually feed and drink relatively close to their nest (<20 m) while remaining vigilant to predators, and 3) they can efficiently deter arctic foxes from their nest (Reed et al. 1995; Bêty et al. 2002). When having access to an undefended nest, an arctic fox can rapidly deplete it by caching eggs close to the nest. Caching may thus allow arctic fox to maximize benefits when a food supply is only available for a limited period of time, as has been observed for red fox (*Vulpes vulpes*) (Macdonald 1976). Secondly, primary caches are vulnerable to cache raiding because arctic fox home ranges overlap extensively in goose colonies with high nest density (Anthony 1997; Eide et al. 2004). Hence, foxes may benefit from investing time and effort in recaching eggs in potentially safer sites (outside the goose colony and/or closer to their den). The higher lifespan of secondary caches suggests that they represented safer places than primary caches.

We cannot exclude that a few biases were introduced in our experiment involving radio-tagged eggs. However, it is difficult to evaluate the most likely direction of potential biases. For example, our visits to caches may have been perceived by foxes and may have led them to move radio-tagged eggs to new cache sites more frequently or farther away than if cache sites had not been visited by us. In this case, we may have overestimated the amount of re-caching. On the other hand, it is possible that when we detected that an egg had been re-cached, foxes may have actually re-cached the egg several times between our two consecutive visits. In that case, we may have underestimated the amount of re-caching. Although a detailed study involving different or more sophisticated techniques would allow to evaluate these potential biases, the fact that they were equal for all caches and had opposite effects on the estimated amount of recaching helps to reduce their overall impact (*sensu* Vander Wall and Joyner 1998).

Increased cache lifespan with distance from the food source was observed in Japanese squirrels (*Sciurus lis*, Tamura et al. 1999), eastern chipmunks (*Tamias striatus*, Clarke and Kramer 1994a) and willow tits (*Parus palustris*, Brodin 1993), presumably because food sources attract other foragers. In our study, the lifespan of primary caches also increased with distance from the nest. This may be because cache pilfering and/or the benefit of recaching decreases when distance from the food source increases.

The rapid-sequestering hypothesis has been supported by two laboratory experiments on Merriam’s kangaroo rats (*Dipodomys merriami*, Jenkins and Peters 1992; Jenkins et al. 1995). Kangaroo rats initially cached items close to food source to maximise harvest rate and to make seeds unavailable to non-digging competitors (birds and ants), and they subsequently redistributed their caches to make them less available to other rodents. However, a field experiment on eastern chipmunks showed that scatter hoard placement was more related to pilferage avoidance ("pilfering-avoidance hypothesis", Macdonald 1976) than to the need of rapidly sequestering food items from an ephemeral patch (Clarke and Kramer 1994a). Subordinate chipmunks (juveniles) were more likely to scatter hoard (Clarke and Kramer 1994b), but also typically recached their food after a competitor had searched the vicinity of the cache (Clarke and Kramer 1994a). In 3 cases where we observed arctic foxes perceiving common ravens in the vicinity of their caches, they never recached the food but rather defended it until the bird left the area (Careau et al. 2006). Although these preliminary observations are limited, they indicate that recaching in arctic fox may not be related to pilferage avoidance.

Because the rapid-sequestering hypothesis does not explain the subsequent recaching from secondary to tertiary caches, our results raise other questions about the adaptive significance of recaching in arctic fox. Given the relatively short distances over which radio-tagged eggs were carried from secondary to tertiary caches, recaching could be a mean of monitoring the quality and quantity of the food reserve (see DeGange et al. 1989). However, this cache-management hypothesis assumes that the hoarder is retrieving its own food, which may not be always the case. If a foraging fox encounters a cache that it did not make, it can increase its own knowledge of the stored resource and reduce the knowledge of its competitors by moving the eggs to a new location (Vander Wall 1995). Therefore, what we interpret as recaching could instead be cache pilfering (Daly et al. 1992; Vander Wall and Jenkins 2003). The paired cache technique is an effective way to estimate cache use by hoarders vs. pilferers (Vander Wall et al. 2006). The system presented in this paper offers a promising opportunity to apply this method to improve our understanding of hoarding behaviour in carnivores.

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References

Anthony RM (1997) Home ranges and movements of arctic fox (*Alopex lagopus*) in western Alaska. Arctic 50:147-157

Bates D, Maechler M (2006) Matrix: A Matrix package for R. In. R package version 0.995-4

Bêty J, Gauthier G, Korpimäki E, Giroux J-F (2002) Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. J. Anim. Ecol. 71:88-98

Board RG (1966a) Course of microbial infection of hens egg. J. Appl. Bacteriol. 29:319-341

Board RG (1966b) The course of microbial infection of the hen's egg. J. Appl. Bacteriol. 29:319-341

Board RG, Fuller R (1974) Non-specific antimicrobial defenses of the avian egg embryo and neonates. Biol. Rev. Camb. Phil. Soc. 49:15-49

Brodin A (1993) Low rate of loss of Willow Tit caches may increase adaptiveness of long-term hoarding. Auk 110:642-645

Careau V, Lecomte N, Giroux JF, Berteaux D (2006) Common ravens raid arctic fox food caches. J. Ethol. in press

Clarke MF, Kramer DL (1994a) The placement, recovery, and loss of scatter hoards by eastern chipmunks, *Tamias striatus*. Behav. Ecol. 5:353-361

Clarke MF, Kramer DL (1994b) Scatter-hoarding by a larder-hoarding rodent - intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. Anim. Behav. 48:299-308

Conover WJ, Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. Am. Stat. 35:124-129

Daly M, Jacobs LF, Wilson MI, Behrends PR (1992) Scatter hoarding by Kangaroo Rats (*Dipodomys merriami*) and pilferage from their caches. Behav. Ecol. 3:102-111

DeGange AR, Fitzpatrick JW, Layne JN, Woolfenden GE (1989) Acorn harvesting by florida scrub jays. Ecology 70:348-356

Eide NE, Eid PM, Prestrud P, Swenson JE (2005) Dietary responses of arctic foxes Alopex lagopus to changing prey availability across an Arctic landscape. Wildlife Biol. 11:109-121

Eide NE, Jepsen JU, Prestrud P (2004) Spatial organization of reproductive Arctic foxes *Alopex lagopus*: response to changes in spatial and temporal availability of prey. J. Anim. Ecol. 73:1056-1068

Elmhagen B, Tannerfeldt M, Verucci P, Angerbjorn A (2000) The arctic fox (*Alopex lagopus*): an opportunistic specialist. J. Zool. 251:139-149

Frafjord K (1993) Food habits of arctic foxes (*Alopex lagopus*) on the western coast of Svalbard. Arctic 46:49-54

Gauthier G, Bêty J, Giroux JF, Rochefort L (2004) Trophic interactions in a high arctic goose colony. Integ. Comp. Biol. 44:119-129

Gendron RP, Reichman OJ (1995) Food perishability and inventory management - a comparison of 3 caching strategies. Am. Nat. 145:948-968

Hadj-Chikh LZ, Steele MA, Smallwood PD (1996) Caching decisions by grey squirrels: A test of the handling time and perishability hypotheses. Anim. Behav. 52:941-948

Hurlbert SH (1984) Pseudoreplication and the desing of ecological field experiment. Ecol. Monogr. 54:187-211

Ihaka R, Gentleman R (1996) R: A language for data analysis and graphics. J. Comp. Graph. Stat. 5:299-314

Jacobs LF (1992) The effect of handling time on the decision to cache by grey squirrels. Anim. Behav. 43:522-524

James PC, Verbeek NAM (1983) The food storage behaviour of the northwestern crow. Behaviour 85:276-291

James PC, Verbeek NAM (1984) Temporal and energetic aspects of food storage in northwestern crows. Ardea 72:207-215

Jenkins SH, Peters RA (1992) Spatial patterns of food storage by merriam kangaroo rats. Behav. Ecol. 3:60-65

Jenkins SH, Rothstein A, Green WCH (1995) Food hoarding by merriams kangaroo rats - a test of alternative hypotheses. Ecology 76:2470-2481

Kotler BP, Brown JS, Hickey M (1999) Food storability and the foraging behavior of fox squirrels (*Sciurus niger*). Am. Midl. Nat. 142:77-86

