UNIVERSITÉ DU QUÉBEC À RIMOUSKI

EFFETS DES MOUVEMENTS, DES COMPORTEMENTS ALIMENTAIRES ET DE LA TÉMÉRITÉ D'UN PRÉDATEUR TERRITORIAL SUR UNE COMMUNAUTÉ DE PROIES

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JEANNE CLERMONT-BEAUDOIN

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RÉSUMÉ

La prédation joue un rôle central dans les processus écologiques. En plus d'affecter la croissance des populations de proies par mortalité directe, les mouvements des prédateurs génèrent un paysage du risque de prédation qui influence la composition et la structure des communautés. Plus spécifiquement, les proies répondent à leur perception du risque en modifiant leurs comportements, et ces changements phénotypiques peuvent ultimement influencer leur aptitude phénotypique et la dynamique de leurs populations. Les mécanismes qui génèrent les effets du risque de prédation sur les populations de proies sont cependant peu compris. En plus de leurs déplacements dans l'habitat, des caractéristiques propres aux prédateurs peuvent également influencer la répartition spatiale du risque de prédation. Notamment, la territorialité chez une espèce prédatrice pourrait influencer les patrons de chasse des individus prédateurs dans leur domaine vital, lorsqu'ils tentent d'éviter d'interagir avec leurs conspécifiques. Également, les individus prédateurs peuvent montrer des différences interindividuelles constantes dans certains traits comportementaux, comme la témérité. Puisque la témérité d'un prédateur peut influencer sa capacité à acquérir des proies, celle-ci pourrait influencer le paysage du risque de prédation. Ainsi, la compréhension des conséquences de la prédation sur une communauté animale nécessite l'étude des comportements des prédateurs, puisque ces derniers influencent directement la répartition du risque de prédation.

L'objectif principal de cette thèse de doctorat est d'évaluer comment l'activité des prédateurs influence le risque de prédation et les comportements des proies, et d'explorer comment la territorialité et la personnalité des prédateurs influencent la répartition du risque de prédation. J'ai étudié les comportements du renard arctique, un prédateur actif qui chasse en se déplaçant et qui agit comme prédateur principal pour la majorité des proies à l'île Bylot au Nunavut (Canada).

Au Chapitre 1, grâce au suivi GPS des mouvements des renards arctiques, j'ai développé un paysage de l'activité des prédateurs et montré son effet sur le paysage du risque de prédation. Je montre ensuite comment la variation spatiale dans l'intensité d'utilisation de l'espace de ce carnivore influence les comportements anti-prédateurs et la répartition de multiples espèces de proies. Ces résultats montrent les mécanismes qui régissent les effets du risque de prédation sur les populations de proies, et permettent de mieux comprendre comment le risque de prédation structure les communautés animales.

Au Chapitre 2, j'ai développé une classification des comportements des renards à partir de données d'accélérométrie, permettant de déterminer où et quand les renards adoptent des comportements associés à la prédation. Il demeure difficile d'identifier les évènements de prédation de prédateurs actifs se nourrissant de petites proies à partir de données télémétriques. La classification des données d'accélérométrie est donc une avancée méthodologique offrant un grand potentiel scientifique, en permettant ultimement de caractériser plus précisément la répartition du risque de prédation qui résulte de l'activité des prédateurs.

Au Chapitre 3, j’ai montré que les interactions entre renards utilisant des domaines vitaux voisins influencent les comportements de prédation des renards non territoriaux, dont les domaines vitaux chevauchent ceux de leurs voisins territoriaux. Je montre ainsi comment les renards utilisent différentes tactiques comportementales pour sécuriser des ressources, soit la territorialité ou l’ajustement des comportements de prédation à la probabilité de rencontrer un voisin. La présence d’individus non territoriaux pourrait également influencer la répartition du risque de prédation en créant des zones ou la densité de prédateurs est plus élevée que la moyenne.

Au Chapitre 4, j’ai évalué la présence de différences interindividuelles dans la témérité des renards arctiques et identifié une variable écologique qui pourrait favoriser le maintien de ces différences. J’ai trouvé que l’abondance de la proie principale des renards, les lemmings, influence la relation entre leur témérité et leur succès reproducteur, puisque lorsque les proies principales sont rares, seulement les renards les plus téméraires se reproduisent. Au contraire, quand les proies sont abondantes, tous les renards ont un grand nombre de jeunes. La force de la sélection qui agit sur la témérité pourrait donc dépendre de l’abondance des proies principales.

En plus d'apporter des connaissances nouvelles sur les comportements des prédateurs, cette thèse montre que le risque de prédation est un important déterminant de la répartition et des comportements des proies d’une communauté, et met en lumière certains mécanismes qui régissent les effets de la prédation sur la biodiversité locale.

Mots clés : accélérométrie, écologie spatiale, interactions prédateurs-proies, mouvements, paysage de la peur, personnalité, renard arctique (*Vulpes lagopus*), risque de prédation, succès reproducteur, territorialité

ABSTRACT

Predation plays a central role in ecological processes. The growth of prey populations and the composition and structure of communities are affected by direct killing of prey, and by the predation risk landscape that results from the movements of predators. More specifically, prey respond to their perception of risk by adjusting their behaviours, and such phenotypic responses can ultimately influence individual fitness and the dynamic of populations. Mechanisms leading to predation risk effects on prey populations however remain poorly understood. In addition to the movements of predators in their habitat, individual characteristics of predators also influence the distribution of predation risk. For example, territoriality in a predator species could influence the hunting behaviours of individuals in their home range, while they try to avoid interacting with conspecifics. Additionally, predators may show consistent among-individual differences in behavioural traits such as boldness. As predator boldness may influence prey acquisition rate, it could also influence the predation risk landscape. As such, the study of predator behaviours, which directly influence the distribution of predation risk, is a necessary step to better understand the consequences of predation on animal communities.

The main objective of this thesis was to evaluate how the activity of predators influences predation risk and prey behaviours, and to explore how the territoriality and personality of predators influence the distribution of predation risk. I studied the behaviours of the Arctic fox, an active hunting predator that searches prey while moving, and that acts as the main predator of most of the prey on Bylot Island in Nunavut (Canada).

In Chapter 1, I used GPS tracking of Arctic fox movements to develop a predator activity landscape and I showed that it was related to the predation risk landscape. I also showed how variation in the intensity of space use of this carnivore influenced anti-predator behaviours and distribution of multiple prey species. These results show mechanisms leading to predation risk effects in prey populations and allow to better understand how predation risk structures animal communities.

In Chapter 2, I developed a behavioural classification of Arctic fox behaviours using accelerometry data, which allowed to determine where and when foxes used behaviours associated to predation. It remains difficult to identify the killing events of active hunting predators that feed on small prey using telemetry data. This classification of accelerometry data is thus a methodological advance that has great scientific potential, by allowing a more precise characterisation of the predation risk landscape that results from predator activities.

In Chapter 3, I showed how interactions among foxes using neighbouring home ranges influenced the foraging behaviours of non-territorial foxes, whom home ranges overlap those of their territorial neighbours. I suggest that foxes may use different behavioural tactics to secure resources, either through territoriality or behavioural adjustments of foraging behaviours to the probability of encountering a neighbour. The presence of non-territorial individuals could also influence predation risk distribution by creating zones where predator density is higher than average.

In Chapter 4, I evaluated the presence of among-individual differences in the boldness of Arctic foxes and identified an ecological variable that could favor the maintenance of such differences. I found that the abondance of fox main prey, lemmings, influenced the relation between fox boldness and reproductive success. Only foxes behaving boldly reproduced when main prey were scarce. On the contrary, when prey were abundant, all foxes had a large number of young. The force of selection acting on boldness could thus depend on the abondance of main prey items.

In addition to bringing knew knowledge on predator behaviours, this thesis shows that predation risk in an important determinant of prey distribution and behaviours in a vertebrate community, and highlights mechanisms that govern the effects of predation on local biodiversity.

Keywords: accelerometry, Arctic fox (*Vulpes lagopus*), landscape of fear, movements, personality, predation risk, predator-prey interactions, reproductive success, spatial ecology, territoriality

INTRODUCTION

0.1 Effets du risque de prédation sur le comportement des proies

La prédation a un rôle central dans les processus écologiques et évolutifs (Menge & Sutherland, 1976; Ford et al., 2014). Elle agit notamment comme force descendante qui structure les communautés animales et végétales, générant parfois une cascade trophique où les prédateurs affectent les communautés végétales via la régulation des populations d’herbivores (Schmitz et al., 2004; Legagneux et al., 2012). De plus, les conséquences écologiques de la prédation dépassent les effets directs liés à la consommation des proies. Par exemple, les prédateurs influencent également les comportements de leurs proies (par ex. temps passé à se nourrir, Laundré et al., 2001), ou d’autres traits physiologiques (par ex. taux d'hormones, Creel et al., 2007), morphologiques (par ex. épaisseur de coquille ou force musculaire, Agrawal, 2001) ou d’histoire de vie (par ex. taille de ponte, Eggers et al., 2006), en modulant le risque de prédation dans le paysage (Schmitz et al., 2004; Peacor et al., 2020, 2022). Le risque de prédation représente la probabilité qu’un individu soit consommé par un prédateur, à une localisation et un temps donnés (Lima & Dill, 1990). Les proies peuvent notamment répondre à leur perception du risque en ajustant leur utilisation de l’habitat ou leur niveau de vigilance afin de réduire le risque de prédation (Laundré et al., 2001; Fortin et al., 2005; Valeix et al., 2009). Ces changements phénotypiques peuvent ensuite se répercuter sur leur survie et leur reproduction (Peckarsky et al., 1993; Peacor et al., 2022), et ultimement influencer la croissance des populations et la structure des communautés (Cresswell, 2008; Teckentrup et al., 2018; Sheriff et al., 2020; Wirsing et al., 2021). Ainsi, les effets de la prédation peuvent être séparés en effets létaux, dus à la consommation des proies, et en effets non létaux, qui résultent de changements phénotypiques en réponse au risque de prédation (Lima & Dill, 1990; Cresswell, 2008; Gaynor et al., 2019; Peacor et al., 2022).

0.1.1 Le paysage de la peur dans son contexte écologique

Bien que les effets létaux et non létaux peuvent tous affecter la dynamique des populations et des communautés, les mécanismes qui expliquent les effets résultant du risque de prédation sont complexes et demeurent mal compris (Peacor et al., 2020, 2022; Sheriff et al., 2020; Wirsing et al., 2021). En effet, de plus en plus d'études suggèrent que les individus modifient leurs comportements en réponse à leur perception du risque de prédation, qui varie spatialement et temporellement (Forstmeier & Weiss, 2004; van der Merwe & Brown, 2008; Valeix et al., 2009; Kohl et al., 2018; Smith et al., 2019b). Toutefois, un manque de clarté dans la définition des variables et des concepts qui sont étudiés a parfois mené à des raisonnements circulaires (Gaynor et al., 2019). Par exemple, afin d'évaluer comment les proies modifient leurs comportements anti-prédateurs, comme la vigilance, en fonction du risque de prédation, certaines études ont utilisé d'autres comportements anti-prédateurs, comme l'émission de cris d'alarme, comme proxys du risque de prédation (par ex. Willems & Hill, 2009). Dans ces cas, c'est plutôt la relation entre deux comportements anti-prédateurs qui est étudiée, et non l'effet du risque de prédation sur les réponses comportementales des proies. Cette confusion dans les définitions des variables qui sont mesurées limite notre capacité à identifier les mécanismes qui expliquent les effets non létaux de la prédation, et notre compréhension de ces mécanismes demeure donc grandement théorique. Une standardisation des méthodes et de la terminologie, ainsi qu'une clarification des concepts permettraient de mieux identifier les variables qui sont réellement mesurées dans nos études, et ainsi d'identifier les mécanismes qui expliquent les effets du risque de la prédation sur les populations et communautés (Gaynor et al., 2019; Peacor et al., 2020).

En se basant sur le concept du paysage de la peur popularisé par Laundré et al. (2001, 2010), Gaynor et al. (2019) ont proposé un cadre conceptuel pour guider les recherches sur les effets du risque de prédation. Dans ce cadre conceptuel, détaillé à la Figure 0.1, le paysage de la peur, soit la répartition spatiale du risque de prédation perçu par les proies, se retrouve parmi une série de paysages interreliés. Au sommet se trouve le paysage physique, soit les caractéristiques de l'habitat pouvant influencer le risque de prédation, telles que celles qui limitent les déplacements du prédateur (par ex. la topographie, Anderson et al., 2015) ou qui influencent la probabilité que la proie détecte un prédateur (par ex. l'ouverture du milieu, Valeix et al., 2009). Différentes caractéristiques biologiques et écologiques des prédateurs (par ex. mode de chasse, territorialité) et des proies (par ex. densité, présence de proies alternatives) déterminent également la répartition des proies et les interactions qu’elles ont avec leurs prédateurs, et interagissent avec le paysage physique pour moduler le paysage du risque de prédation. Ensuite, le paysage du risque de prédation détermine le paysage de la peur. En effet, celui-ci n’est pas nécessairement équivalent à celui du risque de prédation, puisque des contraintes physiologiques, phylogénétiques ou écologiques peuvent affecter comment les individus perçoivent le risque dans leur habitat (Jordan & Ryan, 2015; Gaynor et al., 2019). Finalement, le paysage de la peur influence les réponses des proies à la variation du risque de prédation, et ultimement leur répartition et leurs comportements anti-prédateurs.

