Rôle de la densité d'oies et de la détection du prédateur dans les variations du succès reproducteur de la grande oie des neiges

Mémoire

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Sous la direction de:

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Résumé

Comprendre comment les interactions trophiques varient dans le temps et l'espace est essentiel pour prédire les dynamiques de population et la réponse des espèces animales aux changements environnementaux. La densité-dépendance, qui décrit la relation entre la taille d'une population et son taux de croissance, constitue un mécanisme fondamental dans la dynamique de population au sein des communautés. Ce mémoire explore les mécanismes qui régissent la densité-dépendance du succès reproducteur chez une espèce coloniale, la grande oie des neiges (*Anser caerulescens atlanticus*), dans un système écologique arctique fortement structuré par les relations proies-prédateurs. Dans un premier volet, nous avons analysé un jeu de données à long terme (1999–2023) recueilli sur l'île Bylot (Nunavut, Canada), afin d'évaluer comment la densité de nids d'oies influence leur succès de nidification, en interaction avec l'abondance des lemmings, proie alternative du principal prédateur, le renard arctique (*Vulpes lagopus*). Nos analyses révèlent que la densité-dépendance varie selon l'échelle spatiale considérée (individuelle vs populationnelle) et dépend fortement de l'abondance de lemmings. À l'échelle de la population, un effet positif de la densité n'apparaît que lorsque les lemmings sont peu abondants, tandis qu'à l'échelle de l'individu, un effet négatif se manifeste seulement lors des années de forte abondance de lemmings. Ces résultats soulignent l'importance des interactions indirectes entre proies et du contexte écologique dans la modulation de la densité-dépendance. Dans un second volet, nous avons testé expérimentalement l'un des mécanismes proposés dans la littérature pour expliquer la densité-dépendance : la variation de la probabilité de détection des nids par les renards en fonction de leur densité. En menant une expérience sur le terrain durant trois années consécutives en utilisant des nids artificiels et des pièges photographiques, nous avons montré que la probabilité de détection diminuait avec la distance entre les nids, mais que le même patron se répétait entre les années, malgré des conditions écologiques contrastées (grande variabilité interannuelle en en ce qui concerne l'abondance de lemmings et d'oies). Intégrées dans un modèle mécanistique multi-espèces, ces variations de détection se sont révélées insuffisantes pour expliquer à elles seules les variations interannuelles du succès de nidification observées dans la nature. Dans l'ensemble, ce mémoire montre que la densité-dépendance chez les oies arctiques résulte d'interactions complexes et dynamiques entre espèces, influencées par la structure spatiale, l'abondance des proies alternatives et le comportement des prédateurs. Il souligne également la nécessité d'in-

tégrer des approches empiriques et mécanistiques pour mieux comprendre les fondements des interactions trophiques dans les écosystèmes naturels.

Abstract

Understanding how trophic interactions vary across time and space is essential for predicting population dynamics and species responses to environmental change. Density dependence, which describes the relationship between population size and growth rate, is a fundamental mechanism in population dynamics. This thesis explores the mechanisms underlying density dependence in reproductive success for a colonial species, the greater snow goose (*Anser caerulescens atlanticus*), within an Arctic ecological system shaped by predator–prey relationships. In the first part, we analyzed a long-term dataset (1999–2023) collected on Bylot Island (Nunavut, Canada) to assess how nest density affects goose nesting success, and how this relationship is modulated by the abundance of lemmings, an alternative prey for the main nest predator, the Arctic fox (*Vulpes lagopus*). Our analysis revealed that the direction and intensity of density dependence vary with spatial scale (individual vs population) and lemming abundance. At the population scale, positive density dependence emerged only in years of low lemming abundance, while at the individual scale, negative density dependence was observed only during years of high lemming abundance. These findings highlight the role of indirect interactions between prey and ecological context in shaping density-dependent processes. In the second part, we experimentally tested on the field one potential mechanism for density dependence: variation in nest detection probability by foxes in response to nest density. Over three years, using artificial nests and camera traps, we found that detection probability declined with inter-nest distance and that the pattern remained consistent across years despite contrasting ecological conditions (large interannual variability in goose and lemming abundance). When integrated into a multi-species mechanistic model, variation in detection probability was insufficient on its own to explain the observed interannual variation in goose nesting success. Together, these studies show that density dependence in Arctic-nesting geese is driven by complex and dynamic species interactions influenced by spatial structure, alternative prey abundance, and predator behavior. The results emphasize the value of combining empirical and mechanistic approaches to uncover the underlying drivers of trophic interactions in natural ecosystems.

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À tous les amateurs d'omelettes

La [toundra] chantait
Le Soleil brillait
Au bout des marécages

Et tous ces oiseaux
Qui étaient si bien
La haut dans les nuages
J'[ai tant] aimé les accompagner
Au bout de leur voyage

Adapté de *Le Chasseur*,
Michel Delpech

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Avant-propos

Ce mémoire comprend d'abord une introduction générale présentant le contexte de l'étude. Suivent ensuite deux articles scientifiques rédigés en anglais représentant le coeur de l'ouvrage et, enfin, une conclusion générale résumant les retombées, limitations et perspectives futures du projet.

Chapitre 1 – Spatial scale and indirect interactions modulate density dependence in nest survival of a greater snow goose colony

À soumettre

Auteur principal : Matthieu Weiss-Blais (MWB) Coauteurs : Joël Bêty (JB), Frédéric Dulude-de Broin (FDB), Andréanne Beardsell (AB), Gilles Gauthier (GG), Pierre Legagneux (PL)

Contribution des auteurs : MWB, JB, AB et PL ont défini le projet. GG, PL et MWB ont récolté et assemblé les données. MWB et FDB ont effectué les analyses statistiques. MWB a rédigé l'article. JB, AB, FDB, GG et PL ont révisé plusieurs versions de l'article.

Chapitre 2 – Field experiment suggests that prey density does not change prey detection by the predator

À soumettre

Auteur principal : Matthieu Weiss-Blais (MWB) Coauteurs : Andréanne Beardsell (AB), Pierre Legagneux (PL) et Joël Bêty (JB)

Contribution des auteurs : MWB, JB, AB et PL ont défini le projet. MWB et AB ont récolté et assemblé les données. MWB a effectué les analyses statistiques. MWB a rédigé l'article. AB, PL et JB ont révisé plusieurs versions de l'article.

Introduction

La prédation

Fondamentale en écologie, la prédation est omniprésente dans les milieux naturels et détermine le flux d'énergie entre différents niveaux trophiques au sein d'une communauté (DeLong, 2021; Estes et al., 2011). En plus de représenter une des grandes forces évolutives qui influence de nombreux traits d'histoires de vie chez la plupart des espèces du règne animal (Sih, 1987), la prédation détermine également la persistance de certaines espèces en un endroit donné et ainsi influence leur distribution (Lima, 1998; Wisz et al., 2013). En effet, par ses effets directs (consommation) et indirects (risque de prédation), la prédation détermine largement la structure des communautés (Sih et al., 1985), leur modularité (Brose et al., 2025) ainsi que leur fonctionnement (Schmidt and Ostfeld, 2008; Suraci et al., 2022).

Les réseaux trophiques (réseaux d'interactions au sein d'une communauté caractérisés par des liens de consommation entre espèces ou groupes fonctionnels) sont généralement composés de nombreuses interactions faibles et de quelques interactions trophiques très fortes (Wootton and Emmerson, 2005). La force des interactions trophiques est déterminée par plusieurs facteurs, notamment les composantes physiques de l'environnement (Cherif et al., 2024) ou encore les traits des espèces tels que la taille corporelle (Brose et al., 2006). Bien que la taille corporelle puisse être une bonne indication des interactions trophiques dans certains systèmes (Gravel et al., 2013), dans les écosystèmes terrestres, elle ne permet souvent pas à elle seule de prédire correctement les interactions trophiques et il est nécessaire de considérer d'autres traits comme des traits comportementaux du prédateur (techniques de chasse) ou de la proie (stratégies d'évitement ou de camouflage ; Kalinoski and DeLong (2016)). La force du lien trophique dépendra donc du comportement des prédateurs et des proies, mais aussi de leur densité relative (Abrams and Ginzburg, 2000).

La force d'une interaction trophique peut également dépendre de la densité ou de la présence d'autres espèces au sein du même réseau trophique. Ces interactions dites indirectes, car elles impliquent un effet via une espèce intermédiaire, peuvent survenir à la fois entre niveaux trophiques (interactions verticales) ou sein d'un même niveau trophique (interactions horizontales ; Strauss, 1991; Wootton, 1994). Les interactions indirectes entre niveaux trophiques

peuvent être causées par des cascades de changements de densité dans lesquelles une espèce (a) influence indirectement une autre (c) en modifiant l'abondance d'une espèce intermédiaire (b), qui à son tour affecte celle l'espèce c (Estes et al., 2011). Ces cascades peuvent aussi découler de modifications de traits comportementaux, notamment à travers des effets non létaux de la prédation : par exemple, la survie d'une proie peut augmenter si la présence d'un superprédateur réduit l'activité d'un mésoprédateur (Werner and Peacor, 2003). Les interactions indirectes au sein d'un même niveau trophique, quant à elles, peuvent émerger entre proies partageant un même prédateur (Holt, 1977; Wootton, 1994). Dans ce cas, la présence ou l'abondance d'une proie peut influencer indirectement une autre en modifiant le comportement (réponse fonctionnelle) ou la densité (réponse numérique) du prédateur commun (Holt, 1977). Cette interaction peut être négative (*compétition apparente*) si, par exemple, l'augmentation d'une proie engendre une augmentation de la densité de prédateurs, avec des conséquences délétères pour l'autre proie (Schmidt and Ostfeld, 2008; Holt and Lawton, 1994). À l'inverse, l'interaction indirecte peut être positive (*mutualisme apparent*) si l'abondance d'une proie diminue la pression de prédation sur l'autre, en changeant la réponse fonctionnelle du prédateur commun (ex. réduction de la quête alimentaire, satiété ; Beardsell et al., 2022; Holt, 1977). L'impact de ces interactions indirectes sur la structure des communautés peut être équivalent, voire parfois supérieur, à celui des interactions directes (Strauss, 1991; Wootton, 1994).

La colonialité

Les proies emploient plusieurs stratégies pour réduire le risque de prédation, telles que l'augmentation de la crypticité (Gomez and Théry, 2007), le développement d'armements (Hammill et al., 2008), une réduction des activités (Lima and Dill, 1990), l'utilisation de refuges physiques (Sih et al., 1985; Sih, 1987) ou biologiques (association avec une espèce de plus grande taille ou plus agressive qui peut éloigner les prédateurs ; Quinn and Ueta (2008)) ou encore l'évitement d'habitats perçus comme risqués (Gaynor et al., 2019). La grégarité est une autre stratégie que certaines espèces de proies adoptent afin de réduire le risque de prédation (Caro, 2005). De manière générale, la vie en groupe peut augmenter la vigilance, diluer le risque de prédation, accentuer la confusion du prédateur et améliorer la défense collective, réduisant ainsi la probabilité qu'un individu soit capturé par un prédateur (Giraldeau et al., 2012). Les oiseaux bénéficient des avantages de la socialité en se regroupant pour plusieurs activités, telles que le repos (*roosts*), l'alimentation et la migration (*flocks*) ou encore la reproduction (colonies ; Lima and Dill, 1990). Ces stratégies permettent d'échanger de l'information sur les ressources disponibles ou d'augmenter leur probabilité d'appariement (Danchin et al., 2004; Giraldeau et al., 2012) mais, elles constituent aussi, et surtout, un moyen de défense contre les prédateurs. Cet avantage anti-prédateur est d'autant plus crucial durant la période de reproduction, car la prédation est la principale cause d'échec de

nidification chez les oiseaux (Menezes and Marini, 2017; Ricklefs, 1969; Skutch, 1985; Martin, 1993; Thompson Iii, 2007).

La nidification en colonie est une stratégie qui a évolué indépendamment chez au moins 20 groupes d'oiseaux (Rolland et al., 1998). Jusqu'à 19% des espèces utilisent cette stratégie de reproduction (Crook, 1965). De manière générale, une colonie désigne une agrégation de nids, le plus souvent de la même espèce, d'une densité supérieure à celle observée dans le paysage environnant, et qui est formée de territoires contenant peu ou pas de ressources défendables (Evans et al., 2016). Plusieurs mécanismes peuvent avoir mené à l'émergence de colonies : une réduction de la prédation (Wittenberger and Hunt, 1985), un accès à de l'information sur la localisation de la nourriture (Ward and Zahavi, 1973), une augmentation de l'accès à des partenaires sexuels (Giraldeau et al., 2012). Cependant, aucun de ces mécanismes ne fait actuellement l'unanimité dans la littérature (Rolland et al., 1998; Varela et al., 2007). Plus récemment, il a été proposé de considérer les colonies comme des sources d'information sociale permettant aux individus de prendre de meilleures décisions et d'ainsi augmenter leur valeur adaptative en diminuant leur taux de prédation, en sélectionnant les habitats les plus propices pour la nidification, et en ayant un plus grand accès aux partenaires sexuels (Evans et al., 2016). L'agrégation d'oiseaux en colonies pourrait donc être le résultat d'individus prenant des décisions similaires basées sur de l'information sociale (Evans et al., 2016).

Les fortes densités d'individus caractérisant les colonies peuvent offrir plusieurs avantages aux proies en réduisant la prédation par différents mécanismes comme i) une meilleure détection des prédateurs et une meilleure circulation d'information sociale entre individus (Brown and Brown, 1987; Danchin et al., 2004; Gil et al., 2018), ii) une dilution passive de la pression de prédation par simple jeu de probabilités (Bednekoff and Lima, 1998; Beauchamp and Ruxton, 2008; Becker, 1995) ou iii) le harcèlement de groupe (*mobbing* ; Jungwirth et al., 2015; Robinson, 1985; Arroyo et al., 2001). Ces avantages peuvent être cependant contrebalancés par une augmentation de la compétition pour la nourriture (Forero et al., 2002), une augmentation des interactions agressives entre congénères (Hötker, 2000) et une augmentation du partage de maladies et de parasites (Brown and Brown, 2004). Plusieurs de ces mécanismes peuvent simultanément influencer le succès de nidification. C'est la somme de ces mécanismes qui détermine si l'effet global de la densité d'oiseaux nicheurs sur leur succès reproducteur est positif (Pratte et al., 2016; Götmark and Andersson, 1984), négatif (Ferrer and Donazar, 1996; Both, 1998; Rodenhouse et al., 2003) ou neutre (Padyšáková et al., 2010). Ainsi, l'augmentation de la densité peut générer de multiples effets sur l'aptitude phénotypique des individus et la dynamique des populations, ce qui diminue notre pouvoir de prédiction de cette dernière.

La densité-dépendance

La densité-dépendance est un mécanisme central dans la dynamique des populations, car il correspond à la relation entre le taux de croissance (λ) et le nombre d'individus (N) d'une population (Turchin, 2003). Le taux de croissance est généralement négativement densité-dépendant. En effet, ce taux diminue avec l'augmentation de la densité permettant la stabilisation et ultimement la persistance des populations *via* des mécanismes de régulations (Sinclair and Pech, 1996; Murdoch, 1994; Chesson, 2000). La densité-dépendance peut parfois être positive et expliquer l'agrégation des individus (Courchamp et al., 1999). La densité-dépendance négative est largement documentée chez des centaines d'espèces, allant des vertébrés aux invertébrés, autant en milieu aquatique qu'en milieu terrestre (Brook and Bradshaw, 2006) et peut être générée à la fois par des mécanismes trophiques ascendants (*bottom-up*), tels que la compétition pour des ressources (nourriture, espace, partenaires) et par des mécanismes trophiques descendants (*top-down*) tels que le parasitisme ou la prédation (Sibly et al., 2005; Sinclair, 2003). Ces mécanismes n'agissent pas de façon constante durant le cycle de vie des animaux et font donc que la densité-dépendance peut varier selon les stades de vie d'une espèce (Clutton-Brock et al., 2002; Bland et al., 2025; Hanski, 1990). Chez les espèces longévives comme les anatidés, la survie des nids est l'un des paramètres démographiques (avec la survie des adultes) ayant le plus d'influence sur le taux de croissance des populations et qui est le plus susceptible de générer de la densité-dépendance (Koons et al., 2014).

Il a été observé chez plusieurs taxons d'oiseaux que l'intensité de la prédation peut augmenter avec la densité de proies (Schmidt and Whelan, 1999; Martin, 1988; Elmberg et al., 2009). Cette prédation densité-dépendante peut varier selon la structure de la communauté de proies (Marini and Weale, 1997). Des interactions indirectes par l'intermédiaire d'un prédateur commun (voir la section *La prédation* de l'introduction), peuvent réduire la prédation sur les nids d'oiseaux lorsqu'augmente l'abondance d'une autre proie de ce prédateur (Werner and Peacor, 2003). La densité-dépendance et les interactions indirectes peuvent ainsi interagir. Par exemple, lors des pics d'abondance de petits mammifères, la prédation exercée par les belettes (*Mustela nivalis*) sur les nids de passereaux (*Parus spp.*) est réduite, ce qui compense la pression accrue que subissent les nids dans les zones de forte densité (Dunn, 1977). Ainsi, lorsque la prédation génère de la densité-dépendance, celle-ci peut être modulée par la disponibilité d'autres proies partageant le même prédateur (Sinclair, 2003). Il demeure cependant souvent difficile de bien quantifier et de modéliser précisément les effets de la densité des proies sur leur survie en milieu naturel.

La modélisation des interactions prédateur-proies

Les interactions prédateur-proies sont généralement modélisées à l'aide de la réponse fonctionnelle, où l'on illustre la variation du nombre de proies capturées par le prédateur (taux

d'acquisition) en fonction de la densité de proies (Holling, 1959). De façon générale, cette relation peut avoir une forme linéaire (type I), hyperbolique (type II), sigmoïdale (type III) ou de dôme (type IV ; Holling, 1959; Holling and Buckingham, 1976). La réponse fonctionnelle de type II est la relation la plus souvent observée au sein de dyades prédateurs-proies (Uiterwaal et al., 2022).

L'approche *mécanistique* de la modélisation des interactions trophiques, surtout développée durant la dernière décennie, permet d'intégrer les importants comportements des prédateurs et des proies dans la modélisation du taux d'acquisition des prédateurs et de leurs réponses fonctionnelles (DeLong, 2021; Cherif et al., 2024; Prokopenko et al., 2023). Cette approche dans l'étude de la prédation décompose la séquence de prédation en étapes quantifiables, soit le mouvement, la détection de la proie, la décision d'attaquer, la capture, la manipulation de la proie et l'allocation de l'énergie (Beardsell et al., 2021; Wootton et al., 2023). La réponse fonctionnelle (et le type de réponse) correspond à une intégration de cette séquence en fonction de la densité de proies. Cette approche permet donc de mieux intégrer et modéliser les réponses fonctionnelles multi-espèces en milieu naturel (Abrams, 2022) et d'isoler certains comportements clés. L'approche mécanistique permet aussi d'intégrer aux modèles de réponse fonctionnelle des mécanismes densité-dépendants qui sont généralement peu inclus dans l'étude des réponses fonctionnelles (ex. changements comportementaux, interactions indirectes ; Stouffer and Novak, 2021).

Cette approche est très prometteuse, car elle offre beaucoup de possibilités pour décortiquer et identifier les mécanismes proximaux qui influencent le plus les interactions trophiques. Elle permet notamment d'intégrer les comportements du prédateur et de la proie, lesquels peuvent moduler à la fois la force des interactions trophiques et le type de réponse fonctionnelle (Abrams and Matsuda, 1993). Les modifications comportementales peuvent avoir une influence majeure sur la structure des communautés, comme en témoigne le fait que les cascades trophiques induites par les effets non létaux de la prédation peuvent être plus marquées que celles découlant de simples variations d'abondance des prédateurs et des proies (Preisser et al., 2005; Palmer et al., 2021; Estes et al., 2011).

Ces comportements peuvent intervenir à pratiquement chaque étape de la séquence de prédation. La composante du mouvement inclut le type de chasse (Preisser et al., 2007), la vitesse du prédateur (Daugaard et al., 2021) ou encore la sélection d'habitats par les prédateurs et les proies (Gaynor et al., 2019). La probabilité d'attaque d'une proie peut varier en fonction de sa dangerosité, laquelle est déterminée par ses traits défensifs - qu'ils soient physiques (cornes), chimiques (toxines), comportementaux (morsure ; Mukherjee and Heithaus, 2013) - ou selon l'état énergétique interne du prédateur (Beardsell et al., 2024). La probabilité de capture des proies peut varier selon différents comportements anti-prédateurs (Lima and Dill, 1990). L'allocation des proies capturées (consommation directe, cachage) dépend de traits

du prédateur comme son métabolisme, sa mémoire spatiale ou sa territorialité (Vander Wall, 1990).

Le rôle de la détection dans les interactions trophiques

Capacité de détection des proies par le prédateur peut avoir un grand impact sur le taux d'acquisition des proies, car elle détermine l'efficacité de recherche de proies (α) et, ultimement, le taux de rencontre avec les proies - une composante clé de la réponse fonctionnelle (Holling, 1959). Cette capacité de détection peut être modulée par les caractéristiques physiques de l'environnement. Par exemple, des études portant sur les poissons (grands brochets (*Esox lucius* ; Turesson and Brönmark, 2007) et les chats (*Felis catus* ; McGregor et al., 2015) montrent que la turbidité de l'eau et la densité de la couverture végétale verticale peuvent, respectivement, réduire la capacité de détection des proies chez ces prédateurs. Ces limitations peuvent ainsi non seulement influencer le taux d'acquisition, mais également la capacité des prédateurs à réguler les populations de proies (Jönsson et al., 2013).