Lepage D, Nettleship DN, Reed A (1998) Birds of Bylot Island and adjacent Baffin Island, Northwest Territories, Canada, 1979 to 1997. Arctic 51:125-141

Macdonald DW (1976) Food caching by red foxes and some other carnivores. Z. Tierpsychol. 42:170-185

Machlis L, Dodd PWD, Fentress JC (1985) The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol. 68:201-214

Mainguy J, Gauthier G, Giroux J-F, Bêty J (2006) Gosling growth and survival in relation to brood movements in greater snow geese. Auk, in press

Nur N, Holmes AL, Geupel GR (2004) Use of survival time analysis to analyze nesting success in birds: An example using Loggerhead Shrikes. Condor 106:457-471

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell R, Stair GR (eds) Analysis of ecological systems. Ohio State University Press, Colombus, Ohio, pp 155-177

Phillips DP, Ryon J, Danilchuk W, Fentress JC (1991) Food caching in captive coyotes: stereotypy of action sequence and spatial distribution of cache sites. Can. J. Psychol. 45:83-91

Post D, Reichman OJ (1991) Effects of food perishability, distance, and competitors on caching behavior by eastern woodrats. J. Mamm. 72:513-517

Prestrud P (1992) Food habits and observations of the hunting behaviour of Arctic Foxes, *Alopex lagopus*, in Svalbard. Can. F. Nat. 106:225-236

Reed A, Hughes RJ, Boyd H (2002) Patterns of distribution and abundance of Greater Snow Geese on Bylot Island, Nunavut, Canada 1983-1998. Wildfowl 53:53-65

Reed A, Hughes RJ, Gauthier G (1995) Incubation behavior and body mass of female Greater Snow Geese. Condor 97:993-1001

Reichman OJ (1988) Caching behavior by eastern woodrats, *Neotoma floridana*, in relation to food perishability. Anim. Behav. 36:1525-1532

Richardson H, Verbeek NAM (1986) Diet selection and optimization by Nortwestern crows feeding on Japanese littleneck clams. Ecology 67:1219-1226

Roth JD (2003) Variability in marine resources affects arctic fox population dynamics. J. Anim. Ecol. 72:668-676

Samelius G, Alisauskas RT (2000) Foraging patterns of arctic foxes at a large arctic goose colony. Arctic 53:279-288

Sklepkovych BO, Montevecchi WA (1996) Food availability and food hoarding behaviour by red and arctic foxes. Arctic 49:228-234

Smallwood PD, Peters WD (1986) Gray squirrel food preferences: the effects of tannin and fat concentration. Ecology 67:168-174

Smallwood PD, Steele MA, Faeth SH (2001) The ultimate basis of the caching preferences of rodents, and the oak-dispersal syndrome: tannins, insects, and seed germination. Am. Zool. 41:840-851

Smith CC, Reichman OJ (1984) The evolution of food caching by birds and mammals. Ann. Rev. Ecol. Syst. 15:329-351

Tamura N, Hashimoto Y, Hayashi F (1999) Optimal distances for squirrels to transport and hoard walnuts. Anim. Behav. 58:635-642

Tannerfeldt M, Angerbjorn A (1998) Fluctuating resources and the evolution of litter size in the arctic fox. Oikos 83:545-559

Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago

Vander Wall SB (1995) Dynamics of yellow pine chipmunks (*Tamias amoenus*) seed caches: underground traffic in bitterbrush seeds. Écoscience 2:261-266

Vander Wall SB, Jenkins SH (2003) Reciprocal pilferage and the evolution of food-hoarding behavior. Behav. Ecol. 14:656-667

Vander Wall SB, Joyner JW (1998) Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. Can. J. Zool. 76:154-162

Table 1
Number of food items taken by arctic foxes while foraging in a greater snow goose colony, Bylot Island, Nunavut, 2004-2005. The source of the different items is also shown.

Item	Goose egg		Lemming		Gosling		Observation effort (h)
Source	Nest	Cache	Live-captured	Cache	Live-captured	Cache	
2004	18	18	81	20	10	5	198
2005	118	31	23	0	17	1	363
Total	136	49	104	20	27	6	561

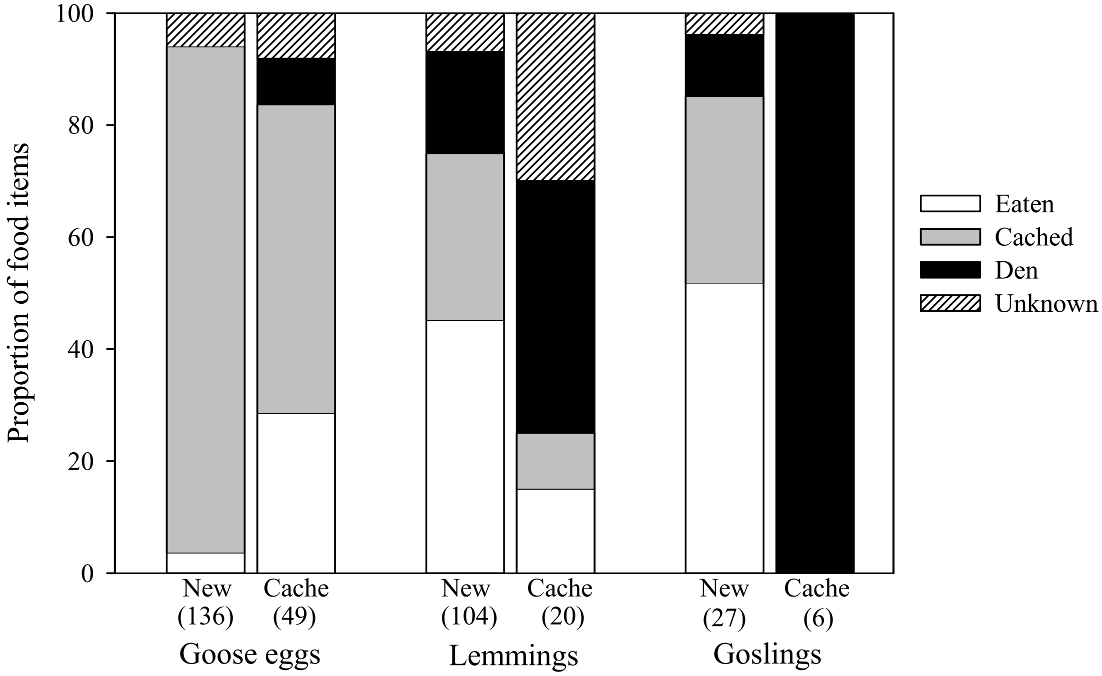

Figure 1 Fate of goose eggs, lemmings, and gosling acquired by arctic foxes according to the source at Bylot Island, Nunavut, 2004-2005. Source is considered to be "new" when a fox took an egg in a nest or live-captured a lemming or a gosling. We considered that food items were brought to the den when foxes left the observation area in the direction of their den. Otherwise the fate is unknown. Sample size is given in parentheses.