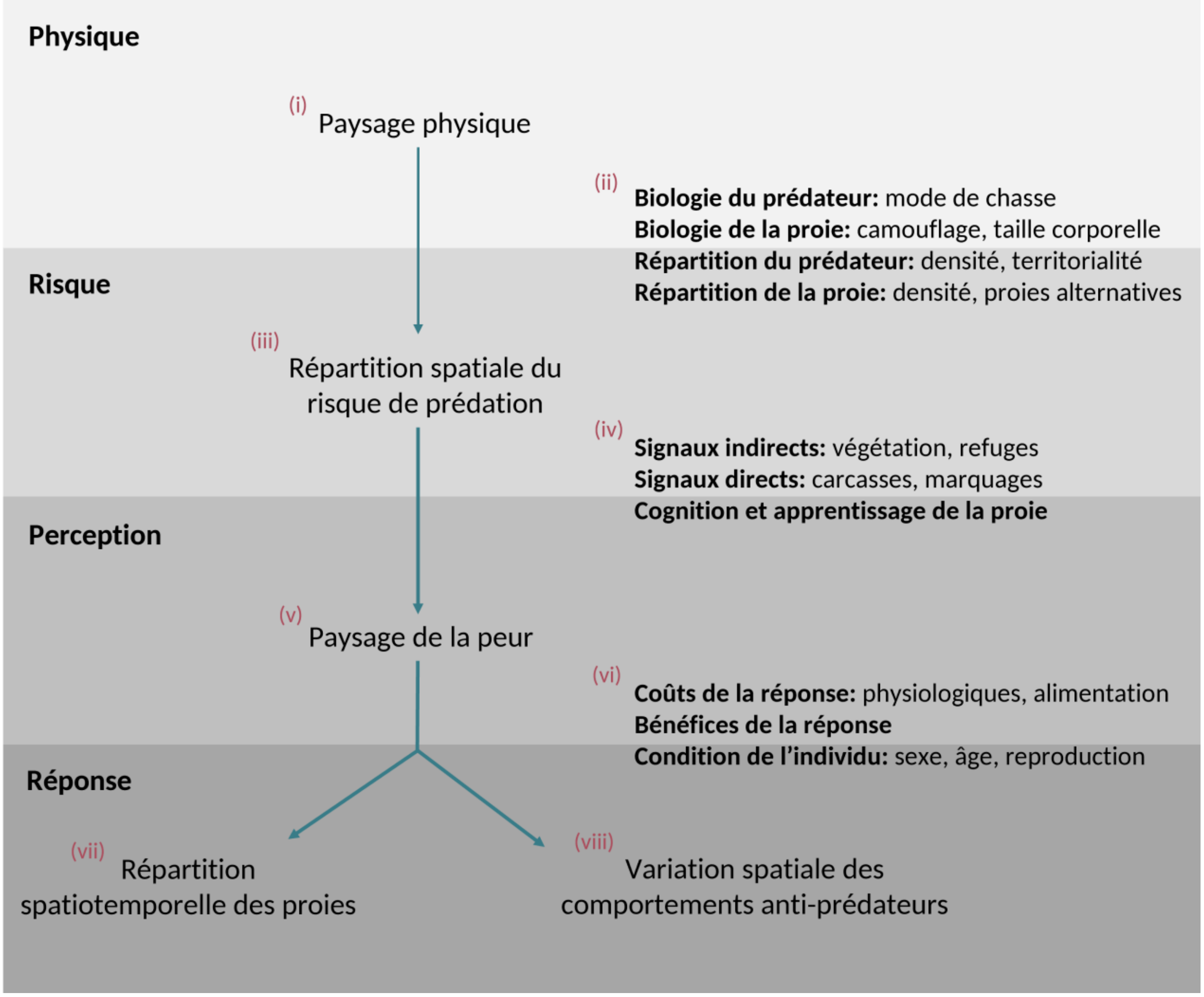

Figure 0. 1 Le cadre conceptuel du contexte écologique du paysage de la peur, proposé par Gaynor et al. (2019). (i) Le paysage physique (par ex. végétation, topographie, couverture neigeuse) influence la visibilité, la probabilité de détection et les mouvements des prédateurs avant et pendant les rencontres entre prédateurs et proies. (ii) Des aspects de la biologie du prédateur et de la proie déterminent la répartition des prédateurs et des proies, et influencent également la répartition du risque. Le paysage physique influence ensuite (iii) la variation spatiale dans le risque de prédation, et la probabilité qu'un évènement de prédation ait lieu. Le risque est ensuite (iv) perçu de manière imparfaite par les proies, en fonction (iv) de différents signaux indirects (associés au paysage physique) et directs (associés aux prédateurs) plus ou moins fiables, et des capacités cognitives des proies, d'expériences passées ou de l'historique évolutif de l'espèce. (v) Le paysage de la peur se manifeste dans les réponses comportementales des proies (vi) qui décident où se déplacer et comment se comporter en fonction des coûts et bénéfices qui sont associés aux différentes options. Deux stratégies peuvent être adoptées pour minimiser le risque, soit (vii) d'éviter les zones les plus risquées, ou (viii) de modifier son comportement afin de réduire la probabilité d'être capturé par un prédateur à une localisation donnée. Figure modifiée de Gaynor et al. (2019).

0.1.2 Réponses comportementales des proies au risque de prédation

Les proies ajustent leurs comportements anti-prédateurs en réponse à leur perception du risque de prédation (Lima & Dill, 1990; Wirsing et al., 2021). Plus précisément, elles peuvent ajuster leurs comportements de manière proactive ou réactive (Creel et al., 2014; Courbin et al., 2016). On parle d'une stratégie proactive d'évitement du risque lorsque les proies modifient leur utilisation de l'espace pour éviter de rencontrer leur prédateur, via une sélection d'habitat (Johnson, 1980). Les animaux sélectionnent les habitats qui leur assurent le plus grand succès reproducteur à long terme, et ce à différentes échelles spatiales, allant de la sélection de l'aire de répartition à la sélection du micro-habitat (Johnson, 1980). Les proies peuvent notamment choisir l'emplacement de leur domaine vital en fonction du risque de prédation (Lima, 2009; Morosinotto et al., 2010), puis modifier leur utilisation de l'espace à l'intérieur du domaine vital afin d'éviter les zones les plus souvent utilisées par leur prédateur (Forstmeier & Weiss, 2004; Anderson et al., 2015). Finalement, lorsque le risque de prédation est imminent, c'est-à-dire lorsqu'une proie rencontre un prédateur, la proie peut adopter un comportement réactif, par exemple se cacher, fuir ou se défendre, pour augmenter ses chances de survie (Ydenberg & Dill, 1986; Montgomerie & Weatherhead, 1988).

La stratégie utilisée pour diminuer le risque peut également dépendre des taux de rencontre entre la proie et son prédateur. Les prédateurs ont généralement des proies principales ou préférées, c'est-à-dire nettement plus consommées ou recherchées que les autres (Hayward & Kerley, 2005; Hayward et al., 2006). Bien que ces proies puissent tenter de sélectionner des habitats où le risque de prédation est le plus faible, elles seront recherchées par les prédateurs et devront également utiliser des stratégies réactives d'évitement du risque lorsque des rencontres auront lieu. Effectivement, on observe souvent un jeu spatial, ou une « course à l'espace » entre les prédateurs et les proies (de l'anglais *predator-prey space race*), où les prédateurs modifient leur utilisation de l'espace pour maximiser le taux de rencontre avec leurs proies, alors que les proies tentent de minimiser les probabilités de rencontre (Sih, 1984; Smith et al., 2019a). En théorie, si la réponse du prédateur est dominante, les répartitions spatiales des prédateurs et des proies devraient être positivement corrélées (Sih, 1984, 2005), ce que l’on observe chez certains prédateurs et leurs proies principales (Fortin et al., 2005; Arias-Del Razo et al., 2012). À l’opposé, pour les proies qui sont consommées de manière opportuniste par leur prédateur (proies accidentelles), et qui ne sont pas recherchées en priorité, la stratégie proactive, soit la sélection d’habitat à faible risque de prédation, peut s’avérer efficace pour réduire le risque de prédation (Forstmeier & Weiss, 2004; Avgar et al., 2015). Dans le cas d’une réponse dominante de la proie, une corrélation négative entre les répartitions des prédateurs et des proies devrait être observée (Sih, 1984, 2005). De plus, les prédateurs vont parfois sélectionner les zones où les ressources recherchées par les proies sont les plus abondantes (par ex. les points d’eau dans les savanes africaines, Valeix et al., 2009), plutôt que de rechercher directement les proies, donnant lieu à un effet « saute-mouton » (de l’anglais *leapfrog effect*, Sih, 1998, 2005). Ceci peut favoriser les prédateurs si les proies dépendent fortement de ces ressources et ne peuvent les éviter (Smith et al., 2019a). Dans certains cas, les proies peuvent être favorisées en évitant temporairement ces zones qui sont dorénavant associées à un fort risque de prédation (Courbin et al., 2016).

0.2 Comportements de prédation et mouvements des prédateurs

Afin de mieux comprendre les mécanismes qui expliquent les effets du risque de prédation sur la répartition et les comportements des proies d’un écosystème, il est nécessaire de comprendre ce qui influence les comportements de prédation des prédateurs. En effet, le paysage du risque de prédation résulte de l’utilisation de l’espace des prédateurs lorsqu’ils sont en quête alimentaire (Lima, 2002; Gaynor et al., 2019). Tout comme les proies, les prédateurs vont sélectionner les habitats qui leur assurent le plus grand succès reproducteur à long terme, à différentes échelles spatiales (Johnson, 1980). À l’échelle de leur domaine vital, les prédateurs vont ainsi favoriser l’utilisation d’habitats où l’abondance de proies est la plus grande (Fortin et al., 2005; Arias-Del Razo et al., 2012; Scrafford & Boyce, 2018), et où leurs déplacements sont facilités ou leur succès de capture plus grand (Schmitz et al., 2004; Lecomte et al., 2008a; Smith et al., 2019a), tout en évitant les zones utilisées par leurs propres prédateurs s’il y a lieu (Brook et al., 2012; Suraci et al., 2016). Ainsi, du point de vue d’une proie, le risque de prédation peut varier dans l’espace en fonction de l’abondance et de la répartition des autres espèces, et selon différentes caractéristiques de l’habitat.

De plus, le mode de chasse des prédateurs influence la manière avec laquelle ils utilisent leur habitat pendant la quête alimentaire, et donc la répartition spatiale du risque de prédation (Schmitz, 2008). Parmi les prédateurs terrestres, on distingue généralement trois modes de chasse principaux, soit 1) le mode de chasse par embuscade (en anglais *ambush* ou *sit-and-wait predator*), 2) le mode de chasse par embuscade incluant la poursuite de la proie (*sit-and-pursue*), et 3) le mode de chasse actif (*cursorial* ou *active hunting predator*) (Schmitz et al., 2004). Les prédateurs qui chassent par embuscade (par ex. le lion, *Panthera leo,* le puma, *Puma concolor*) se cachent dans l’habitat et attendent leur proie, pour ensuite les embusquer et parfois les pourchasser. Les prédateurs actifs (par ex. le loup gris, *Canis lupus*, le renard roux, *Vulpes vulpes*) parcourent leur domaine vital de manière intensive afin de maximiser la probabilité de rencontre avec des proies. En somme, les prédateurs embusqués tentent en général de surprendre des proies en mouvement en restant immobiles, tandis que les prédateurs actifs tentent en général de surprendre des proies immobiles alors qu’ils sont en mouvement. Ainsi, chez un prédateur actif, la distance parcourue par unité de temps influence son taux d’acquisition de proies (Austin et al., 2006; Scharf et al., 2006; Merrill et al., 2010).

Le mode de chasse est un important déterminant des effets du risque de prédation dans un système prédateurs-proies (Preisser et al., 2007; Schmitz, 2007, 2008; Miller et al., 2014; Wirsing et al., 2021). Puisque les prédateurs qui chassent par embuscade tendent à demeurer immobiles et à utiliser préférentiellement des habitats qui leur permettent de se camoufler, le risque de prédation par ce type de prédateur peut être plus facilement perceptible par les proies grâce à des signaux clairs du paysage physique (par ex. herbes hautes et denses) (Preisser et al., 2007; Schmitz, 2007, 2008; Smith et al., 2020; Wirsing et al., 2021). À l’opposé, un prédateur actif qui parcourt de grandes distances dans son domaine vital génère des signaux parfois plus diffus, rendant le risque de prédation plus difficilement perceptible. Ainsi, le paysage de la peur devrait davantage ressembler au paysage du risque de prédation lorsque les prédateurs chassent par embuscade (Gaynor et al., 2019). Les réponses des proies à leur perception du risque pourraient donc être plus importantes quand elles sont susceptibles d'être consommées par des prédateurs embusqués.