La détection des proies par le prédateur peut aussi être influencée par le contexte biologique d'un écosystème. Maintenir un approvisionnement optimal pour un prédateur nécessite de maximiser la probabilité de rencontre, mais aussi la probabilité de détection d'une proie. Il est ainsi attendu que cette probabilité de détection dépende de la densité de la proie en question (Cornell, 1976). En effet, deux mécanismes communément proposés pour expliquer ces différences de détection sont l'*image de recherche*, et le *taux de recherche*. Le premier stipule que la capacité de détection d'une proie par un prédateur augmente avec l'abondance de celle-ci, car il devient plus efficace à reconnaître cette proie (Pietrewicz and Kamil, 1979). Le deuxième correspond à l'ajustement de la vitesse du prédateur pour examiner plus longtemps une zone et ainsi augmenter sa probabilité d'y détecter des proies (Guilford and Dawkins, 1987, 1989). Ces mécanismes pourraient à eux seuls générer une prédation densité-dépendante, mais leur démonstration a surtout été faite en milieu contrôlé (Gendron and Staddon, 1983; Nams, 1997) et ils ont rarement été testés en milieu naturel (Vigallon and Marzluff, 2005). L'une de ces rares expériences en milieu naturel n'a d'ailleurs pu appuyer l'existence de ces mécanismes chez les écureuils (*Sciurus niger*), soulignant l'importance de vérifier à nouveau cette hypothèse dans la nature (Morgan and Brown, 1996).

Système d'étude

Les écosystèmes arctiques sont caractérisés par un réseau trophique et une structure du paysage relativement simple, offrant un contexte idéal pour documenter des mécanismes écologiques en milieu naturel. Le présent mémoire s'appuie sur des données et de nombreuses études réalisées à l'île Bylot, au Nunavut, Canada (Gauthier et al., 2024a). Une trentaine d'espèces d'oiseaux nichent régulièrement sur le site, dont la grande oie des neiges (*Anser*

caerulescens atlanticus) qui représente la plus grande biomasse en été (environ 12 000 couples annuellement, avec un maximum de 24 000 couples). Ces grandes oie des neiges forment une large colonie dont la densité varie substantiellement entre les années (Gauthier et al., 2023; Moisan et al., 2025). L'oie des neiges est une espèce qui a connu une explosion démographique au cours des années 1980 et 1990, mais dont la population a été depuis stabilisée par une libéralisation de la chasse à la fois aux États-Unis et au Québec (Lefebvre et al., 2017). Si la densité de couples nicheurs varie entre les années, celle-ci ne montre pas de tendance à la hausse ou à la baisse au cours des 30 dernières années. Le principal prédateur des nids d'oiseaux, et particulièrement des nids d'oies, est le renard arctique (*Vulpes lagopus* ; Bêty et al., 2001). La prédation sur les nids d'oies est aussi générée, mais en moindre partie, par certains prédateurs aviaires que l'on retrouve sur l'île comme le goéland bourgmestre (*Larus hyperboreus* ; Gauthier et al., 2004), le labbe parasite (*Stercorarius parasiticus*) et le grand corbeau (*Corvus corax* ; Bety et al., 2002). L'écosystème accueille aussi deux espèces de rongeurs (le lemming brun (*Lemmus trimucronatus*) et le lemming variable (*Dicrostonyx groenlandicus*), dont l'abondance est marquée par des cycles aux 3 à 5 ans (Gauthier et al., 2013, 2024a). La pression de prédation sur plusieurs espèces d'oiseaux dépend étroitement de l'abondance de lemmings (Bêty et al., 2001; Mckinnon et al., 2013). De façon générale, lors d'années de faible abondance de lemmings, la pression de prédation sur les nids d'oiseaux et élevée, alors que durant les années de forte abondance de lemmings, la pression sur les nids d'oiseaux est relâchée (Bêty et al., 2001; Lamarre et al., 2017).

Objectifs

Ce mémoire s'attelle à comprendre les différents facteurs et mécanismes qui déterminent une partie des variations de succès reproducteur de la grande oie des neiges. Dans le premier chapitre, nous déterminons, à partir de données issues d'un suivi à long terme sur la reproduction des oies au sein de la colonie, les effets densité-dépendants sur la survie des nids en contrastant deux échelles spatiales et différentes densité de lemmings, une proie importante du système et qui partage les mêmes prédateurs. Dans le second chapitre, nous tentons de déterminer expérimentalement si la probabilité de détection des nids d'oies par les renards dépend de la densité d'oies et/ou de lemmings en répétant la même expérience basée sur des nids artificiels durant 3 années consécutives présentant des densités de lemmings et d'oies très contrastées. Le second objectif de ce chapitre est d'estimer l'effet de la variation interannuelle de la détection des nids sur la réponse fonctionnelle des renards et *in fine* sur la survie des nids d'oies. Pour ce faire, nous avons utilisé un modèle mécanistique de prédation, paramétré au sein de ce système naturel qui intègre explicitement les différentes étapes de la séquence de prédation, dont la probabilité de détection. Les simulations issues de ce modèle permettent d'évaluer l'influence de ce paramètre sur le taux d'acquisition de nids d'oies par les renards ainsi que sur le succès de nidification des oies.

Chapitre 1

Spatial scale and indirect interactions modulate density dependence in nest survival of a greater snow goose colony

1.1 Résumé

La densité-dépendance est un concept central en écologie des populations, mais son occurrence et sa force peuvent varier selon le contexte écologique. Parmi les différents facteurs biotiques et abiotiques façonnant la densité dépendance, peu d'études ont examiné comment les interactions avec les autres espèces de la communauté influencent son expression. À partir de données à long terme (1999–2023) recueillies dans une colonie de grandes oies des neiges (*Anser caerulescens atlanticus*) sur l'île Bylot (Nunavut, Canada), nous avons examiné comment le succès de nidification est influencé par la densité de nids à deux échelles spatiales, soit individuelle et populationnelle, et comment cette relation est modulée par l'abondance de lemmings, une proie alternative du renard arctique (*Vulpes lagopus*), principal prédateur des nids d'oies. Avec plus de 8 000 nids suivis sur 20 ans, nous avons d'abord confirmé que la densité de lemmings a un effet positif sur le succès de nidification, et que la date de ponte influence le succès de manière non linéaire. Nous avons ensuite montré que la direction et la force de la densité-dépendance varient selon l'échelle spatiale et l'abondance en lemmings. À l'échelle populationnelle, une densité-dépendance positive apparait uniquement lors d'années de faible densité de lemmings, ce qui pourrait être généré par des changements dans le mouvement et les comportements de quête alimentaire des renards. À l'échelle individuelle, une densité-dépendance négative a été observée, mais uniquement les années de forte abondance de lemmings, suggérant une quête alimentaire accrue des renards dans les zones à forte densité de nids. Bien que la direction de l'effet reste constante entre les échelles spatiales, son intensité diffère. Nos résultats montrent que la densité-dépendance pendant une phase critique du cycle de vie n'est pas constante dans le temps, mais résulte

d'interactions indirectes dynamiques au sein du réseau écologique. Cette étude souligne l'importance d'intégrer les interactions indirectes entre proies et l'échelle spatiale dans l'étude de la régulation densité-dépendante en milieu naturel.

1.2 Abstract

Density dependence is a central concept in population ecology, yet its occurence can differ across ecological context. From the various biotic and abiotic factors influencing density-dependent processes, few studies have examined how interactions with other species in the community shape its expression. Using long-term data (1999–2023) from a greater snow goose (*Anser caerulescens atlanticus*) colony on Bylot Island (Nunavut, Canada), we investigated how nesting success is influenced by nest density at both population and individual scales, and how this relationship is modulated by the abundance of lemmings—an alternative prey of the Arctic fox (*Vulpes lagopus*), the primary nest predator. Based on >8,000 nests monitored over 20 years, we first confirmed that lemming density has a strong positive effect on goose nesting success and that laying date influences success non-linearly, with peak survival occurring around the median laying date. We then found that the strength and direction of density dependence varied with spatial scale and lemming abundance. At the population scale, positive density dependence in nesting success was detected only in years of low lemming density, consistent with shifts in fox foraging behavior. In contrast, negative density dependence emerged at the individual scale, but only in years of high lemming density, suggesting fox restricted their foraging activity in high-density nesting patches. Although the direction of density dependence was consistent across spatial scales, its magnitude differed: positive effects were more pronounced at the population scale, while negative effects were stronger at the individual scale. These contrasting patterns highlight the importance of predator-mediated interactions and spatial structure in shaping density-dependent outcomes. Our findings demonstrate that density dependence during a critical life stage is not temporally constant, but instead emerges from dynamic, indirect interactions within the broader ecological network. This study underscores the need to account for both multi-prey dynamics and spatial scale when evaluating density-dependent regulation in natural populations.

1.3 Introduction

Density dependence is a fundamental mechanism in population dynamics describing the relationship between a population's growth rate and its size (Turchin, 2003). The growth rate is typically negatively density-dependent, meaning that it decreases as population density increases, thereby contributing to population regulation (Sinclair and Pech, 1996; Hixon and Johnson, 2009). Negative density dependence has been documented across a wide range of

taxa (Brook and Bradshaw, 2006). However, its occurrence troughout a population's annual life cycle does not necessarily imply that all life stages are equally affected (Bland et al., 2025). Moreover, when predation is a major source of mortality, density dependence can be positive due to anti-predator mechanisms, potentially resulting in the spatial aggregation of prey organisms (Courchamp et al., 1999; Gascoigne and Lipcius, 2004).

In birds, density-dependent effects on growth rate are often assumed to arise from mechanisms operating during the breeding season (Rodenhouse et al., 2003; Nolet et al., 2013; Ross et al., 2017). Nest survival is a key component of recruitment (Deeming, 2002; Drent and Daan, 1980) and density dependence on this demographic parameter can strongly impact population dynamics (Hoekman et al., 2002). The effect of density on nest survival varies between species and can be positive (Götmark and Andersson, 1984; Pratte et al., 2016; Ringelman et al., 2014), negative (Ferrer and Donazar, 1996; Rodenhouse et al., 2003; Both, 1998) or neutral (Ackerman et al., 2004; Padyšáková et al., 2010).

The effects of density on nest survival can vary across spatial scales (Schmidt et al., 2001; Ackerman et al., 2004), as each scale may encompass distinct ecological mechanisms (Gunnarsson et al., 2013; Rodenhouse et al., 2003; Mackey et al., 2024; Ringelman et al., 2018). For example, density at large spatial scale (> 10 km) can influence broader processes such as predator numerical response (Ringelman et al., 2018; Holt, 1977) and movement behavior (Kittle et al., 2016). In contrast, density at smaller spatial scales (< 1 km) may affect predator searching strategies (Ringelman et al., 2018) or shape direct interactions among prey, including conspecific aggression (Lebeuf and Giroux, 2014) and the use of social information regarding predator presence (Lima, 2009; Gil et al., 2018). Investigating density dependence across multiple spatial scales is therefore essential to improve our understanding of positive or negative feedback mechanisms influencing bird population dynamics (Ringelman et al., 2014).

Changes in predation pressure can influence the strength of density-dependent effects, especially when those effects are partially driven by predation (Gascoigne and Lipcius, 2004). Predation pressure on bird nests can be strongly influenced by the density of alternative prey species (Werner and Peacor, 2003; Schmidt and Ostfeld, 2008; Abrams and Matsuda, 1996; Abrams et al., 1998). For example, fluctuations in small mammal populations in northern ecosystems can alter predator abundance and behavior, thereby indirectly affecting nest predation rates (Blomqvist et al., 2002; Robinson et al., 2014; Gauthier et al., 2024b). Although the effects of density on nest survival may be shaped by the densities of co-occuring prey species, the role of multi-prey dynamics has rarely been incorporated in studies of density dependence in birds.

In this study, we assessed the effects of nest density on nesting success in a colonial Arctic goose species and examined how these effects are shaped by spatial scale - both at the

population scale (colony-wide nest density) and the individual scale (local nest density around a given nest) - as well as by the density of other prey (small rodents) sharing common predators. Our study system is characterized by a large greater snow goose colony (Gauthier et al., 2023). Nest predation is the primary cause of nest failure, with the arctic fox as the main nest predator. Predation pressure on goose nests is typically reduced in years of high lemming density (Bêty et al., 2001; Bety et al., 2002), partly due to behavioral changes in Arctic foxes (Beardsell et al., 2022, 2024). Goose nest density, primarily driven by snowmelt phenology and breeding propensity, varies considerably across time and space, at both individual and population scales (Figure 1.2). These fluctuations may influence nest predation through multiple mechanisms, potentially enhancing or reducing nest survival.

At the individual scale, geese may benefit from the presence of conspecifics. As they actively defend their nest, most predation events occur during incubation recesses when nests are temporarily unattended (Bêty et al., 2001; Beardsell et al., 2021; Samelius and Alisauskas, 2001). Although geese generally dot not directly protect neighbouring unattended nests (Bêty et al., 2001), the presence of nearby individuals could increase the predator detection for geese in recess through social information sharing (Evans et al., 2016; Lima, 2009; Gil et al., 2018). Geese are highly vocal and exhibit conspicuous anti-predator behaviors - such as running toward their own nest or engaging in aggressive displays - when predators are nearby. However, these potential benefits of individual-scale conspecific density could be offset by increased predator encounter rates, as foraging foxes actively select for areas with high nest density (Grenier-Potvin et al., 2021). At the population scale, prey densities can shape arctic fox space use, daily movement rates, energetic balance and risk-taking behavior (Grenier-Potvin et al., 2021; Beardsell et al., 2022, 2024). While increased prey availability may reduce foraging effort and enhance nest survival (Beardsell et al., 2022, 2024), it can also lead to reduced arctic fox home range size and higher nest encounters, potentially decreasing nest survival (Dulude-de Broin et al., 2023; Beardsell et al., 2023).

Previous work conducted on Bylot Island outlined a positive relationship between the annual average goose nesting success and the average nest density measured at the individual scale (i.e., mean number of nests located within 1-ha circle centred on each goose nest Bêty et al. (2001). However, this positive density-dependent effect was observed only in an area with a relatively high nest density and was based on a relatively short time series (6 years; Bêty et al. (2001)). The present study builds on this previous work by leveraging a substantially longer dataset spanning 20 years. We investigated density-dependent effects on goose nesting success at both individual and population scales and tested whether these effects are modulated by interannual variation in lemming density.

1.4 Methods

1.4.1 Study system

We conducted our study within the greater snow goose colony of Bylot Island, Nunavut, Canada (73°08′N, 80°00′W ; Gauthier et al., 2024a). Annual colony size ranges from approximately 1,250 and 24,000 breeding pairs, averaging around 12,000, and is concentrated within a 50-70 km^2 area that is relatively stable across years (Moisan et al., 2025; Duchesne et al., 2021). The colony habitat consists of a mosaic of wetlands and mesic tundra. Wetlands size ranges from 1 to 6 ha and consist of polygons forming a heterogeneous patchwork of narrow channels, lakes and ponds. Mesic habitats occur in drier valleys, gentle slopes, hills and low-lying plateaus (Lecomte et al., 2008; Gauthier et al., 2023).

Colony size is largely driven by annual variation in goose breeding probability (Reed et al., 2004). The decision to breed is partly determined by the individual's body condition (Bêty et al., 2003). Environmental conditions encountered during winter, spring migration (i.e., hunting disturbance), or shortly after arrival at the breeding grounds (i.e, snow depth), can have long-lasting carry-over effects, leading to reduced breeding propensity (Reed et al., 2004; Legagneux et al., 2012a; Grandmont et al., 2023). Snow melt patterns on the breeding grounds also influence the spatial distribution of nests and determine individual nest density (Lepage et al., 1996). Geese often aggregate in early melting areas, generating high individual scale densities. As in other colonial arctic geese, nests are generally loosely spaced, with nests in denser areas being as close as 10 meters (Anderson and Titman, 1992).

Goose nesting success, defined as the proportion of nests for which at least one egg hatched, varies widely across years, ranging from 12 to 90% (Reséndiz-Infante et al. (2020); Cadieux et al. (2024), 1.2b). Predation is the primary cause of nest failure, with the arctic fox accounting for up to 80% of nest attacks (Bêty et al., 2001; Bety et al., 2002). Fox predation typically results in complete clutch predation, exerting the strongest influence on goose nesting success. Other predators, including parasitic jaegers (*Stercorarius parasiticus*, glaucous gull (*Larus hyperboreus*) and common raven (*Corvus corax*), tend to cause only partial nest predations and have a comparatively smaller impact on nesting success (Bety et al., 2002). During the laying and incubation periods, male geese aggressively defend a restricted area surrounding the female and the nest (Gauthier and Tardif, 1991; Anderson and Titman, 1992). Goose females spend 98% of the day incubating their eggs or near their nest, and the vast majority of nest predation occurs during the briefs incubation recesses (Beardsell et al., 2021; Reed et al., 1995).

Two small mammal species, namely the brown (*Lemmus trimucronatus*) and the collared (*Dicrostonyx groenlandicus*) lemming exhibit high inter-annual and mostly synchronous fluctuations in abundance (Gruyer et al., 2008). These population cycles influence bird nesting success by changing the behavior of shared predators, thereby generating short-term, indirect effects through predation (Bêty et al., 2001; Bety et al., 2002; Mckinnon et al., 2013; Lamarre

et al., 2017). In years of high lemming abundance, Arctic foxes primarily consume small mammals, whereas in low lemming years, goose eggs constitute a larger portion of their diet (Giroux et al., 2012). Recent studies have shown that high lemming densities reduce fox daily movement distances and time spent active, leading to lower nest encounter rates and, consequently, increased bird nesting success (Beardsell et al., 2022).

1.4.2 Lemming density

Lemming density was estimated from live-trapping and capture-mark-recapture methods as described in Fauteux et al. (2018). Trapping was conducted in two 11 ha grids—one in mesic and one in wet habitat—located approximately 30 km north of the goose colony. Densities recorded in June, July and August, were averaged, and each habitat-specific estimate was weighted by the relative area of that habitat type within the Bylot Island plain. Densities of the two lemming species were then combined. Based on the distribution of annual lemming density over the study period, we defined two categories : *low*, < 0.89 lemming/ha, and *high* > 1.7 lemming/ha (Appendix S1). The low-density threshold corresponds to the point at witch arctic foxes shift from a negative to a positive energetic balance, as predicted by a mechanistic model of predation (Beardsell et al., 2024). The high-density threshold reflects the level at which fox reproductive effort increases substantially (Bergeron et al., 2025; Juhasz et al., 2020). We assessed whether using categorical (high vs. low) or continuous representations of lemming abundance were preferred when evaluating the effects of lemming and goose nesting densities on nest survival. The categorical representation was preferred at both spatial scales.

1.4.3 Goose nest monitoring

Our study includes data collected during the nesting period (early June to mid-July) from 1999 to 2023, excluding the years 2005, 2006, 2007, 2020, and 2021 due to either the absence of monitoring or the use of different protocols in those years. Each year, we conducted intensive and systematic nest searching during the laying and early incubation periods using two complementary sampling methodologies. First, we consistently monitored a 23 ha wetland patch located near the centroid of the colony. Second, we surveyed randomly selected square plots in wetland (1 ha) and mesic (4 ha) habitats. For each habitat type, 30 random plots were selected annually, and their coordinates were uploaded to GPS devices prior to the start of the field season. Nest searching in random plots continued until 50 nests had been located in each habitat type (i.e., 50 nests in wetlands and 50 in mesic habitats), resulting in a variable number of plots actually surveyed across years.

Nests were revisited once or twice during incubation, and all eggs were identified with a permanent maker to track egg additions or losses. We visited nests at hatch and post-hatch to record the presence of goslings or membranes. A nest was considered successful if at least one

egg hatched, indicated by the presence of either a gosling or a membrane (Reséndiz-Infante et al., 2020). Despite some interannual variation, the proportion of nests monitored by each sampling method remained relatively consistent across years (Appendix S2).

1.4.4 Goose nest density

Population scale

At the population scale, we used a single annual estimate of goose nest density, representing the average density across the entire colony. This index provides an approximation of the number of goose nests occurring within the average home range of an arctic fox (10.8 km^2 in the goose colony ; Dulude-de Broin et al., 2023). We expected this scale to reflect broad-scale ecological mechanisms, such as changes in fox activity (e.g. movement patterns) or in fox density (homerange overlap) in response to variation in resource availability. Annual average nest density was derived from Moisan et al. (2025), who calculated separate densities for wetland and mesic habitats based on intensive and systematic nest searching. Wetland densities were estimated from 1-ha randomly placed nest-search plots, while mesic densities were derived from a combination of 4-ha plots and breeding pair observations recorded during point counts and transects. These habitat-specific densities were then weighted by the proportion of each habitat type within the goose colony (Figure 1.1a). The approximate boundary of the goose colony was delineated opportunistically using a GPS receiver aboard a helicopter during routine flights across the study area that intersected the colony border. Habitat proportions within the colony were subsequently extracted from satellite maps (Dulude-de Broin et al., 2023).

Individual scale

We relied on the most intensively monitored 23 ha wetland patch for this analysis. Individual scale nest density was computed for each nest within the surveyed area. Individual scale density was defined as the number of nests located within a 100 m buffer around a focal nest, divided by the buffer area (i.e., 3.14 ha ; Figure 1.1b). The 100m buffer corresponds to the core area used by geese during incubation : GPS-tracked geese in our study site spent 98.5% of their time within 100 m of their nests during this period. This area is therefore where most interactions with conspecifics should occur, including public information sharing about predator presence, vocalizations and antagonistic behaviors. We included in the analysis only nests whose buffer overlapped by at least 80% with the 23 ha patch (Figure 1.1b). To account for the partial overlap, individual nest density was calculated as :

$$individual\ density = \frac{Number\ of\ nests\ within\ buffer}{Buffer\ area \cdot Proportion\ of\ overlap} \tag{1.1}$$

where percent of overlap ranged from 0.8 to 1. A sensitivity analysis showed that restricting inclusion to nests with ≥80% buffer overlap did not bias individual scale nest density estimates. In this calculation, we assumed that nest density in the portion of the buffer falling outside the surveyed area was similar to that inside, and that any difference would not significantly affect individual scale density estimates or their relationship to nesting success. We therefore considered our corrected estimates sufficiently accurate to assess the effect of individual density on nesting success. All spatial operations were performed using the `sf` package (v1.0-14; Pebesma, 2018) on the R Statistical Software (v4.4.3; R Core Team, 2024).