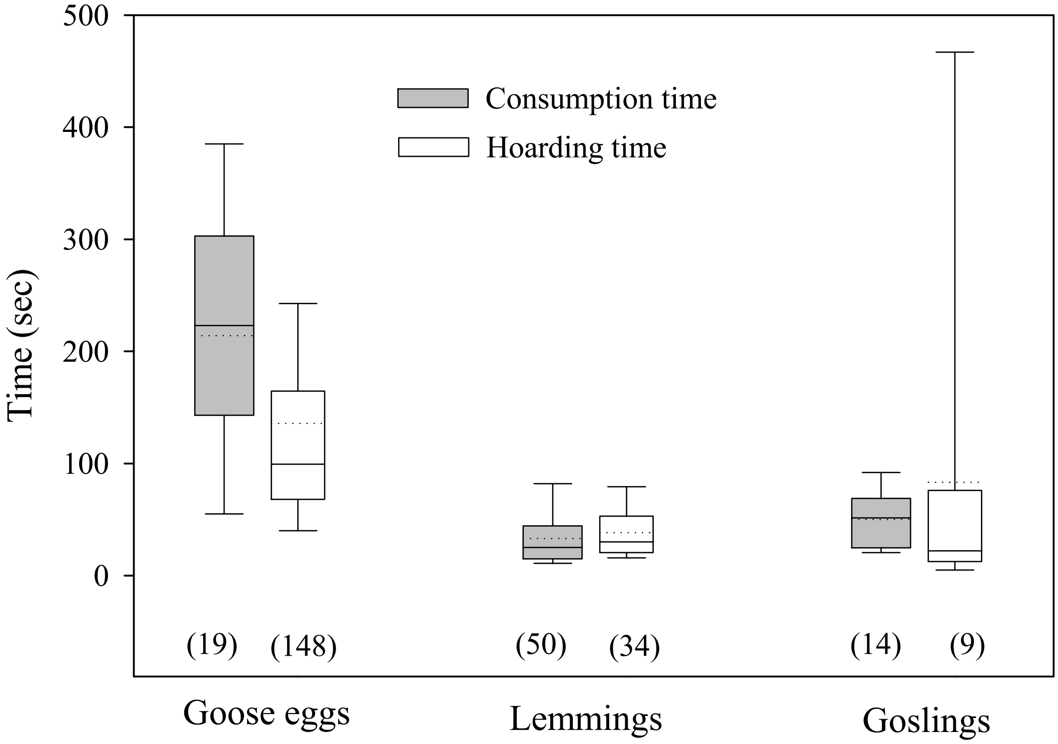

Figure 2 Time spent by arctic foxes consuming and hoarding goose eggs, lemmings, and goslings, Bylot Island, Nunavut, 2004-2005. Hoarding time includes carrying and caching times and numbers in parentheses show sample size for each category. Data are presented as box plots showing the median (*line* within the box), mean (*dotted line*), 25th and 75th percentiles (*box*), and the 10th and the 90th percentiles (*bars*).

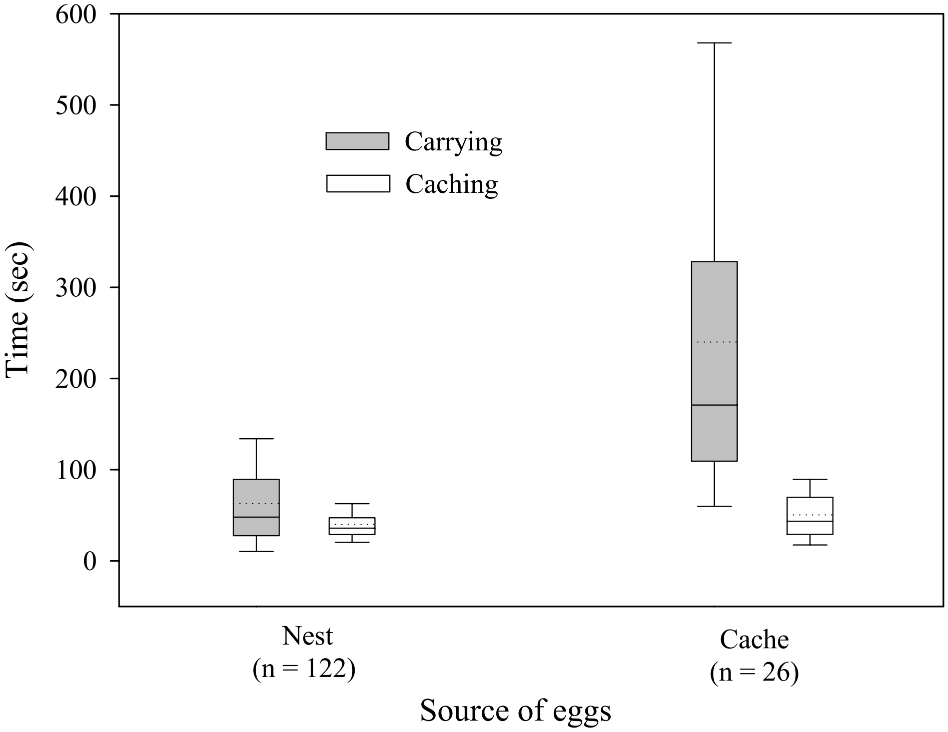

Figure 3 Time spent by arctic foxes carrying and caching goose eggs acquired from nests (primary caches) and caches (recaching), Bylot Island, Nunavut, 2004-2005. Data are presented as in Fig. 2.

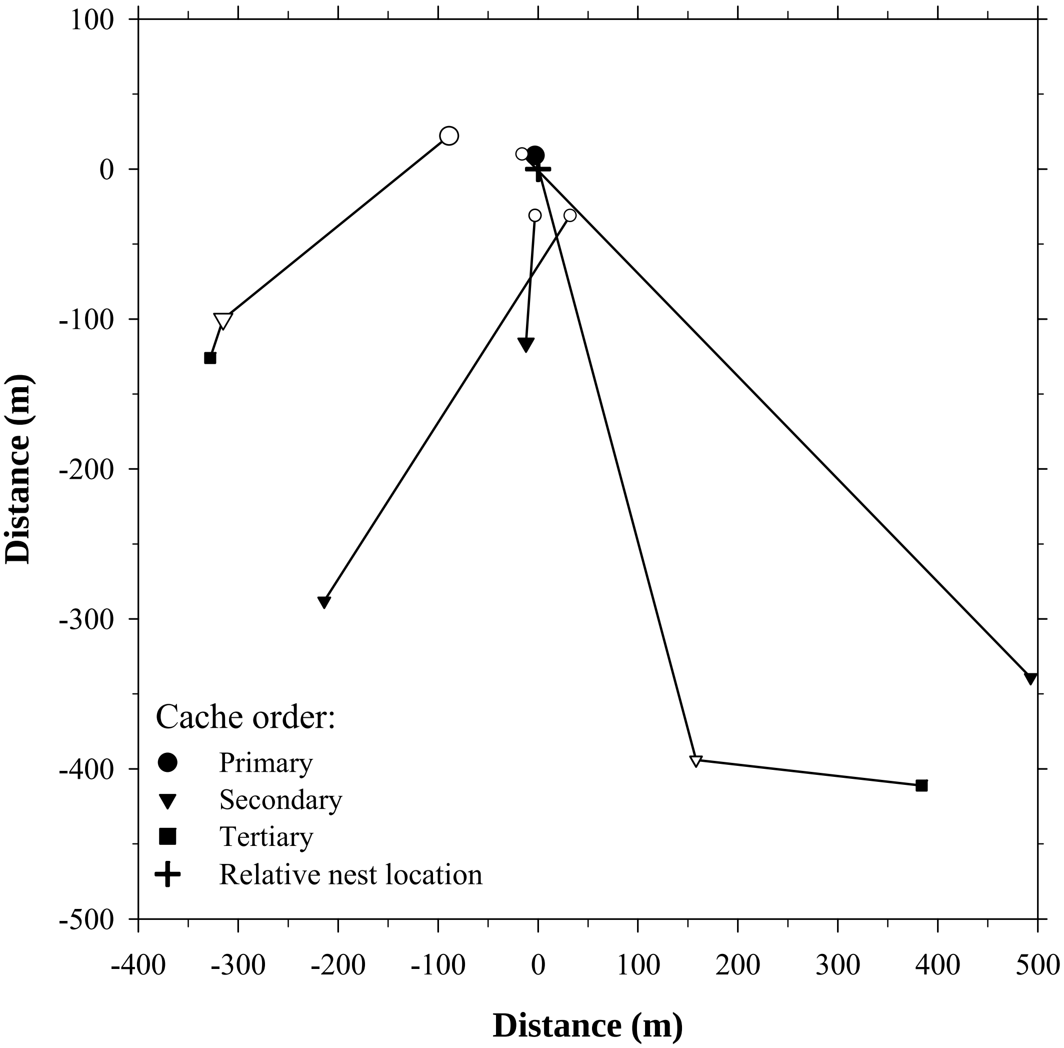

Figure 4 Representative examples of arctic foxes caching radio-tagged eggs (n=5) in a greater snow goose colony at Bylot Island, Nunavut, 2004 and 2005. Although foxes acquired radio-tagged eggs from artificial nests located throughout the colony, all nests are placed at the center of the graph shown by the crosshair to ease illustration. Filled symbols represent caches that survived until 18 August. Lines link radio-tagged eggs from primary to secondary and tertiary caches.