0.2.1 Défis méthodologiques pour étudier les comportements de prédation

Déterminer où et quand les prédateurs capturent leurs proies permet d'établir plus précisément le paysage du risque de prédation. Cependant, les mammifères terrestres prédateurs sont souvent cryptiques et difficiles à observer en milieu naturel. Pour cette raison, des contraintes méthodologiques limitent notre capacité à évaluer où et quand ils capturent des proies. Une méthode couramment utilisée consiste à localiser les évènements de prédation sur le terrain en recherchant les carcasses des proies (Merrill et al., 2010; Thaker et al., 2011; Kohl et al., 2018). Deux autres méthodes plus efficaces utilisent des données de mouvement pour l'identification d'évènements de prédation. La première utilise des données télémétriques (par ex. GPS) pour identifier les localisations potentielles des sites de capture ou de mise à mort (Webb et al., 2008; Merrill et al., 2010; Wilmers et al., 2013). En effet, le temps de manipulation (incluant la consommation) de la proie par le prédateur équipé d'un collier GPS résulte en la création d'un regroupement de localisations, indiquant des sites de capture potentiels. Les sites doivent ensuite être validés sur le terrain en cherchant des carcasses ou des restes. Le succès de cette approche télémétrique dépend grandement du temps de manipulation de la proie, et donc de sa taille, et de la fréquence d'échantillonnage du GPS, qui doit être suffisamment haute pour que plusieurs points soient enregistrés pendant la manipulation de la proie (Knopff et al., 2009; Palacios & Mech, 2011; Petroelje et al., 2020). La deuxième méthode pour identifier les évènements de prédation, utilisée dans quelques études sur des félins, utilise des accéléromètres qui mesurent l'accélération sur trois axes (Wilson et al., 2013; Williams et al., 2014; Wang et al., 2015). Cette fois ci, le succès de la méthode dépend principalement du mode de chasse du prédateur, notamment de la présence d'une embuscade. En effet, le mode de chasse par embuscade est associé à une séquence de comportements dont les patrons d'accélération sont reconnaissables, soit une période de traque ou de repérage suivie de la poursuite, l'attaque et la consommation de la proie.

En raison des contraintes associées à ces deux méthodes, il n'existe à ce jour aucune méthode utilisant des données de mouvement pour identifier les évènements de prédation de prédateurs terrestres qui sont à la fois actifs et qui se nourrissent de petites proies qui demandent un court temps de manipulation. En revanche, il demeurre possible d'identifier des comportements qui sont associés à la quête alimentaire, sans aller jusqu'à l'identification des évènements de prédation. Ceci pourrait tout de même permettre d'en apprendre davantage sur comment les prédateurs génèrent un paysage du risque de prédation. Par exemple, des modèles de mouvement utilisant des données télémétriques permettent la décomposition des trajectoires en plusieurs séquences, associées à différents états comportementaux (Morales et al., 2004; Beyer et al., 2013; Patterson et al., 2017). Ces différents états comportementaux diffèrent l'un de l'autre dans les propriétés statistiques des mouvements qui leur sont associés, soit la longueur des pas et l'angularité des déplacements (angles entre les pas successifs). Cette méthode peut s'avérer intéressante pour identifier les phases d'activité d'un prédateur actif, qui sont principalement associées à sa quête alimentaire (Schmitz et al., 2004). Une classification comportementale de données d'accélérométrie pourrait également s'avérer utile, notamment si les comportements de quête alimentaire génèrent des patrons d'accélération distincts (Chimienti et al., 2017; Tatler et al., 2018).

0.3 Territorialité dans un contexte de prédation

En plus de l'environnement physique, l'environnement social des prédateurs peut influencer leurs mouvements, et potentiellement leur quête alimentaire. Par exemple, la territorialité pourrait influencer la répartition spatiale du risque de prédation. Alors que le domaine vital représente la surface couverte par les déplacements d'un individu (Burt, 1943), le territoire représente plutôt la surface du domaine vital défendue par un individu (ou groupe d'individus mutuellement tolérants), lui assurant ainsi un accès exclusif (Brown & Orians, 1970; Powell, 2000; Hinsch & Komdeur, 2017). Les individus signalent leur motivation à défendre un espace par l'émission de cris territoriaux (Frommolt et al., 2003; Darden & Dabelsteen, 2008) ou de marques olfactives (Sillero-Zubiri & Macdonald, 1998; Giuggioli et al., 2011; Fawcett et al., 2013). Si nécessaire, ils excluent les intrus en les agressant (Eberhardt et al., 1982; White & Harris, 1994). Le degré de territorialité dans une population est majoritairement expliqué par des variables écologiques liées aux ressources alimentaires (Macdonald, 1983; Maher & Lott, 2000), et est souvent quantifié en mesurant la portion de chevauchement entre les domaines vitaux d'individus voisins (Persson et al., 2010; Lebsock et al., 2012; Hernandez-Blanco et al., 2015). Un fort degré de chevauchement indique un faible degré de territorialité, et inversement. Le degré de territorialité ainsi que la taille du territoire résultent de l'optimisation du rapport coûts-bénéfices de la territorialité (Maher & Lott, 2000; Sells & Mitchell, 2020; Ord, 2021). Les coûts (par ex. perte de temps, perte d'énergie, risque de blessures) et bénéfices (par ex. gain en quantité, en qualité ou en prévisibilité de la nourriture) de la territorialité pouvant varier selon le contexte, le degré de territorialité n'est pas nécessairement une caractéristique propre à l'espèce (Powell, 2000) ou même à la population (Macdonald et al., 1999; McLoughlin et al., 2000; Eide et al., 2004).

De manière générale, les individus territoriaux tendent à éviter les interactions physiques avec leurs voisins, qui peuvent s'avérer dangereuses, et évitent donc les frontières (Mech & Harper, 2002; Wrangham et al., 2007; Schlägel et al., 2017). Dans le cas de prédateurs territoriaux, ceci pourrait générer des zones refuges pour les proies entre les territoires des prédateurs. Lewis et Murray (1993) ont notamment montré mathématiquement que le risque de prédation était plus faible entre les territoires de meutes de loups gris, et Mech (1977) a trouvé que les cerfs de Virginie (*Odocoileus virginianus*) étaient plus abondants dans ces zones tampons au Minnesota (États-Unis).

La probabilité de rencontre avec des individus voisins, qui varie au sein des domaines vitaux, peut également influencer la fréquence de certains comportements. Ceci a été observé principalement chez des espèces de primates qui vivent en groupe et chez des canidés. Notamment, les capucins à face blanche (*Cebus capucinus*) sont plus vigilants (Tórrez-Herrera et al., 2020; Noonan et al., 2021) et les loups d'Éthiopie (*Canis simensis*) et les loups gris déposent davantage de marques olfactives en bordure de territoire (Sillero-Zubiri & Macdonald, 1998; Zub et al., 2003). La probabilité de rencontrer un voisin pourrait également influencer les comportements de quête alimentaire des prédateurs, ce qui n'a cependant pas encore été évalué étant donné la difficulté d'étudier les comportements de prédation en milieu naturel (tel que discuté plus haut). Pourtant, une répartition non aléatoire des comportements de prédation pourrait influencer celle du risque de prédation, et conséquemment les comportements et la répartition des proies. Ainsi, la territorialité chez les prédateurs est potentiellement un trait important à considérer dans le contexte écologique du paysage de la peur.

0.4 Différences interindividuelles comportementales

Les individus diffèrent au sein des populations par leur morphologie, leur physiologie et leurs comportements, et lorsqu'elle est héritable, cette variation interindividuelle est à l'origine de l'évolution des espèces et donc de la biodiversité (Darwin, 1859; Bolnick et al., 2003, 2011; Dall et al., 2012). En plus de son influence sur les processus évolutifs, les différences interindividuelles affectent les processus écologiques comme la dynamique des populations, des communautés et des écosystèmes (Wolf & Weissing, 2010; Bolnick et al., 2011; Sih et al., 2012). Par exemple, les différences interindividuelles constantes du niveau d'activité et d'exploration peuvent conduire à des spécialisations individuelles dans la consommation des ressources alimentaires (Toscano et al., 2016). Les termes « personnalité » et « tempérament » font référence aux différences interindividuelles de comportement répétables à travers le temps et les situations (Réale et al., 2007; Bell et al., 2009), alors que l'on parle de syndrome comportemental pour nommer les différents traits de personnalité qui covarient entre eux (Sih et al., 2004).

Les traits de personnalité généralement étudiés sont la témérité (prise de risque), l'exploration (d'un nouvel environnement), l'activité, l'agressivité, et la sociabilité (Réale et al., 2007). Les différences de personnalité dans les populations proviendraient de différences génétiques (van Oers et al., 2005; Réale et al., 2007; Quinn et al., 2009), d'effets maternels ou environnementaux précoces qui affectent la plasticité développementale (Groothuis & Trillmich, 2011; Montiglio et al., 2013; Sih et al., 2015), ou d'une combinaison des deux. Le maintien des différences de personnalité, qui sont associées à des différences d'aptitude phénotypique (Dingemanse et al., 2004; Dingemanse & Réale, 2005; Smith & Blumstein, 2008; Réale et al., 2009), pourrait être expliqué par le lien entre les traits de personnalité et les stratégies individuelles d'histoire de vie (Wolf et al., 2007; Biro & Stamps, 2008; Réale et al., 2010), ou par la présence de sélection fluctuante associée à une importante variation environnementale (Réale & Dingemanse, 2010; Wolf & Weissing, 2010; Dingemanse & Réale, 2013). Cette dernière hypothèse a cependant rarement été testée en milieu naturel (mais voir Dingemanse et al., 2004; Boon et al., 2007; Mouchet et al., 2021).

Bien que de manière générale, une plus grande témérité augmente les opportunités d'alimentation et de reproduction, et est donc associée à un plus grand succès reproducteur (Biro & Stamps, 2008; Smith & Blumstein, 2008; Bubac et al., 2018), des variations dans l'environnement peuvent influencer les relations entre les comportements et différents traits d'histoire de vie (Smith & Blumstein, 2008; Adriaenssens & Johnsson, 2009; Montiglio et al., 2018). On observe notamment que selon l'abondance ou la disponibilité des ressources, ce n'est pas toujours le même type de personnalité qui est avantagé (Boon et al., 2007; Le Cœur et al., 2015; Vetter et al., 2016). Par exemple, les tamias de Sibérie (*Tamias sibiricus*) qui sont les plus téméraires ont un plus grand succès reproducteur annuel que ceux qui le sont moins quand les ressources alimentaires sont rares, mais c'est l'inverse quand la nourriture est abondante (Le Cœur et al., 2015). Ceci génère une sélection fluctuante sur la témérité, qui pourrait maintenir les différences de personnalité dans cette population de tamias (Le Cœur et al., 2015).

0.4.1 Le cas des prédateurs et implications pour le risque de prédation

Les études sur la personnalité animale évaluent souvent les différences comportementales dans un contexte de risque de prédation (Réale et al., 2007; Quinn et al., 2012). En effet, les proies tendent à montrer différents niveaux de témérité face à un risque de prédation, et leurs réactions sont répétables à travers le temps et les situations (Réale & Festa-Bianchet, 2003; Belgrad & Griffen, 2016). Le niveau de prise de risque est également corrélé à d'autres traits de personnalité comme l'agressivité ou l'exploration (Sih et al., 2004; Mazué et al., 2015). Bien que les études sur le sujet soient peu nombreuses, des différences interindividuelles comportementales ont également été observées pour différents traits comportementaux de prédateurs, comme la témérité chez le phoque gris (*Halichoerus grypus*) (Bubac et al., 2018) et le renard nain (*Vulpes macrotis*) (Bremner-Harrison et al., 2018), et l'agressivité, la sociabilité et la témérité chez la hyène tachetée (*Crocuta crocuta*) (Yoshida et al., 2016). Le succès reproducteur des prédateurs étant grandement lié à l'abondance et la disponibilité de leurs proies (Salamolard et al., 2000; Terraube et al., 2015), la variation dans l'abondance des ressources pourrait mener au maintien de différences de personnalité dans les populations de prédateurs, mais ceci n'a jamais été évalué.

On observe également des différences interindividuelles dans des comportements reliés à la quête alimentaire, comme la fidélité aux sites d'alimentation ou le mode d'alimentation (par embuscade ou par recherche active), qui sont parfois liés à des traits de personnalité comme la témérité (Patrick & Weimerskirch, 2014; Spiegel et al., 2017; Harris et al., 2020). De plus, quelques expériences effectuées en laboratoire ou mésocosme ont montré un lien entre les différences de personnalité et la capacité à acquérir de la nourriture (Ioannou et al., 2008; Toscano & Griffen, 2014; Chang et al., 2017). Michalko et Řežucha (2018) ont quant à eux trouvé que la probabilité d'attaquer une proie lors d'une rencontre était plus grande chez les araignées aranéomorphes (*Philodromus cespitum*) les plus agressives. Certains types de personnalité des prédateurs pourraient ainsi augmenter leur capacité à obtenir des ressources quand celles-ci sont en faible abondance, leur assurant un plus grand succès reproducteur. À l'inverse, des coûts associés à la témérité, par exemple une survie diminuée (Smith & Blumstein, 2008), pourraient faire en sorte que les individus les moins téméraires soient avantagés quand les ressources sont très abondantes.

Les prédateurs les plus agressifs et téméraires pourraient donc générer une pression de prédation plus importante et donc influencer plus fortement la dynamique des populations de proies (Sih et al., 2012). Des différences interindividuelles dans des traits comportementaux liés à la capacité de capturer des proies chez des prédateurs en milieu naturel pourrait également faire varier le risque de prédation entre les domaines vitaux des prédateurs. La personnalité des prédateurs pourrait ainsi jouer un rôle important dans le contexte écologique du paysage de la peur. Il est donc nécessaire d’étudier les comportements des prédateurs en milieu naturel, d’évaluer la présence de différences interindividuelles comportementales et d’identifier les variables écologiques qui pourraient favoriser le maintien de ces différences.