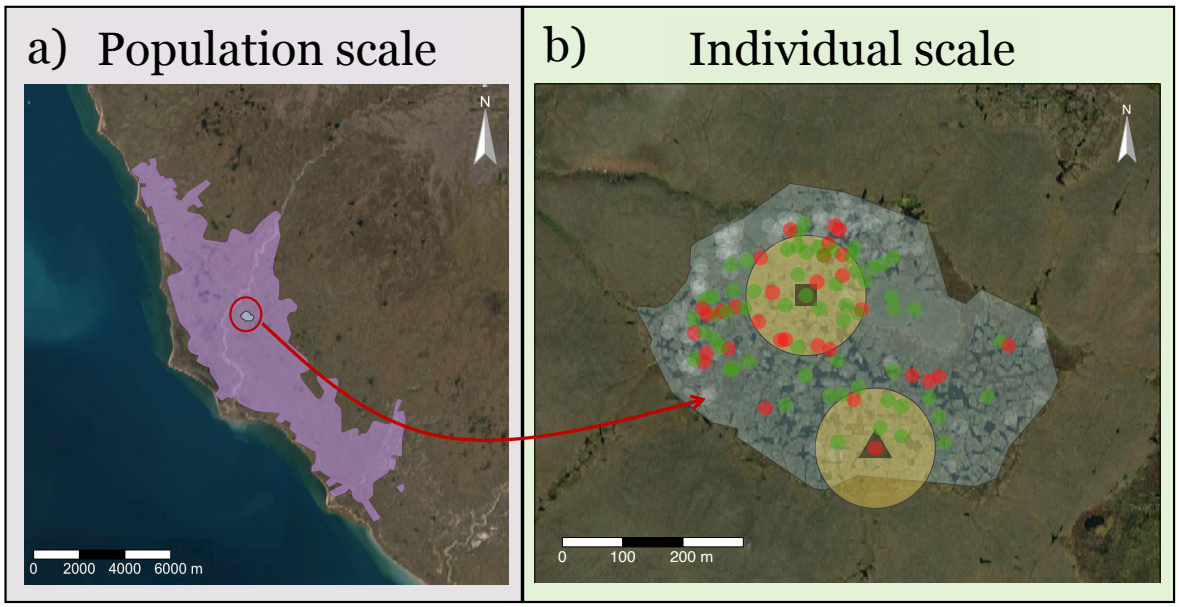

FIGURE 1.1 – Illustration of the two spatial scales of goose nest density used to assess density dependence on nesting success. **a) Population scale :** Average nest density was calculated for the entire colony (purple area). Using multiple monitoring techniques, nest densities were estimated separately for wetland and mesic habitats and then weighted according to the proportion of each habitat type within the colony. **b) Individual scale :** Systematic nest searching was conducted in a large wetland patch near the centroid of the colony (outlined in light blue). Nest of 2017 are show as an example of nest distribution. Individual scale nest density for each nest was calculated as the number of nests within a 100-m (yellow circles) centered on a focal nest (square and triangle), divided by buffer area. We included in the analysis all nests whose buffer was entirely within the surveyed area (e.g., square), allowing up to 20% of the buffer to fall outside the area (e.g., triangle). Green and red represent successful and failed nests, respectively. Dark-colored symbols indicate nests included in the statistical analysis, while pale symbols denote nests excluded due to insufficient buffer overleap or missing data. Nesting success at both spatial scales was determined following the protocols described in the *Goose nest monitoring* section of the Methods.

1.4.5 Statistical analysis

We estimated daily nest survival while accounting for variation in nest exposure periods, as not all nests were discovered at the onset of laying. Maximum exposure for goose nests was

28 days, comprising 5 days of laying and 23 days of incubation. Nest exposure was defined as the number of days between the date of discovery and one of the following endpoints : (i) for successful nests, the observed or estimated hatch date ; (ii) for failed nests, the date of observed predation or the midpoint between the last confirmed active date and the recorded failure date. Nests with undetermined fate were excluded from the analysis. Daily survival rates were converted to nesting success, by extrapolating daily survival rates across the mean nest exposure period within our sample (21 days). For this conversion, we used a power-logistic link function adapted from Shaffer (2004), implemented via code by Mark Herzog and made publicly available by Ben Bolker on RPubs (https://rpubs.com/bbolker/logregexp). This approach models daily survival as a function of covariates while directly incorporating nest exposure time to compute nesting success. We modelled nest fate as a binary response variable (1 = success, 0 = failure ; see *Goose Nest Monitoring* section) using generalized linear mixed models (GLMMs). Fixed effects included goose nest density (population or individual), lemming density (categorical) and relative laying date, previously shown to affect nest success in this system (Lepage et al., 2000). Year was included as a random intercept.

At both scales, each nest corresponds to an observation included in the GLMMs, each nest having a fate and value for the fixed effects. At the population scale (i.e. all nests monitored in a given year) were assigned the same annual density value, whereas at the individual scale (i.e. nests in the large wetland in the colony centroid), each nest was assigned an individual scale density estimate and an annual population scale density estimate. For these nests at the individual scale we were able to compute a population and an individual scale density, allowing us to compare the relative effect of the density at both scales. Nest density values were log-transformed prior to analysis. Predictor collinearity was low (all VIF < 2), justifying inclusion of all covariates in the same model. At the individual scale, we also tested for spatial autocorrelation in nest fate following the methodology described in Fletcher and Fortin (2018) (Appendix S3). No significant autocorrelation was detected, allowing us to consider nests as independent observations. All analyses were performed in R version 4.4.2 (R Core Team, 2024), using the `lme4` package (Bates et al., 2015) for model fitting and the `AICcmodavg` package (Mazerolle, 2023) for model selection.

1.5 Results

The data spans over 20 years, with 11 characterized as high lemming years and 9 as low lemming years (Figure 1.2a). Mean annual goose nesting success across the colony varies more than six fold (12 to 90%) over the study period (Figure 1.2b). Mean nest density at the population scale varied more than twenty-fold, from 0.3 to 7.2 nests/ha, while individual scale nest density varied more than seventy fold (from 0.3 to 23.9 nests/ha ; Figure 1.2).

FIGURE 1.2 – Illustration of the raw data used in the analysis. **a** Time series of lemming densities estimated from capture-mark-recapture. Green and red colors of bars respectively indicate high and low lemming density categories (see *Lemming density* section of methods for the details on this categorization). Years with no data indicate field seasons where logistical constrains impaired comparable field data collection. **b** Time series of mean annual goose nesting success based on all nests monitored each year. Nesting success was estimated by extrapolating daily nest survival rates - calculated from nest exposure time and fate - over the mean nest exposure time period. **c** Time series of mean annual population scale density (mean nest density inside the goose colony). **d** Annual distribution of individual scale density (nest density within 100 m of focal nests) inside a large wetland patch.

1.5.1 Population scale

Goose nesting success was influenced by goose nest density at the population scale, but only in years of low lemming density (Table 1.3, 1.1, Figure 1.3a). In high lemming years, population-scale goose density had no significant effect on nesting success (estimate [95% CI]

= -0.001 [-4.1, 4.8] of change in nesting success (%) per additional nest/ha). In contrast, during low lemming years, population goose density had a strong positive effect on nesting success (25.9 [17.5, 29.1] of change in nesting success (%) per additional nest/ha ; Figure 1.3a and Table 1.3). Models including the interaction between goose and lemming densities explained variation in nesting success better than models without the interaction (1.1). Additionally, laying date had a non-linear effect on nest success, with highest success occurring near the median laying date of each year. Repeating the analysis without accounting for laying date, thus allowing for larger sample sizes, yielded similar results.

TABLE 1.1 – Results of model selection on goose nest density at population scale. K corresponds to the number of parameters estimated for the model ; ΔAICc =AICc of the focal model - AICc of the most parsimonious model ; AICcwt = the rounded Akaike weight. Model parameters are the same as in table1.3, where `population` corresponds to the log of population scale goose nest density that is the same for all nests of a given year, `lemming` corresponds to categorical lemming density and `laying date` represents relative laying date of a nest compared to the median of that year, formulated with a quadratic term. The most parsimonious model based on ΔAICc is highlighted in bold.

Model	K	AICc	Delta AICc	AICcWt
population * lemming + laying date	**7**	**8976.74**	**0.00**	**0.98**
`population + lemming + laying date`	6	8984.35	7.61	0.02
`laying date`	4	8992.17	15.43	0.00
`population * lemming`	5	9069.65	92.91	0.00
`population + lemming`	4	9076.18	99.43	0.00
`lemming`	3	9077.92	101.18	0.00
`Null model`	2	9085.22	108.48	0.00
`population`	3	9086.53	109.79	0.00

1.5.2 Individual scale

Goose nesting success was influenced by individual goose nest density, but only in years of high lemming density (Table 1.3, 1.2, Figure 1.3b). In high lemming years, individual goose nest density had a negative effect of on nesting success (-5.1 [-10.9, 0.4] of change in nesting success (%) per additional nest/ha). Using the within- and between-year comparison proposed by van de Pol and Wright (2009), we found that the negative density-dependent effect was highly consistent within years. In contrast, during low lemming years, individual goose nest density had a slightly positive effect on nesting success (5.1 [-1.9, 13.3]of change in nesting success (%) per additional nest/ha ; figure 1.3 b and table 1.3). However, there was inter-annual variation in the slope of the within year effect of nest density on goose nesting success. This suggests that the effect of density on nesting success varies between low lemming years.

The model including the interaction between individual scale goose nest density and lemming density explained more variation in nesting success than models without the interaction. We were also able to compare the effect of density at both scales with these nests that are in the centroid of the colony. Models that included individual nest density explained more variation in nesting success than models using population-scale density for the same combination of predictors (1.2). Individual nest density was not correlated with relative laying date, suggesting that late-laying individuals did not select or avoid patches of high individual nest density.

TABLE 1.2 – Results of model selection on goose nest density at th individual scale. K corresponds to the number of parameters estimated for the model ; ΔAICc =AICc of the focal model - AICc of the most parsimonious model ; AICcwt = the rounded Akaike weight. Parameters are the same as in table1.3, where `individidual` corresponds to the log of individual scale goose nest density for a given nest, `population` corresponds to the log of population scale goose nest density that is the same for all nests of a given year, `lemming` corresponds to categorical lemming density and `laying date` represents relative laying date of a nests compared to median of that year, formulated with a quadratic term. The most parsimonious model based on ΔAICc is highlighted in bold.

Model	K	AICc	Delta AICc	AICcWt
individual*lemming + laying date	**7**	**2290.37**	**0.00**	**0.38**
individual*lemming + population + laying date	8	2291.06	0.69	0.27
individual*lemming + population*lemming + laying date	9	2292.96	2.59	0.10
population + lemming + laying date	6	2293.61	3.24	0.08
individual + lemming + laying date	6	2293.73	3.36	0.07
population*lemming + laying date	7	2294.33	3.96	0.05
individual + lemming + population + laying date	7	2295.62	5.25	0.03
individual*lemming	5	2298.68	8.31	0.01
lemming	3	2299.66	9.29	0.00
population + lemming	4	2301.44	11.07	0.00
individual + lemming	4	2301.62	11.24	0.00
laying date	4	2302.15	11.78	0.00
population*lemming	5	2302.36	11.99	0.00
Null	2	2310.31	19.93	0.00
population	3	2312.29	21.92	0.00
individual	3	2312.31	21.94	0.00

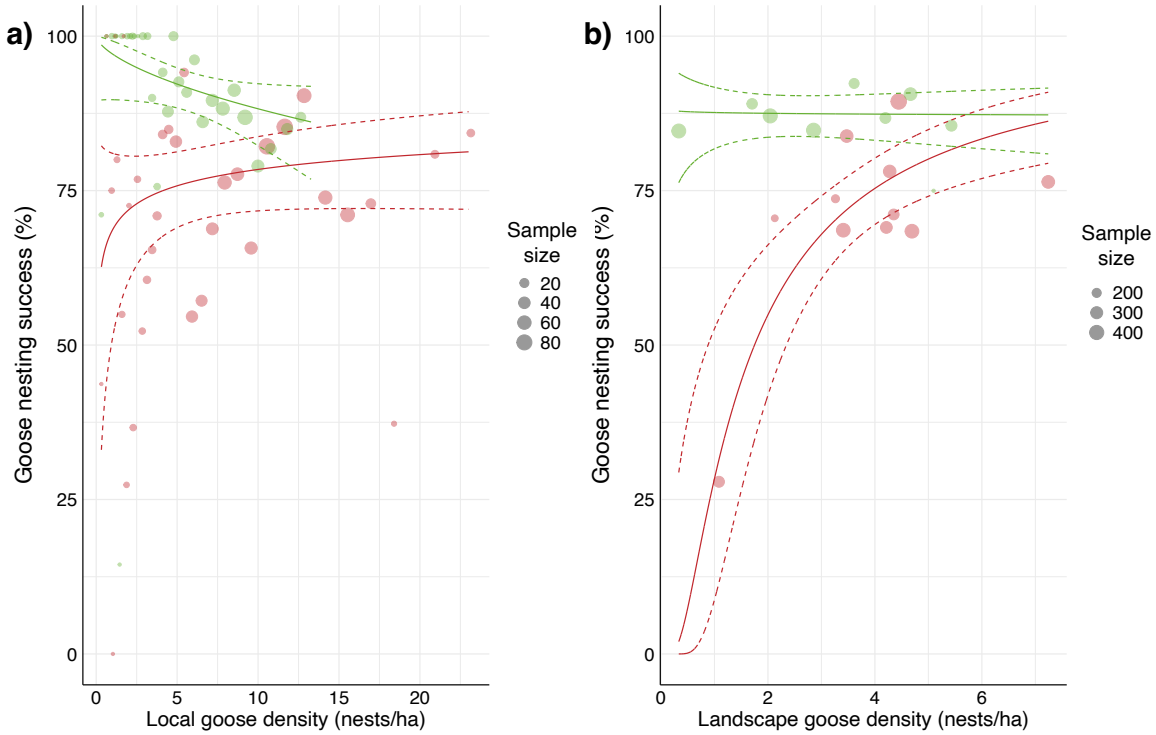

FIGURE 1.3 – Effect of goose nest density on nesting success at the population (a) and individual (b) scales. Nesting success was estimated by extrapolating daily nest survival rates - calculated form nest exposure time and fate - over the mean nest exposure time period (21 days). The interaction with lemming density is indicated by red (low lemming) and green (high lemming) lines. Solid lines represent model predictions, and dotted lines show the 95% C.I. across the mean nest exposure period. Dots represent raw data binned by nest density ; each dot shows the average nesting success within a group of binned nests. Dot size is proportional to the number of nests in that bin. In (a), the raw data are grouped into 40 bins, while in (b) the data are binned by year. Results are based on the most parsimonious model for each spatial scale.

TABLE 1.3 – Parameter estimates of the top-ranked linear mixed model for population and individual scales (see both model selection in table 1.1 and table 1.2). Year was used as a random effect for both models. In both models, log of goose density (respectively `population nest density` and `individual nest density`) in interaction with the categorical `lemming density` (low vs high, with low as the reference level) were used as fixed effects with the additive effect of `relative laying date` specified with a quadratic term.

POPULATION SCALE : `population nest density * lemming + relative laying date`^{2}					
Fixed Effect	Estimate	Std. Error	z value	p-value	
(Intercept)	-2.56	1.54	-1.66	0.096	ns
population nest density	1.10	0.26	4.18	2.87e-05	***
lemming high	7.42	1.82	4.08	4.43e-05	***
relative laying date	-1.59	1.94	-0.82	0.41	ns
relative laying date^2	-18.98	1.68	-11.27	< 2e-16	***
population nest density:lemming high	-1.11	0.31	-3.56	0.00037	***
INDIVIDUAL SCALE : `individual nest density * lemming + relative laying date`^{2}					
Fixed Effect	Estimate	Std. Error	z value	p-value	
(Intercept)	3.77	0.30	12.57	< 2e-16	***
individual nest density	0.19	0.14	1.34	0.18	ns
lemming high	2.57	0.74	3.49	0.00048	***
relative laying date	4.16	2.20	1.89	0.059	.
relative laying date^2	-5.36	1.81	-2.97	0.0030	**
individual nest density:lemming high	-0.83	0.36	-2.27	0.023	*

Significance codes : *** : p-values ≤ 0.001 ; ** : p-values ≤ 0.01 ; * : p-values ≤ 0.05 ; . : p-values ≤ 0.1 ; ns : p-values ≥ 0.1.
`Relative laying date`^{2} represents the quadratic term of the `Laying date` variable.

1.6 Discussion

We investigated density dependence in nest survival using data from >8,000 nests monitored across 20 years within a 25-year study period in a greater snow goose colony. We found evidence that density dependence varied with spatial scale (population vs individual) and was modulated by the density of an alternative prey species - lemmings - that share common predators with geese. The direction of the effect of goose nest density on nesting success was consistent across scales for a given lemming density, while its strength differed between scales : positive effects were stronger at population scale, whereas negative effects were more pronounced at the individual scale.

1.6.1 Population scale

We found a positive density-dependent effect at the population scale, but only in years of low lemming density (Figure 1.3a). In contrast, no density-dependent effect was detected in years of high lemming density. Positive density dependence at population scale aligns with what has been reported by former studies in geese (Bêty et al., 2001; Bousfield and Syroechkovskiy, 1985). We also confirmed that lemming density has a strong positive effect on goose nesting success (Bêty et al., 2001) and validated a non-linear effect of laying date, with highest success occurring near the median laying date (Lepage et al., 2000). Positive density dependence, has been reported in several other bird species (Götmark and Andersson, 1984; Birkhead, 1977; Cuthbert, 2002; Picman et al., 2002) and is particularly likely to emerge when predation is a dominant source of mortality (Gascoigne and Lipcius, 2004).

Our study provides a rare empirical example of density-dependent effects in a prey species being modulated by the fluctuating abundance of other prey species within the same ecological community. Van Dellen and Sedinger (2020) showed that in a black brant (*Branta bernicla nigricans*) colony in Alaska the effect of nest density on nesting success varies accordingly to their index of fox predation pressure. While they do not explicitly describe what determines the intensity of fox predation in their system, their result suggests that density dependence can be influenced by predation. Similarly, in some California waterfowl populations, the direction of the effect of nest density on nest survival appears to change depending on small mammal abundance (Ackerman, 2002). Rodent abundance can have more complex effects on the relation between bird density and nesting success, as small mammal density may also influence the spatial distribution of nests in some colonial bird species. For example, fieldfares (*Tudrus pilaris*) often form colonies of a few dozen individuals, and colonial individuals experience a better nesting success than solitary nesters (Wiklund and Andersson, 1980). However, fieldfares are more likely to establish such colonies in years of high rodent abundance, when predation pressure from mustelids is reduced - likely because these predators can focus their activity in areas where prey are clustered (Hogstad, 1995).

In our system, arctic foxes are territorial and exhibit strong attachment to their territories from year to year, particularly within the goose colony, which provides a predictable food source that can allow for higher breeding ouput compared to areas outside the colony (Clermont et al., 2021; Giroux et al., 2012; Lai et al., 2017). Given the fitness advantage to keep a territory, foxes tend to remain within their territories even in years of low prey availability, relying on cached food or short excursions outside their territory (Lai et al., 2017). This behavior results in sustained predation pressure on the remaining prey within the territory (Bêty et al., 2001). Consequently, geese experience the highest predation pressure during years with both low goose nest density and low lemming abundance (Figure1.3a). In such years, fox sightings near the goose colony centroïd are more frequent (Bety et al., 2002), indicating increased predator activity - and by extension, higher nest encounter rates between fox and geese. This heightened activity may stem from several proximate mechanisms triggered by food scarcity, including increased daily distance traveled (Beardsell et al., 2022), a greater nest attack probability (Bety et al., 2002; Beardsell et al., 2024) or increased overlap with adjacent home ranges, to access additional patches including goose nests. Further studies are needed to disentangle the relative contribution of these potential mechanisms.

We suggest that classical dilution mechanisms, such as predator swamping or prey handling (Hamilton, 1971; Bednekoff and Lima, 1998), are unlikely to be the main drivers of the positive effect of nest density on nesting success we observed. Recent studies challenge the prevalence of saturation in natural systems, emphasizing that predator acquisition rates may rarely be saturated in natural ecosystems (Coblentz et al., 2023). We found little evidence of satiation in arctic foxes within our system, particularly given that this predator is known to engage in surplus killing and cache most of its captured preys for consumption during months where prey are scarce (Beardsell et al., 2021; Careau et al., 2007). Moreover, passive dilution is less likely in species like geese, which actively defend their eggs against predators (Samelius and Alisauskas, 2001).

1.6.2 Individual scale

We found a negative density-dependent effect at the individual scale, but only in years of high lemming density (Figure 1.3b). In contrast, little evidence of density dependence was detected in years of low lemming density. This pattern aligns with findings from several goose populations, where negative density dependence was observed during the breeding period (Layton-Matthews et al., 2019; Thompson, 1998; Lebeuf and Giroux, 2014). Similar patterns have been observed to be created by predation in other birds (Gunnarsson and Elmberg, 2008; Carpio et al., 2016). We thus suspect that shifts in predator behavior may drive the emergence and variability of negative density dependence across years.

Arctic foxes increase their prey searching activity in the areas with high goose nest density (Mckinnon et al., 2013; Grenier-Potvin et al., 2021). We hypothesize that in years of high

lemming abundance, fox activity is concentrated in the densest nesting areas, whereas in low lemming years, when overall food availability is reduced, foxes may search more broadly across all nesting patches, regardless of individual scale nest density. This is consistent with previous studies suggesting that predator foraging behavior can generate density-dependent predation patterns (Schmidt and Whelan, 1999; Whelan et al., 2003). In our system, a field experiment provided strong evidence that arctic fox detection of goose nests does not vary with nest density, allowing us to rule out that changes prey detection rates are a proximate mechanism underlying the observed negative density dependence (Chapter 2 of this thesis).

Individual scale density could also influence interactions among geese. On one hand, nesting in close proximity increases the likelihood of antagonistic encounters, with rates reaching nearly three aggressive interactions per hour (Gauthier and Tardif, 1991). On the other hand, high individual scale nest density can enhance the transmission of social information about predator presence (Evans et al., 2016; Gil et al., 2018). Denser nesting areas include more individuals capable of detecting and reacting to predators, either by directly signalling to conspecifics or through behavioral cues associated with anti-predator defence (Danchin et al., 2004; Lima and Dill, 1990).

