

UNIVERSITÉ DU QUÉBEC À RIMOUSKI

SÉLECTION DES SITES DE TANIÈRES ET DES TANIÈRES DE REPRODUCTION
CHEZ LE RENARD ARCTIQUE À L'ÎLE BYLOT, NUNAVUT

MÉMOIRE PRÉSENTÉ À

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PAR

GUILLAUME SZOR

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AVANT-PROPOS

Ce mémoire est présenté sous la forme d'un article à être soumis à la *Revue canadienne de Zoologie* ainsi que d'un protocole préparé pour l'Agence Parcs Canada et le Comité de gestion conjointe des parcs (Joint Park Management Committee) du Parc national du Canada Sirmilik. Une revue de littérature a été ajoutée au mémoire afin de fournir au lecteur un supplément d'informations sur le sujet d'étude.

Contribution des auteurs

Bien que Dominique Berteaux et Gilles Gauthier soient co-auteurs de l'article principal, le manuscrit doit être considéré comme le mémoire de l'étudiant. L'apport de D. Berteaux et G. Gauthier se limite aux fonctions de supervision. Ils ont guidé l'étudiant lors de la planification du travail de terrain et lors de la rédaction du mémoire. Guillaume Szor a planifié l'échantillonnage, récolté les données de terrain, fait les analyses statistiques et rédigé le mémoire.

RÉSUMÉ

L'utilisation de tanières est une stratégie courante chez plusieurs carnivores terrestres, utilisant ces structures comme site de mise-bas et d'élevage des jeunes, ou simplement comme refuge ou lieu de repos. La localisation de ces tanières semble rarement aléatoire mais plutôt influencée par l'abondance des ressources alimentaires ou la facilité d'échapper à la prédation. Le premier objectif de mon projet était de déterminer quels étaient les paramètres influençant la localisation des tanières d'un carnivore vivant dans un écosystème arctique. Nous avons examiné les caractéristiques et l'environnement de 83 tanières de renards arctiques (*Alopex lagopus*) sur la plaine sud de l'île Bylot, Nunavut, Canada. La topographie, le microclimat et la distribution des ressources alimentaires aux tanières (n = 83) ont été comparés aux caractéristiques de sites aléatoires dans l'aire d'étude (échelle du paysage) ainsi qu'aux caractéristiques d'autres sites potentiels dans un rayon de 100 mètres autour des tanières (échelle locale). Les tanières de renards arctiques étaient majoritairement excavées dans des buttes ou pentes naturelles, préférentiellement aux endroits où le substrat était sablonneux, assurant ainsi un bon drainage du site. Nous avons également observé une préférence pour les sites ayant un faible couvert de neige au printemps et une plus grande exposition au sud, générant ainsi une température du sol plus élevée aux tanières et donc un dégel du sol plus rapide à la fin de l'hiver. Nous suggérons que la sélection de sites bien drainés et où la fonte des neiges est accélérée permet aux renards arctiques d'avoir accès à une couche de sol meuble plus épaisse au-dessus de la strate de pergélisol. L'accès à un sol meuble, dans un environnement arctique, semblerait donc représenter le facteur limitant principal pour l'établissement de tanières chez ce carnivore.

Le second objectif de mon projet était d'identifier les contraintes apparentes auxquelles les renards arctiques sont exposés lors du choix de leur site de reproduction. Nous avons comparé l'environnement de 27 tanières utilisées pour la mise-bas à l'environnement de 53 tanières inactives. La sélection d'une tanière de reproduction semble fortement liée à la distribution des ressources alimentaires ainsi qu'à la compétition intra ou interspécifique. Plus précisément, le renard arctique sélectionne les tanières situées dans les habitats où sa proie principale (lemming) abonde ou celles localisées à proximité d'une importante source de proies alternatives (colonie d'oie). Cependant, la présence de plusieurs tanières à proximité semble diminuer l'attrait d'une tanière donnée, possiblement à cause de la compétition potentielle que ces tanières voisines génèrent. Ainsi, nous suggérons que malgré la grande abondance de tanières existantes, le nombre de tanières de haute qualité disponibles pour la reproduction demeure limité. Considérant la présence grandissante du renard roux dans le haut arctique canadien, il est donc possible qu'une importante compétition s'installe entre ces deux espèces pour l'accès aux tanières de qualité. D'après nos observations, le renard arctique demeure pour l'instant le principal prédateur terrestre à l'île Bylot. Un programme de suivi de la communauté de renards de l'île Bylot est cependant essentiel afin de surveiller l'évolution de ce fragile écosystème. Nous proposons un protocole de terrain adapté pour un tel suivi. Ce protocole constituera pour Parcs Canada un élément important dans le suivi de l'intégrité écologique du Parc National du Canada de Sirmilik.

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

UTILISATION DE TANIÈRES CHEZ LES CARNIVORES

L'utilisation de refuges est un phénomène courant chez de nombreuses espèces animales. Plusieurs carnivores tels que le loup, le renard, le lynx ou la martre utilisent des cavités, naturelles ou excavées, comme site de mise bas, de cache alimentaire ou simplement de repos. Divers paramètres semblent affecter le choix d'un site de tanière, notamment la distance à un point d'eau chez le lynx roux (*Lynx rufus*) (Kolowski et Woolf 2002), l'inclinaison et l'orientation du terrain pour le lynx du Canada (Slough 1999) ou le type de sol chez l'ours grizzly (*Ursus arctos*) (McLoughlin et al. 2002). Le choix d'un site de tanière, plus particulièrement pour la reproduction, semble rarement aléatoire et est souvent basé sur deux principaux facteurs : la facilité d'échapper à la prédation et l'abondance locale de ressources alimentaires. Par exemple, la majorité des tanières de lynx du Canada (*Lynx canadensis*) ou de martre d'Amérique (*Martes americana*) sont situées dans des lieux de haute densité de débris ligneux grossiers, procurant une couverture horizontale et verticale et protégeant ainsi de la prédation, des intempéries et produisant un couvert de fuite additionnel (Ruggiero et al. 1998; Slough 1999). Pour le renard véloce (*Vulpes velox*) ainsi que le renard-chaton à longues oreilles (*Vulpes macrotis*), la présence de haute végétation abritant les insectes dont ils se nourrissent semble être un facteur important lors du choix d'un site de tanière (Pruss 1999; Arjo et al. 2003). Les caractéristiques physiques de la tanière en soi affectent également le choix d'un animal cherchant une tanière pour se reproduire. Le nombre de trous ainsi que leur grosseur sont des caractéristiques importantes chez certaines espèces. Par exemple, les jeunes renards à oreilles de chauve-souris (*Otocyon*

megalotis) vivant dans l'est et le sud de l'Afrique se réfugient fréquemment dans les trous de petits diamètres afin d'échapper à la prédation par de plus gros carnivores (Arjo et al. 2003). L'orientation des trous, la surface totale de la tanière ainsi que la végétation sur et autour de la tanière sont toutes des caractéristiques pouvant également jouer un rôle dans le choix d'une tanière de reproduction (Dalerum et al. 2002). L'identification des éléments influençant le choix d'un site de reproduction peut nous permettre d'identifier les contraintes auxquelles sont exposés les individus d'une espèce donnée lors de cette période critique de leur cycle de vie.

Sélection d'un site de tanière chez le renard arctique

Plusieurs études ont été effectuées sur les tanières de renards arctiques, principalement sur leur morphologie et leur distribution spatiale. Les propriétés des sites de tanières varient considérablement d'une région à l'autre. Différentes caractéristiques ont été relevées comme jouant un rôle potentiel dans l'établissement d'une tanière (tableau-1). Macpherson (1969) nota que les tanières étaient habituellement plus présentes dans les sites sablonneux mais stables, facilement drainés, avec beaucoup de végétation et une pente douce. De plus, les sites surplombant de larges vallées, ou le lit d'une rivière, semblaient préférés dans l'arctique canadien (Macpherson 1969). Certaines études ont indiqué que la température du sol et la profondeur du sol meuble au-dessus du pergélisol seraient des facteurs affectant le choix d'un site de tanière chez le renard arctique (Chesemore 1969; Smits et al. 1988). D'après Prestrud (1992b), les sites avec une épaisseur et couverture de neige plus faible seraient également préférés par les renards. Les études de Chesemore (1969), Smith et al. (1988), Prestrud (1992b) et Dalerum et al. (2002) ont démontré que les pentes orientées vers le sud étaient habituellement plus utilisées, possiblement à cause du microclimat plus chaud qu'on y retrouve et qui mène à une fonte des neiges plus hâtive ainsi qu'à un dégel du sol plus rapide. Au Groenland, cependant, Nielsen et al.

(1994) soutiennent que ce serait plutôt l'orientation des vents dominants qui déterminerait l'orientation des trous des tanières, les entrées étant placées de façon à empêcher au vent de s'engouffrer dans les tanières. Eide et al. (2001) ont démontré que les terrains ayant une structure modérément irrégulière et accidentée semblent être préférés par le renard arctique au Svalbard. D'après les auteurs, ce type de terrain offrirait une plus grande quantité de sites potentiels pour une tanière, puisqu'on y trouverait plus de sites exposés au soleil, ayant une plus haute température et étant plus rapidement libérés de la neige au printemps. Finalement, Tannerfeldt et al. (2002) ont démontré que la présence d'une tanière utilisée par un renard roux à proximité diminuerait les chances d'utilisation d'une tanière par le renard arctique.

Tableau 1: Résumé des différents paramètres affectant la localisation des tanières de renard arctique d'après la littérature. «Oui » indique que le paramètre affecte la localisation des tanières. Les cases laissées blanches indiquent que ce paramètre n'avait pas été étudié.

Lieu	Nombre de tanières	Topographie	Type de sol	Inclinaison du terrain	Orientation de la pente	Température du sol	Profondeur du pergélisol	Végétation environnante	Couvert de neige	Proximité d'un point d'eau	Référence
Alaska	50	oui	variable		oui	oui	oui			variable	Chesemore, 1969
Nunavut	203		oui	oui				oui			Macpherson, 1969
Alaska	42				non					variable	Garrott et al. 1983
Yukon	42	oui	oui		oui	oui	oui				Smits et al. 1988
Svalbard	56			oui	oui				oui		Prestrud, 1992
Groenland	17		oui	variable	oui			oui			Nielsen et al., 1994
Alaska	83	oui									Anthony, 1996
Svalbard	34	oui									Eide et al., 2001
Suède	77			oui	oui						Dalerum et al., 2002

Jusqu'à maintenant, aucune étude n'a exploré les relations possibles entre les sites de tanière et la distribution des ressources alimentaires. Le renard arctique est généralement reconnu comme étant un prédateur opportuniste, se nourrissant principalement de rongeurs, de carcasses de phoques ou de grands ongulés, de poissons et invertébrés marins, et exploitant également les

colonies d'oiseaux marins et d'oies lorsqu'elles sont présentes. Dans la grande majorité de son aire de répartition, sa diète est cependant largement dominée par les lemmings (Dalerum et Angerbjörn 2000; Elmhagen et al. 2000; Frafjord 2000). Les importantes variations de populations souvent cycliques caractéristiques de ces micro-mammifères influencent largement la dynamique des populations de renards arctiques (Hersteinsson et al. 1989; Angerbjörn et al. 1995; Tannerfeldt et Angerbjörn 1998). Lors d'années de forte abondance de lemmings, la proportion de renards reproducteurs augmente considérablement, ainsi que la taille des portées pouvant atteindre jusqu'à 18 renardeaux, la plus importante chez les carnivores (Tannerfeldt et Angerbjörn 1998). À l'opposé, lors des creux de populations de lemmings, l'effort de reproduction ainsi que la taille des portées diminuent de façon significative tandis que le taux de prédation sur les proies alternatives augmente (Angerbjörn et al. 1995; Tannerfeldt et Angerbjörn 1998; Bêty et al. 2001). Selon Roth (2003), les variations d'abondance des ressources marines auraient également une influence sur la dynamique des populations côtières de renards arctiques, principalement lors de creux de population de lemmings. Finalement, Eide et al. (2004) ont également démontré l'influence des variations spatiales et temporelles des proies sur la taille et le degré de chevauchement du domaine vital du renard arctique. Considérant l'influence marquée des ressources alimentaires sur la reproduction du renard arctique, il est probable que la distribution des tanières soit également liée à la distribution des ressources alimentaires. Aucune étude ne s'est penchée jusqu'à maintenant sur cette question.

L'objectif de cette étude était donc d'identifier tout d'abord les facteurs environnementaux (topographie, microclimat et distribution des ressources alimentaires) influençant la sélection d'un site de tanière chez le renard arctique à l'île Bylot. Malgré le grand nombre de tanières existantes dans une région, seulement quelques-unes d'entre elles sont

généralement utilisées répétitivement pour la reproduction. Une comparaison de l'environnement des tanières utilisées à des fins de reproduction et de celles non-utilisées pour la reproduction nous permettra d'identifier les différences existant entre ces deux catégories de tanières. Ce deuxième objectif permettra de mieux cerner les contraintes possibles auxquelles est exposé le renard arctique lors de sa période de reproduction.

STATUT DE LA COMMUNAUTÉ DE RENARDS ARCTIQUES ET ROUX DE L'ÎLE BYLOT

Au cours des derniers siècles, l'aire de répartition du renard roux a drastiquement changé à cause d'introductions anthropiques ou d'expansions naturelles de l'espèce. Le renard roux est maintenant le carnivore ayant l'aire de répartition la plus grande (Voigt 1987), s'étendant à travers la majeure partie de l'Europe, l'Asie, l'Amérique du Nord, l'Australie (où il a été introduit au cours du 19^e siècle) et une partie de l'Afrique du Nord.

Bien qu'indigène en Amérique, au nord du 40-45^e parallèle, le renard roux était auparavant rare ou même absent dans le centre et l'est des États-Unis, ainsi que dans les forêts de feuillus où le renard gris (*Urocyon cinereoargenteus*) était très présent jusqu'à la fin du 17^e siècle (Churcher 1959; Larivière et Pasitschniak-Arts 1996). Lors de la colonisation de l'Amérique du Nord (1650-1750), plusieurs renards roux européens ont été introduits, principalement pour la chasse, dans de nouveaux territoires où le renard roux était encore absent. Il semble y avoir un désaccord dans la littérature au niveau de la parité des espèces de renard roux provenant de l'Europe et celle déjà présente en Amérique (Voigt 1987). Certains auteurs soutiennent que le renard roux indigène, *Vulpes fulva*, serait une espèce différente de son cousin européen, *Vulpes vulpes*, et il s'en suit donc une confusion au niveau de laquelle des populations a par la suite étendu son aire de répartition. Audubon et Bachman (1854, cités par Churcher, 1959)

mentionnent néanmoins que le renard roux était absent jusqu'en 1750 au sud de la Pennsylvanie et ont documenté par la suite une expansion de son aire de répartition jusqu'en Georgie en 1850. Godin (1977) soutient également que le renard roux s'était établi le long de la côte du sud-est des États-Unis en 1750 et y repoussait graduellement le renard gris.

Une expansion nordique de la distribution du renard roux a également été notée plus récemment. Au cours du 20^e siècle, le renard roux a été observé dans des régions du nord de l'Amérique où il n'avait encore jamais été signalé. D'après différentes informations provenant de communautés Inuit, le renard roux aurait été aperçu sur l'île de Baffin pour la première fois en 1918 puis aurait étendu graduellement son aire de répartition vers le nord jusqu'à atteindre les îles de Cornwallis et Ellesmere en 1962 (Macpherson 1964). La première mention de la présence du renard roux sur l'île Bylot remonte à 1977 dans un rapport publié par Kempf et al. (1978). Marsh (1938) signala également l'arrivée de quelques renards roux à Eskimo Point (Arviat) en 1932, puis à Chesterfield pendant l'hiver de 1933-1934, ce qui fut suivi par une hausse importante de la population dans les années suivantes. En Europe et en Russie, une même expansion de l'aire de répartition du renard roux vers de plus hautes latitudes et altitudes a également été observée (Chirkova 1968). D'après Lindström (1989), la population de renards roux aurait environ triplé en Fennoscandinavie entre 1930 et 1960.