0.5 Problématique de recherche et objectifs

Le paysage du risque de prédation influence la répartition et les comportements des proies. Cependant, notre compréhension des mécanismes qui expliquent les réponses comportementales des proies demeure grandement théorique, et les méthodes pour étudier les comportements alimentaires des prédateurs sont limitées. De plus, différentes caractéristiques propres aux individus d’une espèce de prédateur, comme leur territorialité ou leur personnalité, pourraient également influencer la répartition spatiale du risque de prédation. Ainsi, la compréhension des conséquences de la prédation sur une communauté animale nécessite l’analyse des mouvements et des comportements des prédateurs. L’**objectif principal** de cette thèse est d’évaluer comment l’activité des prédateurs influence les comportements et la répartition des proies, et d’identifier des caractéristiques propres aux individus prédateurs qui pourraient influencer la répartition du risque de prédation. Pour répondre à cet objectif principal, j’ai étudié une population de renards arctiques (*Vulpes lagopus*) et ses interactions avec la communauté de proies de l’île Bylot au Nunavut, et j’ai progressé selon quatre objectifs spécifiques (Figure 0.2).

Tout d’abord, mon **premier objectif** était d’évaluer comment la variation spatiale dans l’intensité d’utilisation de l’espace par le renard arctique, un prédateur actif, génère un paysage du risque de prédation qui peut être perçu par les proies. J’ai également évalué dans le cadre de cet objectif si le paysage de l’activité des renards influence les comportements anti-prédateurs d’une proie principale (la grande oie des neiges, *Anser caerulescens atlanticus*), et la répartition de proies accidentelles (plusieurs autres espèces d’oiseaux migrateurs) nichant à Bylot. Comme il demeure difficile d’étudier les comportements de prédateurs actifs qui se nourrissent de petites proies, mon **deuxième objectif** consistait à développer une méthode permettant d’identifier les évènements de prédation du renard arctique. Spécifiquement, j’ai utilisé une classification comportementale de données d’accélérométrie pour identifier des évènements de cache de proies des renards. Pour les deux derniers objectifs, j’ai cherché à comprendre comment certaines caractéristiques comportementales du renard arctique pouvaient influencer la répartition spatiale du risque de prédation. Ainsi, mon **troisième objectif** consistait à évaluer comment la territorialité, et plus spécifiquement les interactions entre individus utilisant des domaines vitaux voisins, influencent les comportements de prédation des renards et donc la répartition du risque de prédation. Finalement, pour mon **quatrième objectif**, je me suis intéressée à l’effet du contexte écologique, soit l’abondance de la proie principale, sur la relation entre le niveau de témérité des renards et leur succès reproducteur. J’ai également évalué la présence de différences interindividuelles dans ce comportement. Ce quatrième objectif est une étape permettant d’évaluer l’importance de la témérité pour l’écologie et l’évolution du renard arctique, dans le but d’évaluer à terme les effets des différences de personnalité entre renards sur la répartition du risque de prédation généré par cette espèce. Les quatre objectifs spécifiques de ce projet sont présentés sous forme d’articles scientifiques dans les prochains chapitres de cette thèse.

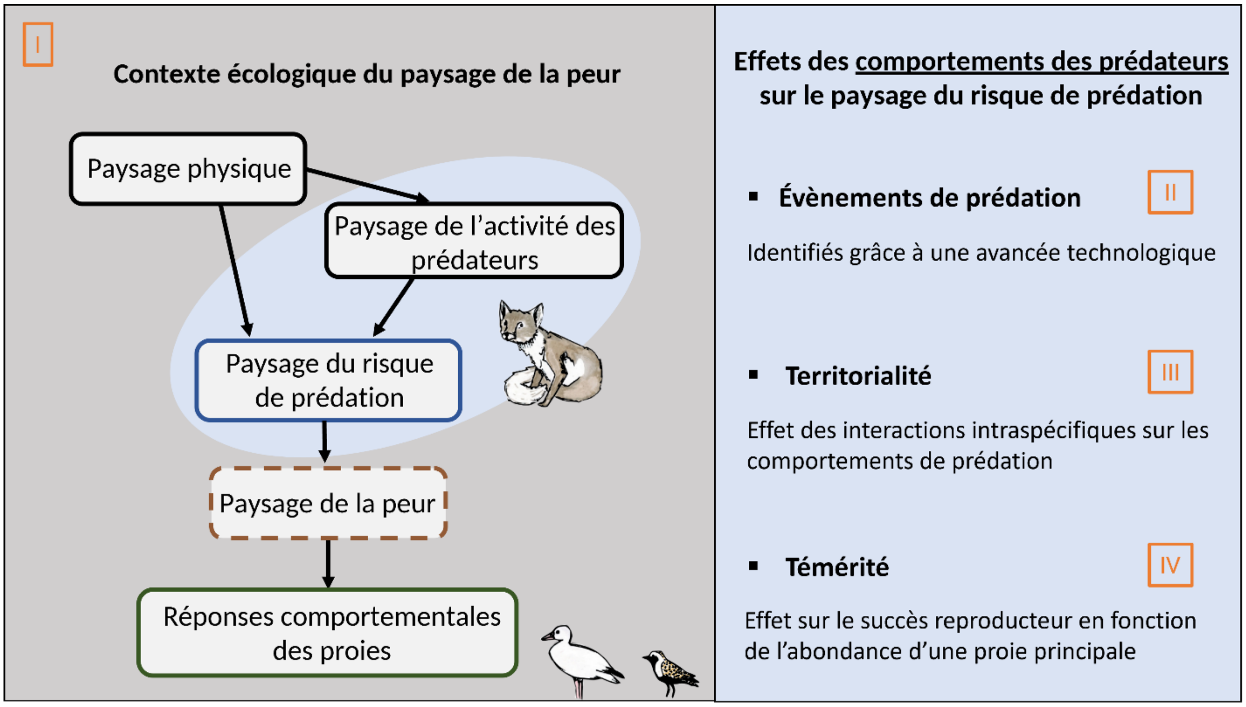

Figure 0. 2 Résumé des objectifs de la thèse (le numéro du chapitre est indiqué et encadré en orange). Le contexte écologique du paysage de la peur est central au projet. Au premier Chapitre, j'évalue les liens entre le paysage de l'activité des renards et celui du risque de prédation, et comment ils génèrent une variation spatiale dans les comportements anti-prédateurs de proies principales, et la répartition de proies accidentelles. Je considère également les effets du paysage physique sur ces interactions. Le paysage de la peur n'est pas mesuré mais omniprésent (encadré pointillé). Ensuite, j'évalue comment différentes caractéristiques des prédateurs pourraient influencer comment ils génèrent le paysage du risque de prédation. D'abord, au Chapitre 2, j'explique que l'identification des évènements de prédation de prédateurs actifs se nourrissant de petites proies demeure un obstacle méthodologique à l'évaluation du paysage du risque de prédation, et je propose de surmonter cet obstacle grâce à une avancée technologique. Au Chapitre 3, j'évalue comment la territorialité, et plus spécifiquement les interactions entre individus voisins, peuvent influencer les comportements de prédation. Finalement, au Chapitre 4, j'évalue comment la témérité d'un prédateur peut affecter son succès reproducteur en fonction de l'abondance d'une proie principale. Je me suis intéressée à cette question puisque des différences interindividuelles dans la témérité pourraient influencer la répartition du risque de prédation.

0.6 Modèle d’étude : le renard arctique et la communauté animale de l’île Bylot

Le renard arctique est un prédateur terrestre de l’Arctique dont la répartition est circumpolaire (Prestrud, 1991; Audet et al., 2002; Angerbjörn et al., 2004). J’ai étudié les renards arctiques de l’île Bylot située au nord de l’île Baffin, dans le parc national de Sirmilik au Nunavut (73° N, 80° W, voir la Figure 1.5 montrant la position géographique du site d’étude). Les habitats dominants sont la toundra mésique et les milieux humides polygonaux. On y retrouve aussi des zones de toundra xérique, des zones humides inondées, des milieux graveleux, des lacs et des rivières.

Le renard arctique est le prédateur principal dans plusieurs écosystèmes arctiques, se nourrissant de petits rongeurs, d’œufs d’oiseaux, de carcasses et d’autres items (Angerbjörn et al., 2004). À Bylot, les renards arctiques ont comme proies principales les lemmings bruns (*Lemmus trimucronatus*) et variables (*Dicrostonyx groenlandicus*) (Gauthier et al., 2011). Ces populations de lemmings montrent d’importantes fluctuations d’abondance avec des pics populationnels généralement espacés de 3 à 4 ans (Gruyer et al., 2008). Certains renards se nourrissent aussi alternativement d’œufs de la grande oie des neiges (Bêty et al., 2001; Gauthier et al., 2004). En effet, une colonie d’environ 20 000 couples d’oies répartis sur environ 70 km^2 niche sur l’île Bylot (Bêty et al., 2001, 2002; Gauthier et al., 2013; Figure 0.3C), créant une courte mais importante période d’abondance en nourriture pendant l’été pour les renards établis dans la colonie ou à sa proximité. Pendant la période de nidification, les renards récoltent et cachent activement les œufs dans leur domaine vital (Careau et al., 2007, 2008b). Ces œufs constituent une source de nourriture importante en dehors de la période de nidification, ce qui permet en partie de réduire les effets des creux d’abondance de lemmings (Samelius et al., 2007). Les particularités des comportements de cache des renards sont détaillées aux Chapitres 2 et 3. De manière opportuniste, les renards se nourrissent durant l’été d’œufs d’autres espèces comme des passereaux ou des limicoles qui viennent nicher à Bylot, mais que l’on retrouve en faible densité (McKinnon et al., 2013; Duchesne et al., 2021). Les lemmings restent la ressource nécessaire pour la reproduction des renards (Chevallier et al., 2020), bien que certains couples dont les tanières sont situées à proximité de la colonie d'oies peuvent parfois se reproduire aussi lors d'années où l'abondance en lemmings est faible (Giroux et al., 2012). La Figure 0.3A résume les relations trophiques entre le renard arctique de l'île Bylot et ses proies principales et alternatives (ces deux types de proies étant activement recherchées par les renards) et ses proies accidentelles (qui ne semblent pas activement recherchées par les renards mais qui sont consommées lorsqu'elles sont rencontrées).

Lorsque la densité en proies principales (lemmings) est faible, les renards compensent cette diminution de ressources en exerçant une prédation supérieure sur leurs proies alternatives (œufs d'oies des neiges) et accidentelles (œufs de limicoles et autres oiseaux) (Bêty et al., 2002; Lamarre et al., 2017). Cependant, la prédation sur les proies accidentelles est supérieure dans les zones où les proies alternatives sont abondantes, probablement à cause d'un effet d'agrégation des renards dans la colonie d'oies (Lamarre et al., 2017). Aussi, la relation positive entre la densité de nids d'oies des neiges et la prédation des nids de limicoles est plus marquée lors d'années à faible abondance de lemmings (McKinnon et al., 2013). Il existe donc des interactions indirectes complexes entre les espèces de proies qui ont le renard arctique comme prédateur commun (Bêty et al., 2002; Gauthier et al., 2004; Ims et al., 2013; McKinnon et al., 2013; Duchesne et al., 2021).

Les renards arctiques sont généralement territoriaux et défendent leur territoire en déposant des marques olfactives (urine, fèces), en émettant des cris territoriaux, et au besoin en chassant activement les intrus par des poursuites voire des contacts agressifs (Eberhardt et al., 1982). Les renards arctiques forment des paires socialement monogames (Eberhardt et al., 1982; Cameron et al., 2011). L'organisation sociale de l'espèce est variable à l'échelle circumpolaire, allant de couples reproducteurs à groupes de trois individus ou plus par territoire (Norén et al., 2012). Le degré de sociabilité est spécifique à l'écosystème et dépend de la répartition et de l'abondance des ressources, qui sont variables à l'échelle circumpolaire, et aussi de la pression de prédation sur le renard arctique, notamment par le renard roux (Eide et al., 2004; Norén et al., 2012; Elmhagen et al., 2014). Chez la population de renards arctiques de l'île Bylot, les groupes de plus de deux individus sont exceptionnels et les territoires sont presque toujours occupés par une paire seulement (Cameron et al., 2011; Lai, 2017), peut-être parce que la prédation sur les renards est rare à ce site, ce qui rendrait la formation de groupes peu bénéfique (Lai, 2017). Les renards utilisent des tanières pour l'élevage des jeunes, l'emplacement de ces dernières étant sélectionné entre autres selon la topographie, la proximité à un cours d'eau et l'abondance en nourriture (Szor et al., 2008).

Pendant l'hiver, bien que surtout résidents, les renards arctiques de l'île Bylot effectuent des déplacements à l'extérieur de leur territoire, parfois à très grande échelle vers la banquise avoisinante, comme décrit à l'aide de balises Argos (Tarroux et al., 2010; Lai et al., 2015, 2017). Récemment, nous avons suivi les mouvements de quelques renards avec des colliers GPS et montré l'ampleur de leurs déplacements dans leur domaine vital pendant l'été, avec des distances parcourues journalières d'en moyenne 52 km, allant jusqu'à 76 km (Poulin et al., 2021). Nous avons également étudié la sélection d'habitat des renards pendant l'été, et découvert que lorsqu'ils sont actifs, les renards sélectionnent les habitats favorables aux lemmings et les zones où la densité en nids d'oies est la plus élevée (Grenier-Potvin et al., 2021). Lorsqu'ils sont inactifs, et donc probablement au repos, ils évitent les zones où la densité en nid d'oies est élevée. Nous avons également observé que les renards évitent les bordures de leur domaine vital, qui sont des frontières entre domaines vitaux voisins, et favorisent plutôt l'utilisation d'habitats à proximité de leur tanière pendant l'élevage des jeunes (Grenier-Potvin et al., 2021).