If interactions among geese - such as competition or information sharing - were the primary drivers of density-dependent effects, we would expect consistent patterns across lemming densities, since geese are unlikely to adjust their behavior in response to lemming dynamics. This would result in either negative density dependence due to competition, or positive density dependence driven by social information sharing. The observed shift in density dependence slope between low and high lemming years suggests that the effects of nest density on nesting success are not generated by prey behaviors, but are instead mediated by predator behavior responding to abundance of another prey.

Success of nests monitored near the colony centroid appears to be more strongly influenced by individual scale nest density than density at the population scale. Geese may thus have an advantage when nesting in the colony centroid - which typically has a higher nest density compared to the rest of the colony - because nests in that area may be more resilient to fluctuations in density at broader spatial scales. At the individual scale, we found a negative relationship between nest density and nesting success. However, this does not imply that colonial nesting is disadvangtageous in terms of nesting success. In fact, our results at the population scale suggest that nesting at very low densities (< 2 nests/ha in the whole colony) increases vulnerability to fluctuations in lemming abundance and thus changes in predator behavior. Thus, although we detect a negative effect of density at the individual scale, our findings support the fitness value of colonial nesting.

1.6.3 Density dependence at the subspecies level

Understanding density dependence in migratory species is particularly challenging because their vital rates - and ultimately population regulation - are influenced by conditions encountered across breeding, wintering and stopover sites. Like resident species, migratory populations can experience negative density dependence when increasing population size limits survival or reproduction (Newton and Brockie, 1998), but identifying when and where such processes operate is complex. We showed that density dependence during a key life stage - the breeding season - varies between years depending on predation pressure. This temporal variability in breeding output component should be integrated into future studies of population dynamics in migratory species. Population level surveys in greater snow geese have not detected strong negative density dependence in this goose subspecies (Morrissette et al., 2010; Lefebvre et al., 2017), unlike in other goose populations (Trinder et al., 2009; Alisauskas et al., 2024), which may reflect the effects of harvest limiting population growth. Alternatively, density dependence might only emerge as population size approaches the carrying capacity of the ecosystem. On Bylot Island, current population levels appear well below this threshold : geese consume only 10% of available primary production (Legagneux et al., 2012b) and many potential nesting sites remain unoccupied. In contrast, density dependence has been linked to the saturation of optimal nesting habitat in other goose colonies (Rodenhouse et al., 1997).

1.7 Conclusion

Our results suggest that variation in predator behavior and abundance - particularly in response to fluctuating prey like lemmings - can modulate the strength and direction of density dependence in colonial arctic-nesting geese. This highlights the critical role of predation pressure during the breeding season and underscores the importance of evaluating density-dependent processes across multiple scales. To our knowledge, such predator-mediated interactions are rarely integrated into studies on density dependence in birds during reproduction (but see Ackerman (2002); Van Dellen and Sedinger (2020)). The underlying mechanisms are likely complex and diverse, warranting future research to isolate and quantify their individual contribution to population dynamics. We also advocate for greater consideration of predator mediated indirect interactions between prey species as a factor shaping density dependence. Had we not accounted for predator mediated interactions, our results would have suggested only weak or absent density dependence. The logistical challenges of community-wide monitoring in remote ecosystems may partly explain why such effects sometimes go undetected (Gunnarsson et al., 2013). Detecting density dependence in natural populations can be difficult (Berryman et al., 2002) and signals may be weak or inconsistent (Strong, 1986). By incorporating both spatial scale and trophic context, our study provides a framework to improve detection and interpretation of density-dependent processes in the wild.

1.8 Supplementary Materials

S1 Identification of lemming density threshold

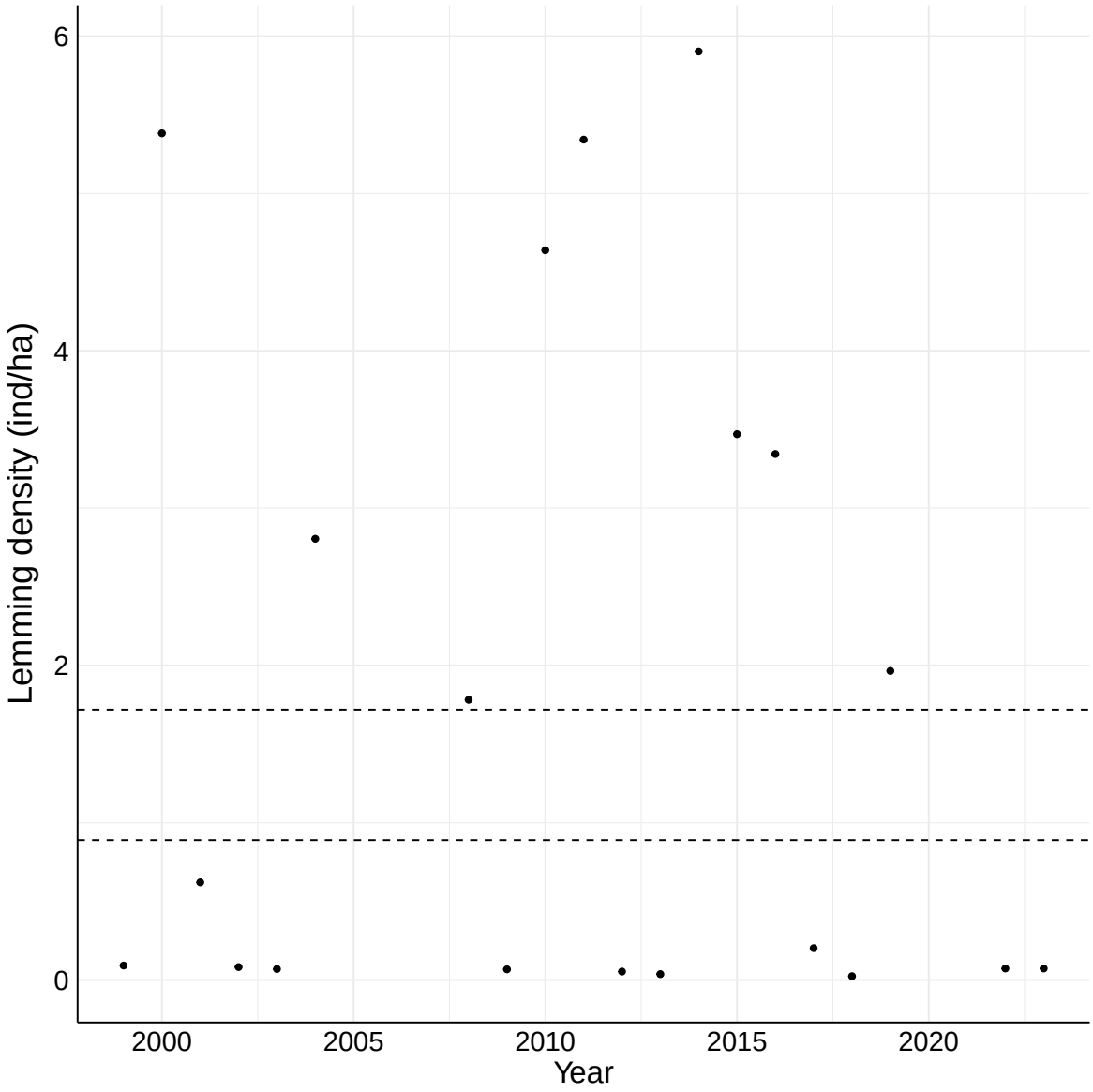

FIGURE 1.4 – Distribution of combined density of brown and collared lemmings. Dashed lines respectively correspond to density thresholds for low, < 0.89 lemming/ha, and *high*, > 1.7 lemming/ha, years. Low threshold correspond to the predicted shift from negative to positive fox energetic balance (Beardsell et al., 2024). High threshold indicates the level at which fox reproductive effort increases markedly Bergeron et al., 2025

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S2 Annual proportion of nests by sampling method

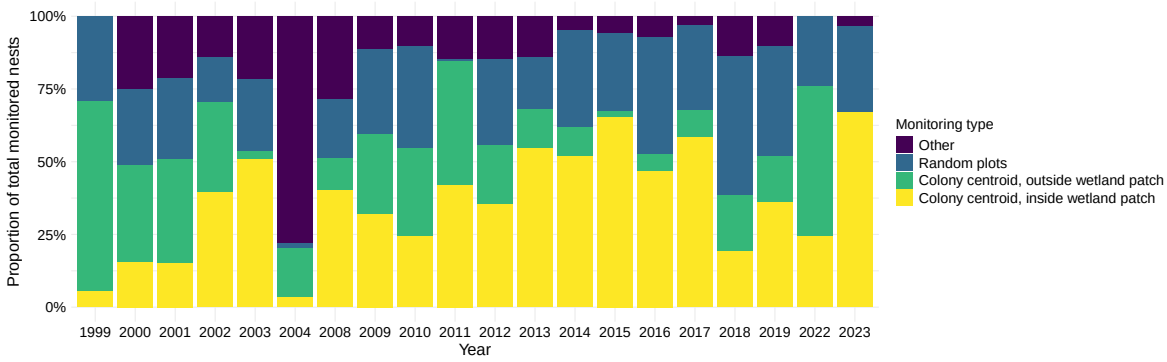

FIGURE 1.5 – Contribution of each monitoring type (colony centroid, random plots and others) to the total number of nests monitored for each year. Yellow corresponds to nests within the 23ha large wetland patch in the centroid of the colony (1.1b). Green corresponds to monitored nests also in the colony centroid, but outside the main wetland patch and rather in the mesic habitat or the wetlands in the vincinity of this patch (Figure 1.1b). Blue corresponds to nests found in random plots that are distributed across the goose colony. Purple corresponds to nests inside the colony that were found opportunistically, outside of the systematically surveyed areas.

All nests were monitored with the same methodology, but come from different nest searching plots and areas of the colony. All monitored nests, regardless of their monitoring type or location in the colony were included in the analysis at the population scale. Daily nest survival of all these nests was converted to yield the annual estimate of nesting success at the population scale. Nests in the colony centroid represent a relatively stable proportion of all monitored nests across years.

Nests included in the analysis at individual scale come from the group in yellow (nests in the colony centroid and inside the thoroughly searched 23ha large wetland patch).

S3 Example of autocorrelation analysis of nesting success

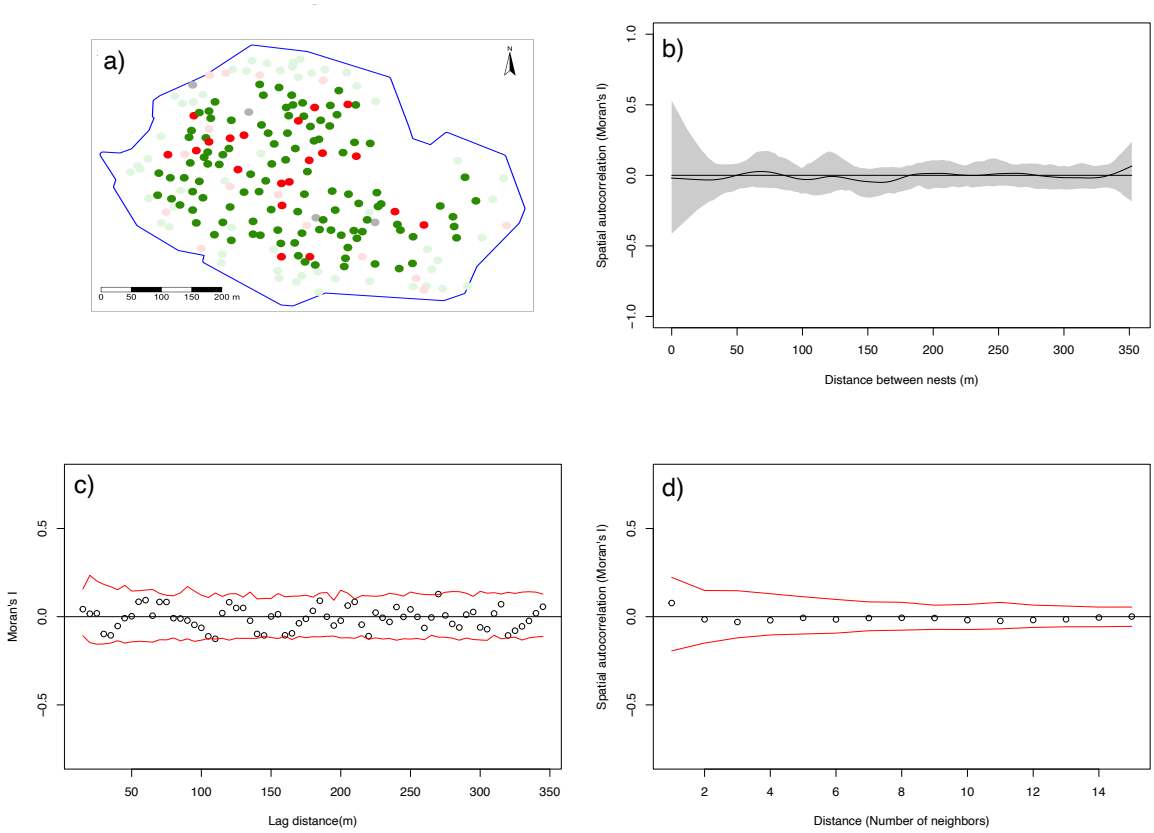

FIGURE 1.6 – Evaluation of spatial autocorrelation in nesting success at the individual scale, using 2015 data as an example, see Fletcher and Fortin (2018) for detailed code. a) Distribution of nests (dots) within the systematically surveyed large wetland patch (blue polygon). Green and red dots respectively represent successful and unsuccessful nests. Dark-colored dots indicate nests included in the analysis, while pale dots were excluded from the analysis but used to calculate individual scale nest density. b) Moran's I correlogram showing the spatial autocorrelation of nest fate as a function of inter-nest distance. The shaded area represents the 95% confidence interval. c) Moran's I correlogram with data points (dots) and null model boundaries (red lines), representing the range of values expected under no spatial autocorrelation. d) Nearest neighbor correlogram, showing the correlation in nest fate between a focal nest and its *n*th neighbor.

Consistent with other years, nesting success showed no evidence of spatial autocorrelation in 2015. The examplified output of the analysis for 2015 is similar to what the test for spatial autocorrelation of nesting succes yielded for other years.

Chapitre 2

Field experiment suggests that prey density does not change prey detection by the predator

2.1 Résumé

La détection des proies par le prédateur influence fortement l'intensité des interactions trophiques. Bien que la variation de la probabilité de détection ait été proposée par plusieurs auteurs comme un mécanisme pouvant générer la densité dépendance ou créer un changement de préférence de proies, elle demeure rarement quantifiée en milieu naturel. Nous avons mené une expérience sur le terrain durant trois années consécutives dans la toundra arctique, en nous concentrant sur l'interaction entre le renard arctique et l'oie des neiges. Nous avons estimé la probabilité de détection des nids d'oies par le prédateur en réponse à la variation de densité de ces proies. Nous avons ensuite intégré ces probabilités de détection dans un modèle mécanistique multi-espèces afin d'estimer la réponse fonctionnelle du prédateur et d'évaluer l'impact de la variation observée de probabilité de détection sur le taux d'acquisition du prédateur et la survie des proies. Nous avons utilisé des paires de nids artificiels disposées à différentes distances les uns des autres (de 10 à 120 m) et évalué le sort des deux nids à l'aide de pièges photographiques placés à proximité de chaque nid. Nous avons observé que la probabilité de détection des nids par les renards diminuait avec la distance entre les deux nids d'une paire. Ce patron restait similaire entre les années, malgré de fortes variations des densités de nids d'oies et de lemmings, les principales proies des renards arctiques. Les simulations avec le modèle mécanistique de prédation ont suggéré que la variation interannuelle du succès de nidification des oies observée sur le terrain ne peut être expliquée par les légers changements dans la probabilité de détection des nids mesurés via notre expérience. Notre étude souligne l'importance de tester les mécanismes en milieu naturel afin que l'interprétation des patrons de prédation observés en nature soit cohérente

avec les mécanismes proximaux qui les génèrent. Nous plaidons pour une augmentation des études utilisant une approche modulaire et des expériences de terrain pour identifier les mécanismes proximaux qui déterminent la force des interactions trophiques.

2.2 Abstract

Prey detection by predators greatly influence the strength of trophic interactions. While detection probability variation has been proposed to generate density dependence or prey switching, it has been rarely quantified in natural settings. We conducted a field experiment in the Arctic tundra focusing on the interaction between Arctic fox and greater snow geese. We estimated the prey detection probability by the predator using paired artificial nests deployed at different distances (10-120m) over three years of contrasted prey densities. We further included these detection probabilities into a multi-species functional response model to evaluate the impact of detection probability on predator acquisition rate and prey survival. We found that nest detection probability by foxes decreased as the distance between paired nests increased. This pattern remained similar in all years, despite strong inter-annual variation in both goose nest and lemming densities, the main prey of arctic foxes. Simulations with the mechanistic model of predation indicated that the observed inter-annual variation in goose nesting success cannot be explained by the changes in nest detection probability measured in our experiment. This study highlights the importance of empirically testing such mechanisms in the field to ensure that predator-prey models incorporate the right proximal mechanisms to generate the observed patterns. We call for an increase in studies using a mechanistic approach and experiments on the field to untangle proximate mechanisms underlying interaction strength.

2.3 Introduction

Predation is a cornerstone of ecosystem structure as it creates energy flow between trophic levels (DeLong, 2021; Brose et al., 2008). The strength of trophic interactions depends on physiological, behavioral and morphological traits of both predators and preys as well as their relative abundance (Abrams and Ginzburg, 2000; Brose et al., 2019). Interactions strength corresponds to number of prey captured per unit of time, which is the product of a series of steps leading to prey capture, namely the predation sequence. Breaking down of this sequence allows for a better parameterization of trophic-interaction models and ultimately the modelization of entire food dynamics (Wootton et al., 2023; Cherif et al., 2024). This modular approach to predation also enables precise study of these steps which will in turn offer a better understanding of mechanisms underlying predator-prey interactions (Spalinger and Hobbs, 1992; Prokopenko et al., 2023; Beardsell et al., 2023; Cherif et al., 2024).

The first step in the predation sequence corresponds to the prey detection by the predator. This parameter is known to have the potential to greatly influence the strength of trophic interactions (Lima and Dill, 1990; Andersson, 1981; Beauchamp, 2013). Prey have developed multiple adaptations to reduce detection probability (cryptic coloration (Dimitrova and Merilaita, 2014; Stevens and Merilaita, 2009) ; increased vigilance (Beauchamp, 2015) ; reduced activity (Lima, 1998)) and predators evolved structures to increase detection (Köppl et al., 1993). Prey detection by the predator can be visual, olfactive, auditive or physical and its importance for interaction strength has been shown for various species (Stevens, 2013), from vertebrates such as bats (Page and Bernal, 2020) to invertebrates such as crabs (Weissburg et al., 2002; Smee, 2012).

Prey detection by predators is a behavior that could change according to prey density (Cornell, 1976; Nams, 1997; Ishii and Shimada, 2010). Predators face cognitive constraints in image interpretation, such as limited attention and memory, which affect effective detection of multiple prey types (Dukas, 2001, 2002). Mechanisms have been proposed and tested in laboratory settings to explain how predators adjust detection with regard to these constraints (changing prey density and limited predator attention) to maintain optimal foraging (Dukas and Ellner, 1993; Dukas, 2004; Bond, 2007; Garay et al., 2018). The most commonly proposed mechanism is the formation of a *search image*, whereby the probability of detecting a particular prey by a predator increases with that prey's abundance because high encounter rate with a prey is supposed to create a more acute illustration of the prey in the predator's mind (Dawkins, 1971; Pietrewicz and Kamil, 1979; Bond, 1983; Lawrence, 1985; Gendron, 1986; Bond and Kamil, 1998, 2002). Detection probability is thus presumed to change with biological context and search image formation is sometimes proposed as a mechanism causing density-dependent nest predation (Schmidt and Whelan, 1999; Whelan et al., 2003; Lloyd, 2006), but few studies have measured detection probability in natural ecosystems where the densities of multiple prey species vary simultaneously. Studies on detection probability and search image were generally conducted through experiments in controlled environments (Gendron and Staddon, 1983; Reid and Shettleworth, 1992; Dukas, 2001; Nams, 1997; Ishii and Shimada, 2010; Price and Banks, 2016), but rarely in natural systems (ex. (Vigallon and Marzluff, 2005; Morgan and Brown, 1996). Evaluating in the wild the variations in detection probability and their impact on prey demographic parameters thus represents a knowledge gap.

The sessile and generally cryptic feature of bird nests offers a valuable opportunity to evaluate detection probabilities under natural conditions. Moreover, interpretation of fluctuations in nest survival can be directly related to predation as it is the main cause for nest failure in birds (Menezes and Marini, 2017; Ricklefs, 1969; Skutch, 1985; Martin, 1993; Thompson Iii, 2007), providing an ideal study system to conduct experiments and assess detection probability of predators. The outcome of such experiments can be further integrated in mechanistic approach models where this specific component of the predation sequence is implemented

to simulate population-level impacts of detection probability and assess its demographic significance (Beardsell et al., 2021, 2022).

Our study system, characterized by i) a generalist predator, the arctic fox (*Vulpes lagopus*), feeding mainly on small mammals and bird eggs during the summer (Bety et al., 2002; McKinnon and Bêty, 2009; Giroux et al., 2012), ii) the presence of a breeding colony of greater snow geese (*Anser caerulescens atlanticus*), with annual variations in goose nest density Gauthier et al., 2013; Moisan et al., 2025) and iii) high-amplitude fluctuations of lemming populations (with peaks occurring every 3-5 years) that indirectly affect bird nesting success (Bêty et al., 2001; Blomqvist et al., 2002) is ideal to setup field experiments to assess detection probability.