CHAPITRE III

COMMON RAVENS RAID ARCTIC FOX FOOD CACHES

Ce chapitre est présentement sous presse dans la revue *Journal of Ethology*
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Abstract Cache recovery is critical for evolution of hoarding behaviour, because the energy invested in caching may be lost if consumers other than the hoarders benefit from the cached food. By raiding food caches, animals may exploit the caching habits of others, that should respond by actively defending their caches. The arctic fox (*Alopex lagopus*) is the main predator of lemmings and goose eggs in the Canadian high arctic and stores much of its prey in the ground. Common ravens (*Corvus corax*) are not as successful as foxes in taking eggs from goose nests. This generalist avian predator regularly uses innovation and opportunism to survive in many environments. Here, we provide the first report that ravens can successfully raid food cached by foxes, and that foxes may defend their caches from ravens.

Key words *Alopex lagopus* · *Corvus corax* · Food caching · Cache raiding · Defence of food caches · Foraging innovation · Bylot Island

Introduction

Hoarding behaviour, a widespread foraging strategy in animals, entails two key processes—delayed consumption of the food and caching of food items to prevent consumption by other individuals (Vander Wall 1990). Cache recovery is a critical component of hoarding behaviour, because the benefits of hoarding decrease if consumers other than the hoarders recover cached food (Andersson and Krebs 1978). Cache raiding is a form of kleptoparasitism that is more likely to occur in open habitats, especially for systems involving birds, because they use visual cues to locate caches (Brockman and Barnard 1979).

In some arctic goose breeding colonies, all factors are present for the behavioural evolution of both cache raiding and mechanisms aimed at reducing cache raiding. First, hoarding behaviour is usually more common at high latitudes because prey items such as goose eggs and lemmings are seasonally abundant (Smith and Reichman 1984). These resources can also be efficiently stored for later use, because of their small size, their natural packaging of skin or shell, and the cold temperature of cache sites. Second, arctic tundra is an open habitat with 24 h daylight during summer, which favours cache raiding after visual cues.

Arctic foxes (*Alopex lagopus*) and common ravens (*Corvus corax*) are opportunist predators that forage on lemmings and goose eggs (Bêty et al. 2002; Elmhagen et al. 2000; Nelson 1934). Arctic foxes are efficient predators on lemmings and goose nests and cache a high proportion of the eggs they take (Samelius and Alisauskas 2000; Stickney 1991). Common ravens are less successful in preying upon lemmings and eggs but have a remarkable capacity to innovate foraging behaviour (Andersson 1989; Bêty et al. 2002; Ficken 1977; Heinrich 1995). Although cache raiding by ravens has been observed, it occurs mostly on caches made by other ravens (Bugnyar and Kotrschal 2002b). In a broad sense, an innovation is a new or modified learned behaviour not previously found in the population (Reader and Laland 2003). Foraging innovation is vital for species with generalist and opportunistic lifestyles, for example ravens, and can be further defined as the ingestion of a new food type or the use of a new foraging technique (Lefebvre et al. 1997). Here, we document the first report of common ravens raiding arctic fox food caches and foxes defending their caches against ravens.

Material and methods

Our observations were made on Bylot Island in the Canadian high arctic (72°53'N, 79°54'W) from June 8 to July 20 in 2004 and 2005. The mean daily temperature during the observation period was 3.7°C (1.0–7.7°C) and the mean daily precipitation was 1.7 mm (0–15 mm). Bylot Island is the primary breeding site for greater snow geese (*Chen caerulescens atlantica*; Reed et al. 2002). Nesting density of other land birds is low compared with that of geese (Lepage et al. 1998). Although we found no raven nest, they are known to breed in the study area (B. Audet and O. Gilg, personal communication). The weight, width, and length of greater snow goose eggs range from 85–145 g, 4.8–5.6 cm, and 7.3–8.9 cm, respectively (n=60; V. Careau, unpublished data). Both brown (*Lemmus sibiricus*) and collared (*Dicrostonyx groenlandicus*) lemmings occur on Bylot Island. The abundance of brown lemmings varies in cycles of large amplitude with peaks every 3–4 years, which affects arctic fox breeding success (Gauthier et al. 2004). Lemming abundance was high in 2004 (peak year) and low in 2005 (declining phase, snap-trap census; G. Gauthier, personal communication). The main goose colony encompassed 16 km^2 with a mean density of 206 nests km^2 during the study (N. Lecomte, unpublished data) and was located in gently slopping hills of mesic tundra and wetlands. We made observations from two blinds and covered an area of 3.4 km^2 using spotting scopes, 20–60×. Foxes were identified by ear tags and/or the distinctive pattern of their pelts, recognition of which was facilitated by their shedding from winter to summer pelage. We counted common ravens inside the observation area for 10 min every second day. We performed focal sampling of foxes foraging in the goose colony and recorded all interactions between foxes and ravens using a digital voice recorder.

Results

We conducted 549 h of observation over 66 days (2004: 29 days, 2005: 37 days) during which we recorded 82 h of arctic fox foraging activity. At least 5 and 7 different adult foxes were frequently seen foraging in the area in 2004 and 2005, respectively. Ravens were present on 30 of 35 counting periods (mean=4 individuals, range 1–30, median=3) and we detected them flying over or perching on top of the adjacent hills on 14 occasions during focal fox observations. During the entire study, we observed foxes caching 169 eggs and 30 lemmings; ravens were present during 10 (5%) of these caching events. On two occasions a fox carrying an egg was followed by a raven walking at a distance of approximately 20 m. In both instances, the animals went out of the observation limit after 5 min with the fox still carrying the egg.

We witnessed five interactions between ravens and foxes involved in food caching, raiding, and defending (Table 1). On two occasions, we observed a raven raiding a food item that had been cached by a fox few minutes previously. On 24 June 2004 at 20:30, on a sunny evening, a fox spent 18 s caching a lemming. While the fox was caching its food, two ravens landed about 15 m away. Immediately after the fox had left the cache and was hunting for other lemmings about 40 m away, both ravens walked directly towards the cache, probing the ground as they approached. One of the ravens retrieved the lemming 121 s after starting its search and took off with the lemming in its beak. The second bird followed. We could not tell whether or not the lemming cached by the fox had been partly visible to the ravens. The second observation of cache raiding by ravens occurred on 8 June 2005, at 16:00, on a sunny afternoon. An arctic fox cached a goose egg in the snow that covered 90% of the study area at this date. Approximately 10 s after the fox had left the cache, and was about 50 m away, a raven arrived from the opposite direction and landed at the cache site. Immediately upon landing, it retrieved the egg and flew off with it in its beak. It is likely the raven was able to detect the cache because the fox had disturbed the snow surface where the egg was cached and left tracks leading to and from the cache.

Foxes did not attempt to defend their caches in either of the successful raids made by ravens. On three other occasions, however, we observed two different individuals defending their cached food. First, on 15 June 2005 at 19:20, we observed a fox spending 40 s caching an egg before spotting a raven on the ground at a distance of 15 m. In a two-minute period the fox charged the raven four times, but was unsuccessful at making it leave the area. Between charges the fox returned to the cache site and lay down for 3 min at a distance of one meter from the cache until the raven flew off at 19:25. The fox left the site one minute after the raven flew away and neither was seen again by the end of the observation period, 95 min later. Another observation of a fox defending its food cache from a raven was made 27 June 2005, at 20:10, on a sunny evening. A fox spent 53 s caching an egg in the ground. While the fox was digging, a raven landed 20 m away. After burying its egg the fox moved approximately 30 m away from the cache in ca. 40 s. It then spotted the raven and returned to the cache. Using its snout, the fox spent 262 s raking more leaves and moss on top of the cache. It then lay down beside the cache and stayed there for 13 min until the raven flew away at 20:30. The fox left the area 28 min after the raven. Neither the fox nor the raven was observed at the cache during the remaining 5 h of observation. The same fox defended a second cache on 7 July 2005, at 17:32, on a sunny afternoon. The fox spent 39 s caching an egg in the ground. A raven landed on a mound 15 m away 6 s before the fox had finished storing the egg. The fox noticed the bird when leaving the site, prowled the area for 15 s and charged the raven for 21 s. The raven flew off but remained near (<20 m) the cache until 17:40. After the initial charge, the fox returned to its cache and lay down nearby until 17:41. Neither the fox nor the raven returned to the site during the remaining 110 min of observation. Other than these three occasions, we never observed foxes staying at the cache site after storing food items.