Conséquences de l'expansion du renard roux pour le renard arctique

Tout organisme vivant nécessite un apport d'énergie en provenance de son habitat afin de combler ses demandes énergétiques basales et répondre à ses besoins présents. Lorsque deux espèces similaires partagent un même habitat, la restriction des ressources mène souvent à une compétition entre les organismes pour l'accès à celles-ci. Deux différents type de compétition

peuvent se produire dans ce cas : une compétition par exploitation (interactions indirectes entre les individus dont les ressources sont diminuées par le compétiteur) ou par interférence (interactions directes et physiques entre les individus pour l'accès aux ressources). Une autre réponse possible à un manque de ressource peut être une modification de la niche écologique fondamentale d'un des organismes, résultant en l'exclusion d'un des compétiteurs de son habitat d'origine et donc en une ségrégation des deux espèces dans le territoire.

Dû aux importantes expansions de l'aire de répartition du renard roux, il existe maintenant une zone importante de chevauchement dans la répartition géographique des renards roux et arctiques (figure 1). Une diminution importante de la répartition et de l'abondance du renard arctique a également été observée, dans toute son aire de répartition circumpolaire, suite aux invasions du renard roux (Marsh 1938; Chirkova 1968; Linnell et al. 1999). Différentes études ont été conduites sur les interactions entre les deux espèces. Grâce entre autres à sa plus grande taille et à son agressivité, le renard roux est dominant par rapport au renard arctique

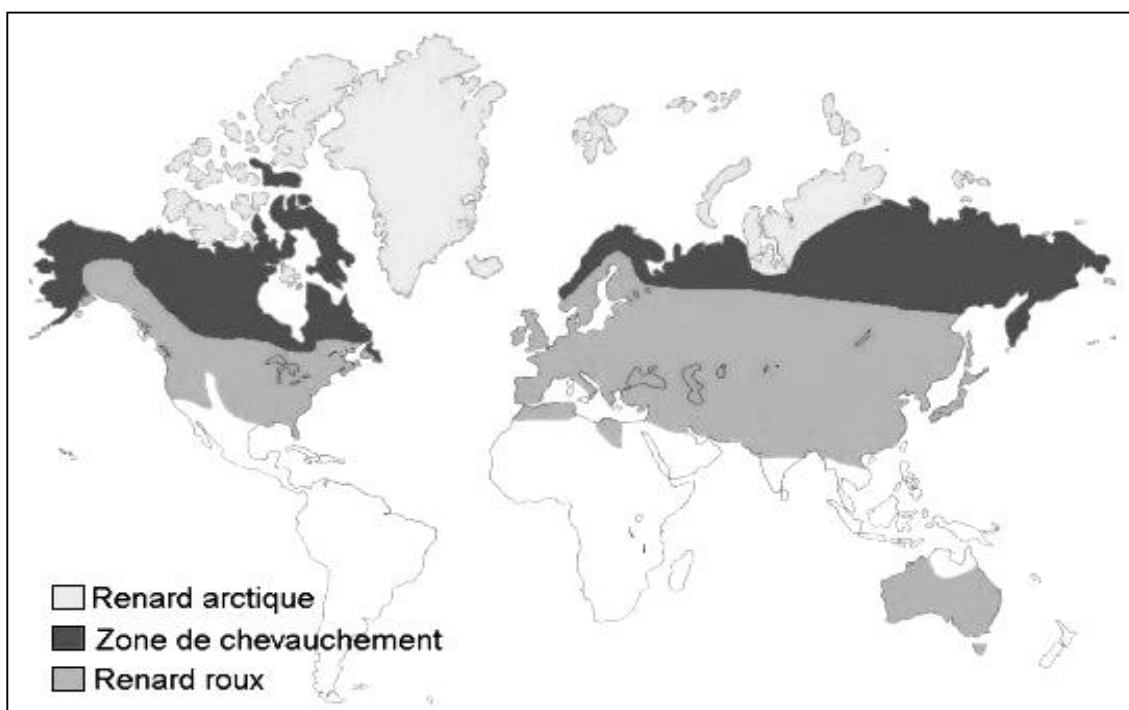


Figure 1: Aire de répartition actuelle des renards roux et arctiques (d'après Larivière et Pasitschniak-Arts, 1996; Audet *et al.*, 2002)

(Rudzinski et al. 1982) et peut même être un prédateur de ce dernier (Frafjord et al. 1989). Ainsi, dans les zones de chevauchement des deux espèces, le renard roux conserve habituellement l'accès aux habitats les plus productifs et le renard arctique est confiné aux territoires plus nordiques ou de plus hautes altitudes et ainsi plus pauvres (Linnell et al. 1999). Hersteinsson and Macdonald (1992) ont proposé l'hypothèse selon laquelle la limite sud de l'aire de répartition du renard arctique serait déterminée par la compétition avec le renard roux. Lors du choix d'une tanière, le renard arctique semble également éviter les sites à proximité de ceux utilisés par le renard roux (Marsh 1938; Tannerfeldt et al. 2002). Cette importante pression du renard roux autant au niveau de l'alimentation que du choix d'un site de tanière semble donc avoir un effet important sur la dynamique des populations de renards arctiques. En Fennoscandinavie, la présence du renard roux semble avoir été un facteur important dans la dégradation des populations de renards arctiques. Le renard arctique est maintenant menacé d'extinction dans cette région malgré sa protection depuis 1928 (Hersteinsson et al. 1989). Aucune étude n'a été conduite en Amérique du Nord sur l'effet de la compétition interspécifique et les dangers potentiels de l'expansion nordique de l'aire de répartition du renard roux sur les populations de renards arctiques.

Compte tenu de la grande similarité entre les niches écologiques des renards roux et arctiques (Elmhagen et al. 2002), ainsi que de la limitation des ressources disponibles dans l'arctique, il est fort possible qu'une importante compétition s'installe entre les deux espèces. L'accès à une tanière de reproduction s'avère une dimension importante de la niche écologique des deux espèces et pourrait donc représenter une source de compétition. Il est donc important de bien comprendre l'écologie actuelle du renard arctique et les facteurs influençant son choix d'un site de tanière afin de pouvoir détecter des changements si l'abondance du renard roux venait à

augmenter. Un suivi intensif de la communauté de renards à la limite de la distribution actuelle du renard roux est également primordial. Ce suivi nous permettra de mieux comprendre les impacts potentiels que pourrait impliquer une augmentation d'abondance du renard roux sur les populations canadiennes de renards arctiques. L'île Bylot est située à la limite nordique de l'aire de répartition actuelle du renard roux et fait partie du Parc National du Canada de Sirmilik depuis 2001. Elle représente donc l'endroit idéal pour instaurer un tel programme de suivi de la communauté de renards dans l'arctique canadien. Le dernier objectif de cette étude était donc d'établir un protocole de suivi des populations de renards de l'île Bylot qui constituera un élément important dans le suivi de l'intégrité écologique de l'écosystème du Parc National du Canada de Sirmilik.

En résumé, l'utilisation de tanières est une pratique courante chez plusieurs carnivores. Cependant, les exigences en terme d'habitat de tanière varient d'une espèce à l'autre en fonction de leurs besoins particuliers. Chez le renard arctique, plusieurs caractéristiques topographiques ont déjà été proposées comme jouant un rôle dans la sélection d'un site de tanière dans différentes régions de sa répartition circumpolaire. Les objectifs du présent projet sont donc d'identifier les caractéristiques d'habitat sélectionnées par le renard arctique lors de l'établissement d'une tanière à l'île Bylot et, en second lieu, de déterminer les variables d'importance pour cette espèce lors de la sélection d'une tanière particulière pour s'y reproduire, parmi l'ensemble de toutes celles disponibles. Troisièmement, considérant les conséquences probables de l'empiètement progressif du renard roux sur l'aire de répartition du renard arctique, le dernier objectif de l'étude est d'établir un programme de suivi à long terme de la communauté de renards de l'île Bylot.

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CHAPITRE 2

DEN ECOLOGY OF AN ARCTIC MAMMAL: SELECTION OF DENNING SITES AND REPRODUCTIVE DENS BY ARCTIC FOXES ON BYLOT ISLAND, NUNAVUT, CANADA

Manuscrit en préparation pour une publication.

Guillaume Szor¹, Dominique Berteaux¹ and Gilles Gauthier²

¹ Chaire de recherche du Canada en conservation des écosystèmes nordiques, Département de biologie et Centre d'études nordiques, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Qc, Canada, G5L 3A1

² Département de biologie et Centre d'études nordiques, Université Laval, Québec, Qc, Canada, G1K 7P4

G. SZOR, D. BERTEAUX AND G. GAUTHIER. Den ecology of an arctic mammal: selection of denning sites and reproductive dens by arctic foxes on Bylot Island, Nunavut, Canada.

The utilization of refuges is a common strategy for numerous animal species in order to maximize their survival and that of their offspring. The majority of carnivores use natural or excavated cavities as rest sites or for parturition and cub rearing. Den site choice, particularly for reproductive purpose, is rarely random but often based on two main factors: the ease to escape from predators and the local abundance of food resources. Due to the small number of predators and the low predictability of cyclic prey species present in arctic ecosystems, characteristics used by arctic carnivores when selecting a denning area may differ from those used by southern species. We examined the environment and characteristics of 83 arctic fox (*Alopex lagopus*) dens on the south plain of Bylot Island, Nunavut, Canada. We compared topography, microclimate and food resource distribution between denning sites and random locations in a 425 km² study area (landscape scale) and with other potential den sites in a 100 m radius around dens (local scale) to determine characteristics used by arctic foxes when selecting a denning area. Den sites were preferably located in mounds or slopes and were closer to streams than expected under a random scenario. Foxes preferred to excavate dens at sites with low snow cover at spring, high ground temperature and depth to permafrost, and steep and southerly exposed slopes with sandy substrate. Of the 83 dens examined in this study, only 27 were used at least once to rear a litter between 2003 and 2005 inclusively. Applying resource selection function analysis (RSF), we found that an attractive force (distribution of food resources) and a repulsive one (presence of other dens in the vicinity) affected selection of dens for reproduction. Despite the high density of dens in our study area (1.84 / 10 km²), we suggest that high quality dens available for reproduction may be limited.

G. SZOR, D. BERTEAUX ET G. GAUTHIER. Écologie des tanières d'un mammifère arctique: sélection des sites de tanière et des tanières de reproduction chez le renard arctique à l'île Bylot, Nunavut, Canada.

L'utilisation de refuges est une stratégie courante chez plusieurs espèces animales afin de maximiser leur survie ainsi que celle de leur progéniture. La plupart des carnivores utilisent des cavités, naturelles ou excavées, comme site de repos ou comme lieu de mise-bas et d'élevage des jeunes. Le choix d'un site de tanière, plus particulièrement pour la reproduction, semble rarement aléatoire et est souvent basé sur deux principaux facteurs : la facilité d'échapper à la prédation et l'abondance locale de ressources alimentaires. Considérant le nombre peu élevé de prédateurs ainsi que la faible prédictibilité des proies cycliques présentes dans les écosystèmes arctiques, il est possible que les caractéristiques utilisées par un carnivore arctique, lors de la sélection d'un site de tanière, diffèrent de celles utilisées par les espèces du sud. Nous avons examiné l'environnement et les caractéristiques de 83 tanières de renards arctiques (*Alopex lagopus*) sur la plaine du sud de l'île de Bylot, Nunavut, Canada. Nous avons comparé la topographie, le microclimat et la distribution des ressources alimentaires entre les sites de tanières et des sites aléatoires dans notre aire d'étude s'étalant sur 425 km² (échelle du paysage). De plus, les caractéristiques de chaque tanière ont également été comparées à celles d'autres sites potentiels, dans un rayon de 100 m autour de la tanière (échelle locale). Les tanières étaient préférentiellement excavées dans des buttes ou pentes naturelles et étaient généralement plus près d'un ruisseau qu'attendu d'une distribution aléatoire. Les renards préféraient creuser leur tanière aux sites ayant une faible couverture de neige au printemps, une température du sol et une profondeur au pergélisol plus élevée, situés sur des pentes abruptes et exposées au sud et ayant un substrat sablonneux. Des 83 tanières examinées dans cette étude, seulement 27 ont été utilisées au

moins une fois pour élever une portée, entre 2003 et 2005 inclusivement. À partir de fonctions de sélection des ressources (RSF), nous avons identifié une force positive (distribution des ressources alimentaires) et une négative (présence d'autres tanières à proximité) influençant la sélection d'une tanière de reproduction chez le renard arctique. Malgré la forte densité de tanières dans notre aire d'étude (1,84 / 10 km²), nous suggérons que les tanières de haute qualité disponibles pour la reproduction pourraient demeurer limitées.

INTRODUCTION

Understanding habitat selection processes and underlying causes is a fundamental goal in animal ecology. Various factors can influence habitat use by individuals, but the general assumption is that individuals will select habitats where their fitness will be maximized in accordance to the activity they need to perform. For many carnivorous mammals, access to a den is essential for successful breeding and cub rearing (Moehlmann 1989). The location of these dens is rarely random but often based on factors such as the ease of escape from predators (Ruggiero et al. 1998; Slough 1999) or the proximity of available food resources (Pruss 1999; Arjo et al. 2003). In the arctic tundra, arctic foxes (*Alopex lagopus*) excavate dens where they give birth to cubs and rear them until the mid-summer weaning period (Macpherson 1969). Access to a den is believed to be essential for successful reproduction, but they can also be used as shelters during winter or summer (Prestrud 1992a). Physical characteristics of arctic fox dens have been described throughout most of the species' range (Chesemore 1969; Macpherson 1969; Garrott et al. 1983; Smits et al. 1988; Prestrud 1992b; Nielsen et al. 1994), but few studies have considered the influence of environmental characteristics on their spatial distribution (Eide et al. 2001). Habitat components such as distance to water sources, vegetation height or distance to a road have been shown to influence the location of den sites in other carnivores (Ruggiero et al. 1998; Pruss 1999; Henner et al. 2004). Identifying factors influencing habitat selection can provide important clues on the ecology, physiology as well as on constraints to which a given species is exposed.

Our objective was to determine environmental characteristics influencing den site selection by an arctic mammal, the arctic fox. Eide et al. (2001) have demonstrated the influence of landscape heterogeneity on the selection of denning areas by arctic foxes in Svalbard. Other

topographical and microclimatic characteristics such as altitude, slope inclination and orientation, snow cover, or presence of streams and other water bodies, have been suggested to influence the location of arctic fox dens (Chesemore 1969; Macpherson 1969; Garrott et al. 1983; Smits et al. 1988; Prestrud 1992b; Nielsen et al. 1994). However, to our knowledge, the actual selection for these variables have never been studied through a utilisation/availability analysis. Considering the low productivity of the arctic tundra, food resource distribution may also be an important driving force for the selection of an adequate denning area. Due to the difficulties of measuring the distribution and abundance of food in space and time, no study has considered the influence of food resources on the location of arctic fox dens. Eide et al. (2004) did, however, show that the size of arctic foxes' home range vary according to the distribution and predictability of food resources. In this study, we investigated the importance of topography, microclimate and food resource distribution on the selection of denning sites by arctic foxes at two spatial scales. At the landscape scale, we evaluated the influence of topography, water bodies, surrounding habitat and the distribution of lemmings and nesting geese, the two main prey items of arctic foxes. At a micro-scale, we assessed the influence of snow cover, substrate type, slope aspect and inclination, and soil depth and temperature.

Despite a relatively high abundance of dens excavated by arctic foxes throughout the tundra, only a small proportion of those are repeatedly used for reproduction (Prestrud 1992a; Anthony 1996). The criteria used to select dens for reproduction are unclear. Assuming that an individual selects a den so as to maximize its fitness, reproductive dens should differ from non-breeding dens in some characteristics of importance to reproducing arctic foxes. Identifying these variables should allow for a better understanding of the constraints to which arctic foxes are exposed during reproduction. The second objective of this study was therefore to identify

environmental features used by arctic foxes when choosing a reproductive den. Again, we evaluated the relative importance of topography, microclimate and the distribution of food resources.

MATERIALS AND METHODS

Study area

We worked on the south plain of Bylot Island (73°N, 80°W), Nunavut, Canada (Fig. 1). The area is characterized by large upland mesic plateaus, covering ca. 90% of the landscape (Masse et al. 2001), intersected by several valleys with lowland moist habitats. This is the most important breeding site of the Greater Snow Goose (*Chen caerulescens atlantica*) with more than 55 000 breeding individuals (Reed et al. 2002). Many other migrating bird species nest in the area but their density is relatively low compared to snow geese (Lepage et al. 1998). Two species of lemmings occur in the area: the brown lemming (*Lemmus sibericus*), which prefers wetlands and feeds largely on graminoids (Gauthier et al. 1996; Negus and Berger 1998), and the collared lemming (*Dicrostonyx groenlandicus*), which prefers drier habitats and feeds primarily on *Dryas* and other forbs (Rodgers and Lewis 1986). The arctic fox is the main terrestrial predator of the system. It preys mainly on lemmings but also feeds on snow goose eggs and chicks, especially when rodent populations drop (Bety et al. 2001).