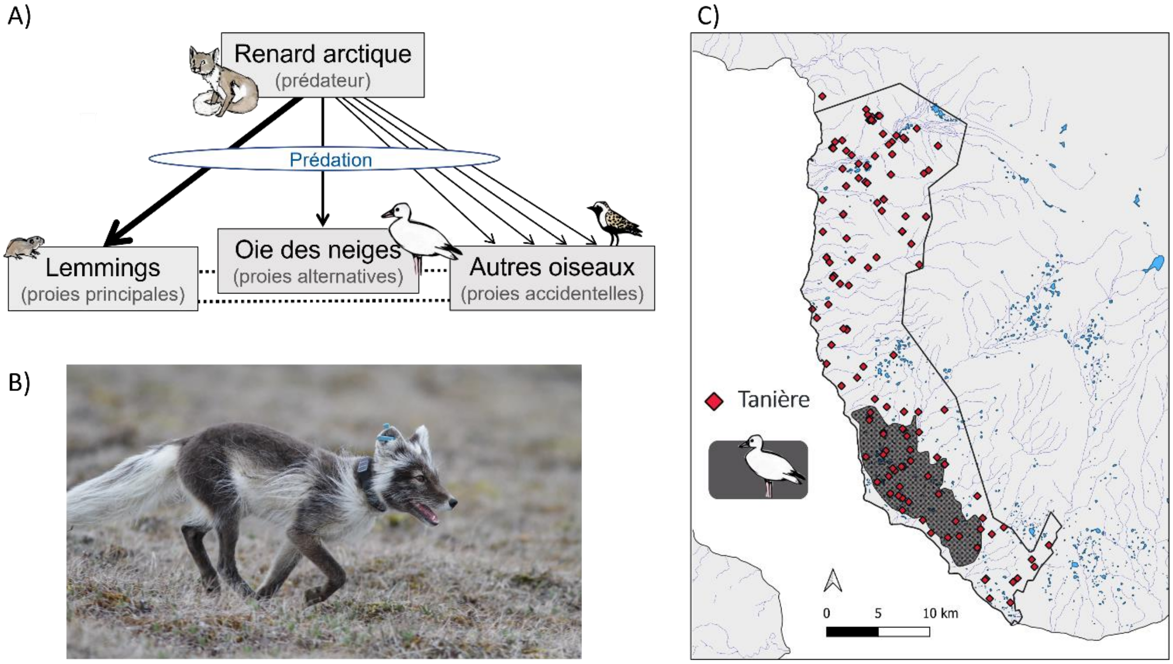

Figure 0. 3 Modèle d'étude. A) Relations trophiques entre le prédateur le plus influent de l'île Bylot et ses proies principales, alternatives et accidentelles (l'épaisseur des flèches représente l'importance de la proie pour le renard). Les lignes pointillées représentent les interactions indirectes entre les proies. Dessins des animaux réalisés par Éliane Duchesne. B) Renard arctique équipé d'un collier GPS avec accéléromètre. Photo prise par Dominique Berteaux. C) Plaine sud de l'île Bylot (73° N, 80° W) au Nunavut (Canada), montrant la zone d'étude (ligne noire), les tanières de renards (losanges rouges) et la colonie d'oies (région grise hachurée).

0.6.1 Méthodologie générale

Les 115 tanières de renards actuellement connues à Bylot (Figure 0.3C) sont visitées chaque année au mois de mai pour identifier celles qui semblent occupées. Des caméras automatiques sont installées et des observations aux tanières sont effectuées pour identifier celles qui sont utilisées pour la reproduction, identifier les individus utilisateurs s'ils sont marqués, et déterminer le nombre de jeunes produits. Les renards sont ensuite capturés à l'aide de cages ou de pièges à patte, dans le but de marquer les individus de la population (avec des boucles d'oreille de couleur). Les individus sont pesés et sexés. Certains individus sont également équipés de colliers munis d'un GPS, d'un accéléromètre, et de batteries rechargeables grâce à des panneaux solaires (Figure 0.3B). Les données sont téléchargées à distance par ondes radio à ultra haute fréquence (UHF) à l'aide d'une station émettrice-réceptrice et d'une antenne. Nous avons équipé 8 renards en 2018 et 15 renards en 2019, et enregistré pour chaque individu une localisation GPS toutes les 4 minutes, ainsi que des séquences d'accélérométrie sur trois axes (vertical, latéral et antéro-postérieur) de 30 secondes séparées entre elles par des pauses de 4 minutes. Nous avons mesuré une erreur moyenne de 11 m pour les localisations GPS enregistrées chaque 4 minutes (Poulin et al., 2021). Les données GPS ont permis de mesurer l'intensité d'utilisation de l'espace des renards (Chapitre 1), de définir les domaines vitaux et mesurer les interactions entre individus voisins (Chapitre 3). Les données d'accélérométrie ont permis de connaître les comportements des renards à partir d'une classification des données par un algorithme d'apprentissage (Chapitre 2). Depuis 2016, à la fin de chaque capture de renards, nous évaluons également leur témérité, soit leur tendance à prendre des risques. Lors du relâché d'un renard après une capture, celui-ci s'enfuit en courant mais se retourne de temps en temps pour observer l'équipe de capture. Nous mesurons la distance entre le renard et les observateurs au moment où il s'arrête pour la première fois, et considérons cette distance comme indicatrice du degré de témérité de l'individu. Cette mesure est décrite en détail au Chapitre 4.

Chaque année, la densité en lemmings est estimée à l'aide de données de capture-marquage-recapture (Gauthier et al., 2013; Fauteux et al., 2015). Bien que la densité puisse varier spatialement sur l'île Bylot, ces variations spatiales sont faibles par rapport aux variations interannuelles (D. Berteaux, comm. pers.). La colonie d'oies de l'île Bylot est toujours située au sud de l'aire d'étude (Figure 0.3C). La densité des nids dans la colonie est spatialement hétérogène et le contour de la colonie varie quelque peu selon les années. Ce contour est tracé annuellement avec un GPS lors d'un survol par hélicoptère, ce qui permet de mesurer le chevauchement de chaque domaine vital de renard avec la colonie. De plus, en 2018 et 2019, nous avons cartographié de façon très précise la densité en nids d'oies dans les domaines vitaux des renards équipés d'un collier (voir le Chapitre 1 et Grenier-Potvin et al., 2021).

Nous avons mesuré également l’intensité de la défense du nid par les oies pendant l’incubation. En approchant les nids, nous avons fait fuir l’oie qui couvait et avons noté la distance entre l’observateur et l’oiseau au moment où celui-ci quittait le nid (voir Chapitre 1). Cette distance était d’autant plus faible que l’intensité de la défense était grande. Les nids des autres espèces d’oiseaux qui nichent à Bylot sont également localisés chaque année dans l’aire d’étude à l’aide de transects et de recherche active aux endroits où des individus reproducteurs sont aperçus ou entendus (Lamarre et al., 2017; Duchesne et al., 2021). Finalement, nous estimons le risque de prédation à l’aide de proies artificielles (morceaux de foie lyophilisé) disposées dans les domaines vitaux des renards. Des revisites permettent de déterminer si les proies ont été consommées (voir Chapitre 1).

CHAPITRE I

THE PREDATOR ACTIVITY LANDSCAPE PREDICTS THE ANTI-PREDATOR BEHAVIOR AND DISTRIBUTION OF PREY IN A TUNDRA COMMUNITY

Jeanne Clermont, Alexis Grenier-Potvin, Éliane Duchesne, Charline Couchoux, Frédéric Dulude-de Broin, Andréanne Beardsell, Joël Bêty & Dominique Berteaux

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1.1 Résumé

La prédation influence les communautés via des effets létaux et non létaux. Dans le cas des effets non létaux, les proies répondent de manière proactive ou réactive à leur perception du risque de prédation, qui varie à différentes échelles spatiales et temporelles. Les concepts de course à l'espace entre prédateurs et proies et du paysage de la peur sont utiles pour mieux comprendre comment le risque de prédation affecte les décisions comportementales et la répartition des proies. Nous avons évalué les effets du risque de prédation dans une communauté terrestre de l'Arctique, où le renard arctique est le prédateur principal d'oiseaux migrateurs. À l'aide de données GPS récoltées à haute fréquence, nous avons estimé le paysage de l'activité des renards arctiques, et validé à l'aide d'une expérience de proies artificielles que les paysages de l'activité des prédateurs et du risque de prédation sont interreliés. Nous avons ensuite mesuré les effets du paysage de l'activité des renards sur les comportements anti-prédateurs d'une proie principale (oie des neiges) activement recherchée par les renards, et sur la répartition des nids de plusieurs espèces de proies accidentelles consommées de manière opportuniste par les renards. Nous avons premièrement trouvé que les oies montraient une plus grande intensité de défense du nid dans les endroits fortement utilisés par les renards, suggérant qu'elles répondent de manière réactive à la variation du risque de prédation. Deuxièmement, nous trouvons que la probabilité d'occurrence des nids de proies accidentelles se trouvant dans des habitats accessibles aux renards était plus faible dans les zones fortement utilisées par les renards. Ceci suggère que ces oiseaux utilisent une stratégie proactive pour éviter la prédation, en sélectionnant des sites de nidification éloignés des zones risquées. Pour les proies accidentelles nichant dans des micro-habitats plus difficilement accessibles aux renards, la probabilité d'occurrence des nids était indépendante du risque de prédation dans l'environnement entourant le nid, puisque ces oiseaux évitent le risque à une échelle spatiale plus fine. En suivant les mouvements de tous les individus de l'espèce de prédateur dominante de notre aire d'étude, nous montrons comment l'étude des patrons de mouvement des prédateurs permet d'évaluer la répartition spatiale du risque de prédation. En somme, nous soulignons la diversité des stratégies de gestion du risque chez des proies qui partagent le même prédateur, ce qui permet une meilleure compréhension des mécanismes régissant la répartition des espèces et la structure des communautés.

Mots-clés : comportement anti-prédateur, course à l’espace, expérience de proies artificielles, interactions prédateurs-proies, paysage de l’activité des prédateurs, paysage de la peur, renard arctique, répartition des nids, risque de prédation

1.2 Abstract

Predation shapes communities through consumptive and non-consumptive effects. In the latter case, prey respond to perceived predation risk through proactive or reactive risk management strategies occurring at different spatial and temporal scales. The predator-prey space race and landscape of fear concepts are useful to better understand how predation risk affects prey behavioral decisions and distribution. We assessed predation-risk effects in a terrestrial Arctic community, where the arctic fox is the main predator of ground-nesting birds. Using high frequency GPS data, we estimated a predator activity landscape corresponding to fox space use patterns, and validated with an artificial prey experiment that this predator activity landscape correlated with the predation risk landscape. We then investigated the effects of the fox activity landscape on multiple prey species, by assessing the anti-predator behavior of a main prey (snow goose) actively searched for by foxes, and the nest distribution of several incidental prey species. We first found that snow geese showed a stronger level of nest defense in areas highly used by foxes, possibly responding with a reactive strategy to variation in predation risk. Then, nests of incidental prey reproducing in habitats easily accessed by foxes had a lower probability of occurrence in areas highly used by foxes, suggesting these birds may use a proactive risk management strategy by shifting their distribution away from risky areas. For incidental prey species nesting in microhabitat refuges difficult to access by foxes, probability of nest occurrence was independent of predation risk in the surrounding area, as they avoid risk at a finer spatial scale. By tracking all individuals of the dominant predator species in our study area, we demonstrated the value of using predator space use patterns to infer spatial variation in predation risk. Overall, we highlight the diversity of risk management strategies in prey sharing a common predator,

hence refining our understanding of the mechanisms driving species distribution and community structure.

Keywords: anti-predator behavior, arctic fox, artificial prey experiment, landscape of fear, nest distribution, predation risk, predation risk effects, predator activity landscape, predator-prey interactions, predator-prey space race

1.3 Introduction

Predation plays a central role in ecological and evolutionary processes (Menge & Sutherland, 1976; Ford et al., 2014). It shapes communities through both direct killing of prey (consumptive effects) and non-consumptive, predation-risk effects (Lima & Dill, 1990; Cresswell, 2008; Laundré et al., 2010; Peacor et al., 2020). Non-consumptive effects of predation can be major drivers of food web structure and dynamics (Cresswell, 2008; Teckentrup et al., 2018).

Prey respond to predation risk with various risk management strategies that are tailored to different spatial and temporal scales. Strategies are either proactive when behavior is adjusted to reduce risk prior to a predator encounter, or reactive when the threat is imminent (Lima & Dill, 1990; Creel et al., 2014; Courbin et al., 2016). At broad spatial and temporal scales, predation risk associated to different areas may influence prey's choice of home range, such as the breeding home range of migrant birds (i.e., proactive home range selection, or second-order habitat selection, Johnson, 1980; Lima, 2009; Morosinotto et al., 2010). At intermediate scales, spatial variation in predation risk within the home range of a prey may affect its space use, particularly during times of high risk (i.e., proactive patch selection, or third-order habitat selection, Johnson, 1980). For example, many bird species maximise their reproduction by nesting where predation risk is the lowest, either where the regional abundance of main predators is low (Forstmeier & Weiss, 2004) or in habitats providing complete or partial refuge against predation (Anderson et al., 2015). At fine scales, in direct presence of a predator, prey show reactive risk avoidance and use anti-predator behavior such as escape behavior (Ydenberg & Dill, 1986). In a breeding context, the threat posed by predators is often much higher for young than for adults (Rosenbaum, 2018). Thus, in many species, parents (such as incubating birds) provide offspring defense rather than flee (Montgomerie & Weatherhead, 1988; Lima, 2009).