During our study, we often observed ravens probing the ground with their beaks while walking on the tundra. On 23 June 2005 at 20:30, a raven landed in the observation area, walked for approximately 5 m, spent 5 s removing moss with its beak, and recovered a cached egg. No fox or raven had been observed in the area during the previous two hours of observation. After spending 4 min eating the egg, the raven walked 150 m to another cache site and recovered another egg. The bird flew off with the egg in its beak in the direction from which it had originally come. In more than 900 h of observation, we have never observed ravens caching goose eggs (this study and Bêty et al. 2001, 2002). The only items cached by ravens on Bylot Island were experimental plastic eggs used for another study. These may have been cached because ravens were unable to break and eat them.

Discussion

To the best of our knowledge, this is the first report of common ravens (alone or in pairs) raiding arctic fox food caches. We argue that the interspecific cache-raiding behaviour of ravens is a foraging innovation that enables them to exploit goose eggs more efficiently. The greater snow goose population has increased from a few thousand in the early 1900s to 50,000 in 1965, and to an estimated 700,000 in 2004 (Gauthier et al. 2005). This 14-fold growth in the last 40 years has obviously increased the number of eggs available to predators throughout the goose breeding range, which in return has probably increased the number of eggs cached by foxes. Arctic foxes can acquire 19–88% of the goose eggs produced annually on Bylot Island (Bêty et al. 2002); of these approximately 80% are cached (V. Careau, unpublished data). In another goose colony on Banks Island, individual foxes were observed to cache up to 1,000 eggs per summer (Samelius and Alisauskas 2000). Foraging innovations enabling ravens to benefit from the increased abundance of goose eggs should be strongly selected for.

Corvids have been observed raiding food caches made by canids in other circumstances. Bugnyar and Kotrschal (2002a) observed wild ravens raiding food caches made by captive wolves (*Canis lupus*). As observed in our study, potential raiders perched close to the wolves that were caching and waited until they moved away before approaching the cache. Similarly, Henry (1986) reported that magpies (*Pica pica*) attempted to raid food caches immediately after they were made in the snow by a red fox (*Vulpes vulpes*). In response to raiding of food caches, hoarders may alter their behaviour to prevent their caches from being detected by kleptoparasites. Macdonald (1976) observed that when a well fed hand-reared red fox became careless in making its caches, the food was almost invariably raided by corvids. On the day after it lost all its stored food to crows (and on which it did not eat because of this) the fox began to cache carefully again, however. All these observations including ours suggest that the kleptoparasitic behaviour of corvids exerts a pressure on foxes to carefully conceal their cached food.

Visual observation is essential for common ravens to achieve conspecific cache raiding (Bugnyar and Kotrschal 2002a). By following foxes carrying eggs, ravens can enhance their raiding efficacy by acquiring visual information about cache location. Henry (1986) suggested that red foxes could deter corvids by carrying food items until the birds give up. This could also be true for the arctic foxes we saw moving away with an egg followed by a raven for more than 5 min.

There is no previous report of foxes chasing, defending, or guarding cached food items against ravens. In response to cache defence, ravens may attempt to remain undetected by foxes and delay cache raiding until the fox cannot actively defend it (Bugnyar and Kotrschal 2002a). Our observation of a raven recovering two cached eggs long after the fox had left them supports this hypothesis. To raid cached food, ravens may conceal themselves when they see a fox caching, remember the cache location, and return later for raiding. Probing the ground as they walk on the tundra may also help ravens to find food caches. We do not yet know whether they concentrate their searches in areas where they have previously observed foxes caching food, however. The behavioural evolution of such a natural system of hoarders and raiders and the cognitive strategies employed warrant further investigation and experimental research.

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References

Andersson M, Krebs J (1978) On the evolution of hoarding behaviour. Anim Behav 26:701-707

Andersson S (1989) Tool Use by the Fan-Tailed Raven (*Corvus rhipidurus*). Condor 91:999-999

Bêty J, Gauthier G, Giroux J-F, Korpimäki E (2001) Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388-400

Bêty J, Gauthier G, Korpimäki E, Giroux J-F (2002) Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. J Anim Ecol 71:88-98

Brockman HJ, Barnard CJ (1979) Kleptoparasitism in birds. Anim Behav 27:487-514

Bugnyar T, Kotrschal K (2002a) Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? Anim Behav 64:185-195

Bugnyar T, Kotrschal K (2002b) Scrounging tactics in free-ranging ravens, *Corvus corax*. Ethology 108:993-1009

Elmhagen B, Tannerfeldt M, Verucci P, Angerbjorn A (2000) The arctic fox (*Alopex lagopus*): an opportunistic specialist. J Zool 251:139-149

Ficken MS (1977) Avian play. Auk 94:573-582

Gauthier G, Bêty J, Giroux JF, Rochefort L (2004) Trophic interactions in a high arctic goose colony. Integr Comp Biol 44:119-129

Gauthier G, Giroux JF, Reed A (2005) Interactions between land use, habitat use and population increase in greater snow geese: what are the consequences for natural wetlands? Global Change Biol 11:856-868

Heinrich B (1995) An experimental investigation of insight in Common Ravens (*Corvus corax*). Auk 112:994-1003

Heinrich B, Pepper JW (1998) Influence of competitors on caching behaviour in the common raven, *Corvus corax*. Anim Behav 56:1083-1090

Henry JD (1986) Red fox: The catlike canine. Smithsonian Institution Press, Washington, D. C.

Lefebvre L, Whittle P, Lascaris E, Finkelstein A (1997) Feeding innovations and forebrain size in birds. Anim Behav 53:549-560

Lepage D, Nettleship DN, Reed A (1998) Birds of Bylot Island and adjacent Baffin Island, Northwest Territories, Canada, 1979 to 1997. Arctic 51:125-141

Macdonald DW (1976) Food caching by red foxes and some other carnivores. Z Tierpsychol 42:170-185

Nelson AL (1934) Some early summer food preferences of the American raven in southeastern Oregon. Condor 36:10-l 15

Reader SM, Laland KN (2003) Animal Innovation. Oxford University Press, Oxford

Reed A, Hughes RJ, Boyd H (2002) Patterns of distribution and abundance of Greater Snow Geese on Bylot Island, Nunavut, Canada 1983-1998. Wildfowl 53:53-65

Samelius G, Alisauskas RT (2000) Foraging patterns of arctic foxes at a large arctic goose colony. Arctic 53:279-288

Smith CC, Reichman OJ (1984) The evolution of food caching by birds and mammals. Annu Rev Ecol Syst 15:329-351

Stickney A (1991) Seasonal pattern of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Can J Zool 69:2853-2859

Vander Wall SB (1990) Food hoarding in animals, Chicago: University of Chicago Press

Table 1

Interactions between arctic foxes and common ravens during caching, cache raiding and cache defending events on Bylot Island, Nunavut, 2004 and 2005.

Date	Time	Food item cached by the fox	Number of ravens attending	Landing distance from cache location (m)	Time between fox leaving and cache raiding (s)	Time the fox spent defending the cache (min)	Raiding successful
24 June 2004	20:30	lemming	2	15	121	-	yes
8 June 2005	16:00	goose egg	1	0	10	-	yes
15 June 2005	19:20	goose egg	1	15	-	6	no
27 June 2005	20:10	goose egg	1	20	-	46	no
7 July 2005	17:32	goose egg	1	15	-	8	no

CONCLUSION GÉNÉRALE

L'objectif de ce projet de maîtrise était de tester l'idée générale qu'un prédateur maximise son accès à une ressource abondante mais éphémère via le comportement de mise en réserve (CMR). Le modèle d'étude était le renard arctique et les ressources principales étaient l'oie (œufs et oisons) et le lemming. De toutes ces ressources, l'œuf est sans doute la meilleure proie à cacher et cette étude démontre que le CMR d'un renard est exprimé à son plus fort lorsqu'il acquiert un œuf (chap. II). Ce projet, qui utilise des données s'échelonnant sur une période de 8 ans, démontre pour la première fois comment les différences annuelles de CMR des renards sont reliées au cycle de lemmings (chap. I). Aussi, en utilisant une nouvelle technique, cette recherche fournit des informations inédites sur le CMR des renards et dévoile un mécanisme leur permettant de séquestrer rapidement la nourriture (chap. II). Enfin, cette étude documente que le grand corbeau peut prélever efficacement les réserves faites par les renards (chap. III), suggérant que les réserves d'œufs cachés par les renards sont également bénéfiques à un autre prédateur.