More than 40 dens had been found opportunistically on the south plain of Bylot island between 1993 and 2002 and were already known at the start of the study. In the summer of 2003 we performed an extensive search for dens by foot and snowmobile to complete the survey throughout the study area. We covered an area of approximately 60 km of coastline that extended between 4 and 15 km inland, depending on the relief. The surveyed area totalled approximately

425 km² (Fig. 1). It was delimited to the west by the sea, and to the north and east by polar semi-deserts where preliminary exploration showed that dens were either rare or absent. Logistic constraints prevented us from surveying the area to the south. To minimize the risks of including arctic hare burrows in our analysis, only structures with more than one entrance were considered as arctic fox dens. Field work performed in subsequent years indicated that virtually all dens (n = 83) in the study area had been found by 2003.

Landscape characteristics of denning sites

Each den was positioned using a Global Positioning System (GPS) receiver (± 5 m) and its surrounding environment was first described at a coarse landscape level. Topographic heterogeneity was evaluated using the terrain ruggedness index (TRI) proposed by Nellemann and Fry (1995). The TRI was derived from a 1:50 000 topographic map (with 20 m contour intervals) at 2 different scales (1 x 1 km and 2 x 2 km). The whole study area was divided into quadrats (of either 1 x 1 km, n = 448 or 2 x 2 km, n = 131), within which four transects of a fixed length (1 or 2 km) were positioned in a rosette, centered in the quadrat, at 45° intervals. The TRI was calculated using the following equation:

$$\text{Terrain ruggedness index (TRI)} = (\text{TNC} \times \text{TNF}) / (\text{TNC} + \text{TNF})$$

where TNC = total number of contour lines intercepted by the transect and TNF = total number of changes in aspect (ups and downs) along the transect (Nellemann and Fry, 1995). For each quadrat, the transect with the highest index value was retained. Each den was attributed the TRI of the quadrat in which it was located. Aspect and slope inclination were measured with a GPS

and clinometer, respectively. The habitat surrounding the den (100 m radius) was visually classified as xeric, mesic, or moist according to the dominant habitat class. Distance to closest coastline, lake and stream were measured on a map using ArcGIS (ESRI® ArcMap™9.0)

Two variables were used to estimate food resource distribution at the landscape scale. The first one was the distance to the main snow goose breeding colony of Bylot island. Since 1991, several hundred adult females are marked with plastic neck-collars annually during brood-rearing (Gauthier et al. 2001). Each year, systematic searches of collared females on nests are conducted throughout the colony and the position of each nest is recorded using a GPS. Assuming that collared geese are distributed randomly in the colony, we used the 95% kernel of the position of their nests from 2000 to 2005, to map the average extent of the colony. We then measured the distance separating dens from the closest edge of the colony with ArcGIS and used it as an index of goose availability for foxes.

Second, an index of lemming habitat quality (ILHQ) was derived from the vegetation communities and topographical features, in order to reflect lemming availability to foxes. The study area was classified into ten habitats: graminoid wet meadow, moist meadow, moist shrub tundra, mesic tundra, graminoid mesic tundra, shrub-heath tundra (dominance of *Cassiope*), shrub-heath tundra (dominance of *Dryas*), stream edge, moist polygons and mesic polygons (table 1; see Duclos et al. (2006) for detailed habitat description). Lemming's relative use of each habitat was estimated through counts of lemming burrows and faeces during summer 2004. Since both faeces and burrows were observed to persist for multiple years, the derived index represents a multi-annual average use by lemmings of each habitat category. We sampled ten sites per

habitat. Sampling sites were chosen in the field by selecting patches of at least 3000 m² of uniform habitat, to avoid influence of other surrounding habitats. For each sampling site, we positioned two parallel transects (20 m apart) on which three 1.5 x 1.5 m quadrats were located 20 m apart. We estimated the number of lemming faeces within each quadrat. We also counted lemming burrows in six 40 m² quadrats (2 x 20 m) positioned in-between the quadrats used to estimate faeces. The total N per habitat for both faeces and burrows is thus 60 quadrats (10 sites x 2 transects x 3 quadrats). For each site, the mean number of scats and burrows were transformed to values constrained between 0 and 1. This was accomplished by dividing the mean number of faeces or burrows of site i by the highest value obtained across all sites. The value for faeces and burrows were then added up for each site to obtain a value between 0 and 2 representing lemming utilization of the site. An index of lemming habitat use (ILHU) was then created for each habitat category by calculating the mean value for all sampled sites of a given habitat. Using a digital vegetation map and aerial photographs of Bylot Island, we then measured the proportion occupied by each of the ten habitats within a 0.5, 1 and 2 km radius around each den using ArcGIS. An index of lemming habitat quality (ILHQ) was then assessed for each den, at these three scales, by summing the product of the proportion occupied by each habitat (P_i) by its index of lemming habitat use ($ILHQ = \sum(P_i * ILHU_i)$).

To determine whether arctic foxes *select* for particular environmental characteristics when establishing their den, we also measured each variable at random locations ($n = 92$) within the study area. We compared characteristics of den locations to those of random locations using two-sample t-tests or Mann-Whitney U tests, depending on the normality of the variable. G-tests were used to compare nominal variables.

Local characteristics of denning sites

Preliminary observations showed that most dens were excavated in natural ridges and/or in slopes of 10° or more (95% of dens satisfied at least one of these conditions). Therefore, we assumed that the presence of at least one of these features was essential for the establishment of a den. Sites with such characteristics (hereafter called “potential denning sites”) were abundant in the study area and did not appear limiting. To determine the importance of micro-climatic and micro-topographic features on the selection of a denning site, we compared den characteristics with those of nearby potential denning sites. In the field, we randomly selected two to four potential denning sites, depending of their availability, within a 100 m radius of each studied den using a table of random angles and distances. For each den and potential site, we measured the same variables as follows. We measured height of ridges, by averaging maximum height on each side, and/or the inclination and orientation of the slope using a clinometer and GPS, respectively. We estimated ground snow cover in a 10 m radius (<5%, 5-25%, 25-50%, 50-75%, >75%) at the beginning of June. We classified the substrate as sand, loam, gravel, rock or a combination of these. Finally, we measured ground temperature (5 cm below surface) and depth of loose soil (depth to permafrost or rocky substrate) at five random locations on the den and its periphery. We compared heights of ridges and ground temperatures using paired sampled t-tests. We applied Wilcoxon signed-rank tests to compare snow cover (using the median of each class of cover), slope aspect and inclination, as well as depth of loose soil because data were not distributed normally. Finally, we compared types of substrate between dens and potential den sites using G-tests.

Comparisons of reproductive and non-breeding dens

From 2003-2005, 83 dens were visited at least twice during the summer (mid-June and mid-July) to check for signs of fox presence. Dens where cubs were observed at least once during this period were classified and will be referred to as “reproductive dens” in the following sections, while those with no reproduction observed during the three years of the study were classified as “non-breeding dens”. Since arctic foxes have been observed to move their litter between dens during the rearing period, reproductive dens were further divided into “natal” (cubs observed at beginning of breeding season) or “rearing” (movement of litter directly observed or cubs only appeared late in the breeding season) dens. We compared environmental characteristics of each set of dens using ANOVAs or Kruskal-Wallis tests, depending on the normality of the data, followed by Dunn’s multiple comparison tests, to determine if any variable could explain the different utilisation made of these three categories of dens. Table 2 summarizes the complete set of variables measured at each den.

Second, we used resource selection function (RSF) analysis (Manly et al. 1993) to determine the relative importance of each variable in distinguishing between reproductive and non-breeding dens. Since the movement of a litter from its natal den to another rearing den may be prompted by our visits and the trapping conducted at dens, rearing dens were excluded from this analysis and only natal dens were considered as reproductive dens. We used logistic regression to estimate the resource selection probability functions (RSPF) which took the form:

$$W^*(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}$$

where $W^*(x)$ is the probability of a den being used for reproduction for a given combination of variables (x_i) and their coefficients (β_i). We only included in the models variables that were not strongly correlated to each other (Pearson correlation < 0.7) and for which measurement were repeated at most dens. SNOW was therefore eliminated for RSF analysis because of missing values for many dens while TRI_2KM, LEMM_1KM and NBRDEN_5KM were removed because of multicollinearity with other variables. Finally, only one variable of the following pairs was used in a given model due to strong correlation: ALTITUDE/INCLINATION and DISTDEN/EXPO_EW. We performed multiple logistic regressions (MLR), using forward and backward stepwise approaches, to do a preselection of the best variables allowing for discrimination of the two classes of dens. Different models were then built and evaluated using Akaike's information criterion (AIC) to select the best while most parsimonious RSF models. Due to our small sample size, we used the second-order AIC (AICc) (Burnham and Anderson 2002). McFadden's Rho-squared statistic was also calculated for each model to assess model performance. McFadden's Rho-squared is intended to mimic r-squared used in linear regression (Steinberg and Colla 2004) but tends to have lower values. According to Hensher and Johnson (1981), values between 0.20 and 0.40 should be considered very satisfactory. The discriminatory power of each model was also evaluated through receiver operating characteristic (ROC) curves analysis. According to Pearce and Ferrier (2000), the area under ROC curves represents an adequate estimation of the discrimination performance of a model. Estimated by the c-statistic, ROC values between 0.7 and 0.8 are considered acceptable while values between 0.8 and 0.9 are considered excellent discrimination (Hosmer and Lemeshow 2000). The area under the curve was evaluated using the Mann-Whitney W statistic approach proposed by Hanley and McNeil (1982).

RESULTS

Index of lemming habitat quality

The index of lemming habitat use (ILHU) varied according to habitat type (Kruskal-Wallis Test Statistic = 40.499, $p < 0.001$) but every habitat categories did not always differ significantly from each other. Of the ten habitat categories, stream edge was the most heavily used by lemmings while lemmings scats and burrows were almost totally absent in graminoid wet meadow (Fig. 2).

Landscape characteristics of den sites

We compared the environment surrounding 83 fox dens to that surrounding 92 random sites (Table 3). First, we confirmed the strong selection for mounds. Furthermore, dens were located on steeper slopes than random sites and were also located closer to streams than expected. Finally, neither slope orientation, terrain ruggedness, distance to lakes, surrounding habitat (moist, mesic or xeric), distance to coastline, distance to goose colony nor lemming habitat quality influenced the location of arctic fox dens.

Local characteristics of denning sites

Comparison of dens characteristics with those of potential denning sites revealed that snow cover on dens was lower than on other potential sites while ground temperature and depth of loose soil was significantly higher at dens (Table 4). Dens were also usually located on steeper slopes than other potential sites and had a more southerly orientation, but there were no significant differences in the height of mounds selected by arctic foxes. Finally, dens were preferentially excavated in sandy substrate while loam was avoided despite its relatively high availability in the ecosystem.

Comparisons of reproductive and non-breeding dens

We compared 83 dens (20 natal, 7 rearing and 56 non-breeding) which were monitored over three consecutive years (2003-2005). Natal dens were closer to the goose breeding colony than non-breeding dens and were farther away from another den than non-breeding or rearing dens (Table 5). The number of dens in a 1, 3 and 5 km radius was significantly lower around natal dens than non-breeding ones. Finally, rearing dens were closer to a stream than non-breeding dens and both natal and rearing dens were situated in better lemming habitats than non-breeding dens at all scales.

Lemming's habitat quality around reproductive (natal and rearing) dens (1 km radius) was correlated to the distance separating the den from the goose colony (one outlier excluded from analysis; Fig. 3). Reproductive dens closer to the goose colony were situated in low quality lemming habitats while those farther away from the colony were located in high quality habitats for lemmings. The opposite relationship is observed when considering the distribution of all existing dens pooled together (Fig. 3).

Seventy-six dens (20 natal and 56 non-breeding) were used to build the RSFs using logistic regressions. Nine variables were retained through the forward and backward stepwise approach: GEESE, NBDEN_3KM, LEMM_500M, LEMM_2KM, EXPO_NS, DISTCOAST, DISTDEN, DISTSTREAM and TRI_1KM. Table 6 summarizes the six best models obtained. All six models had a $\Delta AICc$ lower than 2.0, suggesting substantial evidence for each of them (Burnham and Anderson 2002). The most parsimonious model (model 1) allowing for

discrimination of the two sets of dens included three variables (distance to the goose breeding colony, number of dens in the vicinity, and lemming's habitat quality) and had the following equation:

$$W^*(x) = \frac{\exp(V)}{1 + \exp(V)}$$

where

$$V = -2.393 - 0.074(\text{GEESE}) - 0.375(\text{NBDEN_3KM}) + 24.2(\text{LEMM_500M})$$

According to this model, the probability of a den being used for reproduction increases with lemmings habitat quality around it, while it decreases as its distance to the colony and the number of dens in a three kilometres radius increase. These three variables were all retained in the top six models, which strongly suggests that they were the most important criteria explaining the selection of reproductive dens by arctic foxes. This model had a high discriminatory power as its likelihood of correctly classifying a den as reproductive, within a pair of reproductive and non-breeding dens, was 88.5%. Three additional variables were retained in the other five top models: distance to closest coastline (negative effect as distance increases), distance to closest den (positive effect as distance increases), and north/south component of slope exposition (negative effect as exposition becomes northward).

We used the most parsimonious model (model 1) to predict the probability of reproduction at each den of the study area (Fig. 4a) and compared it with the actual frequency of utilisation of each den by arctic foxes (Fig. 4b). According to the model, dens located inside the limits of the goose colony usually had a lower probability of use than those located in its periphery, which was consistent with field observations. Comparison of both figures shows that

only seven dens had a high predicted probability of utilization (> 50%) but were not actually used as natal dens between 2003 and 2005. Of those seven dens, four were actually rearing dens while only three dens were truly never used for reproductive purpose. While most natal dens had a high predicted probability of use, five out of the 20 natal dens were used more often than predicted by the model. Finally, when plotting the actual frequency of utilization of a den for reproduction against the probability predicted by our model (Fig. 5), we can see that highly used dens usually have a higher probability predicted by our model, confirming the high adequacy of our model in predicting arctic fox use.

DISCUSSION

Selection of denning sites

Few landscape variables explained the spatial distribution of fox dens on Bylot Island. The availability of favourable topographical structures, such as ridges and slopes, and the proximity of streams, were the only features selected by arctic foxes.

According to Macpherson (1969), the permafrost layer in the arctic tundra represents a physical barrier for arctic foxes trying to dig new dens in spring. Den sites may then be limited to areas where the active layer is sufficiently deep and where soil conditions allow burrowing. Ridges and mounds typically consist of warm mineral soil with coarse texture, are well drained, and have a deep layer of soil over the permafrost or bedrock (Swanson 1996). Terrains with steep slopes should also be well drained and thus reduce the formation of permafrost. Our analysis at the local scale further highlighted the high importance of slope aspect and inclination on the selection of a specific denning site by foxes. The prevalence of arctic fox dens on southerly rather than northerly exposed slopes has often been reported (Chesemore 1969; Garrott et al. 1983;

Smits et al. 1988; Dalerum et al. 2002), and is believed to be linked to the warmer microclimate associated with southerly exposed locations. The southerly orientation and steep slope of denning sites may be responsible for their lower snow cover, higher soil temperature and higher depth to permafrost compared to other nearby potential sites. Furthermore, considering the high permeability of sand (Gluyas 2005), selection of sites with sandy rather than loam substrate may also provide a better drainage of the site, allowing for a faster warming of the ground, reducing the formation of permafrost and thus allowing for an easier digging. The combination of these criteria may therefore result in a deep active layer allowing arctic foxes to excavate sufficiently large structure for an efficient protection from hazardous weather or even for potentially giving birth and rearing a litter.

The utilisation of streamside cutbanks for denning is a common phenomenon in arctic foxes (Chesemore 1969; Macpherson 1969; Smits et al. 1988). In our study area, 35 out of 83 dens (42%) were located directly along the banks of rivers, streams or temporary water channels. We suggest two hypotheses to explain this observation. First, the good drainage found on the slopes along water channels may provide a good ground stability, an easy digging, and a reduction of flooding risks. Second, stream sides was the most heavily used habitat by lemmings (Fig. 2). Choosing a site near a stream could thus ensure that a reliable source of food is present nearby. Having a patch of very good lemming habitat at proximity of the den may be sufficient to meet foxes' needs, which could explain why the lemming's habitat quality index (ILHQ) had no influence on den site selection. This second hypothesis could be tested by analysing space use and foxes movements around the den.