Prey risk management strategies also depend on predator and prey encounter rates and on the outcome of the predator-prey space race, where predators are searching for prey and prey are moving to avoid predators (Sih, 1984; Lima, 2002; Smith et al., 2019a). Indeed, space use patterns of predators and their main prey (which are often the most abundant and profitable prey) tend to correlate since predators actively search for them (Fortin et al., 2005; Arias-Del Razo et al., 2012). Thus, main prey species can hardly avoid predation risk by shifting their distribution, and they lose the space race. This is also most likely to occur when prey are relatively immobile (Sih, 1984) since their distribution is predictable, such as in the case of breeding birds after nest establishment. Such prey will rather adopt reactive risk management strategies like defense or vigilance behaviors. On the other hand, incidental prey species, which are consumed when encountered but are not affecting predator movements in the landscape, may win the predator-prey space race and manage risk of predation proactively by avoiding areas highly used by predators (Forstmeier & Weiss, 2004; Avgar et al., 2015).

The landscape of fear concept offers another useful framework to understand how predation risk affects prey behavior (Laundré et al., 2010; Gaynor et al., 2019; Peacor et al., 2020). Laundré et al. (2010) defined the landscape of fear as the spatial variation in prey perception of predation risk. Gaynor et al. (2019) then framed the landscape of fear as part of a series of interdependent landscapes. First, the physical landscape represents habitat features that interact with the biology (hunting mode, body size, etc.) of predators and prey to determine their distributions and interactions. These interactions then modulate the predation risk landscape and, accordingly, the landscape of fear. Finally, the landscape of fear determines the responses of prey to predation risk, which ultimately shape spatiotemporal variations in prey distribution and anti-predator behavior. Many studies have used proxies of predation risk, such as habitat features (Dupuch et al., 2014), or proxies of perceived predation risk, such as prey behavior (Willems & Hill, 2009). Proxies are useful but they can also lead to circular reasoning (Gaynor et al., 2019).

For cursorial predators (in opposition to ambush or sit-and-wait predators), the space use of active individuals, which can be measured at a fine scale through GPS tracking, should closely approximate the landscape of predation risk since they continuously prowl in search of prey (Schmitz et al., 2004). Some landscape of fear studies measured predator movements to explain prey behavior while considering local density or space use of predators, but with only a limited number of locations (Thaker et al., 2011; Kohl et al., 2018). For very active predators, a detailed assessment of movements is required to infer the predation risk landscape (Poulin et al., 2021). Fortunately, improved GPS telemetry (Wilmers et al., 2015) and modelling techniques (e.g., hidden Markov models, Patterson et al., 2017) now allow researchers to assess the behavior and active periods of predators from their fine scale movements. However, the active periods of predators may sometimes be associated with activities other than hunting (such as long-distance movements), therefore the correlation between fine scale predator space use patterns and the predation risk landscape should be demonstrated.

Conceptualization of the landscape of fear has generated hypotheses about the role of predation risk in driving animal behavior across contexts (Laundré et al., 2010; Gaynor et al., 2019). Empirical studies are needed to simultaneously evaluate how predators generate the distribution of predation risk and how different prey species respond proactively or reactively to this distribution. Arctic terrestrial food webs are good models to study vertebrate predator-prey interactions because they are relatively simple. One example is the tundra community of Bylot Island (Nunavut, Canada), where the arctic fox (*Vulpes lagopus*) is the main terrestrial predator. This canid is a cursorial, active hunting predator that travels extensive daily distances within its territory (Poulin et al., 2021). On Bylot, it feeds on lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) which show annual density fluctuations (Gruyer et al., 2008). Apart from lemmings, arctic foxes prey on nesting birds and pose a greater threat to eggs and chicks (Bêty et al., 2001; McKinnon & Bêty, 2009).

During the nesting season, they collect eggs of the colonial nesting greater snow goose (*Anser caerulescens atlanticus*) (Bêty et al., 2001), and thus select both productive lemming habitats and patches of high snow goose nest density (Grenier-Potvin et al., 2021). While geese can decide where to nest, once this decision is made they can no longer rely on proactive spatial avoidance of predators, since foxes seek out their nests. Highly conspicuous snow geese however actively defend their nests when closely approached by a fox (Bêty et al., 2002). This defense strategy is effective as long as geese remain close to their nest during incubation (Reed et al., 1995; Bêty et al., 2002). Foxes also opportunistically prey upon nests of other ground nesting birds and are their main nest predator (McKinnon & Bêty, 2009; Gauthier et al., 2011). These incidental prey mainly nest in mesic tundra, but some of them nest in microhabitat patches that constrain fox movements and can thus offer protection. For example, islets of just a few square meters located in ponds may serve as refuges in the tundra landscape (Gauthier et al., 2015).

We assessed the effects of the predation risk landscape in the tundra community of Bylot Island. We first defined and assessed empirically the predator activity landscape, that is the utilization distribution of active foxes, using high frequency GPS data coupled with hidden Markov models. We then experimentally tested if this predator activity landscape predicted (P1) the probability of consumption of artificial prey, thus reflecting the predation risk landscape. Then, we investigated the effect of the fox activity landscape on risk management strategies of the bird community. We assessed the nest defense behavior of a main prey (snow geese), predicting (P2) that nest defense when approached by a potential predator should be stronger in areas most used by foxes, where predation risk of unattended nests is higher. We also assessed the effect of the predator activity landscape on the nest distribution of incidental prey, composed of bird species from different guilds, and predicted (P3) that the probability of nest occurrence should be lowest in areas most used by foxes.

1.4 Methods

1.4.1 Study system

We conducted fieldwork during May-July 2019 in the southwest plain of Bylot Island (72°53' N, 79°54' W), in Sirmilik National Park of Canada, Nunavut (Appendix S1: Figure 1.5). The ecosystem is characterized primarily by mesic tundra and polygonal wetlands (Grenier-Potvin et al., 2021). In this system, arctic fox pairs have virtually no predators and are territorial. Territories of all studied individuals overlapped a snow goose colony composed of > 20,000 nesting pairs distributed over 70 km^2 (Bêty et al., 2001, 2002).

1.4.2 Fox captures and movement tracking

During May and June 2019, we captured 13 foxes using Softcatch #1 padded leghold traps (Oneida Victor Inc. Ltd., Cleveland, OH, USA). These foxes represented 6 neighboring territorial pairs and one additional individual, whose small home range overlapped two territories (Figure 1.1). Each fox was marked with colored ear tags allowing identification at a distance, and was fitted with a GPS collar (95 g, 2.6–3.3% of body mass; Radio Tag-14, Milsar, Poland) equipped with rechargeable batteries, a solar panel, and UHF transmission allowing remote data download. We used a GPS fix interval of 4 min and average GPS location error was 11 m (Poulin et al., 2021). The 6 fox territories comprise our study area. The general contour of the study area was drawn using the concave hull of fox GPS data (QGIS version 3.8.3, QGIS Development Team, 2019), excluding a few extra-territorial trips (Figure 1.1). For each individual, we used locations from 10 days at the end of June. These ten days correspond to a major part of the laying and incubation periods of tundra nesting birds and are of utmost importance for their annual reproductive success. Datasets were synchronized (± 2 days depending on capture day and the timing of missing data; the 2 days following capture were excluded). Daily observations and automated cameras at fox dens confirmed that we tracked all foxes foraging in the study area. Of the 6 monitored fox pairs, 5 reproduced.

Capture techniques and immobilization procedures were approved by the UQAR Animal Care Committee (CPA-64-16-169 R3) and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada (SIR-2018-28021).

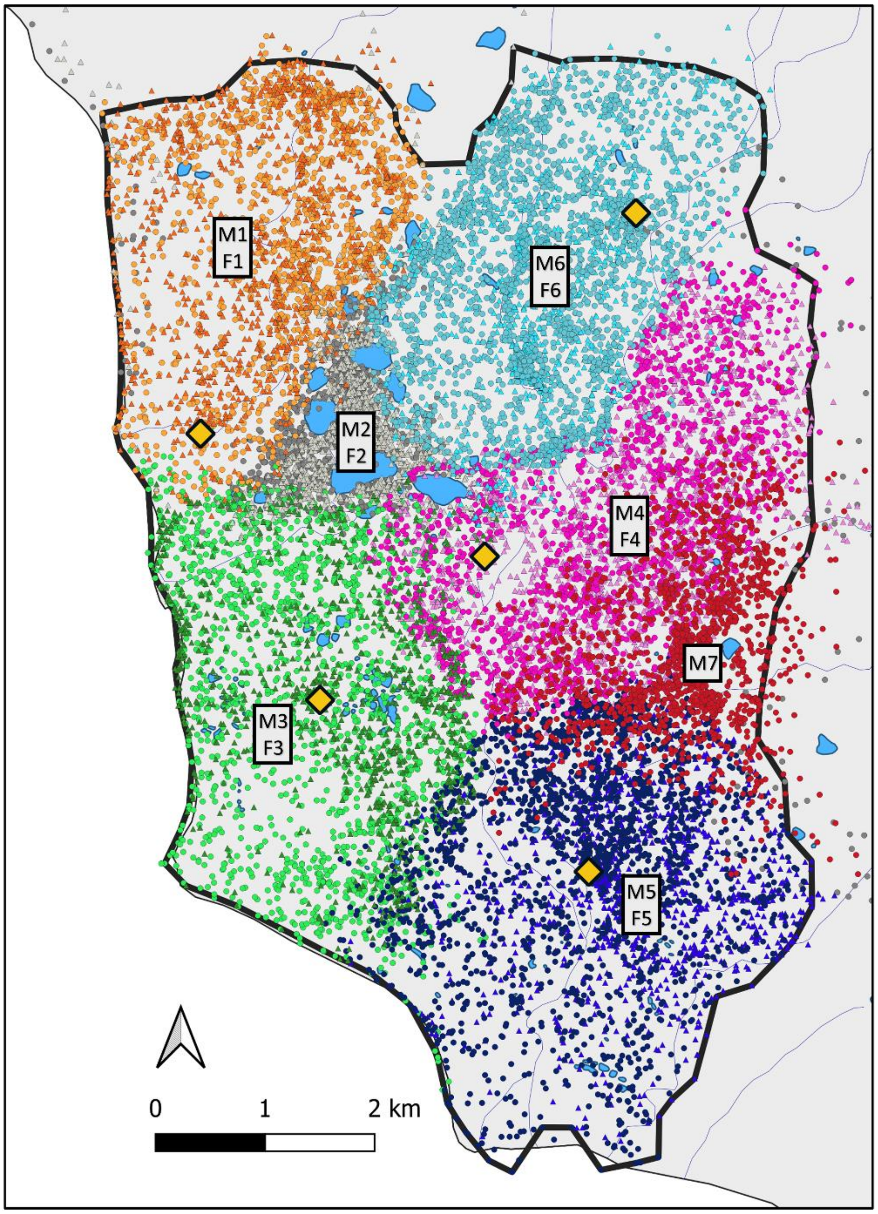

Figure 1. 1 Study area on Bylot Island (Nunavut, Canada) featuring GPS locations (dots for males and triangles for females) of 13 arctic foxes tracked during 10 days at the end of June 2019. Foxes occupied 6 territories (M7 had a small home range overlapping two territories) and pair members have related colors, as detailed in Appendix S1: Table 1.4. GPS locations were collected at 4-min fix intervals and the 20,961 data points shown are those classified in

the active state by a hidden Markov model. Yellow diamonds locate the 5 reproductive dens (M2, F2 and M7 did not reproduce). The thick black line is the contour of the study area. Lakes and large ponds are in blue. See Appendix S1: Figure 1.5 for the geographical context of the study area.

1.4.3 Artificial prey experiment

We conducted an artificial prey experiment using 8-g pieces of dried beef liver (measuring ca. 0.5 x 2 x 2 cm; Benny Bullys Sales Inc., ON, Canada; hereafter, baits) to assess predation risk. Predation on artificial prey is a good proxy for predation risk on bird nests, as probability of predation approximates 100% when a fox initiates an attack on an unattended goose nest or on any passerine or shorebird nest (Beardsell et al., 2021). Like baits, most nest contents are thus readily available once detected. The experiment started on 4 July, after we had tracked fox movements. We placed in each of the 6 fox territories 6–8 lines of ca. 10 baits each (total of 428 baits distributed in 44 curved lines each measuring 293 ± 77 m (mean ± SD), see bait locations in Appendix S1: Figure 1.6A). Each bait line was located in a homogeneous habitat patch and bait lines were distributed equally between wetland polygons and mesic tundra patches, at least 300 m from the study area limits. Avoiding study area borders ensured that baits could not be taken by unknown foxes from adjacent territories. Distance between adjacent baits within bait lines was 79 ± 7 m and distance between adjacent lines was 297 ± 118 m. We covered baits with moss or lichen to exclude predation by avian predators (as done for artificial nests, Léandri-Breton & Bêty, 2020) and visited baits after 4 days to assess their removal by foxes. A piece of orange flag placed under each bait became visible when a bait had been removed, thus facilitating assessment of predation events. To confirm that foxes were the only bait consumers, we placed some camera traps during 5 ± 2 days after the experiment at 6 locations (in 3 fox territories) to monitor the fate of baits, which were replaced if consumed. Thirteen baits were taken, all by foxes.