We conducted an artificial goose nest experiment over three years of contrasted prey densities, to estimate detection probability and we further assessed how interannual variation in predator detection influences functional response and prey survival, using a multi-species mechanistic model (Beardsell et al., 2021, 2022, 2023). Specifically, we tested the following hypothesis : The *detection adjusment hypothesis* predicts a predator's ability to detect a given prey to increase with its density (Pietrewicz and Kamil, 1979), such that detection probability of artificial goose nests should increase in years of high goose nest density. Additionally, following this hypothesis, a high lemming density could enhance lemming detection while reducing detection of goose nests (Dukas, 2001).

2.4 Methods

2.4.1 Study system

This study was conducted over three consecutive summers from 2022 to 2024 within a large greater snow goose colony located on the southern plain of Bylot Island, Nunavut, Canada (73°08′N, 80°00′W ; Gauthier et al., 2023, 2024a). The colony supports approximately 12 000 breeding pairs in an area of 50-70 km^2 characterized by a mosaic of wetland polygons, small lakes, ponds and mesic tundra (Moisan et al., 2025; Lecomte et al., 2008). Two species of small mammals are present : the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings. Brown lemmings exhibit pronounced population cycles with a periodicity of 3 to 5 years, while collared lemmings cycles are of smaller amplitude (Gruyer et al., 2008).

Goose nesting success fluctuates substantially between years (Cadieux et al., 2024), with predation by the arctic fox causing the majority of nesting failure (Bêty et al., 2001; Gauthier et al., 2024a). Nesting success is positively associated with lemming abundance, as low lemming density typically increases predation pressure on goose nests (Royer-Boutin, 2015). This is partly explained by changes in fox movement patterns - specifically, increased daily

distance traveled when lemming numbers are low (Dulude-de Broin et al., 2023; Beardsell et al., 2022). In all years, goose eggs constitute a large proportion of the diet of foxes foraging within or close to the goose colony (Giroux et al., 2012). During the summer, arctic foxes acquire more prey than they consume in the short-term as they cache a large number of prey items for future consumption (Careau et al., 2008; Samelius et al., 2007).

Goose nest density varies greatly between years and is known to influence fox acquisition rate (Bêty et al., 2001 ; Chapter 1 of this thesis). Goose females spend 98% of the day incubating their eggs or near their nest (<10m), and the vast majority of nest predation occurs during the brief incubation recesses away from the nest (Reed et al., 1995; Beardsell et al., 2021). We thus focused our study on fox detection probability of unattended goose nests.

2.4.2 Study design

We here describe the general structure of our study (Figure 2.1a). To evaluate if fox nest detection varied between years, and test the *detection adjusment hypothesis*, we leveraged natural variation in annual prey density. In **2022**, both goose and lemming densities were low, with goose nest density among the lowest recorded since the beginning of our long-term monitoring in 1989 (Moisan et al., 2025). In contrast, **2023** was characterized by high goose density but low lemming density, while **2024** featured high densities of both prey species (Figure 2.2a and b). Over this period, goose nest density varied more than threefold, and lemming density increased by a factor of twenty (Figure 2.2 a and b). Goose nesting success also fluctuated by a factor of two across the same three years (Figure 2.2c).

In those three years, we used pairs of artificial nests spaced by 10 to 120 m apart within each pair to estimate i) the detection probability function within the fox's detection range, and ii) whether this function varied between years (see details in the *Artificial nest experiment* section below and in figure 2.1b).

To further investigate the *detection adjustement hypothesis*, we integrated our experimental estimates of unattended nest detection probability into a mechanistic model simulating fox predation. Altough the model is not spatially explicit, we used the mean detection probability within detection range, which likely reliably reflects nest acquisition rates at observed density of unattended nests (see the *Functional response of arctic fox to goose nests* section below for details on this transformation). In the simulations, we varied fox detection probability using annual means from the artificial nest experiment, while keeping all other model parameters constant (see model details in the sections below and in Figure 2.1c).

2.4.3 Goose and lemming density

For 2022 and 2023, we used the average goose nest density in the colony as estimated by (Moisan et al., 2025). Nest density in wet habitat was obtained through intensive, systematic

nest searching plots, whereas density in mesic habitat was derived from a combination of systematic nest searching plots and observations of breeding pairs recorded during points counts and transects. Density by habitat was then weighted by the proportion of each habitat within the goose colony. In both years, we opportunistically mapped sections of the goose colony boundary with a GPS receiver aboard a helicopter. Proportion of each habitat within the colony was then derived from satellite maps (Dulude-de Broin et al., 2023). In 2024, due to a major logistic constraint, we were only able to visit the study area shortly after the goose hatching period and hence we were able to obtain a minimal nest density from remaining empty nest bowls found during survey. We conducted an intensive systematic nest search in a 0.23 km^2 wetland and in 8.5 0.04 km^2 mesic plots distributed randomly in the colony to compute the wetland and mesic densities respectively. These densities were weighted within the average colony polygon between 2010 and 2023. We then classified each year as having a *low* or *high* goose nest density based on whether it was below or above the long-term average derived from data in (Moisan et al., 2025 ; Appendix S1).

Lemming density was estimated from mark-recapture with live-trapping as described in (Fauteux et al., 2018). Trapping was conducted 30 km north of the goose colony in two 0.11 km^2 grids, one in mesic and one in wet habitat. We averaged the densities measured during June, July and August, then weighted density in each habitat by its occurrence in the Bylot Island plain and finally combined the two lemming species. Lemming density appears to have a non-linear effect on other species in our system, where beyond a certain density threshold various ecological processes increase substantially, namely presence of nesting avian predators (snowy owls (*Bubo scandiacus*), long-tail jaegers (*Stercorarius longicaudus*)) and fox reproduction (Gauthier et al., 2024a). As other studies in our system (Dulude-de Broin et al., 2023; Duchesne et al., 2021), we considered lemming density categorically : *low* lemming (< 170 lemming/km^2) and *high* lemming (>170 lemming/km^2). This is the threshold for the marked increase in fox reproduction (Bergeron et al., 2025), which is coherent with fox switch to a positive energetic balance (Beardsell et al., 2024 ; see Chapter 1 of this thesis for details on this threshold).

2.4.4 Empirical goose nesting success

For 2022 and 2023, goose nests were searched systematically in a 0.23 km^2 wetland in the centroid of the colony and in random plots of 0.01 and 0.04 km^2 for wetland and mesic habitats, respectively. Nests were searched during laying and incubation period to find all nests, including early-failed nests. Nests were revisited once or twice during incubation and all eggs were identified with a permanent marker to monitor new or missing eggs. We revisited nests at hatch and after hatching to record presence of gosling or membranes. We considered nests successful if at least one egg hatched (i.e. if at least one gosling or one membrane was recorded in the nest ; Reséndiz-Infante et al., 2020. Nesting success for a given

year is derived from daily nest survival of all monitored nests. Daily nest survival rates were extrapolated across the mean nest exposure period (time between a nest was found and when its fate was determined) within our sample (21 days) to calculate overall nesting success. For 2024, we conducted an intensive systematic nest searching in a 0.23 km^2 wetland and in 0.34 km^2 from 8.5 mesic plots distributed randomly within the colony. This monitoring was done after hatching and nests were considered successful if at least one membrane was found in the empty nest. For that year, nesting success corresponds to the proportion of successfull nests.

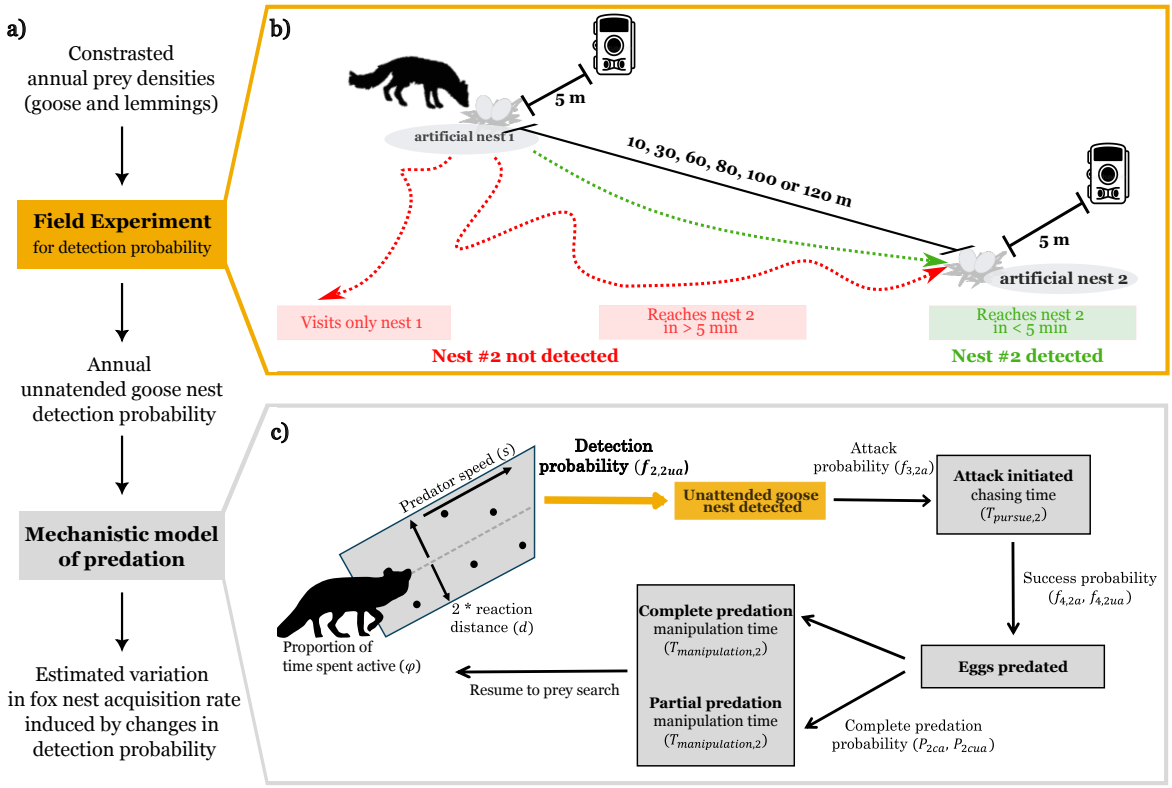

FIGURE 2.1 – **a)** Study design. In three consecutive years marked with contrasted prey densities (lemmings and goose nests), we conducted a field experiment (detailed in b) to measure detection probability of artificial unattended goose nests by arctic foxes. For each year, data from the experiment was averaged to generated a mean annual detection probability. We then evaluated the impact of the annual variation in detection probability on goose nest acquisition rate by arctic foxes using a mechanistic model of predation (detailed in c). **b)** Illustration of the field experiment conducted using artificial goose nests. Each nest consists of two hen eggs covered with goose down. Paired nests were located at 10, 30, 60, 80, 100 or 120 meters apart. We considered that there was a detection if a fox predated nest #1 and reached nest #2 in less than 5 minutes. Other scenarios were considered as non detections. **c)** Simplified illustration of the mechanistic model of predation showing, for unattended nests, the breaking of fox predation sequence in into 6 steps : (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) capture and (6) manipulation. We highlighted the parameter that was measured experimentally in the field (unattended goose nest detection probability). For full model equations, see Beardsell et al. (2023).

2.4.5 Artificial nest experiment

Goose eggs were simulated using domestic chicken eggs, which, despite being slightly smaller, closely resemble goose in shape and color. Each artificial nest contained two hen eggs placed in a 15 cm-wide nest bowl made of goose down collected from nests that showed no signs of predation (Beardsell et al., 2021; Lecomte et al., 2008; Bêty et al., 2001 ; Figure 2.1b). This method has been validated and widely used in our study system (Bety et al., 2002; McKinnon and Bêty, 2009; Mckinnon et al., 2013). Artificial nests were placed in pairs, spaced 10 to 120 meters apart, in a relatively flat terrain. Motion-triggered cameras (model PM35T25, Reconyx) were set on small tripods five meters from each nest to identify nest predators and record the time of predation (Figure 2.1b ; see Appendix S2 for an example of a predation event). By replicating this set-up multiple times, we were able to estimate the probability that an actively foraging fox would detect a second unattended nest at varying distances (Figure 2.1b).

A successful detection was considered when both nests of a given pair were predated by the same fox within five minutes. An unsuccessful detection occurred when only one nest was predated by a fox or when the two nests were predated in more than five minutes (Figure 2.1. When nests were predated by other species (glaucus gull (*Larus hyperboreus*), parasitic jeager (*Parasitic jeager*), common raven (*Corvus corax*)) or when the camera didn't detect the predator, the pair was excluded from the analysis. The five minutes threshold for a detection was determined from the estimated time spent by the fox carrying and caching the eggs of the first nest found (Careau et al., 2007). In pairs where we could assume there was always a detection ; (i.e where nests were 10 m apart, time to reach the second nest went up to near 5 minutes, supporting this threshold value (Appendix S3). We also conducted a sensitivity analysis by changing this parameter and showed that a higher threshold tended to damp the expected negative effect of distance on nest detection (Appendix S3). We identified individual foxes based on fur molt pattern and thus made sure that the same individual predated both nests.

Interference of our detection probability estimates by encounters with other preys are very unlikely as i) foxes consume roughly 10 lemmings per day by travelling 50 km/day (Beardsell et al., 2023; Poulin et al., 2021), it is doubtful that they would regularly catch them when moving between nests of our experimental pairs, ii) other prey density is relatively low (average of 3.1 nests/km^2 for sandpipers, Beardsell et al., 2023) and iii) nests pairs were always set at least 60 meters away from natural goose nests. Moreover, to minimize interference from nearby artificial nest pairs, pairs were deployed at least 250 meters from each other and set in a way topography hides them from each other.

To minimize the risk of Arctic foxes associating cameras with a potential food source, camera traps and tripods were installed at least 12 hours prior to artificial nest deployment at each site. Previous research in the same area reported no effect of camera presence on nesting

success (McKinnon and Bêty, 2009), indicating that foxes are unlikely to use cameras as cues for locating nests. To limit human scent contamination, all equipment—including cameras, eggs, and goose down—were handled using nitrile gloves (Bêty et al., 2001; Lecomte et al., 2008). To avoid creating human scent trails that could link the two nests of a pair at the moment of nest deployment, pairs of fieldworkers separated approximately 250 meters from the eventual nest deployment site. Nests were deployed after 18:00, which coincides with the peak of fox activity and lower avian predator activity (Bety et al., 2002; Appendix S4)). Nests were revisited between 12 and 24 hours after their deployment and revisited until one or two predation occurred, after which we retrieved both cameras and tripods. This experimental approach captures a combination of detection and attack probabilities (Beardsell et al., 2021). However, because unattended nests pose little or no risk of injury to the predator and offer relatively high energetic rewards, the probability of attack is assumed to be very close to 1 and constant across years. Thus, we are confident that this standardized experiment reliably reflects inter-annual variation in detection probability.

2.4.6 Statistical analysis

All analyses were performed using `R` Statistical Software (v4.4.2; R Core Team, 2024). We modeled detection probability (detections vs. non-detection) as a function of distance (distance between artificial nests within a pair) using a generalized linear model with a binomial distribution from the `lme4` package in `R` (Bates et al., 2015). The resulting detection function for each year was used to estimate the mean annual detection probability for unattended nests by averaging the model-predicted values for each meter across the 120 meter arctic fox detection range.

To formally test the *detection adjustement hypothesis*, we fitted a second a binomial model, in which each observation was a nest pair. The response variable was detection (1 = detected, 0 = not detected) and fixed effects included (i) the distance between nests within the pairs (in kilometers), and (ii) the year of pair deployment (treated as a categorical variable). An interaction term between distance and year was included to assess whether the effect of distance on detection probability varied acros years with contrasting prey densities. The null hypothesis of this model was that the effect of distance on detection probability remained constant between years.

2.4.7 Functional response of arctic fox to goose nests

We used the multi-prey mechanistic model of arctic fox functional response developed for this study system (Beardsell et al., 2021, 2023) to examine the effect of variable detection probabilities on goose nest functional response. This model generates estimates of goose nest acquisition rates that are consistent with field observations (Beardsell et al., 2021, 2023). Using Holling disk equation as a starting point, the model integrates the theoretical framework of

(Wootton et al., 2023). The model was derived by breaking down fox predation into 6 steps : (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) capture and (6) manipulation. Each step was adapted to each prey species according to their anti-predator behavior and fox hunting behavior. In our simulations, we only considered lemming (prey 1) and goose (prey 2). We excluded other bird species such as passerines and shorebirds because they nest at relatively low density (Moisan et al., 2025) and also represent a very small proportion of fox energy budget (Beardsell et al., 2024).

As it is the scope of the manuscript, we only detail the equations for the unattended goose nest functional response, but see Beardsell et al. (2023) for full equations and parameter values of the model. As stated above, geese can actively protect their nests from arctic foxes and their presence at the nest strongly influences fox foraging behavior (Bety et al., 2002). The model was thus separated into two components : a first for the acquisition rate of unattended goose nests (FR_{2ua}), when both adults are more than 10 m from the nest (incubation recesses) and a second for the acquisition rate of attended goose nest (FR_{2a}), when a protective adult is less than 10 m from the nest :

$$FR_2(N_1, N_2) = FR_{2ua}(N_1, N_{2ua}) + FR_{2a}(N_1, N_{2a}) \tag{2.1}$$

where N_1 and N_2 respectivetly represente lemming and goose nest density (ind/km^2). N_2 is the sum of unattended and attended nests (N_{2ua} and N_{2a}). N_{2ua} (unattended nests density) is the product of goose nest density (N_2) and the complement of goose nest attendance probability (w) :

$$N_{2ua} = N_2 \cdot (1 - w) \tag{2.2}$$

and N_{2a} (attended nest density) is the product of goose nest density (N_2) and nest attendance probability. Fox functional response to unattended goose nests (number of nest acquired per fox per day) is expressed as :

$$FR_{2ua}(N_1, N_{2ua}) = \frac{\phi_{active}(N_1) \cdot \alpha_{2ua}(N_1) \cdot N_{2ua}}{1 + \alpha(N_1) \cdot h_1 \cdot N_1 + \alpha_{2ua}(N_1) * h_{2ua} * N_{2ua} + \alpha_{2a}(N_1) * h_{2a} * N_{2a}} \tag{2.3}$$

where ϕ_{active} is the mean proportion of time fox spend active in a day, α the capture efficiency (km^2·day^{-1}) and h the handling time per prey item (days/prey item). Handling time of lemmings and of goose attended nest are added to the denominator as they can reduce unattended nest acquisition rate. As shown by Beardsell et al. (2022), fox time spend active (ϕ_{active}) and daily distance traveled (s, which is inside the α component) are negatively correlated with lemming density.

As successful fox attack do not necessarily result in predation of the whole clutch (Bety et al., 2002), we included the probability that an attack would result in complete clutch predation

(P_{2cua}) in the capture efficiency of unattended nests (α_{ua} ; km^2/day). Unattended nest capture efficiency corresponds to the sum of complete and partial unattended predations :

$$\alpha_{2ua}(N_1) = s(N_1) \cdot (2 \cdot d_{2ua}) \cdot f_{2,2ua} \cdot f_{4,2ua} \cdot P_{2cua} + \frac{s(N_1) \cdot (2 \cdot d_{2ua}) \cdot f_{2,2ua} \cdot f_{4,2ua} \cdot (1 - P_{2cua})}{3.7} \tag{2.4}$$

where each of the two components corresponds to the product of daily distance traveled by the predator (s; km·day^{-1}), reaction distance (d_2ua; km), detection probability ($f_{2,2ua}$; the parameter that is measured in the artificial nest experiment), attack probability ($f_{3,2ua}$; assumed to be equal to 1 and thus not showed in the equation 2.4), success probability of an attack ($f_{4,2ua}$) and complete clutch predation probability (P_{2cua}). The partial predation component is divided by a constant, 3.7, that corresponds to mean goose clutch size (Gauthier et al., 2013). To evaluate the effect of the change in detection probability on acquisition rate, we varied fox unattended nests detection ($f_{2,2ua}$) based on mean values obtained with the artificial nest experiment while keeping all other parameters constant.

As the model is not spatially explicit, we used in the simulations the mean experimental detection probability for a given year and assumed it was uniform within fox detection range. We are confident that this reliably reflects nest acquisition rates given the observed unattended nest density in our system. For instance, the maximal goose nest density (N_2) recorded in the colony was 664 nests/km^2, but only a fraction (2%) would be unattended (i.e. no protective adult within 10 m) at any given time. The maximal density of unattended nests in the colony was thus 13 nests/km^2 and assuming a uniform goose nest distribution in the colony, distance between unattended nests was 137 meters. As this distance between unattended nests was estimated in the year with the highest nest density, we could assume that distance between unattended nests is always larger than the 120 m fox detection range. Considering a uniform detection probability within fox detection range does not appear to be a potential bias for our simulations of acquisition rate.

2.4.8 Simulation of goose nesting success

To compute the total number of goose nest predated by foxes per unit of surface, we combined fox multi-species functional response and fox density. Predator density (NR; number of predators per km^2) was estimated as follows :

$$NR = \frac{Np}{H \cdot (1 - V)} \tag{2.5}$$

where Np corresponds to number of predators in a given home range (assumed to be 2 as fox pairs share their home range in our system (Clermont et al., 2021), H corresponds to home range size and V is the proportion of overlap between neighboring home ranges. We did not consider the passage of non-resident floaters in the number of predators. Number of goose nests predated per day per km^2 (P_2) corresponds to the product of fox acquisition rate

($FR_2(N_1, N_2)$; nests/fox/day) and predator density (NR; fox/km^2).

$$P_2(N_1, N_2) = FR_2(N_1, N_2) \cdot NR. \tag{2.6}$$

To evaluate the effect of the change in detection probability on nesting success in these simulations, we varied fox unattended nests detection ($f_{2,2ua}$) based on mean annual values obtained with the artificial nest experiment while keeping all other parameters constant. Goose nest density was set at the average nest density in the colony between 2010 and 2023 (N_2= 358 nests/km^2 ; Appendix S1 ; Figure2.2a) and at mean fox home range size in the colony (10.8 km^2 ; Beardsell et al., 2023). Using differential equations, we calculated the total number of nests predated per km^2 over the geese nesting period (i.e., the average duration between the laying date and hatching date, 28 days for goose) while considering that nest density decreases each day. We assumed that the goose nesting period is synchronized, that fox predation is the only cause of nest failure, and that predated nests are not replaced.