Neither lemming's habitat quality nor distance to the goose colony affected the distribution of dens. Considering the large energy expenditure related to reproduction, we expected a greater influence of these parameters. However, given that, over the last 12 years, only 42% of all existing dens have a record of reproduction (Gauthier et al., unpublished data), this means that dens used for this purpose only represent a portion of all existing dens. This appears to be a common feature of arctic fox denning behaviour since other studies also found a proportion of reproductive dens varying between 23% and 55% (Prestrud 1992a; Anthony 1996; Dalerum et al. 2002). This suggests that arctic foxes dig out a large number of dens but only use some of them for reproductive purpose. Hence, the criteria used by foxes to select sites for the excavation of a new den may differ from those used to select a reproductive den.

Selection of reproductive dens

Food resource distribution seems to be the major criterion influencing the selection of reproductive dens by arctic foxes. Food resources clearly affect cub survival, as was demonstrated by Tannerfeldt et al. (1994) through a supplementary feeding experiment. Although the importance of food resources on the dynamic of arctic fox populations is widely recognized (Angerbjorn et al. 1995; Kaikusalo and Angerbjorn 1995; Tannerfeldt and Angerbjorn 1998; Angerbjorn et al. 1999; Roth 2003), the influence of food resource distribution on the selection of reproductive dens has never been demonstrated.

The positive association between lemming's habitat quality around reproductive dens and distance to the goose colony suggests that arctic foxes trade off between these two food sources and must maximize the availability of at least one of them when selecting a reproductive den. As distance separating the den from the colony augments, it becomes increasingly important to be

located in a good lemming habitat to fulfill the alimentary requirements of a growing litter. The fact that this relationship is positive for reproductive dens, but becomes negative when considering all dens (Fig. 3), suggests that this result is not due to a biased distribution of high quality lemming habitats far away from the goose colony. It actually reinforces the idea that foxes breeding far away from the colony will select dens located in the best lemming habitats even though such sites are scarcer.

Although dens closer to the goose colony had a higher probability of being used for reproduction according to our model, curiously dens located inside the limits of the colony were rarely used by reproducing foxes. The intensive exploitation of this extremely aggregated resource by several foxes, as well as the high density of geese present, may increase disturbance, intraspecific competition for food, as well as risks of predation for cubs, thus reducing the potential fitness of foxes reproducing inside the colony. For a territorial species such as the arctic fox, it may become impossible to defend a territory and raise a litter in such an area. This territoriality would therefore explain the strong avoidance of areas with high density of dens (ie. the third parameter recurring in all top models), in order to reduce intraspecific competition as well as energy investment for defending the territory against potential neighbours.

Few dens had a high predicted probability of use ($> 50\%$) according to our model but did not have any record of reproduction. This suggests that our model accurately predicts the selection of reproductive dens by arctic foxes. Furthermore, the fact that the most heavily-used dens also had a high probably of utilization predicted by our model further reinforces the high adequacy of our model. However, considering that a few dens selected by reproducing foxes had a very low probability of use predicted by our model, this suggests that some variables of

importance may be missing in our model. For example, a secondary variable retained in other top models was the minimal distance to coastline. Marine resources have been shown to represent up to 70% of arctic fox diet in coastal areas (Angerbjorn et al. 1994). The proximity of a den to the coastline may thus provide additional food sources, such as seals, seabirds or other marine wildlife, and could thus compensate for the poor lemming habitat or the high distance of a den from the goose colony. Additional variables may be missing in our model to accurately explain den site use by reproducing foxes but the 88.5% discriminatory power of our model suggests that food resource distribution and territoriality are probably the most important parameters influencing den selection by reproductive arctic foxes.

CONCLUSION

We suggest that topography and micro-climate are the main factors influencing den site selection by arctic foxes. The presence of permafrost under a very thin layer of active soil may be the dominant factor limiting the excavation of new dens. Selection of sites with early snowmelt, southerly exposition, and good drainage, increases the chance of having a deep active layer over permafrost, and thus represent favourable conditions for the excavation of a den. However, the high abundance of non-breeding dens suggests that foxes dig out many dens wherever physical characteristics of the site allow it, but only those located in areas with sufficient food resources and far enough from other dens are used for reproductive purpose. Hence, despite the high abundance of dens in the arctic tundra, high quality dens suitable for reproductive purpose may still be limited. The growing occurrence of red foxes in the high arctic (Marsh 1938; Macpherson 1964; Chirkova 1968) may therefore represent a potential threat for arctic fox populations through competition for adequate reproductive dens. Monitoring of fox communities and studies

of both species preferences in term of reproductive dens are required to evaluate the potential impacts of red foxes' range expansion on arctic fox populations.

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TABLES AND FIGURES

Fig. 1 Map of study area on Bylot Island (73°0' N, 80°0' W), Nunavut, Canada, with location of arctic fox dens (black triangles).

Fig. 2 Index of lemming habitat use (ILHU) for the 10 habitat recognized on the south plain of Bylot Island, Nunavut, Canada. Means \pm standard errors are given. GWM = graminoid wet meadow, MP = moist polygons, GMT = graminoid mesic tundra, MT = mesic tundra, MST = moist shrub tundra, MM = moist meadow, SHTD = shrub-heath tundra (*Dryas*), SHTC = shrub-heath tundra (*Cassiope*), MEP = Mesic polygons, and SE = stream edges.

Fig. 3 a) Correlation between distance to the goose colony and lemming's habitat quality around reproductive dens (1 km radius). Natal dens are illustrated by black circles and rearing dens by white circles. One outlier is illustrated by the black square symbol. With outlier included $n = 27$, Pearson $r = 0.454$, $p = 0.017$; with outlier excluded $n = 26$, Pearson $r = 0.633$, $p = 0.001$. b) Correlation between distance to the goose colony and lemming's habitat quality around all dens (1 km radius). Natal dens are illustrated by black circles, rearing dens by white circles and non-breeding dens by black triangles; $n = 83$, Pearson $r = -0.419$, $p < 0.001$.

Fig. 4 Use of dens by arctic foxes on the south plain of Bylot Island, Nunavut, Canada. a) Probability of use of dens for reproduction according to the most parsimonious model selected (see results and Table 6) and b) observed frequency of use of dens by arctic foxes for reproduction between 2003 and 2005.

Fig. 5 Frequency of utilization by arctic foxes of each den as a natal den, between 2003 and 2005, compared with the probability predicted by the most parsimonious model (model 1). Means with standard errors are illustrated for each category of frequency.

Table 1: Environmental and floristic description of the 10 habitats recognized on the south plain of Bylot Island, Nunavut, Canada.

Habitat types	Description
<i>Based on vegetation</i>	
Graminoid Wet Meadow	Flat microtopography dominated by mosses and graminoids (<i>Dupontia fisheri</i> , <i>Eriophorum russeolum</i> , <i>Eriophorum scheuchzeri</i>).
Moist Meadow	Hummocky or flat microtopography dominated by graminoids (<i>Eriophorum triste</i> , <i>Carex</i> spp., <i>Arctagrostis latifolia</i>), dwarf-shrubs (<i>Salix arctica</i> , <i>Dryas Integrifolia</i>) and mosses.
Moist Shrub-Tundra	Hummocky microtopography dominated by dwarf-shrubs (<i>S. arctica</i> , <i>Salix reticulata</i> , <i>D. integrifolia</i>), mosses and lichen.
Mesic tundra	Hummocky microtopography dominated by mosses, graminoids (<i>A. latifolia</i> , <i>Luzula</i> spp) and dwarf-shrubs (<i>S. arctica</i> , <i>Cassiope tetragona</i>).
Grass Mesic Meadow	Flat microtopography dominated by mosses, graminoids (<i>Alopecurus alpinus</i> , <i>Luzula nivalis</i>) and dwarf-shrubs (<i>S. arctica</i>).
Shrub Heath- Tundra (<i>Dryas</i>)	Flat or hummocky microtopography dominated by dwarf-shrub (<i>D. integrifolia</i> , <i>Salix</i> spp) and lichen.
Shrub Heath- Tundra (<i>Cassiope</i>)	Hummocky or flat microtopography dominated by dwarf-shrub (<i>C. tetragona</i> , <i>Salix</i> spp), mosses and graminoids (<i>A. latifolia</i> , <i>Carex</i> spp., <i>Luzula</i> spp., <i>E. triste</i>).
<i>Based on topography</i>	
Moist Polygons	Polygons with concave or flat center usually filled with wet meadow or moist shrub tundra vegetation.
Mesic Polygons	Polygons with convex or flat center covered by mesic vegetation and separated by deep and narrow water canals.
Stream edge	Twenty meters on each side of streams.

Table 2: Description of all habitat variables measured at dens.

Variable	Description	Method
ALTITUDE	Elevation above sea level (m)	GPS
EXPO_EW	East-west component of slope exposition	Sin(orientation)
EXPO_NS	North-south component of slope exposition	Cos (orientation)
SLOPE	Degree of inclination of slope (°)	Clinometer
HABITAT	General habitat in 100m radius (humid, mesic or xeric)	Visual assessment in the field
SUBSTRATE	Substrate (sand, loam, gravel, rock or combination)	Visual assessment in the field
TEMP	Ground temperature at 5cm	Thermometer; averaged over 5 locations
DEPTH	Depth of loose soil (depth to permafrost or rocky substrate)	Measured with metal rod; averaged over 5 locations
GEESE	Minimal distance to edge of goose breeding colony (km)	Distance to 95% kernel of collared goose nests
DISTCOAST	Distance to closest coastline (km)	ArcGis
DISTDEN	Distance to closest den (km)	ArcGis
NBDEN_1KM	Number of dens present in a 1km radius	ArcGis
NBDEN_3KM	Number of dens present in a 3km radius	ArcGis
NBDEN_5KM	Number of dens present in a 5km radius	ArcGis
TRI_1KM	Terrain ruggedness index at 1x1 km scale	Method of Nelleman and Fry (1995)
TRI_2KM	Terrain ruggedness index at 2x2 km scale	Method of Nelleman and Fry (1995)
DISTSTREAM	Distance to closest stream (km)	ArcGis
DISTLAKE	Distance to closest lake (km)	ArcGis
LEMM_500M	Index of lemming's habitat quality in 0.5 km radius	Field sampling + ArcGis
LEMM_1KM	Index of lemming's habitat quality in 1 km radius	Field sampling + ArcGis
LEMM_2KM	Index of lemming's habitat quality in 2 km radius	Field sampling + ArcGis

Table 3: Comparison of environmental parameters between arctic fox dens (n = 83) and random sites (n = 92) on the south plain of Bylot Island, Nunavut, Canada. Means \pm standard errors are given. Sites are compared using Mann-Withney U test (U) unless mentioned otherwise.

Parameter	Den sites	Random sites	Statistic value	p
	Mean \pm SE	Mean \pm SE		
Sites located on mounds (%)	31	1	33.1 [†]	< 0.001
Slope inclination (°)	18.2 \pm 1.5	3.6 \pm 0.8	1112	< 0.001
N/S exposition (1.0=N/-1.0=S)	-0.208 \pm 0.097	-0.114 \pm 0.141	909	0.726
E/W exposition (1.0=E/-1.0=W)	-0.194 \pm 0.078	-0.455 \pm 0.089	673	0.070
Terrain ruggedness index (1km)	1.06 \pm 0.10	1.11 \pm 0.07	3626	0.452
Terrain ruggedness index (2km)	2.12 \pm 0.16	2.22 \pm 0.15	3434	0.603
Surrounding habitat (% of sites)				
Moist	12 %	16 %		
Mesic	84 %	81 %	0.185 [†]	0.911
Xeric	4 %	3 %		
Distance to closest stream (km)	0.191 \pm 0.022	0.221 \pm 0.019	4536	0.032
Distance to closest lake (km)	1.15 \pm 0.10	1.05 \pm 0.11	3341	0.154
Distance to coastline (km)	3.82 \pm 0.26	4.14 \pm 0.29	3988	0.611
Distance to goose colony (km)	14.7 \pm 1.2	11.9 \pm 1.13	3363	0.174
Lemming habitat quality (0.5 km)	0.170 \pm 0.005	0.180 \pm 0.004	4030	0.526
Lemming habitat quality (1 km)	0.181 \pm 0.005	0.191 \pm 0.003	4079	0.436
Lemming habitat quality (2 km)	0.183 \pm 0.004	0.186 \pm 0.003	3929	0.740

[†]: G-test statistic (G)

Table 4: Comparison of environmental parameters between arctic fox dens and potential denning sites in a 100 m radius around the den, on the south plain of Bylot Island, Nunavut, Canada. Means \pm standard errors are given. Numerical variables are compared using Wilcoxon signed-rank test (W) unless mentioned otherwise. Values with asterisk (*) differed significantly according to Bonferonni 95% interval.

Parameter	Den sites	Potential sites	Statistic value	df	p
	Mean \pm SE	Mean \pm SE			
Height of mound (m)	1.31 \pm 0.36	0.839 \pm 0.124	1.72 [†]	8	0.124
Ground temperature (°C)	8.60 \pm 0.33	7.42 \pm 0.31	5.10 [†]	77	< 0.001
Depth of loose soil (cm)	32.3 \pm 0.6	27.7 \pm 0.7	5.29	76	< 0.001
Slope inclination (°)	21.6 \pm 1.5	17.7 \pm 0.6	3.03	57	0.002
N/S exposition (1.0=N/-1.0=S)	-0.258 \pm 0.114	-0.055 \pm 0.083	-2.04	42	0.042
E/W exposition (1.0=E/-1.0=W)	-0.094 \pm 0.092	-0.239 \pm 0.065	1.38	42	0.167
Snow cover (%)	17.9 \pm 5.7	40.3 \pm 7.2	-2.62	17	0.009
Substrate (% of sites)					
Sand	39 % *	15 % *			
Loam	34 % *	66 % *			
Gravel	1 %	0 %			
Loam + sand	9 %	3%	32.6 [‡]	6	< 0.001
Loam + Gravel	9 %	9 %			
Sand + Gravel	6 %	6 %			
Loam + Rocks	1 %	1 %			

[†]: Paired t-test statistic (t)

[‡]: G-test statistic (G)

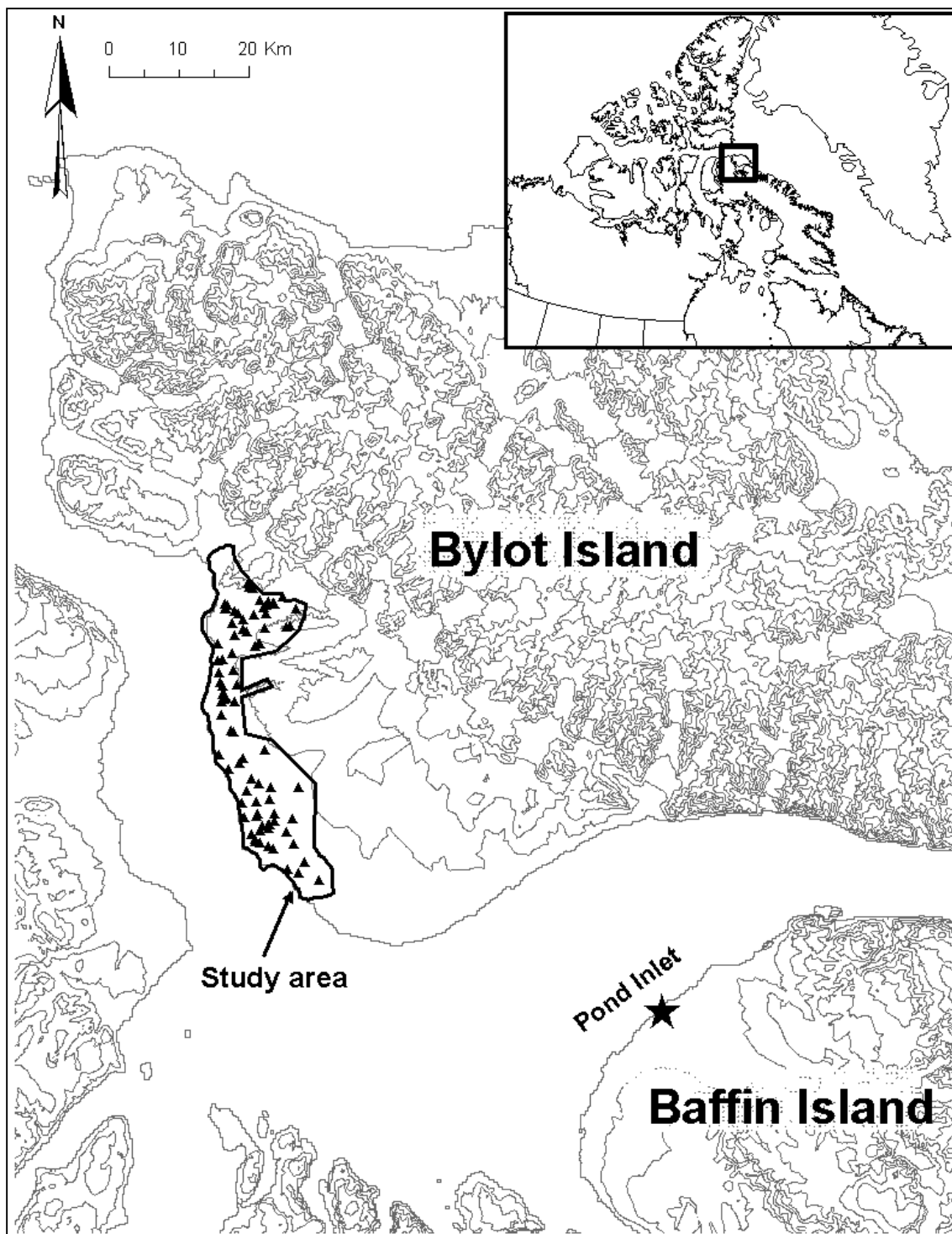
Table 5: Comparison of environmental parameters between natal (n = 20), rearing (n = 7) and non-breeding (n = 56) arctic fox dens on Bylot Island. Means \pm standard errors are given. Variables are compared using Kruskal-Wallis test. Values with the same letter on the same line do not differ significantly ($p > 0.05$, Dunn test).