1.4.4 Snow goose nest defense behavior

Flushing distance from an approaching human is often used to assess a prey’s anti-predator strategy (Blumstein, 2003) and represents a good proxy for nest defense intensity. We measured the flushing distances of 458 incubating females as an indicator of their level of nest defense (see nest locations in Appendix S1: Figure 1.6B). We chose sampled nests randomly within sites visited during field work activities. A small flushing distance (the observer is close to the nest when the female leaves) indicates a high level of nest defense (Clermont et al., 2019). An observer approached a focal nest by walking silently at a slow and constant pace, in a straight line, and measured flushing distance with a telemeter or handheld GPS. To limit potential effects of incubation stage on goose nest defense (Clermont et al., 2019), we performed 85% of flushing distance measures within 5 days from June 14 to June 18 (we did remaining measures in the following days), which corresponds to the first half of the incubation period. We also assessed clutch size as it generally influences nest defense intensity (Montgomerie & Weatherhead, 1988), and we measured the starting distance of the approach as it affects flushing distance (Blumstein, 2003). Starting distance ranged from 15–508 m and was assessed with a telemeter or handheld GPS. Focal nests were located at least 300 m from the study area limits, thus ensuring that fox activity around nests was not underestimated due to visits by uncollared foxes from adjacent territories.

1.4.5 Nest distribution of incidental prey

During the incubation period, we conducted thorough searches of bird nests other than snow geese (i.e., incidental prey). In June, we walked repeatedly throughout the study area to detect signs of reproductive birds (calling, distraction displays, bird flushing at close distance). We did this through transect surveys conducted in mesic tundra, and intensive nest searches performed in wetland patches, stony riverbanks and slopes, which are all easily accessible to foxes. We also inspected microhabitats surrounded by water (hereafter refuges, mostly islets in ponds), which are not easily accessed by foxes. We georeferenced 377 islets in the study area (Appendix S1: Figure 1.7).

We found 109 nests from 13 species in the study area (see nest locations in Appendix S1: Figure 1.6C). A total of 44 nests from 10 species were located in areas easily accessible to foxes: common-ringed plover (*Charadrius hiaticula*, n = 3), american golden plover (*Pluvialis dominica*, n = 9), white-rumped sandpiper (*Calidris fuscicollis*, n = 2), arctic tern (*Sterna paradisaea*, n = 2), rough-legged hawk (*Buteo lagopus*, n = 1), lapland longspur (*Calcarius lapponicus*, n = 16), parasitic jaeger (*Stercorarius parasiticus*, n = 1), long-tailed jaeger (*Stercorarius longicaudus*, n = 6), long-tailed duck (*Clangula hyemalis*, n = 1) and king eider (*Somateria spectabilis*, n = 3). A total of 65 nests from 3 species were located in refuges: cackling goose (*Branta hutchinsii*, n = 38), glaucous gull (*Larus hyperboreus*, n = 11) and red-throated loon (*Gavia stellate*, n = 16).

1.4.6 Predator activity landscape

We defined the predator activity landscape as the utilization distribution (see below) of all foxes in the active state within the study area. For opportunist active hunting predators like arctic foxes, all travelling phases can be associated with hunting, therefore we used a hidden Markov model (HMM) to assign GPS locations to an active or resting state (R package moveHMM, Michelot et al., 2016). HMM decomposes GPS tracks into sequences associated to different behavioral states, which differ from one another in their step lengths and turning angles (Langrock et al., 2012). The active state is characterized by long step lengths and small turning angles, and the resting state with short step lengths and large turning angles. The HMM included time of the day as a covariate to reflect the circadian rhythm of foxes (Grenier-Potvin et al., 2021). Models using a Weibull distribution for step lengths and a wrapped Cauchy distribution for turning angles yielded the most parsimonious model (HMM construction and model selection is detailed in Grenier-Potvin et al., 2021).

Then, we used Kernel Density Estimation (QGIS Heatmap plugin) to map the fox utilization distribution (UD) using only active locations. UDs quantify the intensity of space use (from low to high probability density of GPS locations) by tracked animals and thus identify areas where animals are most likely to be found (Fortin et al., 2005; Thaker et al., 2011). We used 10 x 10 m pixels to map UD scores, allowing fine spatial scale assessment of variation in fox

UD, and a fixed UD smoothing parameter (called radius in QGIS, which is equivalent to the kernel bandwidth) to specify the distance at which GPS locations influence UD scores. As the choice of the UD smoothing parameter can affect prediction tests, we performed a sensitivity analysis. We ran statistical models (presented in the following section) for 5 UD smoothing parameters ranging from 200 to 400 m (50-m increments). As foxes in their active state traveled 232 ± 145 m (mean ± SD, see Results) between GPS fixes obtained at 4-min intervals, the chosen range of smoothing parameters yielded fine resolution activity landscapes that reflected the scale of our data. Using smaller parameter values would have underestimated the use of areas located between GPS locations, whereas using larger parameter values would have overestimated the use of areas located on each side of the fox track. UD scores were standardized from 0 to 1 in each of the 5 UDs.

1.4.7 Statistical models

We tested the effect of the fox activity landscape on the probability of predation of baits (P1), snow goose nest defense behavior (P2) and the nest distribution of fox incidental prey (P3). A first step consisted in extracting the fox UD score at all locations used in the models, that is locations of baits, nests of tested snow geese, as well as nests and available nesting locations of incidental birds (see below).

1) Probability of predation of baits

We used a generalized linear mixed model (R package lme4, Bates et al., 2015) with a logit-link function and a binomial distribution to test the effect of fox UD score on the probability of predation of baits (0 = not predated, 1 = predated), with the ID of the bait line nested in the ID of the fox territory as random effects. We fitted one model for each of the 5 UDs defined with different smoothing parameters.

2) Snow goose nest defense behavior

We used a linear mixed model to test the effect of fox UD score on goose flushing distance. We square-root transformed goose flushing distance to respect the assumption of normality and homoscedasticity in models' residuals. The other fixed effects included in the models were clutch size, starting distance of the approach, and date of observation. All covariates were centered and standardized to facilitate interpretation of model estimates (Schielzeth, 2010). We included as random effects the ID of the fox territory and the ID of the observer performing the approach. We fitted one model for each of the 5 UDs. As the effect of fox UD score on flushing distance was weak (see Results), we investigated whether few influential points were driving the relationship. We identified outliers using the R package car (Fox & Weisberg, 2020) and tested models without those points, which yielded results similar to those we present.

3) Nest distribution of incidental prey

We used conditional logistic regressions with a use-available design (function clogit in R package survival, Therneau et al., 2020) to test the effect of fox UD score on the distribution of bird nests of fox incidental prey species (P3). Since fox UD scores are smoothed values obtained from locations with a ± 11 m error and collected at 4-min intervals, they reflect a spatially-averaged fox utilization of the area rather than microhabitat use. Hence, the UD score of an islet could be > 0 even if no fox visited this small patch, and the spatial resolution of the fox activity landscape was unable to reflect the fine spatial scale of refuges. We thus analyzed separately species nesting in habitats easily accessible to foxes (first set of models) and species nesting in microhabitat refuges (second set of models).

In the first set of models, we compared fox UD scores at bird nests (used locations) to fox UD scores at potential nesting sites (available locations). We considered as available locations a set of random sites located in the study area and out of water bodies. We paired each bird nest location to 50 random locations drawn from an area surrounding the nest (hereafter, the nest area). As tundra nesting birds have various natural histories, including nesting habitat and social system, they likely select nesting sites at different spatial scales, which are unknown. Hence, we could not justify a priori a single radius for the nest area. We therefore repeated analyses after forcing random locations within 5 radii varying from 1000 m to 3000 m (increments of 500 m), thus fitting 25 models (5 UDs x 5 nest area radii).

In the second set of models, we again compared fox UD scores at bird nests (used locations) to fox UD scores at available sites. However, we used as available locations potential nesting sites located in the study area and surrounded by water, drawing from our 377 georeferenced islets. We paired each bird nest location to 50 islets chosen randomly from the area surrounding the nest. Less than 50 islets were sometimes available within the nest area, so we assessed whether this affected results (Appendix S2). As for the first set of models, we fitted 25 models (5 UDs x 5 nest area radii).

All analyses were conducted in R (version 3.6.1, R Development Core Team, 2019). We validated the assumptions of normality, homoscedasticity, non-collinearity among fixed effects, and independence of residuals for all models. Values are expressed as mean ± SD.

1.5 Results

1.5.1 Fox activity landscape

We acquired a total of 45,140 fixes for 13 foxes tracked for 10 days (Figure 1.1). The active behavioral state was assigned to 46 ± 9% of locations per individual (range 31–60%, Appendix S1: Table 1.4) for a total of 20,961 GPS locations. Average step length and turning angle were 232 ± 145 m and 55° for active locations, and 9 ± 9 m and 116° for resting locations (see Grenier-Potvin et al., 2021). Representations of the fox activity landscape show heterogeneity in the intensity of space use by foxes, that remained as smoothing parameters varied from 200 m to 400 m (Figure 1.2, Appendix S1: Figure 1.8). The predator activity landscape identified areas intensively used by some foxes, such as the small central territory of M2 and F2 and the space that M7 shared with the M4-F4 or M5-F5 pairs (Figures 1.1, 1.2).

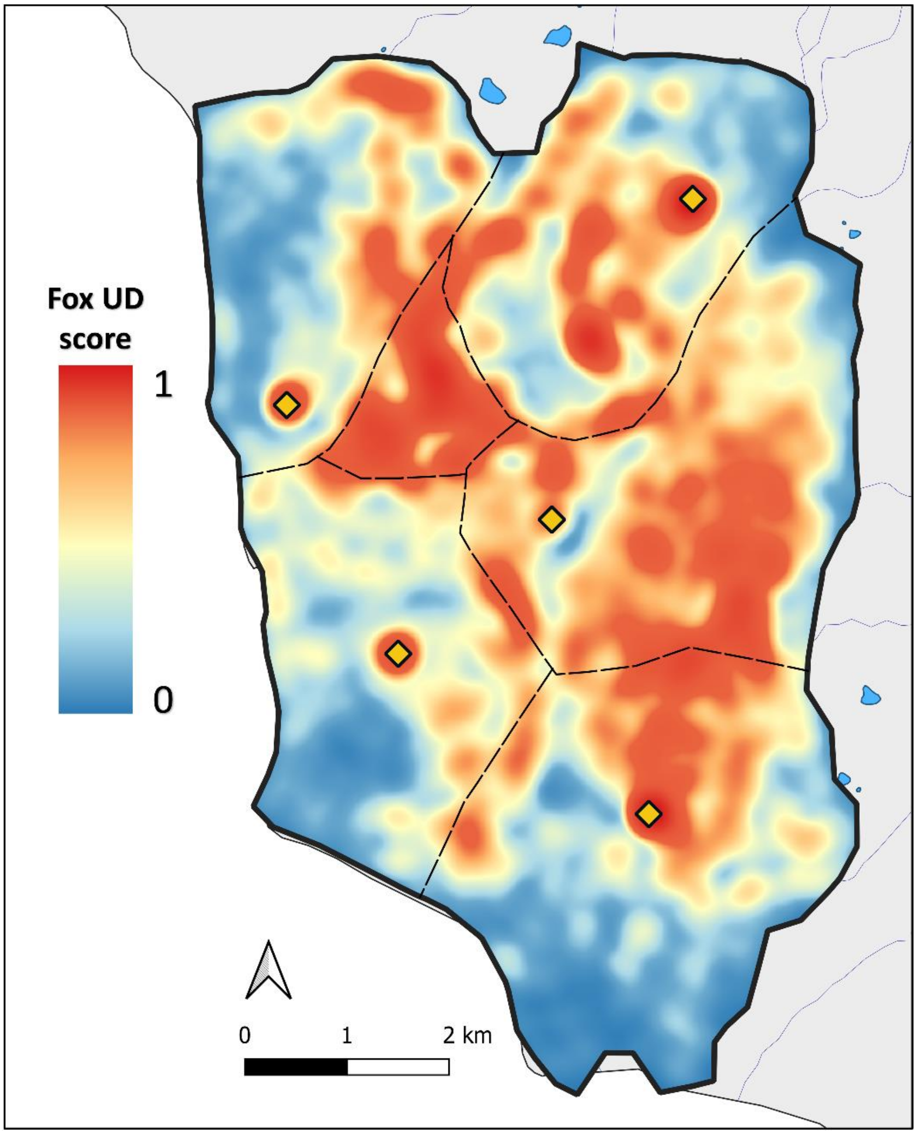

Figure 1. 2 Arctic fox activity landscape generated from 20,961 GPS locations classified in the active state by a hidden Markov model. The activity landscape reflects fox utilization distribution (UD) based on data from 13 individuals living in 6 territories and tracked during 10 days at the end of June 2019, on Bylot Island. A UD smoothing parameter of 300 m was used to generate this activity landscape (see Appendix S1: Figure 1.8 for activity landscapes generated from other smoothing parameters). The color scale reflects fox UD score (from 0 to 1) and thus probability of presence of an active fox. Yellow diamonds locate the 5 reproductive dens, dashed lines identify the approximate boundaries of fox pair territories, and the thick black line is the contour of the study area.

1.5.2 Probability of predation of baits

The artificial prey experiment showed that the predation risk landscape was positively linked to the predator activity landscape. Baits were more likely to be consumed where fox UD score was high (Table 1.1, Figure 1.3a), whatever the UD smoothing parameter (Table 1.1).