Le pillage des œufs cachés

Tout au long de cette étude, il a été impossible de déterminer si un individu qui récupère un œuf caché est celui qui avait antérieurement caché cet œuf (chap. I et II). Ainsi, ce que nous interprétons comme étant une récupération ou recache peut possiblement être un cas de pillage (Vander Wall et Jenkins 2003). Ceci représente la limite majeure de cette étude. Les prochains développements portant sur le CMR du renard arctique toucheront fort probablement à cet aspect. Il est cependant très difficile d'obtenir des informations sur cet aspect en milieu naturel.

Le déploiement de caches artificielles est une manière simple et courante pour évaluer les variations spatio-temporelles en intensité de pillage. Comme ces caches ont été créées par l'homme, leur récupération représente un cas de pillage. Cette méthode n'offre aucun point de comparaison pour vérifier la validité des résultats et il est connu qu'elle peut sous-estimer le taux de pillage (Vander Wall *et al.* 2006). Néanmoins, cette méthode peut s'avérer utile pour estimer la variation annuelle et saisonnière en intensité de pillage et la comparer entre différentes colonies. Il serait alors recommandé d'utiliser le même protocole que Samelius (2004) afin de comparer la colonie de Karrak Lake (densité de nidification élevée) avec celle de Bylot (densité de nidification moyenne).

Il a été récemment démontré que la technique de la cache appariée (où l'on créée une cache artificielle à proximité d'une vraie cache) est une bonne méthode pour estimer la proportion des caches récupérées par les cacheurs vs. pilleurs (Vander Wall *et al.* 2006). Cette technique serait envisageable puisque les œufs émetteurs nous permettent de localiser des « vraies » caches (chap. II). Aussi, la technique des œufs émetteurs pourrait être d'autant plus révélatrice si elle était combinée à d'autres techniques. Le suivi satellite d'individus marqués nous permettrait de savoir si certains déplacements d'œufs cachés se font d'un territoire à l'autre. Certaines techniques plus poussées sont potentiellement réalisables, comme l'identification du renard à l'aide de transpondeurs (dans l'œuf ou sur le renard) ou à l'aide de l'ADN contenu dans la salive laissée par un renard lorsqu'il transporte un œuf (Williams *et al.* 2003). Cependant, il se peut que le développement de telles techniques soit coûteux et implique beaucoup de temps par rapport aux informations qu'elles rapporteront.

La prédation durant la ponte et l'estimation des paramètres phénologiques des oies

Le mécanisme comportemental de séquestration rapide permet à un renard arctique d'acquérir plusieurs œufs contenus dans un même nid lorsqu'il n'est pas défendu (chap. II). Ce mécanisme expliquerait en partie pourquoi les renards ont pu acquérir les œufs à un taux si élevé durant la ponte (chap. I). Ce haut taux d'acquisition peut avoir une implication au niveau de l'estimation de certains paramètres phénologiques des oies. Il est entendu depuis longtemps que la taille de ponte est sous-estimée puisque le nombre d'œufs auparavant prélevés par les prédateurs est inconnu au moment de la découverte d'un nid. Le taux de prédation élevé durant la ponte suggère que la sous-estimation du nombre d'œufs pondus peut potentiellement être plus importante que ce qui est admis. Cette sous-estimation de la taille de ponte peut à son tour avoir un effet sur l'estimation d'un autre paramètre, la date médiane d'initiation de la ponte (date du premier œuf pondu). Puisqu'une oie pond un œuf à toutes les ~33 h (Poussart *et al.* 2000), la date du premier œuf pondu est estimée en retranchant un jour par œuf à la date de la découverte d'un nid (en sautant un jour après le troisième oeuf, voir Lepage *et al.* 1999 pour les détails). La prédation d'un ou plusieurs œufs durant la ponte a donc comme effet de fausser d'un ou plusieurs jours l'estimation de la date à laquelle le premier œuf du nid a été pondu. Si plusieurs nids ont subi ce sort, la date médiane de ponte estimée est plus tardive que ce qu'elle est réellement.

Le CMR et la survie en hiver

L'hiver (octobre à avril) est une période critique pour le renard arctique (Angerbjörn *et al.* 1991; Anthony *et al.* 2000; Macpherson 1969; Roth 2002). Plusieurs auteurs ont souligné l'importance des réserves de nourriture dans la survie des renards arctiques en hiver (Bantle et Alisauskas 1998; Fay et Stephensen 1989; Prestrud 1992b; Stickney 1991). D'autres, cependant, sont plutôt d'avis que la nourriture d'origine marine est le facteur le plus important pour la survie en hiver (Anthony *et al.* 2000; Hammill 1983; Roth 2002). En effet, il a été observé que les renards arctiques sont nomades durant cette période et qu'ils peuvent se déplacer sur de très longues distances sur la glace (Chesemore 1968a; Eberhardt et Hanson 1978) alors qu'ils se nourrissent de carcasses de phoques laissées par les ours polaires (Andriashek *et al.* 1985; Hiruki et Stirling 1989). Cette hypothèse est vraisemblable puisqu'il a été démontré que la survie du renard arctique en hiver est reliée à la production marine, spécialement durant les périodes de faible abondance de lemmings (Frafjord et Prestrud 1992; Roth 2003). Même si l'approvisionnement sur la glace en hiver est un aspect peu connu de l'écologie comportementale du renard arctique, cette option peut s'avérer risquée puisque l'abondance des ressources y est imprévisible et distribuée de façon hétérogène (Ferguson *et al.* 2000).

La mise en réserve pourrait être une stratégie alternative plus sécuritaire que la dispersion hivernale, spécialement durant les années où la production marine est faible (Fay et Stephensen 1989). Eberhardt *et al.* (1983) ont observé que des juvéniles sont restés dans leur territoire natal jusqu'à la fin janvier. Jepsen *et al.* (2002) ont aussi observé que les adultes visitaient une colonie d'oies même après le départ des oies et Anthony (1997) a documenté que certains renards arctiques utilisaient leur territoire estival durant toute l'année. Quoique le renard arctique puisse rester sur terre et chasser le lemming en hiver, toutes les observations citées ci haut pourraient être reliées à la récupération de caches faites en été. Ceci suggère que les renards arctiques utilisent une partie de leurs réserves avant de quitter la terre pour se disperser sur la glace à la recherche de nourriture. D'après nos observations à l'île Bylot, les années où la réserve en oeufs est la plus basse, correspondent à la troisième année après le pic d'abondance de lemmings (chap. I). Ainsi, la proportion d'œufs dans la diète automnale et/ou hivernale des renards devrait être à son plus bas trois ans après le pic de lemming. Ceci peut s'évaluer à l'aide de la technique d'analyse des isotopes stables (Samelius 2004).