2.4.9 Theoretical influence of detection probability

We quantified the theoretical effect of variation in unattended nests detection probability ($f_{2,2ua}$) on the nest acquisition rate by foxes (nests/fox/day) through simulations using the historical average goose nest density in the colony (358 nests/km^2 ; 1.3a ; Appendix S1) and low lemming density (5 individuals/km^2), with all other parameters remaining constant and $f_{2,2ua}$ ranging from a minimal value (0 ; no unattended nests are detected) to a maximal value (1 ; all unattended nests are detected). With the same set of parameters, we quantified the potential of $f_{2,2ua}$ to change goose nesting success in our model by simulating predation of foxes with minimal and maximal $f_{2,2ua}$ through the goose nesting period (28 days).

2.5 Results

In 2022, 2023 and 2024 respectively, a total of 44, 51 and 58 pairs were deployed randomly near the centroid of the goose colony. In total, 38 pairs were excluded because avian predators depredated artificial nests before arctic foxes or due to camera malfunction. This led to a sample size of 28, 40 and 47 for each year. Thus, 75% of all deployed pairs were included in the analysis.

2.5.1 Detection probability

Annual detection probability curves showed strong overlap, with no significant inter-annual differences in the relationship between detection probability and distance (Figure 2.2d). Neither intercepts ($Beta_{intercept\ 2023}$ = -1.12, 95% CI : [-7.79, 7.43], $Beta_{intercept\ 2024}$ = -1.62, [-6.95, 3.17]) nor slopes ($Beta_{slope\ 2023}$ = 16.65, [-64.01, 79.82], $Beta_{slope\ 2024}$ = - 14.95, [-33.85, 68,16]) differed significantly from the 2022 reference year. When pooling data across all years, we

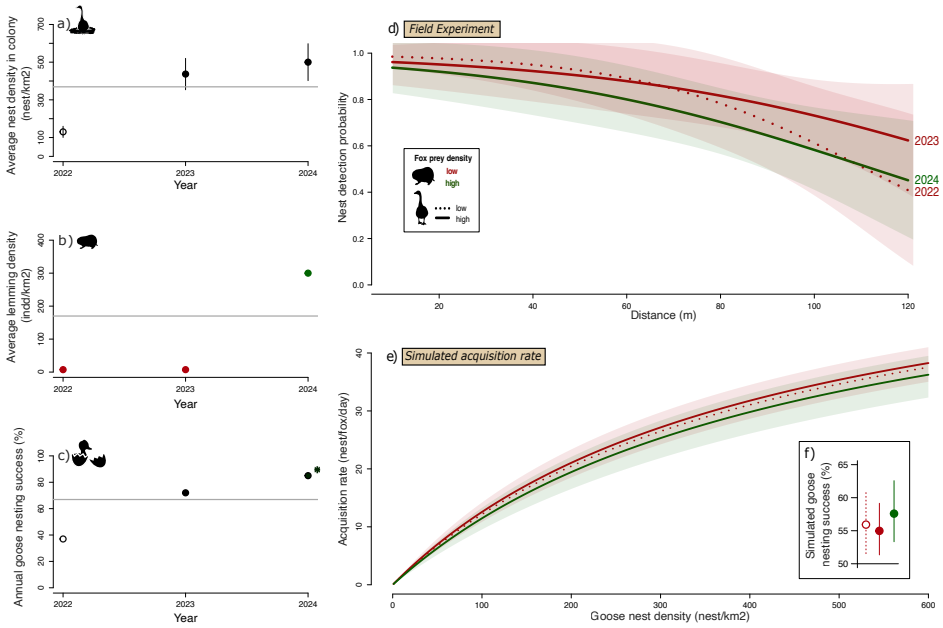

FIGURE 2.2 – **a)** Annual goose nest density during experimental years. Solid line corresponds to the long term (2010-2023) average nest density. Empty and full dots correspond to low and high goose nest density. **b)** Annual lemming density during experimental years. Solid line corresponds to lemming density threshold known to increase markedly fox reproduction. Red and green dots correspond to low and high lemming density. **c)** Annual goose nesting success in the colony during experimental years. Solid line corresponds to mean observed nesting success between 1989 and 2023. **d)** Fox unattended nest detection probability functions determined through a field experiment with artificial goose nests as described in *Artificial nest experiment* of the Methods section. Model-predicted values and 95% confidence interval are shown. Red and green lines correspond respectively to low and high lemming density. Dashed and solid lines correspond respectively to low and high goose density. Detection functions with sample size at each distance are in Appendix S3. **e)** Simulated fox functional responses on goose nests derived with the multi-species mechanistic model. All parameters remained constant and annual unattended nest detection probabilities were inserted in the model to generate the different functional responses. Color and line type code are identical to panel d). Functional responses are simulated at low lemming density (5 individuals/km^2). Range of acquisition rate come from the confidence interval on nest detection shown in d). **f)** Simulated nesting success through whole incubation period using the different functional responses shown in e). Simulations were ran at low lemming density and at average historical goose nest density in the colony (358 nests/km^2). Ranges of simulated nesting success come from the confidence interval on nest detection shown in d)

found that detection probability decreased significantly with increasing distance ($Beta_{distance}$ = -27.82, 95% CI : [-43.52, -13.83]; Figure 2.2d). However, estimated detection probability did not vary much according to prey abundance. For instance, across the gradient of goose nest density, mean annual detection probability increased by 3.4 %, from 0.81 (CI 0.64 to 0.98) at low density to 0.84 (CI 0.70 to 0.98) at high density. Conversely, detection probability declined by 9.2% in the range of lemming density, from 0.84 (CI 0.70 to 0.98) at low density to

0.75 (CI 0.59 to 0.90) at high density. While these observed differences where not statistically significant (strong overlap between CI), their potential biological significance can be explored using simulations derived from mechanistic models (see below).

2.5.2 Simulations of fox acquisition rate and goose nesting success

In the mechanistic model, variation in detection probability ($f_{2,2ua}$) from 0 to 1 can increase goose nest acquisition rate more than tenfold, namely from 3 to 33 nests/fox/day. Applied over the goose nesting season, this variation in acquisition rate attributed to $f_{2,2ua}$ could theoretically change goose nesting success by 44.1%. Unattended nest detection could thus theoretically explain a large part of the empirical goose nesting success variations that span a range of 79 % (Chapter 1 of this thesis).

We found a strong overlap between functional response curves derived with the mechanistic model and the mean annual detection probabilities of unattended artificial goose nests, estimated using field experiments repeated over three years of contrasting prey densities. At the average goose nest density in the colony (358 nests/km^2), fox daily nest acquisition rate (AR) would vary by 0.7 nests/fox/day when integrating detection probability variation induced by changes in goose nest density (AR varying from 29.8, range [25.9, 33.0] to 30.5, range [27.4 to 33.1] ; dashed and solid lines of Figure 2.2e). When integrating variation in the mean detection probability induced by changes in lemming density, fox nest acquisition rate varied by 1.9 nest/fox/day (AR at low and high lemming density is 30.4, range [27.4 to 33.1] and 28.5, range [24.9 to 31.7], respectively ; red and green lines of Figure 2.2e).

Simulations of goose nesting success using the variation in acquisition rates illustrated in Figure 2.2e suggest that the observed variation in nest detection probability induced by changes in goose nest or lemming density can generate very limited impact on annual goose nesting success (changes of 0.9% or 2.6%, respectively ; Figure 2.2f). Nesting success of natural nests varied by 33% between 2022 and 2023, but only 0.9% of that change could be attributed to detection probability variation resulting from an interannual change in goose nest density. Nesting success varied by roughly 15% between 2023 and 2024, but only 2.6% of that change could be attributed to detection probability variation obtained in years of contrasted lemming density (Figure 2.2f).

2.6 Discussion

2.6.1 Detection probability

We conducted an artificial nest experiment over three years characterized by contrasting prey densities to measure variation in a important component of the predation sequence—prey detection probability. Despite strong fluctuations in both goose nest and lemming densities,

we found evidence that the detection probability of goose nests by foxes remained very similar between years. Since fox detection did not significantly increase with goose nest density, nor under substantial changes in lemming availability, the *detection adjustment hypothesis* was rejected.

While the *detection adjustement hypothesis* has received some support from trials in controlled environments (Dawkins, 1971; Pietrewicz and Kamil, 1979; Bond, 1983; Lawrence, 1985; Gendron, 1986; Bond and Kamil, 1998, 2002), demonstrating its role in natural systems requires dedicated field experiments. Studies investigating search image formation in the wild often infer its presence without directly measuring detection probability (Vigallon and Marzluff, 2005; Duca et al., 2019; Husby and Verdal, 2024), typically relying on daily survival rates of artificial nests—an approach that cannot exclude alternative behavioral mechanisms. Our design, using paired artificial nests and camera traps, allowed for precise identification of predation events (Figure 2.1b ; Appendix S2), strengthening inference on detection processes. Search image has also been proposed as a mechanism underlying prey switching (van Leeuwen et al., 2013; Price and Banks, 2016), where an increase in the density of a prey *a* enhances its detection and acquisition by the predator while decreasing the detection and acquisition of a prey *b*. However, in our study, goose nest detection remained relatively stable across variation in lemming density, suggesting that foxes do not shift their attention toward lemmings when they are abundant (Figure 2.2b, d). Although we did not directly measure lemming detection probability, our findings suggest that search image formation for lemmings is likely limited or absent. Alternatively, as foxes are opportunistic generalists that cache prey extensively (Careau et al., 2007), they may allocate cognitive resources toward cache management rather than selective prey detection. Under such a strategy, prey encounter rates, driven by movement patterns, likely dominate prey acquisition processes. We indeed have indications that fox behavior adjustments relative to prey availability will arise through other proximate mechanisms such as daily distance traveled (Beardsell et al., 2022) or risk taking relative to energy budget (Beardsell et al., 2024).

2.6.2 Simulation of acquisition rate and prey nesting success

Recent modelling of trophic interactions in our system shows that detection probability is a step in the predation sequence with a great impact on fox's acquisition rate of goose nests (Beardsell et al., 2021). As most predation occurs on unattended nests (Bety et al., 2002), variation in unattended nest detection probability could theoretically have a strong impact on goose nesting success, as shown by our simulations. Our results showed that marked variations in goose nesting success could not be explained by the slight changes in nest detection probability measured in the field. Simulations that incorporated these slight variations in detection probability had a negligible effect on prey acquisition rate and prey nesting success (Figure 2.2c, f). Variation in detection probability observed in the field is thus

not responsible for the differences observed in nesting success between low and high goose densities (2022 to 2023) or between low and high lemming densities (2023 to 2024), suggesting that other mechanisms may play a greater role in driving fluctuations in nesting success. For instance, nest acquisition rate has been shown to decrease with increasing lemming density, due to both a reduction in the time foxes remain active and their daily distance traveled (Beardsell et al., 2022).

Further simulations using the mechanistic model suggest that changes in predator activity could reduce nest acquisition rate by nearly half. Specifically, as lemming density increases from low (5 ind/km^2) to high (700 ind/km^2), the resulting decline in fox daily distance traveled causes the acquisition rate to drop from 30.5 nests/fox/day, [27.4, 33.2] to 17.3 nests/fox/day, [15.3, 19.2], assuming average goose nest density and holding all other parameters constant. This reduction is over five times greater than the variation caused by changes in detection probability (Figure 2.2d).

Similarly, variation in detection probability accounted for a maximum change of only 2.6% in goose nesting success, whereas changes in fox activity - specifically time spent active and distance traveled in response to increased lemming density - led to an 18.0% change. This strongly suggests, that detection probability in not a primary driver of nesting success variations in our system, and that other fox behavioral responses to prey density play a more significant role. Additionally, artificial nest pairs were discovered more quickly (i.e., first egg predation occurred sooner after deployment) under conditions of low lemming and low goose density, further supporting the idea that the number of prey encountered is at least in part influenced by predator movement rate or predator density, but not by inter-annual differences in detection (Appendix S5). A recent study in our system described the relationship between goose nest density and goose nesting success (Chapter 1 of this thesis). In light of our results we can confidently rule out that change in dectection probability by arctic fox generate these density-dependent patterns of nesting success.

2.6.3 Robustness of our approach

We believe that our conclusions are robust to the limitations of the experimental design. We nevertheless acknowledge below four aspects of our methodology and discuss their implications. (1) As other canids, foxes rely on multiple senses, but mainly on olfaction to detect prey (Lawson et al., 2019), while search image has been mostly showed in predators using visual search (Murton, 1971; Blough, 1991; Getty and Pulliam, 1993; Langley, 1996; Langley et al., 1996). However, search image formation has been shown for various animals using olfaction (*olfactory search image*, in this case), such as skunks (Nams, 1997), search dogs (Gazit et al., 2005) and parasitoïds (Ishii and Shimada, 2010). In our experience, foxes both rely on visual and olfactive cues since our artificial eggs were setup with real down taken from goose nests. (2) Our experiments were conducted over three years with contrasting

prey densities, but each year presented a unique combinations of lemming/goose densities with no replicates of these combinations in our study design. However, since all three years yielded very similar results, we are confident that fox detection probability remains relatively constant, and that additional experimental years would likely yield similar outcomes. (3) In 2024, experiments were conducted at a slightly different timing (i.e., 10 days after the end of goose hatching), but yielded similar results to the two other years. We argue that this does not impact our conclusions since the largest goose density difference was found between 2022 and 2023. (4) The use of a camera and a tripod close to the experimental nests might have increased their detection by foxes and reduced our ability to detect interannual differences. Tripods were set least 12 hours before setting the artificial nest specifically to limit association between tripods and nests, possibly reducing this bias. For instance, a fox was once observed detecting both tripods and cameras within 5 minutes, but failed to detect both nests 12 hours after. Moreover, we conducted a pilot study in 2019 with cameras but no tripods. We obtained a detection function that was not significantly lower using camera traps without tripods (Beardsell et al., 2021 ; Appendix S6). Tripods in 2022-2024 were added to increase our ability to detect the predator in the pictures.

2.7 Conclusion

Prey detection and search image formation are frequently proposed as mechanisms driving variation in acquisition rates under fluctuating prey availability (ex. Schmidt and Whelan, 1999; Whelan et al., 2003; Lloyd, 2006), yet empirical support from natural systems remains limited. In our study, we found no support for the *detection adjustment hypothesis* in explaining variation in Arctic fox predation rates in the High Arctic Tundra. Similarly, a field experiment on red squirrels using giving-up density across prey availabilities also failed to detect evidence of search image formation (Morgan and Brown, 1996). These findings suggest that, contrary to previous assumptions, search image formation may not be a significant driver of density-dependent nest predation and indirect interactions between prey species in the wild.

Our study demonstrates the added value of integrating behavioral and population ecology approaches to better understand predator–prey dynamics. Recently developed modular frameworks (Beardsell et al., 2023; Wootton et al., 2023; Cherif et al., 2024) are particularly well suited for incorporating field experiments that identify the proximate drivers of interaction strength. We provide one of the first empirical applications of such an integration by presenting an 'ecological toolbox' that combines *in situ* and *in silico* approaches to assess detection rates in natural conditions. This framework is especially relevant for systems where detection probability may influence more trophic interactions. The experimental design can be readily adapted to other ecosystems, and advances in biologging technologies (e.g., (Studd et al., 2021) will further facilitate the implementation of mechanistic approaches (Merrill et al., 2010). By testing behavioral mechanisms directly in the field, we align our interpretation of

predation patterns with their actual drivers. We call for an increase in studies using the modular approach and experiments on the field to untangle proximate mechanisms determining interaction strength and ecosystem structure.

2.8 Supplementary Materials

S1 Average goose nest density in the Bylot Island greater snow goose colony

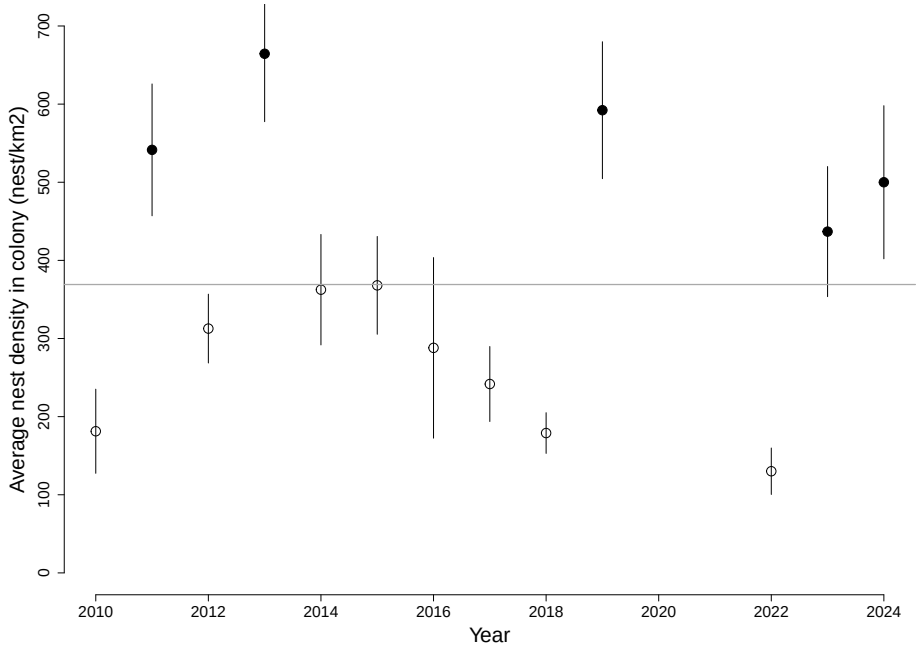

FIGURE 2.3 – Long term time series of goose density derived from data available in (Moisan et al., 2025). Empty and full dots represent respectively low and high goose years. Mean and 95% confidence interval are shown.

S2 Picture sequence of a fox predation on an artificial goose nest

FIGURE 2.4 – Example of a predation event on an artificial nest. Fox a) arrives at the artificial nest, b) searches through goose down, c) captures the hen egg, d) takes the egg out of the nest, e) urinates on the detected nest and f) leaves with the egg.

S3 Support for the 5 minutes threshold on detection

Distribution of time between predation of nest #1 and predation of nest #2 (*delta egg*)

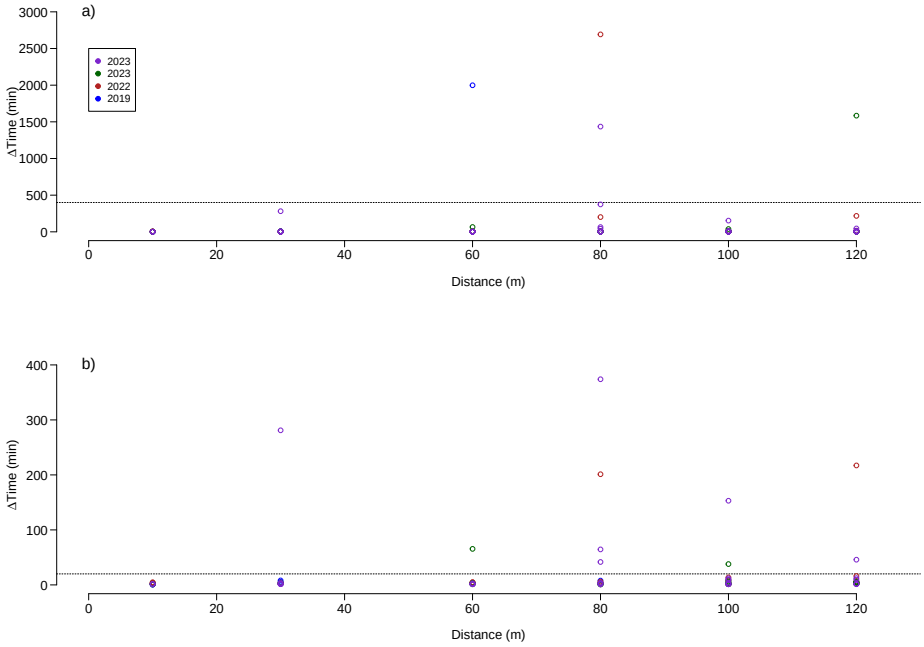

FIGURE 2.5 – Visualization of the distribution of time between predation of nest #1 and predation of nest #2 (*delta egg*) for all distances between nests of a pair. This is the time that is used to determine if a nest was detected or not (Figure 2.1b). a) All pairs, including those with the longest *delta egg*. Horizontal line indicates the upper limit of the range displayed in panel b. b) A subset of experimental pairs, for which the *delta egg* was between 0 and 400 minutes. The horizontal line indicates the upper limit of the range displayed in Figure 2.6

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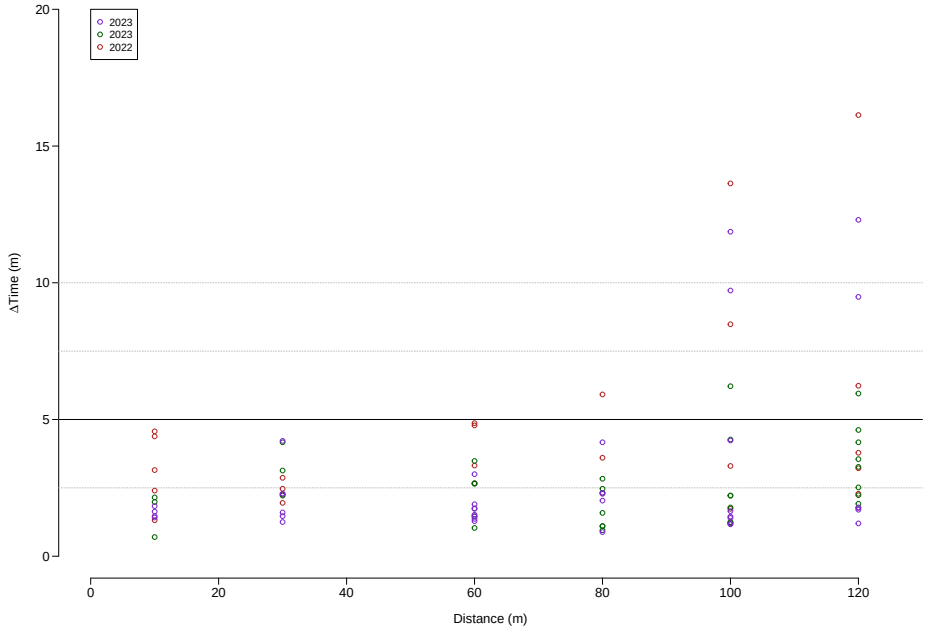

FIGURE 2.6 – Visualization of the distribution of time between predation of nest #1 and predation of nest #2 (*delta egg*) for all distances between nests of a pair, in relation with the potential detection thresholds. Horizontal lines indicate potential detection thresholds. Black solid line (5 minutes) indicates chosen threshold, grey dashed lines correspond to other evaluated thresholds (2.5, 7.5, 10 minutes). The detection probability functions that are derived with these threshold are shown for 2022, 2023 and 2024 in the figures 2.7, 2.8 and 2.9

For pairs with nests placed at 10, 30 and 60 meters from each other, most of the time between predation of nest #1 and predation of nest #2 (*delta egg*) are below 5 minutes. Pairs with nests placed at 10 and 30 meters from each other are expected to practically always be detections. They thus give an index of handling time for a detected nest, which is between 2 and 4.5 minutes (Figure 2.6), which corresponds to that reported in Careau et al. (2007) on natural nests. For pairs with nests at 80, 100 and 120 meters, most *delta egg* are clumped below 5 minutes (when a detection occured), supporting the chosen threshold (Figure 2.6).