Parameter	Natal dens	Rearing dens	Non-breeding dens	Test Statistic	p
	Mean \pm SE	Mean \pm SE	Mean \pm SE		
Distance to closest stream (km)	0.141 \pm 0.042 ^{ab}	0.060 \pm 0.030 ^a	0.225 \pm 0.029 ^b	8.05	0.018
Distance to goose colony (km)	7.33 \pm 1.78 ^a	13.6 \pm 3.5 ^{ab}	17.5 \pm 1.5 ^b	10.0	0.007
Lemming habitat quality (0.5km)	0.208 \pm 0.006 ^a	0.224 \pm 0.005 ^a	0.173 \pm 0.006 ^b	17.7	<0.001
Lemming habitat quality (1 km)	0.200 \pm 0.006 ^a	0.208 \pm 0.009 ^a	0.175 \pm 0.005 ^b	13.7	0.001
Lemming habitat quality (2 km)	0.192 \pm 0.007 ^a	0.203 \pm 0.011 ^a	0.175 \pm 0.004 ^b	14.4	0.001
Distance to closest den (km)	1.62 \pm 0.24 ^a	0.631 \pm 0.317 ^b	0.735 \pm 0.087 ^b	12.3	0.002
Number of dens in 1km radius	1.00 \pm 0.37 ^a	2.57 \pm 0.72 ^{ab}	2.55 \pm 0.35 ^b	7.00	0.003
Number of dens in 3km radius	4.80 \pm 0.74 ^a	6.14 \pm 1.12 ^{ab}	9.02 \pm 0.47 ^b	18.2	<0.001
Number of dens in 5km radius	11.8 \pm 1.3 ^a	13.1 \pm 2.4 ^{ab}	16.4 \pm 0.5 ^b	12.8	0.002

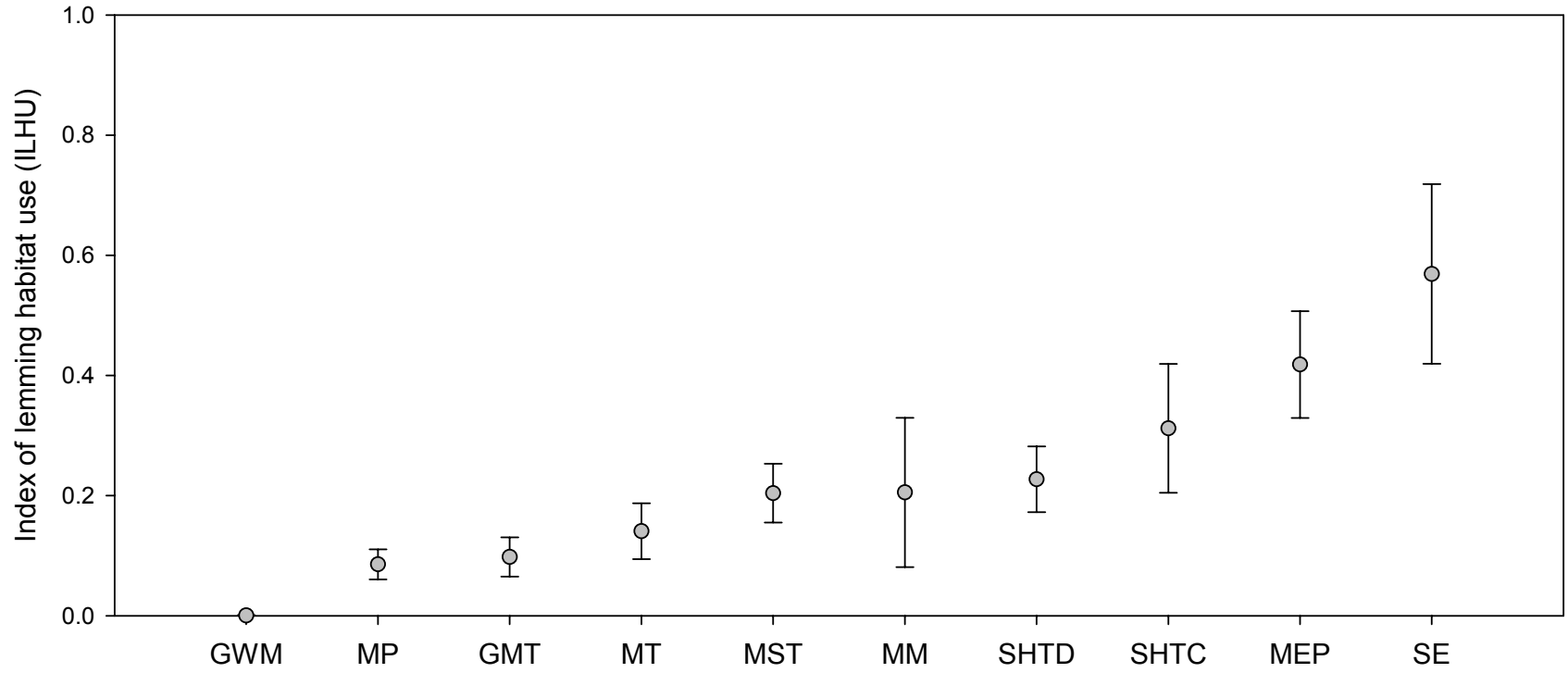
Table 6: Second order Akaike's Information Criterion (AIC_c), McFadden's rho squared (MF) and Receiver operating characteristics curve c-statistic (ROC) for the six top logistic models discriminating between reproductive (natal) and non-breeding arctic fox dens on Bylot Island, Nunavut, Canada.

	Models parameters ¹	AIC _c	Δ AIC _c	MF	ROC
1	GEESE, NBDEN_3KM, LEMM_500M	62.56	0.000	0.384	0.885
2	GEESE, NBDEN_3KM, LEMM_500M, DISTCOAST	62.99	0.124	0.405	0.902
3	GEESE, NBDEN_3KM, LEMM_500M, DISTDEN	63.03	0.468	0.405	0.895
4	GEESE, NBDEN_3KM, LEMM_500M, GEESE x LEMM_500M	63.28	0.722	0.402	0.894
5	GEESE, NBDEN_3KM, EXPO_NS, DISTCOAST, LEMM_2KM, DISTDEN	64.03	1.472	0.444	0.921
6	GEESE, NBDEN_3KM, LEMM_500M, EXPO_NS, DISTCOAST	64.43	1.876	0.411	0.905

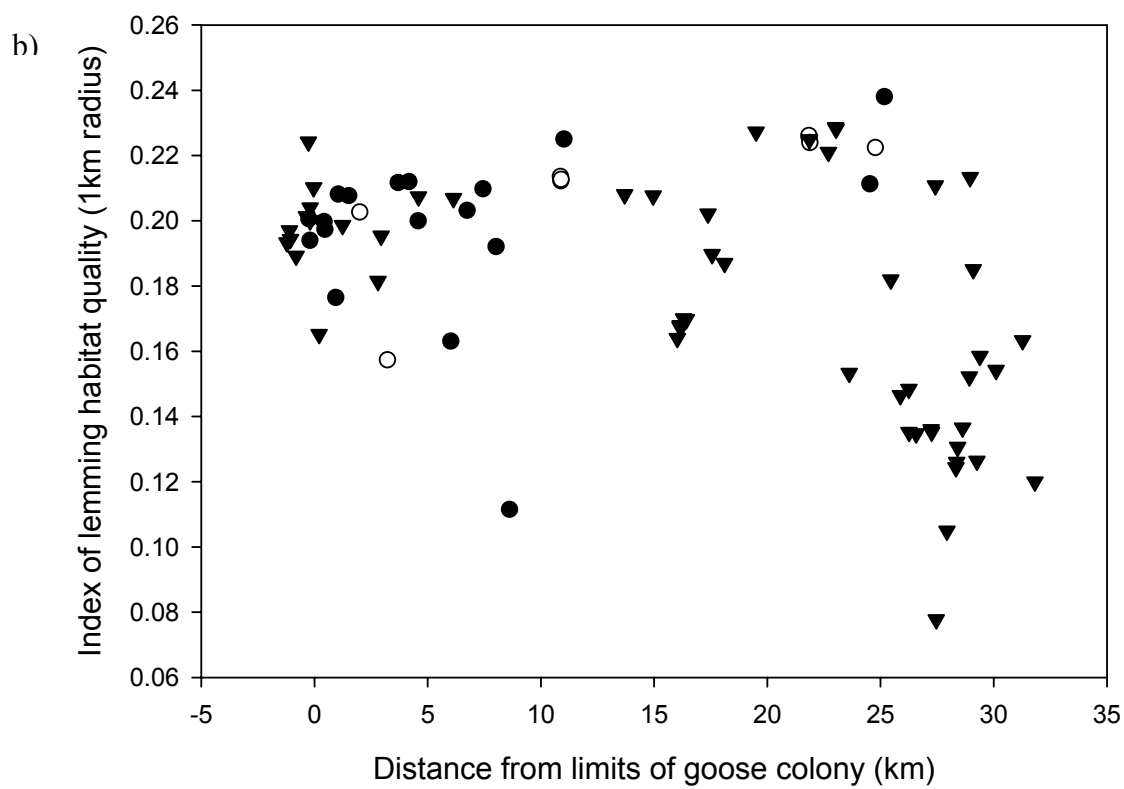
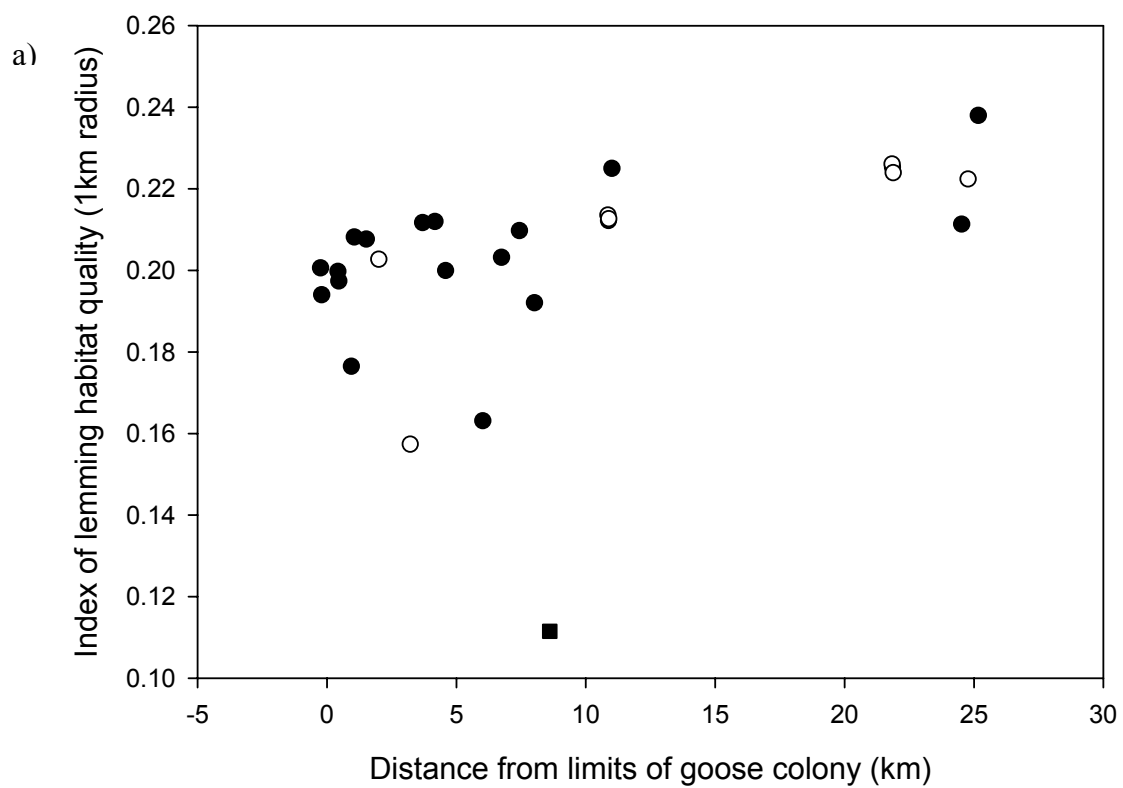
¹Parameter definitions are given in Table 2



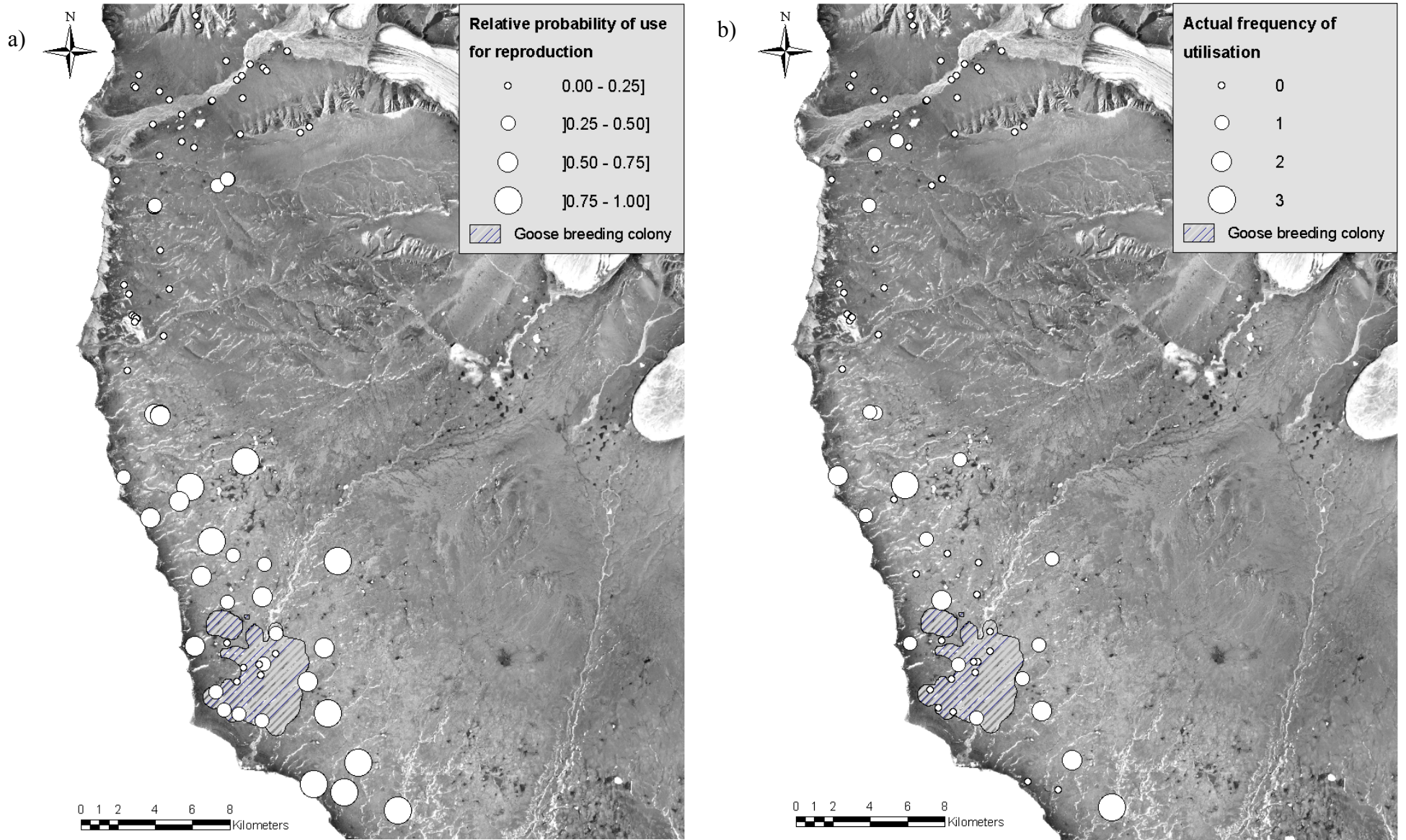
G. Szor, D. Berteaux and G. Gauthier. Fig. 1.