Subside allochtone

La population de la grande oie des neiges n'a cessé d'augmenter depuis un siècle, passant de quelques milliers d'individus au début du siècle, à 50 000 en 1965 et 700 000 en 2004 (Gauthier *et al.* 2005). Cette augmentation bénéficie non seulement aux renards arctiques, mais aussi aux grands corbeaux puisque ces derniers ont la capacité de prélever la nourriture cachée par les renards arctiques. Au même titre que ces derniers, le grand corbeau fait partie du niveau trophique des prédateurs. Le CMR du renard arctique augmente donc le flux d'énergie et éléments nutritifs entre les oies et le niveau trophique supérieur. Le CMR pourrait permettre aux renards arctiques de subsister à des densités plus élevées durant les creux de lemmings et ainsi avoir un pouvoir régulateur plus fort sur ceux-ci quand leurs populations recommencent à augmenter (Bêty *et al.* 2002). La plus forte pression de prédation exercée par les renards sur les lemmings serait alors un des facteurs qui empêcherait ces derniers d'endommager la végétation, contrairement à la théorie d'exploitation des écosystèmes présentée par Oksanen *et al.* (1981) et aux observations rapportées en Scandinavie (Virtanen *et al.* 1997). En étant concentrée sur le comportement des renards arctiques, cette étude a identifié un mécanisme potentiellement important dans les interactions trophiques du système arctique. Cela suit l'approche mise de l'avant par Schoener (1986) et Kingsolver (1989) qui ont invoqué l'utilisation de concepts écologiques basés sur les individus pour comprendre les patrons à l'échelle des communautés. Maintenant que nous comprenons mieux comment le renard arctique change en quelque sorte les contraintes alimentaires de son environnement, la question suivante est de savoir à quel niveau les avantages procurés par le CMR peuvent altérer la structure des communautés (Vander Wall 1990).

BIBLIOGRAPHIE GÉNÉRALE

Abrams, P. A. et H. Matsuda. 1996. "Positive indirect effects between prey species that share predators". *Ecology*, vol. 77, p. 610-616.

Andersson, M. et J. Krebs. 1978. "On the evolution of hoarding behaviour". *Animal Behaviour*, vol. 26, p. 701-707.

Andriashek, D., H. P. K. Kiliaan et M. K. Taylor. 1985. "Observations on foxes, *Alopex lagopus*, and *Vulpes vulpes*, and wolves, *Canis lupus*, on the off-shore sea ice of northern Labrador". *Canadian Field Naturalist*, vol. 99, p. 86-89.

Angerbjörn, A., B. Arvidson, E. Norén et L. Strömgren. 1991. "The effect of winter food on reproduction in the arctic fox, *Alopex lagopus*: a field experiment". *Journal of Animal Ecology*, vol. 60, p. 705-714.

Angerbjörn, A., P. Hersteinsson, K. Liden et E. Nelson. 1994. "Dietary variation in arctic foxes (*Alopex lagopus*) - an analysis of stable carbon isotopes". *Oecologia*, vol. 99, p. 226-232.

Angerbjörn, A., M. Tannerfeldt, A. Bjarvall, M. Ericson, J. From et E. Noren. 1995. "Dynamics of the arctic fox population in Sweden". *Annales Zoologici Fennici*, vol. 32, p. 55-68.

Anthony, R. M. 1997. "Home ranges and movements of arctic fox (*Alopex lagopus*) in western Alaska". *Arctic*, vol. 50, p. 147-157.

Anthony, R. M., N. L. Barten et P. E. Seiser. 2000. "Foods of arctic foxes (*Alopex lagopus*) during winter and spring in western Alaska". *Journal of Mammalogy*, vol. 81, p. 820-828.

Bantle, J. L. et R. T. Alisauskas. 1998. "Spatial and temporal patterns in arctic fox diets at a large goose colony". *Arctic*, vol. 51, p. 231-236.

Bêty, J., G. Gauthier, J.-F. Giroux et E. Korpimäki. 2001. "Are goose nesting success and lemming cycles linked? Interplay between nest density and predators". *Oikos*, vol. 93, p. 388-400.

Bêty, J., G. Gauthier, E. Korpimäki et J.-F. Giroux. 2002. "Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese". *Journal of Animal Ecology*, vol. 71, p. 88-98.

Board, R. G. 1966. "The course of microbial infection of the hen's egg". *Journal of Applied Bacteriology*, vol. 29, p. 319-341.

Board, R. G. et R. Fuller. 1974. "Non-specific antimicrobial defenses of the avian egg embryo and neonates". *Biological Reviews of the Cambridge Philosophical Society*, vol. 49, p. 15-49.

Bugnyar, T. et K. Kotrschal. 2002. "Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception?" *Animal Behaviour*, vol. 64, p. 185-195.

Chesemore, D. L. 1968a. "Distributions and movements of white foxes in northern and western Alaska". *Canadian Journal of Zoology*, vol. 46, p. 849-854.

———. 1968b. "Notes on the food habits of Arctic foxes in northern Alaska". *Canadian Journal of Zoology*, vol. 46, p. 1127-1130.

Clarke, M. F. et D. L. Kramer. 1994. "The placement, recovery, and loss of scatter hoards by eastern chipmunks, *Tamias striatus*". *Behavioral Ecology*, vol. 5, p. 353-361.

Dalerum, F. et A. Angerbjorn. 2000. "Arctic fox (*Alopex lagopus*) diet in Karupelv valley, East Greenland, during a summer with low lemming density". *Arctic*, vol. 53, p. 1-8.

Dally, J. M., N. S. Clayton et N. J. Emery. 2006. "The behaviour and evolution of cache protection and pilferage". *Animal Behaviour*, vol. 72, p. 13-23.

Eberhardt, L. E., R. A. Garrott et W. C. Hanson. 1983. "Winter movements of arctic foxes, *Alopex lagopus*, in a petrolum development area". *Canadian Field Naturalist*, vol. 97, p. 66-70.

Eberhardt, L. E. et W. C. Hanson. 1978. "Long distance movements of arctic foxes tagged in northern Alaska". *Canadian Field Naturalist*, vol. 92, p. 386-389.

Elmhagen, B., M. Tannerfeldt, P. Verucci et A. Angerbjorn. 2000. "The arctic fox (*Alopex lagopus*): an opportunistic specialist". *Journal of Zoology*, vol. 251, p. 139-149.

Fay, F. H. et R. O. Stephensen. 1989. "Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea". *Canadian Journal of Zoology*, vol. 67, p. 1986-1994.

Ferguson, S. H., M. K. Taylor et F. Messier. 2000. "Influence of sea ice dynamics on habitat selection by polar bears". *Ecology*, vol. 81, p. 761-772.

Frafjord, K. 1992. "Behavioural ecology and behavioural energetics in the arctic fox *Alopex lagopus*". Thèse de doctorat, Bergen, University of Bergen, 125 p.

———. 1993. "Food habits of arctic foxes (*Alopex lagopus*) on the western coast of Svalbard". *Arctic*, vol. 46, p. 49-54.

Frafjord, K. et P. Prestrud. 1992. "Home range and movements of arctic foxes *Alopex lagopus*". *Polar Biology*, vol. 12, p. 519-526.

Fuglei, E. 2000. "Physiological adaptations of the arctic fox to high Arctic conditions". Thèse de doctorat, Oslo, University of Oslo, 105 p.

Gauthier, G., J. Bêty, J. F. Giroux et L. Rochefort. 2004. "Trophic interactions in a high arctic goose colony". *Integrative and Comparative Biology*, vol. 44, p. 119-129.

Gauthier, G., J. Bety et K. A. Hobson. 2003. "Are greater snow geese capital breeders? New evidence from a stable-isotope model". *Ecology*, vol. 84, p. 3250-3264.

Gauthier, G., J. F. Giroux et A. Reed. 2005. "Interactions between land use, habitat use and population increase in greater snow geese: what are the consequences for natural wetlands?" *Global Change Biology*, vol. 11, p. 856-868.

Gauthier, G. et J. Tardif. 1991. "Female feeding and male vigilance during nesting in greater snow geese". *Condor*, vol. 93, p. 701-707.

Gendron, R. P. et O. J. Reichman. 1995. "Food perishability and inventory management - a comparison of 3 caching strategies". *American Naturalist*, vol. 145, p. 948-968.

Hadj-Chikh, L. Z., M. A. Steele et P. D. Smallwood. 1996. "Caching decisions by grey squirrels: A test of the handling time and perishability hypotheses". *Animal Behaviour*, vol. 52, p. 941-948.

Hammill, M. O. 1983. "The arctic fox, *Alopex lagopus*, as a marine mammal; physical condition and population age structure". Mémoire de maîtrise, Montréal, McGill University, 72 p.

Henry, J. D. 1986. *Red fox: The catlike canine*. Washington: Smithsonian Institution Press, 174 p.