Sensitivity analysis on the detection threshold

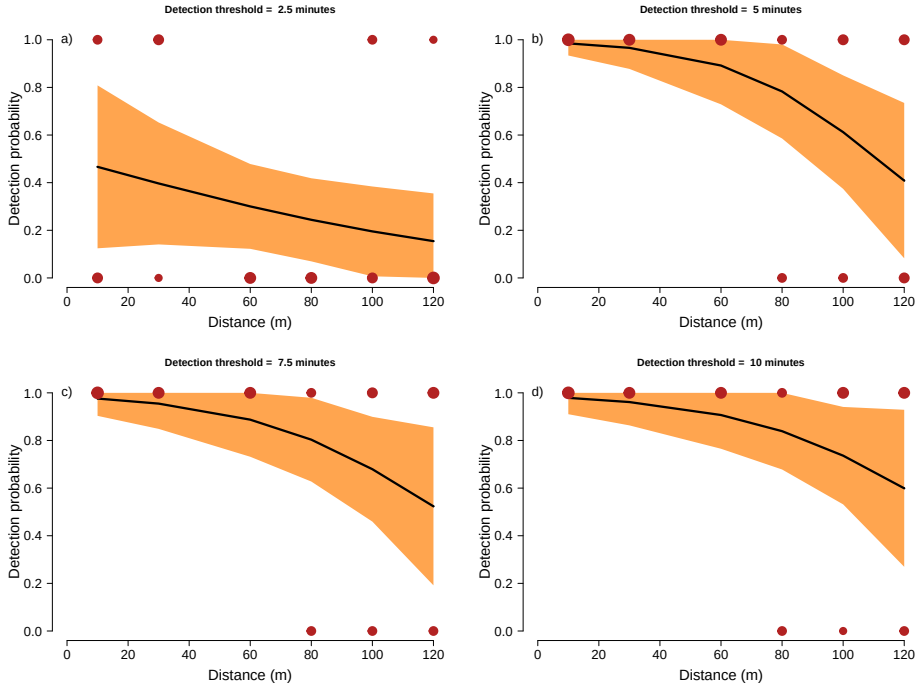

FIGURE 2.7 – Sensitivity analysis on detection threshold (threshold for the time between predation of nest #1 and predation of nest #2) in 2022. detection functions with detection threshold set at 2.5, 5, 7.5 and 10 minutes are respectively shown in panel a), b), c) and d).

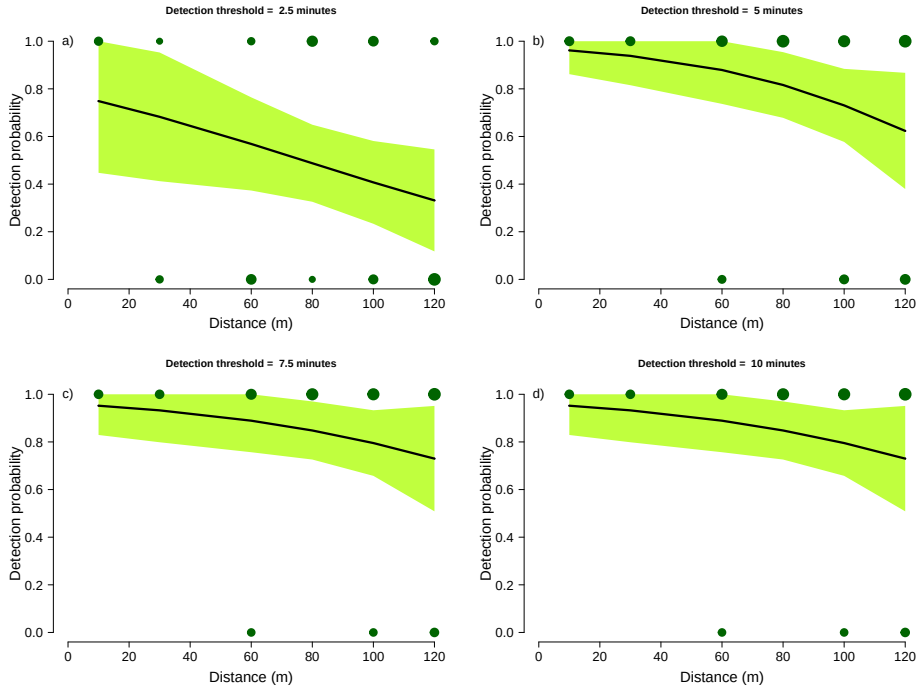

FIGURE 2.8 – Sensitivity analysis on detection threshold (threshold for the time between predation of nest #1 and predation of nest #2) in 2023. detection functions with detection threshold set at 2.5, 5, 7.5 and 10 minutes are respectively shown in panel a), b), c) and d).

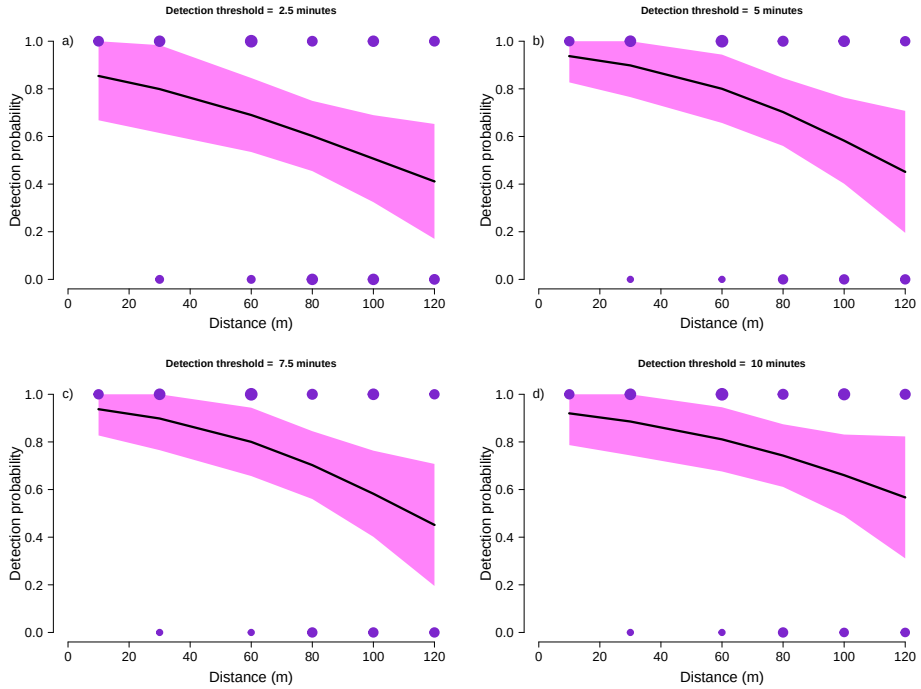

FIGURE 2.9 – Sensitivity analysis on detection threshold (threshold for the time between predation of nest #1 and predation of nest #2) in 2024. detection functions with detection threshold set at 2.5, 5, 7.5 and 10 minutes are respectively shown in panel a), b), c) and d).

We selected the 5 minute threshold as it yielded no non-detections for pairs with nests at 10m and did not damp the negative effect of distance between nests on detection probability.

S4 Details on field experiment

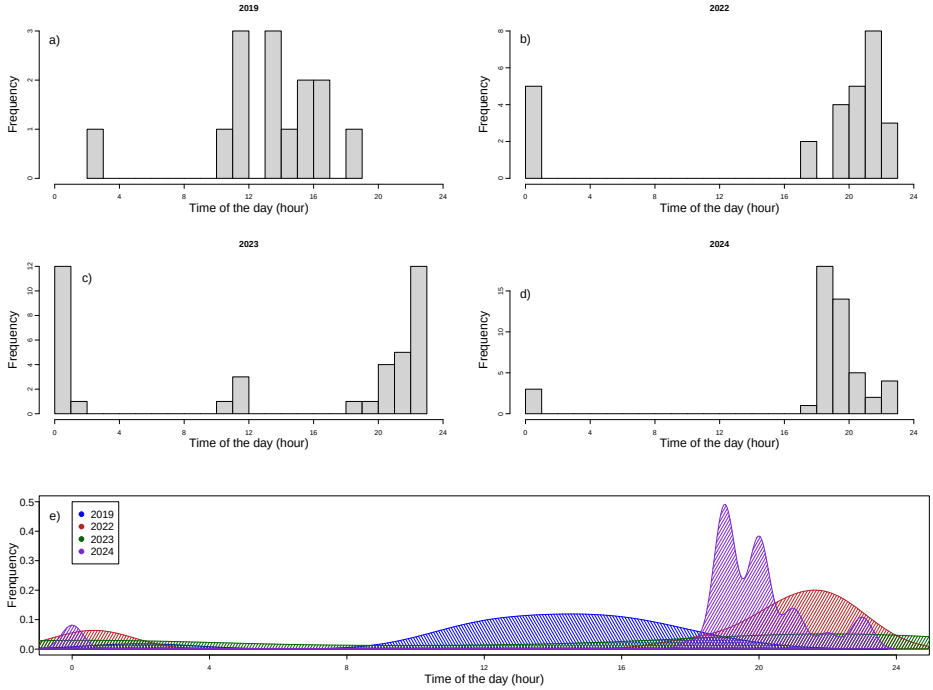

FIGURE 2.10 – Distribution of deployment time of artificial nest pairs within the day. a) Deployment times in the pilot study (2019). b) Deployment times in 2022. c) Deployment time in 2023. d) Deployment time in 2024. e) Comparison of deployment time between years

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Figure 2.10e shows that experimental nest pairs were deployed at a relatively similar time of the day across all years, namely after 18:00, when fox activity increases.

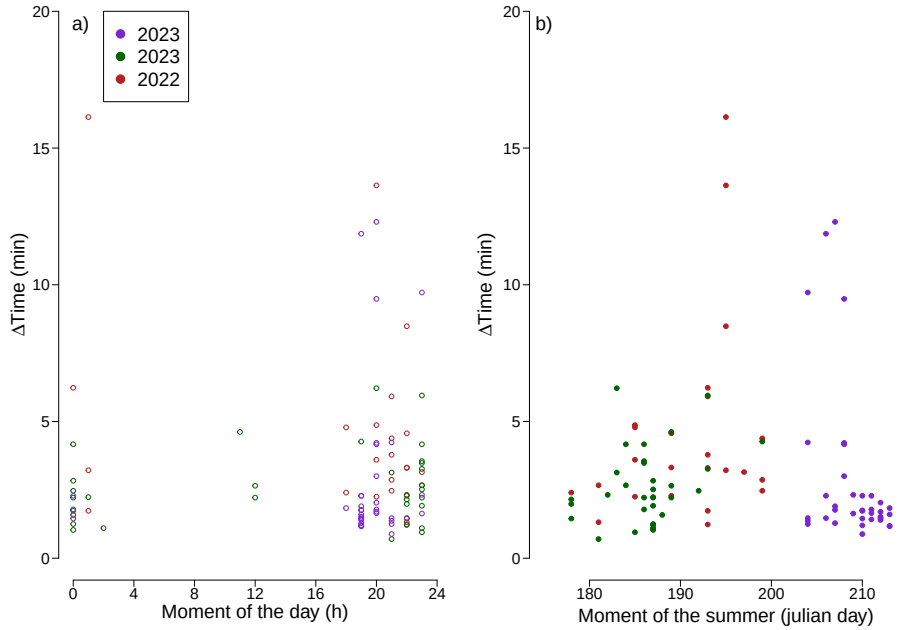

FIGURE 2.11 – Variation of time between predation of nest #1 and predation of nest #2 (*delta egg*) as a function of the moment of pair deployment. a) Variation of pair *delta egg* as a function of the moment of the day that pairs were deployed. b) Variation of pair *delta egg* as a function of the Julian day that pairs were deployed.

We find relatively similar values and distributions of *delta egg* between years, suggesting that deployment time (moment of the day or moment of the year) does not create a bias on our experimental results (2.11). Figure 2.11b illustrates that nests were deployed slightly later in the summer in 2024 compared to other years due to logistical constraints.

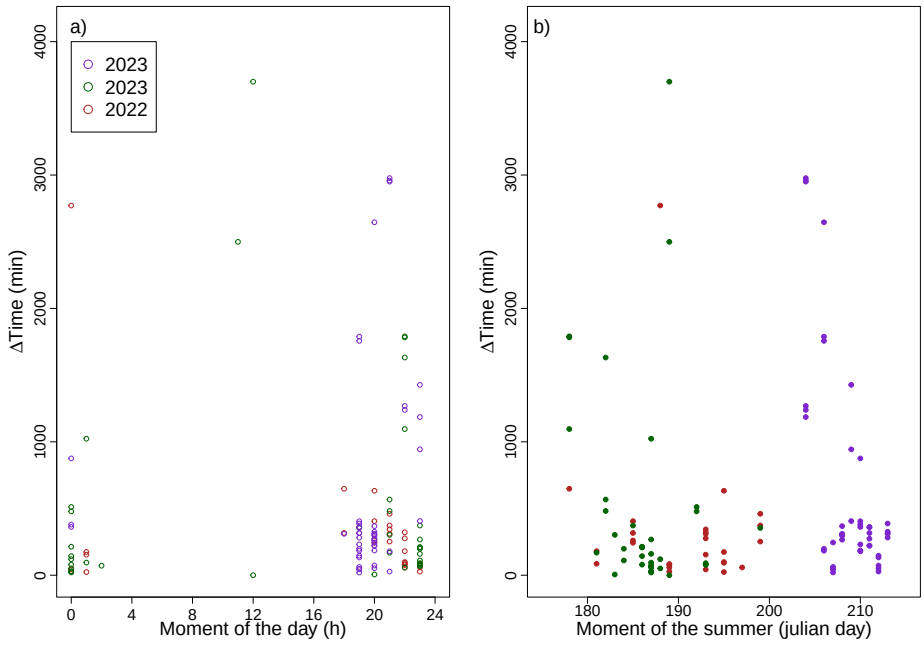

FIGURE 2.12 – Variation of *pair detection time* (time between deployment of a pair in the field and the predation of the first egg of that pair) as a function of the moment of pair deployment. a) Variation of *pair detection time* as a function of the moment of the day pairs were deployed. b) Variation of *pair detection time* as a function of the Julian day that pairs were deployed.

We find relatively similar values and distributions of *pair detection time* across years, suggesting that deployment time (moment of the day or moment of the year) does not create a bias on our experimental results (Figure 2.12). Figure 2.12b illustrates that pair detection time declined during the experimental period in 2024. We however do not think that this was enough to bias our results on predator detection probability.

S5 Inter-annual variation in pair detection time

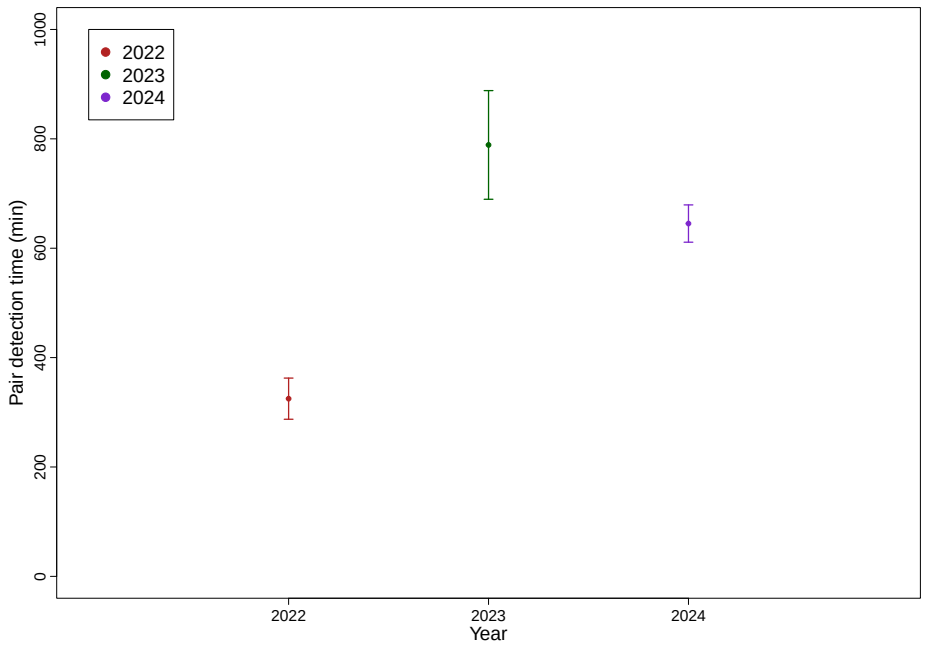

FIGURE 2.13 – Inter-annual comparison of *pair detection time* (time between deployment of a pair in the field and the predation of the first egg of that pair). Mean and 95% confidence interval are shown.

Pair detection time is significantly lower in 2022 than in 2023 and 2024, suggesting that fox prey encounter rate was greater in 2022 than in other years (2.13). This could be a result of increased fox daily distance travelled or fox density (because of an increased overlap between fox home ranges). The plausible proximate mechanisms behind this difference are numerous and remain to be explored.

S6 Evaluation of the tripod effect on detection probability

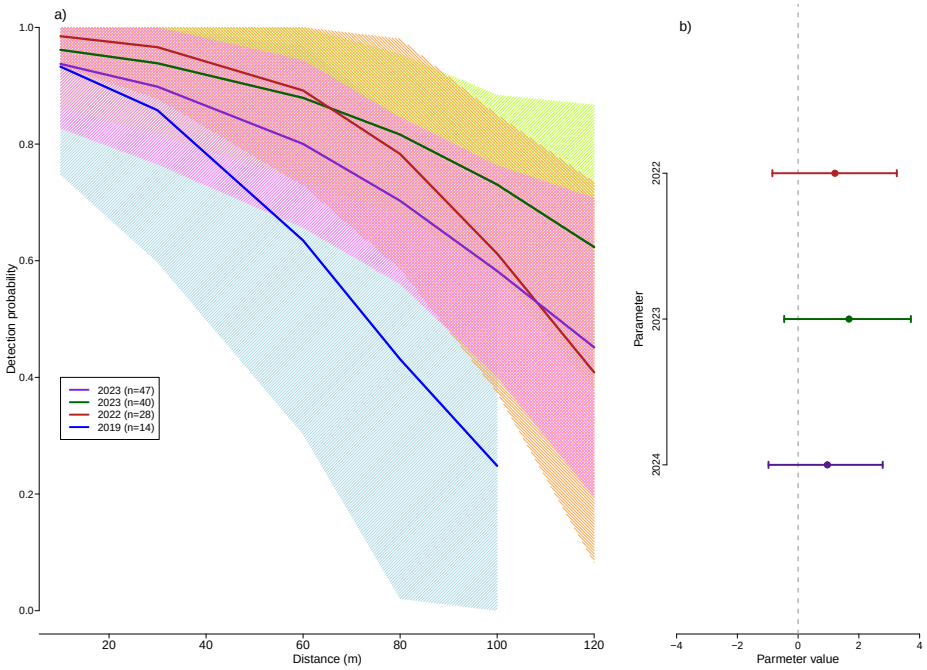

FIGURE 2.14 – Evaluation of the effect of tripod use in the field experiment on the estimated detection probability. a) Comparison of detection functions between a pilot study using only camera traps and no tripod (2019 ; blue curve) with the three other years where camera traps were combined with small tripods (2022, 2023, 2024). Mean model predictions along with 95% confidence interval are shown. Sample size are indicated in the legend. b) Parameter estimates of a generalized linear model using a binomial distribution and comparing detection in 2019 with detection of all other years (2019 is the reference level). Mean prediction of the model and 95% confidence are shown.

Detection probability appears to be a little lower without tripods, however, this difference is not statistically significant. Indeed, confidence interval on detection function of the year without tripod (2019) and those of years with tripod (2022, 2023 and 2024) overlap each other (Figure 2.14a). Moreover, using a generalized linear model, we found no significant difference between the year where no tripods were used compared to the years where tripods were used (all confidence intervals on the detection probability overlap 0 ; Figure 2.14b).

Conclusion

Pour espérer réduire les impacts négatifs des bouleversements qui fragilisent l'intégrité écologique des milieux naturels, nous devons améliorer nos connaissances sur les interactions entre espèces et, notamment, le fonctionnement des réseaux trophiques composant les écosystèmes (Brose et al., 2025). La combinaison d'approches en écologie permet de mieux comprendre le fonctionnement des écosystèmes et d'augmenter notre pouvoir prédictif afin d'anticiper les effets de perturbations (McCarthy et al., 2012). Sans être directement lié aux changements des écosystèmes, le présent mémoire fournit néanmoins des connaissances fondamentales sur les interactions trophiques, contribuant à notre compréhension des interactions intra et interspécifiques au sein de la toundra arctique.