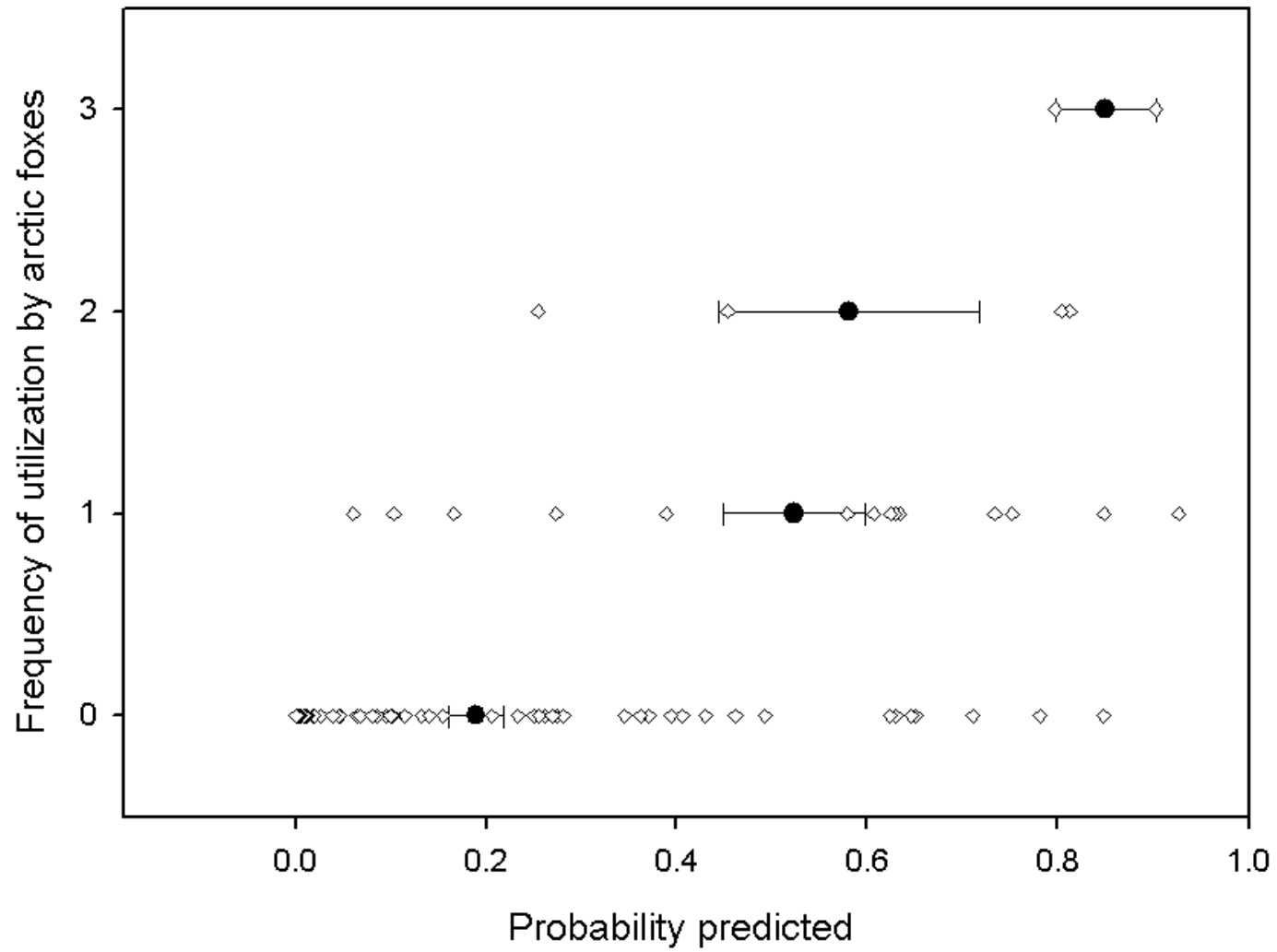
G. Szor, D. Berteaux and G. Gauthier. Fig. 2.



G. Szor, D. Berteaux and G. Gauthier. Fig. 3.



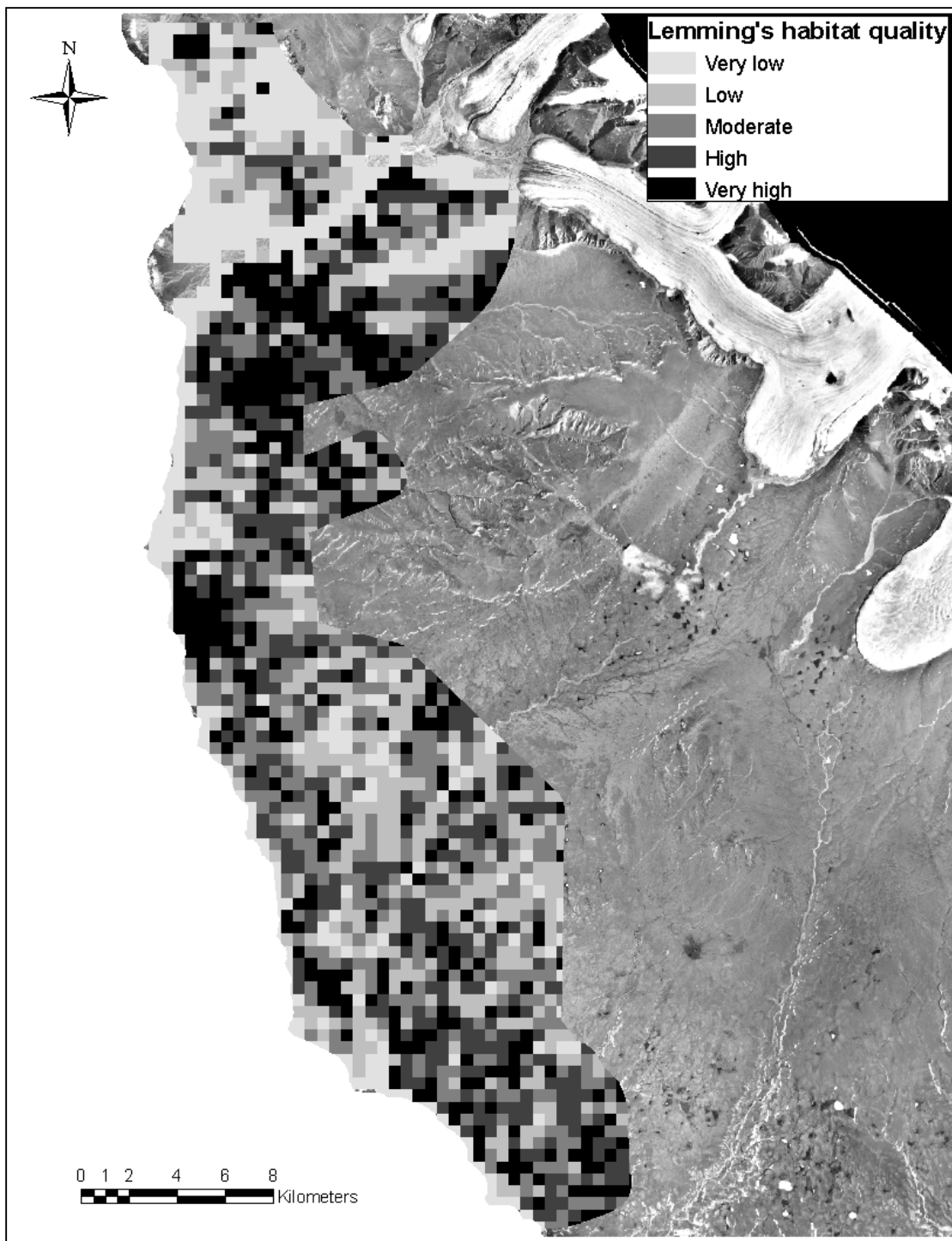
G. Szor, D. Berteaux and G. Gauthier. Fig. 4.



G. Szor, D. Berteaux and G. Gauthier. Fig. 5.

ELECTRONIC SUPPLEMENTARY MATERIAL

S1 Variations in lemming's habitat quality (ILHQ) throughout study area on the south plain of Bylot Island, Nunavut, Canada. Each category of ILHQ, from very low to very high, regroups 20% of the total area.



CHAPITRE 3

SUIVI DE LA COMMUNAUTÉ DE RENARDS DE L'ÎLE BYLOT

Les études écologiques sur l'île Bylot ont débuté en 1988 par une collaboration entre l'Université Laval et le Service canadien de la faune (région du Québec). Cette étude fut tout d'abord initiée en raison de l'importante colonie de nidification de la grande oie des neiges (*Chen caerulescens*) se trouvant sur l'île Bylot. Au cours des années, le programme de recherche s'est progressivement élargi afin d'y inclure les autres composantes de l'écosystème. Un thème central régissant la recherche sur l'île Bylot est maintenant l'étude des interactions trophiques (plantes, herbivores, prédateurs). Dans le contexte des changements climatiques des études sur la végétation, les lemmings, les renards et d'autres espèces d'oiseaux sont maintenant en cours en plus des travaux sur la grande oie des neiges qui continuent.

Les recherches sur l'île Bylot ont révélé la présence de deux espèces de renards s'y reproduisant : le renard arctique (*Alopex lagopus*) et le renard roux (*Vulpes vulpes*). La présence du renard arctique dans l'arctique canadien remonte à plusieurs dizaines de milliers d'années mais l'arrivée du renard roux à de si hautes latitudes est beaucoup plus récente. D'après les communautés Inuit, le renard roux aurait été observé pour la première fois sur l'île de Baffin au début du 20^e siècle et dans les environs de l'île Bylot vers 1950. Les premiers registres rapportant la présence du renard roux sur l'île Bylot remontent à 1977 (Kempf et al. 1978).

Lorsqu'ils coexistent, les renards arctiques et roux deviennent d'importants compétiteurs mais grâce à sa plus grande taille et à son agressivité, le renard roux est habituellement dominant. Suite à l'augmentation de l'abondance du renard roux en Norvège, une ségrégation des deux espèces a

été observée. Les renards arctiques utilisent à présent les tanières situées dans les habitats pauvres de hautes altitudes tandis que les renards roux occupent les tanières situées dans les habitats plus proches de la limite des arbres et donc plus productifs. En Suède, Tannefeldt et al. (2002) ont démontré que les renards arctiques évitent de s'installer dans une tanière située à moins de 8 km d'une tanière de renard roux, le contraire pouvant mener à une prédation de leur portée. Ainsi, l'augmentation de l'abondance du renard roux en Fenno-Scandinavie depuis 1930 est considérée comme un facteur important ayant mené au statut précaire du renard arctique dans cette région.

Depuis 2003, un programme de suivi des populations de renards arctiques et roux a été instauré sur la plaine sud de l'île Bylot. Ceci représente l'unique programme de suivi des deux espèces de renards dans l'arctique canadien. Considérant les impacts déjà évidents du réchauffement climatique sur l'arctique canadien et sur les espèces qu'on y retrouve, un tel programme de suivi est essentiel afin d'évaluer les changements que la faune arctique pourrait subir. La présente section contient le protocole de suivi de la communauté de renards de l'île Bylot préparé pour l'Agence Parcs Canada et le Comité de gestion conjointe des parcs (Joint Park Management Committee) du Parc national du Canada Sirmilik.

Inventory Methods for Bylot Island Fox Populations

Prepared by
Guillaume Szor and Dominique Berteaux

Canada Research Chair in Conservation of Northern Ecosystems and Centre
d'études nordiques
Université du Québec à Rimouski
300 allée des Ursulines, Rimouski (Québec), Canada, G5L 3A1

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Field work was conducted by Guillaume Szor, Ilya Klvana, Patrick Bergeron and Marie-Andrée Giroux under the supervision of Dr. Dominique Berteaux.

INTRODUCTION

The current ecological studies on Bylot Island started in 1988 as a joint collaboration between Université Laval and the Canadian Wildlife Service (Quebec region). The study was first initiated due to the large colony of Greater Snow Geese breeding on the island but over the years, the research program has broadened considerably. With the contribution of many different researchers now working on Bylot Island, we are moving towards a more holistic understanding of the ecosystem. A central theme of the project is now to study the trophic interactions (plants, herbivores, predators) in the context of global changes. In addition to the work that is still being conducted on the Greater snow geese, vegetation, lemmings, foxes, and other birds species are now part of the monitoring and research program.

The monitoring program on Bylot Island has confirmed the presence of two fox species breeding on the island: arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*). The presence of arctic foxes in the Canadian arctic may date from somewhere around late Rancholabrean (130,000 – 10,000 years ago) according to remains found in Alaska and the Yukon (Wright 1987; Youngman 1993). The arrival of the red fox in the high arctic is much more recent. According to historical records, red foxes arrived on southern Baffin Island in the early 1900s and spread to northern Baffin Island by the 1950s (Macpherson 1964). The first mention of a red fox on Bylot Island goes back to 1977, in a report by Kempf et al.(1978).

Several studies demonstrated that when they are sympatric, these two fox species are direct competitors and the larger red fox is dominant and may even kill arctic foxes (Chirkova 1968; Frafjord et al. 1989; Rudzinski et al. 1982). In Norway, a segregation in the altitude of dens

used by each species is observed with arctic fox using dens at higher altitudes while red foxes use those in more productive habitats, closer to the tree line (Linnell et al. 1999). Avoidance of high quality dens by arctic foxes when red foxes were present in the vicinity (up to 8 km) was also observed in Sweden (Tannerfeldt et al. 2002). The increasing abundance of red foxes in Fennoscandia since the 1930s has thus been proposed as a significant factor in the drastic decline in arctic fox populations in this region.

Since 2003, a monitoring of arctic and red fox populations has been established on the south plain of Bylot Island. As far as we know, this represents the only monitoring program for the two fox species in the Canadian Arctic. Such a monitoring program is needed as the consequences of climate warming are quickly spreading across the Arctic and consequences on wildlife are already apparent. The relation between the arctic and red foxes is thought to be a good indicator of the changes that the arctic wildlife community might undergo due to climate change. This report outlines a detailed protocol to continue the monitoring of the fox community of Bylot Island.

GENERAL BIOLOGY OF ARCTIC AND RED FOXES

*Arctic fox (*Alopex lagopus*)*

This account has been synthesized from Audet et al. (2002), Tannerfeldt et al. (2003), Underwood and Mosher (1982) and Garrott and Eberhardt (1987). Information specific to the arctic fox population of Sirmilik National Park of Canada has been included.