Hersteinsson, P. et D. W. Macdonald. 1996. "Diet of arctic foxes (*Alopex Lagopus*) in Iceland". *Journal of Zoology*, vol. 240, p. 457-474.

Hiruki, L. M. et I. Stirling. 1989. "Population dynamics of the arctic fox, *Alopex lagopus*, on Banks Island, Northwest Territories". *The Canadian Field Naturalist*, vol. 103, p. 380-387.

Holt, R. D. 1987. "Prey communities in patchy environments". *Oikos*, vol. 50, p. 276-290.

Jacobs, L. F. 1992. "The effect of handling time on the decision to cache by grey squirrels". *Animal Behaviour*, vol. 43, p. 522-524.

Jenkins, S. H. et R. A. Peters. 1992. "Spatial patterns of food storage by merriam kangaroo rats". *Behavioral Ecology*, vol. 3, p. 60-65.

Jenkins, S. H., A. Rothstein et W. C. H. Green. 1995. "Food hoarding by merriams kangaroo rats - a test of alternative hypotheses". *Ecology*, vol. 76, p. 2470-2481.

Jepsen, J. U., N. E. Eide, P. Prestrud et L. B. Jacobsen. 2002. "The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*)". *Canadian Journal of Zoology*, vol. 80, p. 418-429.

Kapel, C. M. O. 1999. "Diet of arctic foxes (*Alopex lagopus*) in Greenland". *Arctic*, vol. 52, p. 289-293.

Kingsolver, J. 1989. "Weather and the population dynamics of insects: integrating physiological and population ecology". *Physiological Zoology*, vol. 62, p. 314–334.

Klir, J. J. et J. E. Heath. 1992. "Metabolic rate and evaporative water loss at different ambient temperatures in 2 species of fox: the red fox (*Vulpes vulpes*) and the arctic fox (*Alopex lagopus*)". *Comparative Biochemistry and Physiology a-Physiology*, vol. 101, p. 705-707.

Kotler, B. P., J. S. Brown et M. Hickey. 1999. "Food storability and the foraging behavior of fox squirrels (*Sciurus niger*)". *American Midland Naturalist*, vol. 142, p. 77-86.

Lepage, D., A. Desrochers et G. Gauthier. 1999. "Seasonal decline of growth and fledging success in Snow Geese Anser caerulescens: an effect of date or parental quality?" *Journal of Avian Biology*, vol. 30, p. 72-78.

Lepage, D., G. Gauthier et S. Menu. 2000. "Reproductive consequences of egg-laying decisions in snow geese". *Journal of Animal Ecology*, vol. 69, p. 414-427.

Macdonald, D. W. 1976. "Food caching by red foxes and some other carnivores". *Zeitschrift fur Tierpsychologie*, vol. 42, p. 170-185.

Macdonald, D. W., L. Brown, S. Yerli et A.-F. Canbolat. 1994. "Behavior of red foxes, *Vulpes vulpes*, caching eggs of loggerhead turtles, *Caretta caretta*". *Journal of Mammalogy*, vol. 75, p. 985-988.

Macdonald, D. W. et C. Sillerio-Zubiri. 2004. *The biology and conservation of wild canids*. Oxford: Oxford University Press, 450 p.

Macpherson, A. H. 1969. "The dynamics of Canadian arctic fox populations". *Canadian Wildlife Service report series*, no 8, 160 p.

Oksanen, L., S. D. Fretwell, J. Arruda et P. Niemelä. 1981. "Exploitation ecosystems in gradients of primary productivity". *American Naturalist*, vol. 118, p. 240-261.

Phillips, D. P., W. Danilchuk, J. Ryon et J. C. Fentress. 1990. "Food caching in timber wolves, and the question of rules of action syntax". *Behavioural Brain Research*, vol. 38, p. 1-6.

Phillips, D. P., J. Ryon, W. Danilchuk et J. C. Fentress. 1991. "Food caching in captive coyotes: stereotypy of action sequence and spatial distribution of cache sites". *Canadian Journal of Psychology*, vol. 45, p. 83-91.

Poussart, C., J. Larochelle et G. Gauthier. 2000. "The thermal regime of eggs during laying and incubation in Greater Snow Geese". *Condor*, vol. 102, p. 292-300.

Prestrud, P. 1991. "Adaptations by the arctic fox *(Alopex lagopus)* to the polar winter". *Arctic*, vol. 44, p. 132-138.

———. 1992a. "Arctic foxes in Svalbard: population ecology and rabies". Thèse de doctorat, Oslo, University of Oslo, 216 p.

———. 1992b. "Food habits and observations of the hunting behaviour of Arctic Foxes, *Alopex lagopus*, in Svalbard". *Canadian Field Naturalist*, vol. 106, p. 225-236.

Roth, J. D. 2002. "Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice". *Oecologia*, vol. 133, p. 70-77.

———. 2003. "Variability in marine resources affects arctic fox population dynamics". *Journal of Animal Ecology*, vol. 72, p. 668-676.

Samelius, G. 2004. "Foraging behaviours and population dynamics of arctic foxes". *Arctic*, vol. 57, p. 441-443.

Samelius, G. et R. T. Alisauskas. 2000. "Foraging patterns of arctic foxes at a large arctic goose colony". *Arctic*, vol. 53, p. 279-288.

Schmidt, K. A. 1999. "Foraging theory as a conceptual framework for studying nest predation". *Oikos*, vol. 85, p. 151-160.

Schoener, T. W. 1986. "Mechanistic approaches to community ecology: a new reductionism?" *American Zoologist*, vol. 26, p. 81-106.

Scholander, P. F., V. Walters, R. Hock et L. Irving. 1950. "Body Insulation of Some Arctic and Tropical Mammals and Birds". *Biological Bulletin*, vol. 99, p. 225-236.

Sklepkovych, B. O. et W. A. Montevecchi. 1996. "Food availability and food hoarding behaviour by red and arctic foxes". *Arctic*, vol. 49, p. 228-234.

Smallwood, P. D. et W. D. Peters. 1986. "Gray squirrel food preferences: the effects of tannin and fat concentration". *Ecology*, vol. 67, p. 168-174.

Smith, C. C. et O. J. Reichman. 1984. "The evolution of food caching by birds and mammals". *Annual Review of Ecology & Systematics*, vol. 15, p. 329-351.

Stickney, A. 1991. "Seasonal pattern of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area". *Canadian Journal of Zoology*, vol. 69, p. 2853-2859.

Sutherland, W. J. 1996. *From individual to population ecology*. Oxford: Oxford University Press, 224 p.

Tannerfeldt, M. 1997. "Population fluctuations and life history consequences in the arctic fox". Thèse de doctorat, Stockholm, Stockholm University, 90 p.

Tannerfeldt, M., A. Angerbjorn et B. Arvidson. 1994. "The effect of summer feeding on juvenile arctic fox survival - a field experiment". *Ecography*, vol. 17, p. 88-96.

Vander Wall, S. B. 1990. *Food hoarding in animals*. Chicago: University of Chicago Press, 445 p.

———. 1995. "Dynamics of yellow pine chipmunks (*Tamias amoenus*) seed caches: underground traffic in bitterbrush seeds". *Écoscience*, vol. 2, p. 261-266.

Vander Wall, S. B., J. S. Briggs, S. H. Jenkins, K. M. Kuhn, T. C. Thayer et M. J. Beck. 2006. "Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food". *Animal Behaviour*, vol. 72, p. 189-197.

Vander Wall, S. B. et S. H. Jenkins. 2003. "Reciprocal pilferage and the evolution of food-hoarding behavior". *Behavioral Ecology*, vol. 14, p. 656-667.

Vander Wall, S. B. et J. W. Joyner. 1998. "Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success". *Canadian Journal of Zoology*, vol. 76, p. 154-162.

Virtanen, R., H. Henttonen et K. Laine. 1997. "Lemming grazing and structure of a snowbed plant community - a long-term experiment at Kilpisjarvi, Finnish Lapland". *Oikos*, vol. 79, p. 155-166.

Williams, C. L., K. Blejwas, J. J. Johnston et M. M. Jaeger. 2003. "A coyote in sheep's clothing: predator identification from saliva". *Wildlife Society Bulletin*, vol. 31, p. 926-932.