Retombées du mémoire

Dans ce mémoire, nous avons d'abord exploité un jeu de données issues d'un suivi écosystémique à long-terme (chapitre 1), puis y avons ajouté une expérience en milieu naturel dont les résultats ont alimenté des simulations avec une approche de modélisation intégratrice (chapitre 2). Cette intégration fait la force de ce mémoire, car elle nous a permis d'explorer diverses échelles spatiales (du nid à la colonie ; chapitre 1) et d'organisation du vivant (d'expériences au niveau individuel jusqu'aux simulations sur la dynamique de population ; chapitre 2).

Les interactions trophiques sont au cœur de ce mémoire. Notre approche alliant l'écologie comportementale et l'écologie des communautés a permis d'illustrer des tendances générales sur l'intensité de la prédation à l'échelle de la population (chapitre 1) et de se pencher sur un mécanisme proximal pouvant générer ces patrons (chapitre 2). Il est complexe d'appréhender l'ensemble des implications des interactions prédateurs-proies car elles vont bien au-delà des interactions de consommation directe. Influencée par des interactions indirectes entres des proies partageant un prédateur commun ou encore par des changements comportementaux des proies et des prédateurs, la force des interactions prédateur proies peut être difficile à prédire (Mayfield and Stouffer, 2017; Schmitz, 2007; Estes et al., 2004). Des avancées récentes permettent néanmoins d'identifier certaines généralités au sein d'interactions trophiques à travers les taxons et les écosystèmes (Coblentz et al., 2025). Les résultats présentés dans

ce mémoire portent surtout sur les dynamiques trophiques des milieux arctiques, mais la méthodologie employée pourrait être généralisée à d'autres écosystèmes. Nous nous concentrons sur les interactions de prédation entre les renards arctiques et leur deux proies principales, les oies des neiges (une espèce migratrice et coloniale) et les lemmings (des espèces à l'abondance cyclique).

Dans un premier temps, nous avons évalué comment l'effet de la densité de nids sur le succès reproducteur des oies était influencée par des facteurs spatiaux et par les interactions indirectes. À partir des données issues de 20 années de suivi de la reproduction des oies à l'Île Bylot, nous avons montré que la force et la direction de la densité-dépendance varient selon l'échelle spatiale et l'abondance de lemmings, en plus de confirmer que la densité de lemmings a un effet positif sur le succès reproducteur des oies. À l'échelle de la population (densité dans l'ensemble de la colonie), une densité-dépendance positive a été détectée seulement lors d'années de faible densité de lemming, suggérant que ce patron est généré par des changements dans le mouvement et la quête alimentaire des renards arctiques. À l'échelle individuelle (densité à promixité d'un nid focal), en revanche, une densité-dépendance négative a été observée uniquement lors des années de forte abondance de lemming, possiblement parce que les renards concentrent alors leurs activités dans les zones de fortes densité de nids. Bien que pour une densité de lemmings donnée, la direction de la densité-dépendance soit similaire entre les échelles, son intensité diffère : les effets positifs sont plus marqués à l'échelle de la population, alors que les effets négatifs le sont davantage à l'échelle individuelle. Ces résultats mettent en évidence la variabilité des effets densité-dépendants au sein au sein d'un même stade de vie chez une espèce, tout en soulignant le rôle central de la prédation et des interactions indirectes dans la structuration de ces patrons.

Dans un second temps, nous avons cherché à mieux comprendre les mécanismes générant ces patrons densité-dépendants en évaluant expérimentalement un mécanisme proximal potentiel : le changement de la probabilité de détection des nids par les renards en fonction de la densité de nids (*hypothèse de l'ajustement de la détection*). Cette hypothèse fait référence à un mécanisme régulièrement mentionné dans la littérature, soit la formation d'une *image de recherche* chez les prédateurs. À partir de cette expérience utilisant des nids artificiels d'oies des neiges, nous avons démontré que la probabilité de détection des nids varie peu entre les années, malgré des fluctuations importantes des densités d'oies et de lemmings. Par ailleurs, les simulations réalisées à l'aide d'un modèle mécanistique multi-espèces indiquent que ces variations de probabilité de détection ne peuvent à elles seules expliquer les différences interannuelles observées dans le succès de nidification des oies. Ces résultats mettent en évidence la nécessité d'une approche intégrative combinant des expériences en milieu naturel et des simulations avec l'approche mécanistique de la prédation pour relier les mécanismes proximaux aux patrons écologiques à large échelle.

Ensemble, ces deux volets révèlent que les variations de succès de nidification observées sont principalement déterminées par les changements de comportement du renard arctique, eux-mêmes largement influencés par la densité de lemmings. Ces résultats renforcent l'idée que, dans notre système, la densité de lemmings constitue un paramètre clé pour prédire l'intensité de la prédation sur les nids d'oiseaux (Bêty et al., 2001; Mckinnon et al., 2013; Lamarre et al., 2017). Toutefois, nos analyses suggèrent également que la densité d'oies peut moduler cet effet, en influençant la manière dont les renards exploitent l'espace et les ressources disponibles.

Concernant les oies, nos résultats permettent de mieux comprendre certains avantages associés à la nidification en colonie. Lorsque la densité d'oies est élevée à l'échelle de la population, le succès de nidification demeure relativement stable et élevé, peu importe la densité de lemmings. En revanche, à faible densité d'oies, le succès reproducteur chute considérablement lors des années de faible abondance de lemmings comparativement aux années de forte abondance. Cela suggère que si les oies nichaient pas en colonie et que leurs nids étaient très dispersés dans la plaine de l'Île Bylot, leur succès reproducteur pourrait être significativement plus faible que dans leur configuration actuelle, où elles nichent à une en colonie et généralement à une densité modérée (entre 2 et 7 nids/ha).

Ces résultats soutiennent l'idée que, pour les colonies d'oiseaux en milieu toundrique, la réduction du risque de prédation constitue un mécanisme central expliquant le maintien de la stratégie de nidification en colonie (Eichholz and Elmberg, 2014). Dans le cas des grandes oie des neiges qui sont capables de défendre activement et individuellement leur couvée, il est probable que d'autres mécanismes que la dilution passive du risque de prédation - tels que des changements des comportements de chasse des prédateurs - jouent un rôle important dans les bénéfices associés à la nidification en colonie.

Enfin, en montrant que la détection des nids par les renards demeure pratiquement constante malgré les variations de disponibilité des proies, nous renforçons l'idée que la stratégie de chasse de ce prédateur généraliste repose avant tout sur son mouvement. C'est en ajustant leur distance parcourue quotidiennement ou via la sélection de zones de plus fortes densité d'oies que les renards parviennent à consommer davantage de proies (Beardsell et al., 2022; Grenier-Potvin et al., 2021). En effet, les renards arctiques peuvent couvrir plusieurs dizaines de kilomètres par jour (Poulin et al., 2021), et leurs déplacements sont particulièrement efficaces sur le plan énergétique : Beardsell et al. (2024) ont estimé un coût énergétique moyen de 24,7 KJ/km pour un renard de taille moyenne. En montrant que la détection des renards demeure relativement constante, nous appuyons les études stipulant que les ajustements à la distance parcourue par jour sont un facteur déterminant du taux de rencontre et du taux d'acquisition entre les renards et leurs proies (Beardsell et al., 2022).

Limites de l'étude

Chapitre 1 : Densité-dépendance

Les suivis écosystémiques à long terme fournissent des données particulièrement précieuse pour caractériser la complexité des interactions entre les organismes et pour alimenter la théorie sur le fonctionnement des écosystèmes (Lindenmayer et al., 2012). Par exemple, les covariables intégrées à nos analyses ont permis de décrire plus en profondeur la densité-dépendance du succès reproducteur des oies. Toutefois, notre approche corrélative ne permet pas de vérifier formellement les mécanismes proximaux à l'origine des tendances détectées, ni d'en évaluer l'importance relative. Bien que certaines hypothèses puissent être formulées à partir de notre connaissance du système, leur validation sur le terrain sera nécessaire au cours des années à venir. Cela dit, le deuxième chapitre de ce mémoire a permis, à partir d'une approche expérimentale, de tester et de réfuter l'un des mécanismes régulièrement évoqué dans la littérature pour expliquer la densité-dépendance (un ajustement de la détection des proies selon leur densité).

D'autres expériences pourraient être envisagées pour approfondir l'étude des mécanismes en jeu. Dans le chapitre 2, nous avons utilisé une proie artificielle pour isoler certaines composantes de la relation trophique. Une avenue complémentaire consisterait à manipuler le prédateur, par exemple à l'aide de prédateurs artificiels (comme des effigies ou des prédateurs empaillés). De telles manipulations ont été utilisées dans plusieurs systèmes, notamment dans des colonies d'oiseaux pour tester des hypothèses portant sur le partage d'information sociale, la vigilance ou la défense collective (Arroyo et al., 2001; Elliot, 1985; Fuchs et al., 2019). De tels prédateurs artificiels pourraient permettre de contraster la capacité de vigilance et de détection du prédateur entre des oies de diverses densités et expliquer une éventuelle réduction du succès des attaques avec l'augmentation de la densité (densité-dépendance positive). Appliquer ce type de méthodologie dans la toundra arctique comporte cependant des défis logistiques particuliers. D'une part, le terrain accidenté et irrégulier de la toundra peut compliquer le déplacement ou l'installation de ces dispositifs expérimentaux, comparativement aux champs ou à la savane où ils sont typiquement utilisés (Elliot, 1985; Palmer and Packer, 2021). D'autre part, pour minimiser l'influence des humains sur le comportement des proies, il est crucial que les expérimentateurs demeurent le moins visible possible. Or, en l'absence de structures végétales verticales dans la toundra, et compte tenu de la capacité des oiseaux à détecter la présence humaine à grande distance, l'installation discrète de ces dispositifs est plus complexe et pourrait limiter le nombre de réplicats réalisables. Par ailleurs, le suivi télémétrique des renards arctiques mené à l'Île Bylot fournit des données particulièrement riches qui pourraient contribuer à identifier les mécanismes proximaux à l'origine de la densité-dépendance observée (Clermont et al., 2021; Beardsell et al., 2021; Dulude-de Broin et al., 2023).

Un autre limite de notre approche empirique concerne l'évaluation de la densité-dépendance à l'échelle individuelle, réalisée uniquement en milieu humide. Cette restriction s'explique par le fait que les parcelles de recherche de nids situées en habitat mésique étaient trop petites pour appliquer la même approche statistique (nombre de nids dans un rayon de 100 mètres). Obtenir des données comparables en milieu mésique impliquerait un effort de terrain considérable. Toutefois, les dynamiques de prédation dans ce type d'habitat sont inclues dans nos analyses à l'échelle de la population, qui intègrent les estimés de densité de nids et de succès de nidification issus à la fois les milieux humides et mésiques.

Chapitre 2 : Probabilité de détection

Bien que nous croyons nos conclusions robustes aux potentielles limitations de notre approche expérimentale. Il convient néanmoins de mentionner certaines caractéristiques susceptibles d'affecter notre capacité à détecter des variations de la probabilité de détection entre les années et à écarter formellement l'hypothèse de *l'ajustement de la détection*. Tout d'abord, bien que nos expériences aient été menées sur trois années avec des densités de contrastées de proies, chaque année correspondait à une combinaison unique de densités d'oies et de lemmings, sans réplicats pour ces combinaisons. La probabilité de détection était similaires d'une année à l'autre, malgré les forts contrastes de densité de proies, ce qui nous permet d'être raisonnablement confiants que l'ajout de nouvelles années d'expérimentation mènerait à des résultats similaires quant à la probabilité de détection des renards. Par ailleurs, notre dispositif expérimental comprenait une caméra montée sur un trépied à proximité des nids artificiels, ce qui pourrait avoir augmenté leur détectabilité. Nous avons toutefois limité ce biais potentiel en installant les trépieds au moins 12 heures avant la pose des nids afin de dissocier l'arrivée d'une trépied et d'une caméra avec l'arrivée d'un nouvelle proie dans le territoire des renards. De plus, une étude pilote utilisant des caméras sans trépieds n'a pas révélé de différence significative dans les courbe de détection. Enfin, comme ce dispositif expérimental était identique entre les années, nous estimons qu'il aurait permis de détecter d'éventuelles variations interannuelles de probabilité de détection.

Un autre aspect à considérer dans l'influence potentielle de la densité sur le taux d'acquisition des renards est la distance entre les nids. Si l'on assume une distribution uniforme des nids, au sein d'une année de densité élevée, la distance entre les nids sera plus petite que durant une année de faible densité. Puisque la probabilité de détection diminue avec la distance entre le renard et un nid, il se pourrait que la détection des nids soit plus élevée dans une année de forte densité d'oies parce que les nids rencontrés sont généralement plus proches du renard (portion de la courbe de détection où sa détection est élevée). Ce mécanisme n'a pas été pris en compte dans nos simulations, où nous avons supposé une probabilité de détection uniforme dans toute la zone de détection. Toutefois, notre étude porte sur la détection des nids inoccupés (laissés vulnérables par les parents lors des rares pauses d'incubation (2% du

temps)). Ces nids sont relativement rares dans le paysage puisqu'ils représentent environ 2% des nids rencontrés par les renards. Si l'on suppose une distribution uniforme des nids dans la colonie, la plus petite distance moyenne entre les nids inoccupés depuis le début du suivi de la reproduction des oies serait de 137 mètres (lors de l'année où a été recensée la plus forte densité de nids d'oies). Ainsi, peu importe la densité d'oies dans la colonie, la distance entre les nids inoccupés est plus grande que la distance de détection maximale des nids par les renards (environ 120 mètres), ce qui rend d'autant plus acceptable le fait d'utiliser une probabilité de détection uniforme dans toute la zone de détection des renards.

Perspectives

Changements potentiels du réseau trophique à l'Île Bylot pouvant affecter la dynamique de population des oies

La taille de la colonie d'oie de l'Île Bylot est relativement stable depuis le début de notre suivi il y a plus de 30 ans (Moisan et al., 2025), et les effectifs globaux de grande oie des neiges semblent également stables, excepté une certaine diminution depuis les années 2020 (Lefebvre et al., 2017 ; P. Legagneux, comm. pers.). Jusqu'à présent, les oies ne semblent pas être négativement affectées par les changements climatiques. En effet, aucune preuve claire de découplage phénologique entre leur reproduction et le pic de disponibilité alimentaire n'a été observé (Reséndiz-Infante et al., 2020), et aucun bouleversement majeur n'a été observé dans la communauté de l'Île Bylot au cours des 30 dernières années, à l'exception de l'installation de la bernache de Hutchins (*Brenta hutchinsii* ; Gauthier et al., 2023).

Cependant, la réduction de la période pendant laquelle la mer est recouverte de banquise restreint l'accès des ours polaires (*Ursus maritimus*) à leurs proies principales, les phoques, les incitant à se tourner davantage vers des ressources terrestres pour s'alimenter (Rode et al., 2015). Cette modification de leur régime alimentaire peut avoir des conséquences négatives substantielles pour les colonies d'oiseaux nicheurs, comme cela est actuellement observé en région subarctique (Iverson et al., 2014), notamment chez certaines populations d'oies (Rockwell et al., 2011; Drent and Prop, 2008). Bien que les ours polaires soient encore relativement rarement observés à l'Île Bylot (quelques occurrences par année), leur présence pourrait éventuellement, à moyen ou long terme, représenter une menace pour les oies nicheuses. En août 2021, nous avons documenté un événement de prédation au cours duquel un ours a utilisé une technique encore jamais rapportée - la submersion dans un lac pour surprendre un oiseau par dessous - afin de capturer deux grandes oies des neiges (Weiss-Blais et al., 2024). Cet événement illustre la plasticité comportementale des ours polaires et leur capacité à exploiter de nouvelles ressources alternatives. Un événement de prédation similaire sur une oie des neiges a de nouveau été observé à l'Île Bylot en juillet 2025. La progression

de la présence de ce prédateur à l'Île Bylot devra être suivie étroitement, car elle pourrait modifier les interactions entre espèces et, ultimement, la structure de la communauté.

Les changements climatiques pourraient également éventuellement réduire les contraintes environnementales qui limitent actuellement l'établissement ou l'expansion de certains prédateurs à l'Île Bylot. C'est le cas du renard roux (*Vulpes vulpes*), dont l'aire de répartition s'étend vers le nord dans plusieurs régions arctiques historiquement dominées par le renard arctique (Verstege et al., 2023). À ce jour, quelques renards roux sont présents et se reproduisent sur l'Île Bylot, principalement dans les zones montagneuses où se trouvent des proies comme le lièvre arctique (*Lepus arcticus*) et le lagopède alpin (*Lagopus muta* ; Lai et al., 2022). Toutefois, si cette espèce venait à s'implanter ailleurs dans la plaine sud de l'Île - où se situe la colonie d'oies et la majorité des oiseaux nicheurs - elle pourrait profondément perturber les dynamiques de prédation locales. Grâce à leur plus grande taille, les renards roux pourraient être plus aptes à s'attaquer à de grands oiseaux, comme les oies, qui parviennent actuellement à défendre généralement efficacement leur nid contre les renards arctiques (Samelius and Alisauskas, 2001, 2006). L'impact de ce remplacement de prédateur de nids a déjà été observé ailleurs en Arctique, où les plongeons à bec blanc (*Gavia adamsii*) font face à une augmentation de la pression de prédation par les renards roux, alors qu'ils peuvent se défendre avec succès contre les renards arctiques (Parrett et al., 2023).

Autres mécanismes et facteurs pouvant générer la densité-dépendance chez les oies

En mettant en évidence un effet densité-dépendant positif sur le succès reproducteur, nous avons, du moins en partie, expliqué l'un des avantages pour les oies de nicher en colonie à l'Île Bylot. Toutefois, la question demeure quant à la raison pour laquelle les oies choisissent précisément cet emplacement, situé à environ 30 kilomètres d'une des principales zone d'élevage des jeunes. Pour mieux comprendre les facteurs historiques qui ont influencé ce choix, il pourrait être pertinent de recourir à des analyses chimiques des sols pour estimer depuis combien d'années les oies nichent à l'Île Bylot et établir les événements climitatiques ou météorologiques qui coïncident avec cette installation.

Dans le présent mémoire, nous avons considéré l'effet de la densité de lemming de l'année en cours (t_0) sur le succès reproducteur des oies. Il serait toutefois également éclairant d'examiner les effets interannuels, notamment l'influence de la densité de lemmings de l'année précédente (t_{-1}) sur le succès reproducteur. Certaines études suggèrent la présence d'une réponse numérique des renards suite aux pics de lemmings (Holt, 1977; Angerbjorn et al., 1999; Royer-Boutin, 2015). Ceci pourrait entraîner un effet temporellement décalé : une forte densité de lemmings une année pourrait mener à une augmentation du nombre de prédateurs l'année suivante, réduisant ainsi le succès reproducteur des oiseaux l'année suivante. L'évaluation de ce mécanisme dans la relation trophique entre renards et oies permettrait de mieux

comprendre les dynamiques interannuelles en jeu et de les intégrer aux effets décrits au chapitre 1.

Il serait aussi judicieux d'examiner le rôle de la condition physique des oies dans les patrons de densité-dépendance. Par exemple, les oies en meilleure condition pourraient assurer une occupation du nid plus élevée, offrant ainsi une meilleure protection de leur couvée, ce qui augmenterait leur succès reproducteur. Cette hypothèse est appuyée par le fait que l'on recense des taux d'occupation légèrement plus élevés (environ 5 a 10%) chez les oies dont la couvée a atteint l'éclosion, comparativement à celles dont le nid a échoué (Rozell et al., 2024). Cela pourrait engendrer des patrons densité-dépendants si la proportion d'individus en bonne condition n'est pas constante à travers le gradient de densité de nids au sein d'une année ou entre les années.

La météo constitue un autre facteur susceptible d'interagir avec les patrons de densité-dépendance que nous avons décrits dans cette étude. En effet, il a été rapporté dans notre système que les effets bénéfiques d'une forte densité de lemmings sur le succès reproducteur des oies peuvent être atténués ou annulés par des conditions météorologiques comme la température au printemps ou les précipitations à l'été (Dickey et al., 2008). Les quelques mécanismes suggérés ci-haut pourraient être secondaires comparativement à l'effet dominant de l'abondance de lemmings. Cependant, leur intégration pourrait préciser la part encore inexpliquée de la variation de succès de nidification des oies. Cette compréhension fine des facteurs en jeu est essentielle pour bâtir des modèles de dynamique de population robustes, qui constitueraient des outils de gestion faunique particulièrement précieux pour une espèce dont l'abondance peut entraîner des répercussions négatives à la fois écologiques en Arctique et économiques en région méridionale.

Enfin, notre étude s'est concentrée sur la densité-dépendance au sein d'une colonie d'oiseaux arctiques vivant dans un environnement plat et structuré en deux dimensions. La dimensionnalité du paysage est une caractéristique qui peut largement influencer la force des interactions trophiques et la structure des communautés (Pawar et al., 2012; Cherif et al., 2024; Mohd, 2022). Dans ce contexte, il serait intéressant de comparer les mécanismes que nous décrivons dans le présent mémoire et observons dans notre site d'étude à ceux agissant des environnements comportant une structure verticale (arbres, falaises, structures anthropiques) et ainsi une troisième dimension. Ceci permettrait de déterminer si les mécanismes générant la densité-dépendance et les variations de succès reproducteur diffèrent selon la complexité spatiale de l'habitat.

La toundra est caractérisée par une structure du paysage et des réseaux trophiques relativement simples, ce qui permet d'identifier finement les mécanismes générant la dynamique de population. Pour certaines questions en écologie, elle peut agir comme un laboratoire en milieu naturel. Pour profiter au maximum de l'exceptionnel potentiel de ces milieux naturels,

il est d'autant plus pertinent de confronter les principes et les patrons découverts en Arctique à d'autres écosystèmes afin d'améliorer notre compréhension du fonctionnement de ces derniers. Par exemple, notre approche qui combine une méthode expérimentale et des simulations avec des modèles mécanistiques de prédation offre de grands potentiels pour comprendre les mécanismes influençant la force des interactions trophiques. La communauté scientifique a avantage à utiliser et adapter cette approche au sein d'autres écosystèmes. Ceci contribuerait à une compréhension holistique des mécanismes déterminant la structure et le fonctionnement des communautés écologiques.

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