Distribution and habitat

Arctic foxes have a circumpolar distribution, occupying the arctic tundra of Europe, Asia and North America as well as the alpine tundra of Scandinavia. They are mainly found into four categories of habitat: coastal, inland, alpine and marine. Coastal populations usually feed largely on nesting seabirds on rocky outcrops and cliffs as well as marine life in the intertidal zone. Inland habitats are characterized by extensive flatlands, tundra vegetation and continuous permafrost just below a shallow active-soil layer. Available food resources vary seasonally with usually a wide variety of breeding birds during summer, and small rodent (lemmings and voles) and large ungulate (caribou or reindeer) populations present year-around. Alpine habitats are very similar to inland tundra habitats and are mainly occupied by arctic foxes in Scandinavia. In marine habitats, arctic foxes feed primarily on carcasses of sea mammals, fish or marine invertebrates found on the sea ice. In the region of Sirmilik National Park of Canada, arctic foxes use both coastal and inland habitats during summer and probably use more marine habitats during winter although exact habitat use during winter is still unknown.

Life history and population dynamics

Arctic fox are monogamous, form pairs and mate between February and April. They are usually established at a natal den no later than early May and parturition occurs somewhere between May and June, after approximately 52 days of gestation. Litter size varies greatly from year to year and among regions. In areas where lemmings or voles are present like in Sirmilik National Park of Canada, breeding success seems to be strongly related to the density of these small mammals with usually large litters in years of high rodent density and small or no litter in years of low densities. On Bylot Island, mean litter size in 2003, a year of low lemming abundance, was 4.3 cubs while in 2004, a peak lemming year, mean litter size was 8.8 cubs. Peak densities of fox populations usually occur about every 4 years, following the cyclic fluctuations of rodent populations.

Cubs are born blind, with a dark natal pelt and stay in the den until 3-4 weeks old. They are then visible outside the den and will gradually shed their natal pelt until 8 weeks of age. Cubs are weaned at 6-7 weeks and become independent by the end of August, when they are 12-14 weeks old. Growth is rapid and adult body sized is reached at 14-28 weeks of age. Arctic foxes are sexually mature at 9-10 months and some individuals will breed in their first year depending on the food resources available. Under natural conditions, arctic foxes have an average lifespan of 3-4 years but may reach 9-10 years.

Den sites

Arctic foxes are strongly dependent on dens for breeding. Due to the shallow permafrost-free layer in most of arctic fox's range, new dens are rarely dug and existing ones are often used repeatedly year after year. They can therefore become impressive structures with more than a

hundred entrances and covering more than 500 m². With the accumulation of organic matter from faeces and prey remains, dens sites may become covered with lush green vegetation, contrasting with the barren tundra landscape. Preferred dens are usually situated on mounds, ridges or river banks, lie higher above the permafrost layer on well drained soil, and are often south facing and rapidly free of snow in spring.

The openings of arctic fox dens are round or slightly oval, measuring 15-20 cm in diameter, and may vary between one to more than a hundred in a single den (mean number of entrances for Bylot Island = 17, n = 97). New openings are gradually dug by cubs and adults and dens are progressively excavated deeper and deeper as the permafrost layer drops due to increased ventilation and better soil drainage. Where habitat is favourable, complexes of multiple dens separated by only a few meters can sometimes be observed. The construction of a den may spread over hundreds of years and can sometimes be used by other species such as red foxes or arctic hare.

Many signs are typical of an active or whelping den. Strong fox odor in the openings, extensive trampling of the vegetation, freshly excavated openings, high abundance of scats (juvenile scats can be differentiated from adult scats by their small size) and prey remains are usually characteristic of a den used for reproduction. Furthermore, arctic fox pups will often bark from inside the den when approached by a human.

Status

In North America, the arctic fox is abundant wherever it occurs. Its abundance and distribution may however be affected by the ongoing climate changes. According to the

population census conducted in 2003-2004 on Bylot Island, arctic foxes are clearly more abundant than red foxes in our 425 km² study area. A total of 4 arctic fox and no red fox litters were observed in 2003, in a low lemming abundance year, while 15 arctic fox and 1 red fox litters were produced in 2004, in a peak lemming year.

Red fox (*Vulpes vulpes*)

This account has been synthesized from Samuel and Nelson (1982), Voigt (1987) and Larivière and Pasitschniak-Arts (1996). Information specific to the red fox population of Sirmilik National Park of Canada has been included.

Distribution and habitat

The red fox is the most widely distributed carnivore in the world. It occurs throughout most of North America and Europe (except in the extreme north of Nunavut and Siberia), as well as in Asia, northern Africa and more recently in Australia where it was introduced in 1868. Red foxes were apparently native to North America north of 40-45°N but further introductions from England in the 18th century have resulted in an increase in fox populations and expansions into areas previously unoccupied. The extirpation of the gray wolf (*Canis lupus*) and red wolf (*C. rufus*), as well as the human-caused decreased in coyotes (*C. latrans*) populations are believe to have played an important role in the increase of red fox range. Another more recent expansion of red foxes' range has been observed in the last century. According to information from Inuit communities and Hudson's Bay Company fur trade records, red foxes were first observed on Baffin Island in 1918, in the region of Lake Harbour, and gradually expanded northward until they reached Ellesmere and Cornwallis Islands in 1962 (Macpherson 1964). A similar expansion

of red fox populations towards northern latitudes and higher altitudes has also been noted in Russia and especially in Fennoscandinavia where populations have almost tripled between 1930 and 1960 (Chirkova 1968; Lindstrom 1989). In accordance with their worldwide distribution, red foxes are found in a large variety of habitats including arctic tundra, boreal forest, deciduous forest, prairie and grasslands, shrublands, semi-arid deserts, agricultural landscapes and urban environment. Food availability year around and presence of competitors, particularly larger canids, may be the main factors limiting their abundance.

Life history and population dynamics

Red foxes breed from December to April, depending on latitude. Gestation is 51 to 54 days and parturition occurs from March, to as late as June in the highest latitudes. Both sexes are able to breed in their first year, but pregnancy rates and reproductive success are highly variable depending on food availability and fox density. In area of low fox density in Canada, 80-90% of yearlings and 95% of adults may breed successfully. Until now, there has never been more than a single litter of red foxes observed on Bylot Island in a given summer. Average reported litter size, based on pups observations, ranges from 3.8 to 5.6. On Bylot Island, the average litter size observed between 1996 and 2003 was 4.3 pups ($n = 6$). Red fox pups are born with a greyish-brown silky fur, changing to pale buff at 8-14 days and to red at 9-14 weeks of age. Eyes open at 3 weeks of age when pups begin to walk. They are weaned between 8-10 weeks and attain adult size in about 6 months. Life expectancy in the wild can be as high as 8.6 years but few individuals live until 6 years.

Den sites

Like the arctic fox, red foxes use dens for parturition and rearing of cubs. They may dig their own den, which are small and rarely used more than once, or use those abandoned by other species such as woodchucks, badgers, hares or other foxes. Most dens are found in sandy soil and have several entrances up to 40 cm high. Due to the presence of permafrost in the region of Bylot Island, red foxes probably reproduce in already existent arctic fox dens. Therefore, differentiation of arctic and red fox dens usually requires the observation of an individual at the den. More sophisticated techniques, such as DNA probing of fresh faeces, could also allow for species determination at the den, but this has not yet been implemented at Bylot Island.

Status

Red fox populations have been subjected to a severe harvest throughout North-America, mainly because of their importance as vectors of rabies but also because of their impacts on game or rare species. However, the red fox remains the most common species in the genus *Vulpes*, which includes 10 other species worldwide. Despite its high abundance throughout North America, red foxes in the high Arctic are still relatively scarce. The proportion of red fox trapped in Inuit communities has however increased significantly in the last 30 years (Canac-Marquis and Dubois 2000) (figure-1). Hersteinsson and Macdonald (1992) suggested that this northward expansion of red foxes' range may be linked to the increase in summer temperatures recorded during the same period. According to their hypothesis, the warming climate may have resulted in a higher primary productivity, on which the foxes' prey depend, and thus allowed the larger red fox to survive in areas previously occupied by arctic foxes only. On Bylot Island, there has never been more than one litter of red foxes observed in a given year but reproduction has been observed in 1996, 1998, 1999, 2000, 2001 and 2004.

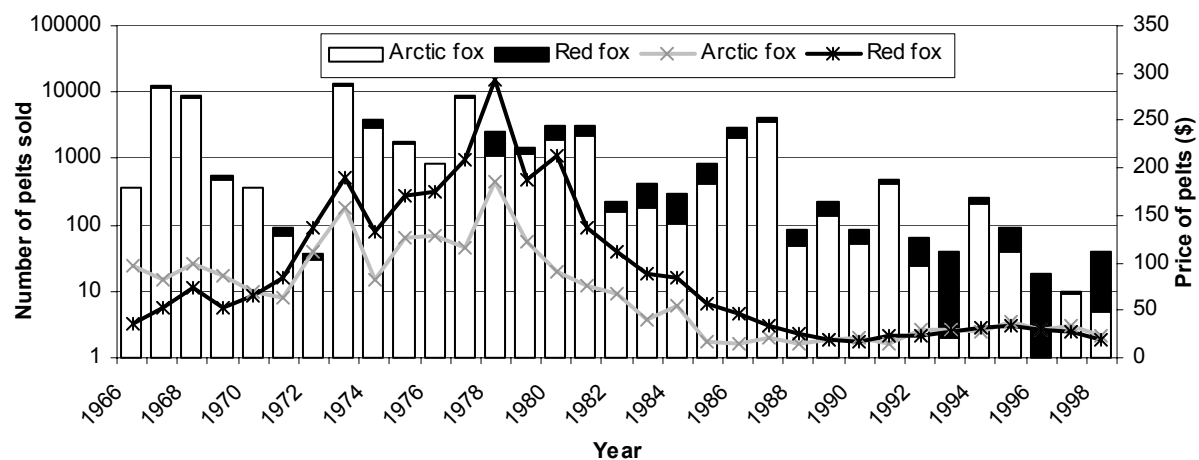


Figure 1 : Changes in the number of arctic and red fox pelts sold (bars) by Nunavik Inuit communities during the end of the 20th century. Variations in pelt price are shown by solid lines. A general trend toward increased proportion of red fox pelts sold, despite the comparable price of each species, suggests a relative increase in red fox abundance. (Data from Canac-Marquis and Dubois 2000)

PROTOCOLS

This section details the methods used in the monitoring program of the fox populations of Sirmilik National Park of Canada, particularly on the south plain of Bylot Island. An effective way to census fox populations is to take advantage of their dependence on den sites for reproduction and cub rearing. With a good knowledge of every available denning site in a study area, an annual visit of each den at the time of reproduction becomes an effective and rapid method for evaluating the total number of reproductive adults, the number of litters produced, and the approximate number of cubs in each litter. A good estimate of the status of each fox species can then be obtained from this information.

Den search

Den search is an efficient survey method when denning habitat is known, dens are easily recognisable and they occur in relatively open areas. This method is thus quite efficient in the case of fox populations in Sirmilik National Park of Canada. In 2003, an exhaustive survey of fox dens was conducted on the south plain of Bylot Island, covering a total of 425 km² (figure-1). Details of the method used during this census are exposed below. They can be used in other study area with minimal modifications.

Equipment

- Map of the area (1:50 000 recommended)
- Geographic Positioning System (GPS) receiver

- Wood batten and marker pen to identify den sites
- Binoculars
- Helicopter and/or snowmobile
- Temporary camp site material (optional)

Planning and field procedures

- Den search should be carried out during end of spring or summer to maximize chances of finding the dens. At the end of summer, some dens can be easier to spot due to the lush vegetation present on them but not every den possesses this characteristic. Please refer to “Den sites” section, under the general description of fox biology, and to figure-2 for effective identification of arctic fox dens.
- One person alone can cover an area of approximately 5-8 km² per day when surveying for dens on foot, and 12-25 km² by snowmobile, depending on the topography and the distance separating the area to cover from the camp site.
- Den search using a snowmobile can be a very efficient method to cover rapidly a large area when there is still a small cover of snow on the ground. Dens are usually situated on sites free of snow early in spring and can therefore be relatively easily spotted among the snow covered tundra. However, this technique may miss some smaller dens or lesser quality ones, still covered by snow. When using a snowmobile, avoid getting too close to dens as this can prompt foxes to abandon their den.
- Den search on foot is a labour intensive and longer process than on snowmobile but allows for a higher confidence level regarding effectiveness of search.

- In both cases, the most efficient method consists in following parallel transects 600 meters apart, and scanning for potential den sites, using binoculars, up to 300 meters on each side of this transect. When the topography is relatively flat, it is fairly easy to spot a den inside this 300 meters range. However, when the topography is rough, observers need to quit the transect line more often to visit potential den sites hidden by topography. A particular attention should be given to river and stream banks which are highly used by foxes but easily overlooked. When a potential den site is spotted, the observer should walk up to that site and verify the presence or absence of a den. We recommend using a 1:50 000 map of the area to record the regions surveyed.
- A handy method to minimize transportation by helicopter consists in establishing a temporary camp site in the middle of a large zone to be surveyed.
- When a den is found, its position should be recorded using the GPS, and a pair of wood battens should be installed on the den to be able to spot it easily during future visits of dens. Den sites are numbered sequentially according to the sector where they are located. Dens located in sector “Camp1” (see figure-3) are numbered between 001 and 099, in sector “Camp2”, between 101 and 199, and in sectors Flycamp1 and Flycamp2, between 301 and 399.

Visit of dens and populations monitoring

With a good knowledge of most den sites available to foxes, it is relatively easy to determine the reproductive effort of each species by visiting these dens at the appropriate time of the year. The following section contains instructions to carry out the monitoring of Bylot Island

fox populations. This protocol could be used with minimal modifications in any other study area previously searched for fox den presence.

Equipment

- Map of the area indicating location of every den
- Geographic Positioning System (GPS) receiver
- Geographical coordinates of dens
- Binoculars or spotting scope
- Helicopter for transportation
- Temporary camp site material

Planning and field procedures

- Visit of dens should be conducted during the denning season, especially during the period when pups are visible outside the den. For red foxes, this period corresponds to beginning of June to mid July while for arctic foxes, it is from end of June to beginning of August. We recommend doing the den survey at the beginning of July (around July 5th) to maximize the chances of observing the majority of litters from both species.
- There are presently 98 known fox dens in our study area (see figure-1). The visit of every den requires approximately 14-16 person-day (7-8 days for a team of 2 persons recommended). The majority of dens can be visited from either Base Camp1 or Base Camp2. However, the utilisation of an helicopter is required for visiting den sites located to the north of Camp1 (river from Qarlikturvik valley to cross) as well as in the sectors Flycamp1 and Flycamp2

(see figure-3). In addition to the ferrying time necessary to travel between Pond Inlet and Bylot island, approximately 3 hours of helicopter is required for transporting the visiting team to and from the sectors where no base camp are present. Each of these sectors require 1 full day for a team of 2 persons to visit every den present. The establishment of temporary camp sites in sector Flycamp1 and 2 can be useful if additional work has to be done at dens (eg. observations, sample collection, etc.) Locations of the recommended camp sites are shown in figure-3.

- Before approaching a den, verify from a distance with your binoculars or spotting scope the presence of foxes at the den.
 - If foxes are present, identify the species and the minimum number of cubs in the litter. Since several arctic foxes have been tagged since 2003 as part of the monitoring program of the fox community, also verify the presence of tags on the ears of adult foxes. Each tagged individual possesses a unique combination of 4 coloured plastic tags. Note the colour of each tag you can observe and specify its location (left/right, inner ear/outer ear). Note the date, time and duration of the observation period.
 - If no fox is observed, walk up to the den and observe for signs of utilisation. Strong fox odor in the openings, extensive trampling of vegetation, freshly excavated openings, high abundance of scats (juvenile scats can be differentiated from adult scats by their small size) and fresh prey remains are usually characteristic of a den used for reproduction. Furthermore, arctic fox pups will often bark from inside the den when approached by a human. If a den seems to be active, try to confirm its status by observing it for an hour from a location at least 500 m away. Note the date, time and duration of the observation period.

- Continuous observation during several hours is required to get an accurate estimate of the number of cubs at an active den. We therefore recommend doing a first visit of every den and subsequently coming back and establishing temporary camp sites at some of the active dens to estimate accurately the litter size. It is useful to identify a potential camp site at each active den during the first visit to minimize the disturbance when returning to establish the camp. Try to find a camp site at least 500 m away from the den but with a good view on it. Some dens already have a recommended fly camp site identified in Table-1 (labelled as "FLY ___").
- When the status of every den is confirmed, at least 5 active dens should be randomly selected to estimate the average litter size for each fox species. To estimate litter size, establish a camp site at least 500m away from the den but with a good view on it. Cubs are mostly active from dusk until dawn but can also be observed during daytime. A continuous observation for 48 hours is usually required to have a good estimate of the litter size. If it is impossible to carry out observations for such a long period, several shorter observation periods can also be conducted. In both cases, it is primordial to note the date, time and duration of the observations to ease the subsequent interpretation of data on litter size. Since it is never possible to be absolutely sure of litter size, “minimum litter size” is usually reported.

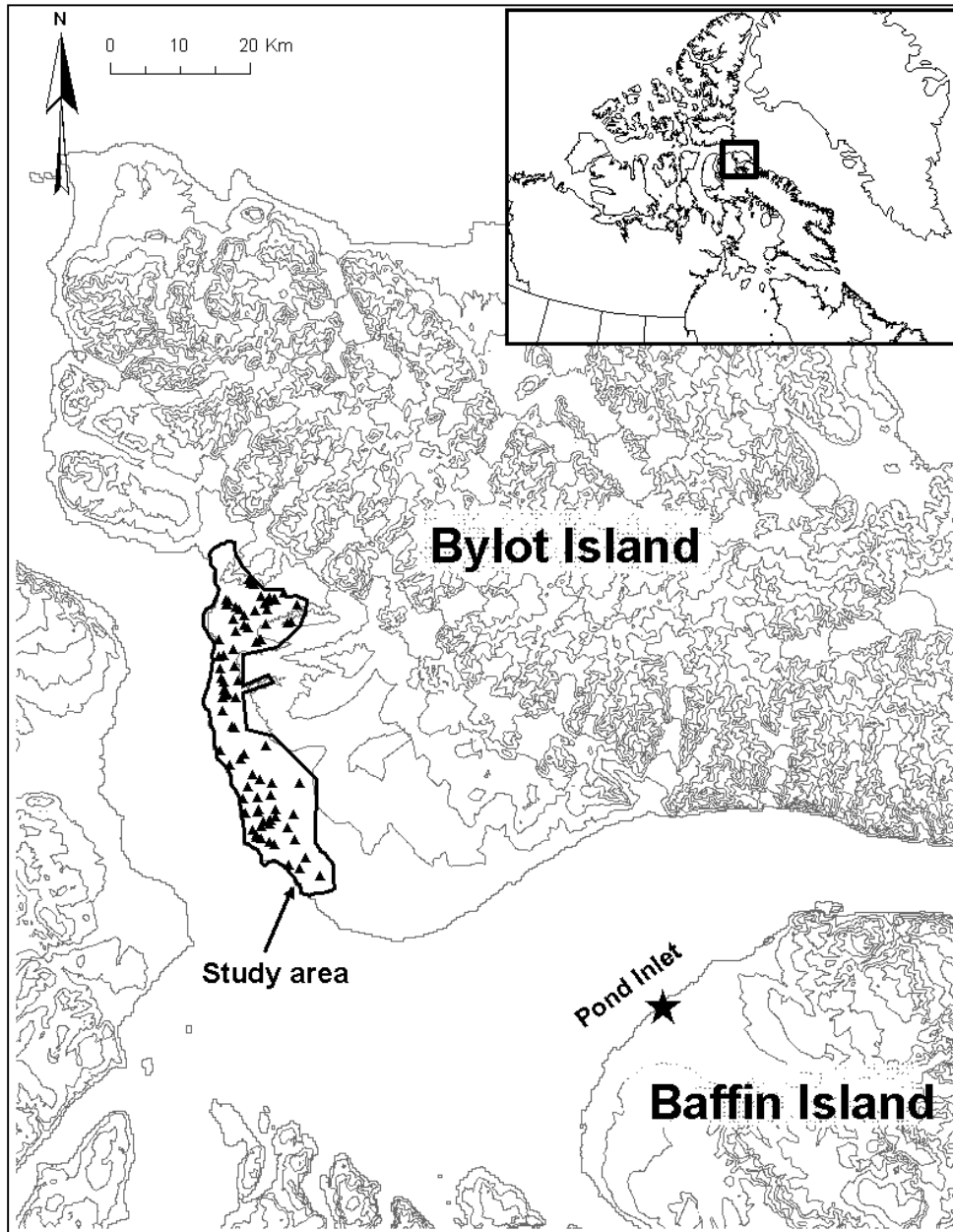


Figure-1: Study area on Bylot Island (73°0' N, 80°0' W), Nunavut, Canada, with location of arctic fox dens (black triangles).



Figure-2: Sample of arctic fox dens on Bylot Island, Sirmilik National Park of Canada.

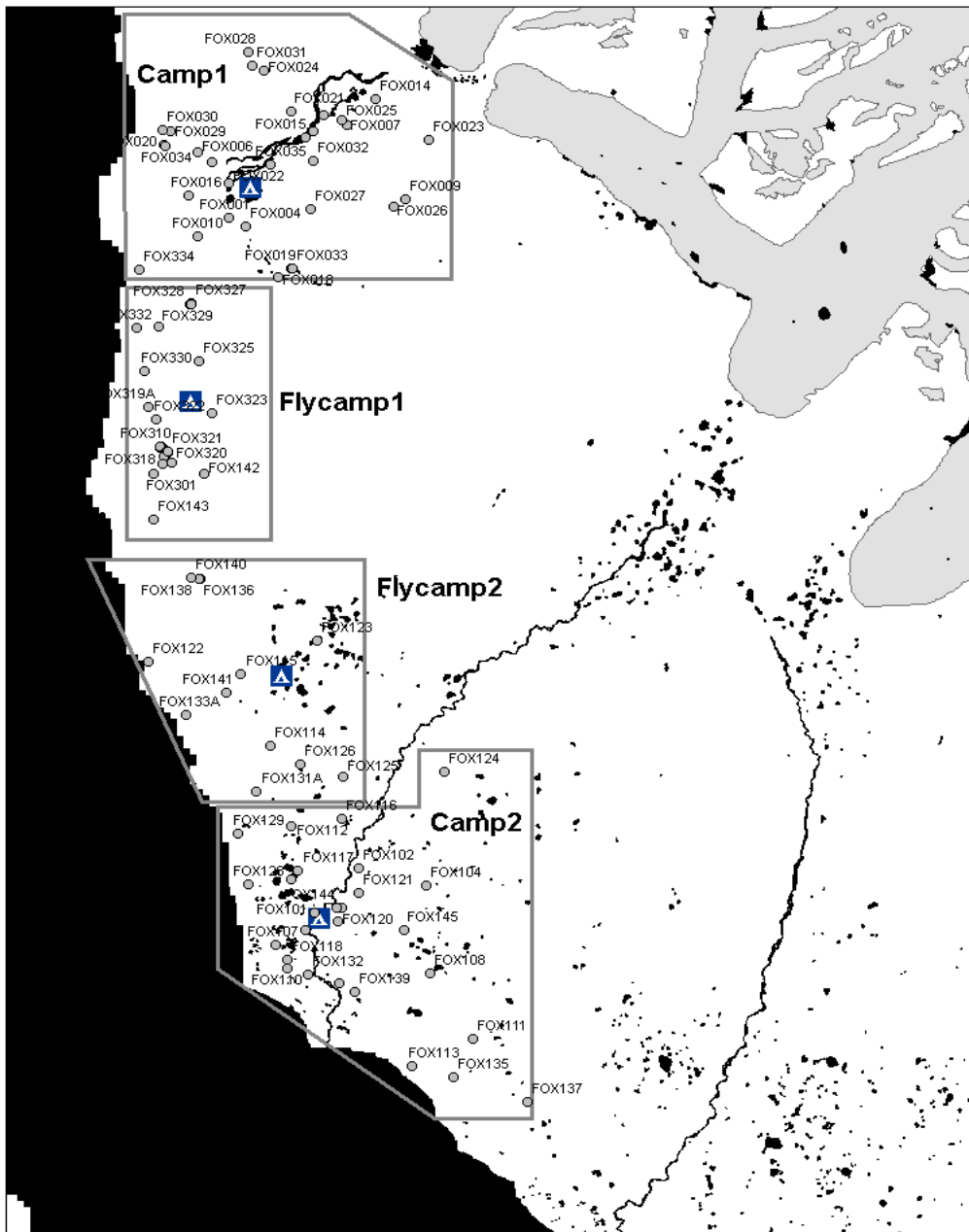


Figure-3: Location of surveyed fox dens and of main camp sites on the south plain of Bylot Island, Sirmilik National Park of Canada. The study area is divided into four different sectors that are used to organize the logistic of the monitoring. Base camp 1, base camp 2 and two recommended temporary camps are positioned on the map with the white tent icons. Position of all fox dens is identified by grey circles. Black areas represent sea or lakes, grey areas represent glaciers.

Table-1: Coordinates (NAD 83) of fox dens (FOX___) and recommended observation sites (FLY___) when these have been identified.

DEN			EAST	NORTH	DEN			EAST	NORTH
FOX001	17	X	532451	8117043	FOX124	17	X	540778	8094571
FOX002	17	X	535676	8120561	FOX125	17	X	536848	8094385
FOX003	17	X	534035	8119187	FOX126	17	X	535180	8094854
FOX004	17	X	533103	8116694	FOX127	17	X	534847	8090222
FOX005	17	X	531772	8119281	FOX128	17	X	533159	8090016
FOX006	17	X	531247	8119700	FOX129	17	X	532795	8092047
FOX007	17	X	536975	8120818	FOX131A	17	X	533496	8093793
FOX008	17	X	536099	8121178	FOX131B	17	X	533489	8093805
FOX009	17	X	539257	8117804	FOX132	17	X	535474	8086368
FOX010	17	X	531241	8116276	FOX133A	17	X	530786	8096904
FOX014	17	X	538096	8121866	FOX133B	17	X	530786	8096888
FOX015	17	X	535377	8120314	FLY133	17	X	531629	8096939
FOX016	17	X	530884	8117963	FOX134	17	X	531310	8102408
FOX018	17	X	534344	8114654	FOX135	17	X	541107	8082192
FOX019	17	X	534863	8114996	FOX136	17	X	531295	8102382
FOX020	17	X	529902	8119998	FOX137	17	X	543981	8081208
FOX021	17	X	534815	8121348	FLY137	17	X	543510	8080768
FOX022	17	X	532447	8118458	FOX138	17	X	531294	8102409
FOX023	17	X	540162	8120183	FOX139	17	X	537300	8085638
FOX024	17	X	533780	8122996	FOX140	17	X	530977	8102452
FOX025	17	X	536791	8120976	FOX141	17	X	532321	8097767
FOX026	17	X	538778	8117503	FOX142	17	X	531489	8106636
FOX027	17	X	535581	8117399	FOX143	17	X	529518	8104795
FOX028	17	X	533177	8123748	FOX144	17	X	536601	8089053
FOX029	17	X	530163	8120569	FOX145	17	X	539181	8088138
FOX030	17	X	529881	8120606	FLY145	17	X	539158	8088498
FOX031	17	X	533340	8123210	FOX301	17	X	529514	8106667
FOX032	17	X	535705	8119358	FOX303	17	X	530085	8107535
FOX033	17	X	534899	8114975	FOX304	17	X	530055	8107536
FOX034	17	X	529991	8119939	FOX305	17	X	530053	8107562
FOX035	17	X	534056	8119211	FOX305B	17	X	530047	8107574
FOX101	17	X	535753	8088880	FOX306	17	X	529894	8107640
FOX102	17	X	537449	8090687	FOX307	17	X	529929	8107648
FOX104	17	X	540076	8089962	FOX308	17	X	529798	8107722
FOX105	17	X	535370	8088132	FOX309	17	X	529815	8107748
FOX106	17	X	536708	8086017	FOX310	17	X	529771	8107758
FLY106	17	X	537027	8085386	FOX313	17	X	530013	8107575
FOX107	17	X	534253	8087571	FOX317	17	X	529937	8107368
FOX108	17	X	540224	8086405	FOX318	17	X	529869	8107060
FLY108	17	X	540213	8085465	FOX319A	17	X	529338	8109370
FOX109	17	X	536809	8089069	FOX319B	17	X	529329	8109344
FOX110	17	X	531239	8116274	FOX320	17	X	530241	8107120
FOX111	17	X	541874	8083762	FOX321	17	X	530074	8107548
FOX112	17	X	534854	8092374	FOX322	17	X	529633	8108877
FOX113	17	X	539477	8082619	FOX323	17	X	531783	8109135
FOX114	17	X	534023	8095623	FOX324	17	X	530929	8113532
FLY114	17	X	534588	8095923	FOX325	17	X	531278	8111211
FOX116	17	X	536769	8092672	FOX326	17	X	530945	8113519
FOX117	17	X	535094	8090583	FOX327	17	X	530971	8113566
FOX118	17	X	534689	8086968	FOX328	17	X	530954	8113547
FOX120	17	X	536658	8088484	FOX329	17	X	529704	8112647
FOX121	17	X	537460	8089650	FOX330	17	X	529157	8110832
FOX122	17	X	529320	8099045	FOX332	17	X	528871	8112569
FOX123	17	X	535834	8099886	FOX334	17	X	528955	8114944

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CONCLUSION DU MÉMOIRE

L'utilisation de tanières est une stratégie partagée par plusieurs carnivores. Bien que généralement, la localisation de ces tanières soit largement influencée par la distribution des ressources alimentaires et la facilité d'échapper à la prédation, cette étude nous a permis de démontrer que les critères de sélection d'un site de tanières peuvent varier fortement en fonction de l'environnement dans lequel une espèce se trouve. Ainsi, pour un mammifère arctique tel que le renard arctique, les conditions environnementales semblent jouer un rôle majeur lors de la sélection d'un site de tanière. Plus particulièrement, la présence de pergélisol dans la toundra arctique semble être le principal facteur limitant l'établissement d'une nouvelle tanière. Nous avons ainsi observé une forte sélection du renard arctique pour des sites situés sur des buttes ou sur des pentes, préférentiellement où le substrat est sablonneux, favorisant ainsi le drainage et minimisant l'accumulation d'eau dans le sol. De plus, la sélection de sites rapidement déneigés au printemps et exposés au sud maximise l'ensoleillement et le dégel du sol. On retrouve ainsi aux sites de tanières une plus grande profondeur de sol meuble au-dessus de la strate de pergélisol.

Malgré la grande abondance de tanières présentes dans notre aire d'étude, seulement certaines d'entre elles sont utilisées pour la mise-bas. La comparaison de l'environnement des tanières de reproduction et des tanières non-utilisées à cette fin nous a permis de développer un modèle de sélection de tanières de reproduction chez le renard arctique et a révélé deux principales forces influençant cette sélection : une positive, l'abondance des ressources alimentaires, et une négative, la présence d'autres tanières à proximité. Les tanières utilisées pour la reproduction sont principalement situées dans les habitats fortement utilisés par le lemming (proie principale) et à proximité de la colonie de nidification de la Grande oie des neiges (proie alternative). Cependant, la présence de plusieurs autres tanières à proximité semble diminuer l'attrait d'une tanière donnée, vraisemblablement en raison de la compétition intra-spécifique potentielle qui pourrait s'en suivre si un autre renard reproducteur venait s'installer dans le même territoire.

Nous avons développé au cours de cette étude un protocole d'évaluation de la distribution spatiale des ressources alimentaires à grande échelle et ainsi démontré l'importance majeure de ce critère pour la reproduction du renard arctique. Cet outil nous a permis d'évaluer plus précisément la disponibilité de tanières de haute qualité, élément essentiel au maintien de cette espèce. Considérant la difficulté que représente l'excavation de nouvelles tanières en présence de pergélisol, une telle étude pourrait donc être répétée afin d'évaluer la capacité de support d'un milieu donné en fonction des tanières qui s'y trouvent.

Malgré la présence grandissante du renard roux dans le haut arctique canadien, le renard arctique demeure jusqu'à maintenant le principal prédateur terrestre du Parc national du Canada Sirmilik. Grâce au protocole de suivi de la communauté de renards instauré dans le parc au cours de ce projet de recherche, la présence de renards roux reproducteurs a été confirmée sur la plaine sud de l'île Bylot. L'application de ce protocole au cours des prochaines années permettra de surveiller l'évolution de cet écosystème et d'évaluer les conséquences d'une éventuelle augmentation de la population de renards roux. De plus, grâce au modèle de sélection de tanières de reproduction développé pour le renard arctique au cours de ce projet nous pourrions désormais identifier les tanières de haute qualité pour cette espèce et ainsi les comparer avec celles utilisées par le renard roux afin d'évaluer l'amplitude du chevauchement de cet aspect de leur niche écologique.