Table 1. 1 Results from binomial mixed models testing the effect of fox UD score on the probability of predation of baits, with patch ID nested in territory ID fitted as random effects, for the 5 UDs with smoothing parameter ranging from 200 to 400 m (n = 428 baits). See Appendix S1: Table 1.5 for variance values of random effects.

UD smoothing parameter (m)	Fixed effect	Estimate [95% CI]	z value	p value
200	(Intercept)	-0.25 [-1.17, 0.68]	-0.60	0.546
	Fox UD score	3.56 [-0.02, 7.45]	1.91	0.056
250	(Intercept)	-0.35 [-1.29, 0.60]	-0.82	0.414
	Fox UD score	3.28 [0.31, 6.49]	2.12	0.034
300	(Intercept)	-0.48 [-1.44, 0.49]	-1.07	0.284
	Fox UD score	3.24 [0.59, 6.09]	2.36	0.013
350	(Intercept)	-0.61 [-1.61, 0.38]	-1.31	0.191
	Fox UD score	3.23 [0.79, 5.84]	2.56	0.011
400	(Intercept)	-0.73 [-1.77, 0.29]	-1.50	0.133
	Fox UD score	3.18 [0.89, 5.62]	2.69	0.007

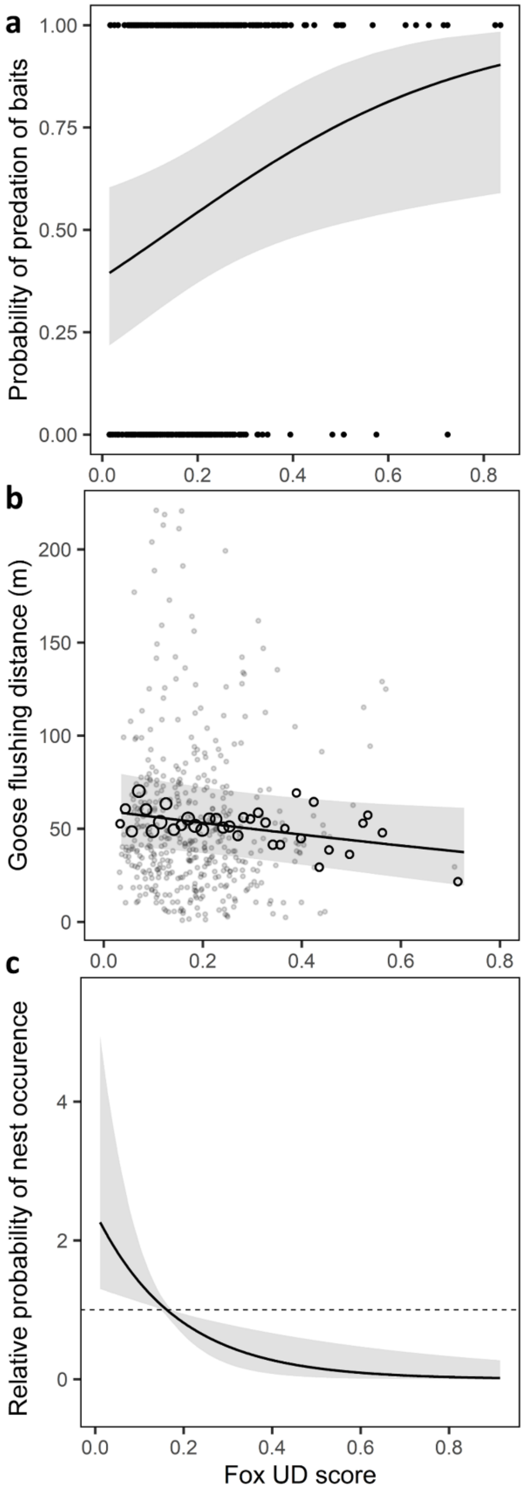

Figure 1. 3 Predicted effect of fox UD score on (a) probability of predation of baits (0 = bait not eaten, 1 = bait eaten, n = 428), (b) goose flushing distance (n = 458) and (c) relative

probability of occurrence of nests from birds nesting in habitats easily accessible to foxes (n = 44 nests from 10 species). In (b), we back-transformed goose flushing distance and fox UD score before plotting (goose flushing distance had been square-root transformed and fox UD score had been centered and standardized in linear models). Dots are raw data and circles are partial residuals divided in 50 bins of equal fox UD score interval after accounting for the effects of the number of eggs, the observer's starting distance and the date. Circle size is proportional to the number of observations in each bin. In (c) the dashed horizontal line represents a relative probability of occurrence of 1, with values below and above 1 indicating lower and higher probabilities of occurrence than random, respectively. The gray area represents the 95% confidence interval of (a) the fitted logistic regression, (b) the linear regression and (c) the relative probability of occurrence obtained by bootstrap. For these representations we used fox UD scores generated with an intermediate smoothing parameter of 300 m, and (c) nest areas generated with an intermediate radius of 2000 m.

1.5.3 Snow goose nest defense behavior

Snow geese showed higher level of nest defense when nesting in areas of high predation risk, as shown by the negative relationship between flushing distance and fox UD score (Table 1.2, Figure 1.3b). Although slope estimates were consistently negative for the 5 UDs, the slope lessened and lost its significance as the UD smoothing parameter increased, suggesting that geese only responded to risk at the finest spatial scales that we explored. Geese also showed a weaker level of nest defense when they had a relatively small clutch and saw the observer approaching from far away, as shown by the significant effects of clutch size and starting distance on flushing distance (no effect of smoothing parameter, Table 1.2). Flushing distance did not vary with observation date.

Table 1. 2 Results from linear mixed models testing the effect of fox UD score on goose flushing distance. Number of eggs, starting distance of the observer and date were included as covariates. Territory ID and observer ID were fitted as random effects and models were repeated for the 5 UDs with smoothing parameter ranging from 200 to 400 m (n = 458 goose nests). All fixed effects are centered and standardized. Significant effects are in bold. See Appendix S1: Table 1.6 for variance values of random effects.

UD smoothing parameter (m)	Fixed effect	Estimate [95% CI]	df	t value	p value
200	(Intercept)	7.34 [5.98, 8.74]	2.79	11.7	0.002
	Fox UD score	**-0.26 [-0.47, -0.04]**	**417.61**	**-2.36**	**0.019**
	Number of eggs	**-0.30 [-0.48, -0.11]**	**424.33**	**-3.15**	**0.002**
	Starting distance	**1.46 [1.25, 1.67]**	**265.55**	**13.72**	**<0.001**
	Date	-0.17 [-0.46, 0.10]	42.69	-1.29	0.203
250	(Intercept)	7.34 [5.98, 8.74]	2.79	11.71	0.002
	Fox UD score	**-0.25 [-0.47, -0.03]**	**410.57**	**-2.25**	**0.025**
	Number of eggs	**-0.3 [-0.49, -0.11]**	**424.34**	**-3.15**	**0.002**
	Starting distance	**1.45 [1.25, 1.67]**	**264.14**	**13.7**	**<0.001**
	Date	-0.17 [-0.45, 0.11]	42.14	-1.27	0.211
300	(Intercept)	7.33 [5.99, 8.71]	2.78	11.87	0.002
	Fox UD score	**-0.23 [-0.45, 0.01]**	**402.52**	**-1.98**	**0.049**
	Number of eggs	**-0.3 [-0.49, -0.11]**	**424.37**	**-3.15**	**0.002**
	Starting distance	**1.46 [1.25, 1.67]**	**264.68**	**13.69**	**<0.001**
	Date	-0.16 [-0.45, 0.11]	42.35	-1.21	0.230
350	(Intercept)	7.33 [6.01, 8.68]	2.78	12.08	0.002
	Fox UD score	-0.20 [-0.42, 0.04]	396.55	-1.69	0.091
	Number of eggs	**-0.30 [-0.48, -0.11]**	**424.42**	**-3.13**	**0.002**
	Starting distance	**1.46 [1.25, 1.67]**	**266.50**	**13.67**	**<0.001**
	Date	-0.16 [-0.44, 0.12]	43.01	-1.17	0.250
400	(Intercept)	7.33 [6.03, 8.66]	2.78	12.25	0.002
	Fox UD score	-0.17 [-0.39, 0.07]	392.59	-1.46	0.146
	Number of eggs	**-0.30 [-0.48, -0.11]**	**424.48**	**-3.12**	**0.002**
	Starting distance	**1.46 [1.25, 1.68]**	**268.83**	**13.67**	**<0.001**
	Date	-0.15 [-0.44, 0.12]	43.69	-1.13	0.265

1.5.4 Nest distribution of incidental prey

For bird species nesting in habitats easily accessible to foxes, nests were more likely to occur where fox UD score was low, compared to random locations (Table 1.3, Figure 1.3c). The probability of nest occurrence declined steeply as fox UD score increased (Figure 1.3c). The effect of fox UD score on nest distribution was significant or almost significant (with p values only slightly over 0.05 and the upper limit of confidence intervals slightly over 0) for all 5 fox activity landscapes (smoothing parameters of 200–400 m) and 5 nest area sizes (radii of 1000–3000 m) (Table 1.3). Coefficient estimates were larger for the smallest UD smoothing parameters (Table 1.3), suggesting that risk was more likely to affect bird nest distribution at the at finest spatial scales.

For bird species nesting in refuges, fox UD score did not affect the probability of nest occurrence, whatever the smoothing parameter or nest area radius (Table 1.3). Fox UD scores of nesting locations were not statistically different from those of random islets (Table 1.3). Variation in the number of random islets available for testing did not affect results (Appendix S2).

Table 1. 3 Results from conditional logistic regressions with a use-available design testing the effect of fox UD score on the nest distribution of (A) birds nesting in habitats easily accessible to foxes (n = 44 nests from 10 species) and (B) birds nesting in microhabitats providing a refuge against foxes (n = 65 nests from 3 species). Coefficient estimates are presented for 25 models, each reflecting a given size of the nest area (from 1000 to 3000 m) and UD smoothing parameter (from 200 to 400 m). Significant effects are in bold.

Radius of nest area (m)	UD smoothing parameter (m)	(A) Nests in easily accessible habitats			(B) Nests in refuges		
		Coefficient [95% CI]	z value	p value	Coefficient [95% CI]	z value	p value
1000	200	**-9.81 [-18.42, -1.20]**	**-2.23**	**0.026**	0.93 [-7.36, 9.23]	0.22	0.826
	250	**-7.12 [-13.86, -0.39]**	**-2.07**	**0.038**	0.50 [-6.14, 7.13]	0.15	0.884
	300	**-5.58 [-11.17, -0.002]**	**-1.96**	**0.050**	1.13 [-5.45, 5.70]	0.04	0.965
	350	-4.46 [-9.23, 0.32]	-1.83	0.067	-0.20 [-5.06, 4.67]	-0.08	0.937
	400	-3.53 [-7.69, 0.63]	-1.66	0.097	-0.46 [-4.84, 3.92]	-0.20	0.838
1500	200	**-10.61 [-18.60, -2.61]**	**-2.60**	**0.009**	4.43 [-1.66, 10.52]	1.43	0.154
	250	**-7.70 [-13.82, -1.57]**	**-2.46**	**0.014**	3.24 [-1.47, 7.96]	1.35	0.178
	300	**-6.04 [-11.05, -1.04]**	**-2.37**	**0.018**	2.40 [-1.49, 6.30]	1.21	0.226
	350	**-4.89 [-9.13, -0.66]**	**-2.26**	**0.024**	1.79 [-1.54, 5.12]	1.05	0.293
	400	**-4.01 [-7.68, -0.34]**	**-2.14**	**0.032**	1.36 [-1.58, 4.31]	0.91	0.365
2000	200	**-9.87 [-17.33, -2.41]**	**-2.59**	**0.009**	3.50 [-1.79, 8.78]	1.30	0.195
	250	**-7.04 [-12.67, -1.41]**	**-2.45**	**0.014**	2.44 [-1.64, 6.51]	1.17	0.241
	300	**-5.42 [-9.95, -0.88]**	**-2.34**	**0.019**	1.74 [-1.63, 5.11]	1.01	0.312
	350	**-4.29 [-8.07, -0.50]**	**-2.22**	**0.026**	1.28 [-1.60, 4.16]	0.87	0.385
	400	**-3.44 [-6.68, -0.21]**	**-2.09**	**0.037**	0.97 [-1.56, 3.50]	0.75	0.453
2500	200	**-8.05 [-14.82, -1.28]**	**-2.33**	**0.020**	3.47 [-1.82, 8.76]	1.29	0.199
	250	**-5.68 [-10.77, -0.59]**	**-2.19**	**0.029**	2.55 [-1.51, 6.60]	1.23	0.218
	300	**-4.35 [-8.44, -0.26]**	**-2.08**	**0.037**	1.92 [-1.41, 5.25]	1.13	0.258
	350	**-3.45 [-6.86, -0.04]**	**-1.98**	**0.048**	1.47 [-1.38, 4.31]	1.01	0.312
	400	-2.78 [-5.69, 0.14]	-1.87	0.062	1.15 [-1.36, 3.64]	0.90	0.371
3000	200	**-7.03 [-13.61, -0.45]**	**-2.10**	**0.036**	3.78 [-1.48, 9.05]	1.41	0.159
	250	**-4.99 [-9.90, -0.08]**	**-1.99**	**0.047**	2.79 [-1.21, 6.80]	1.37	0.171
	300	-3.83 [-7.75, 0.09]	-1.91	0.056	2.16 [-1.11, 5.43]	1.30	0.195
	350	-3.02 [-6.28, 0.23]	-1.82	0.068	1.70 [-1.07, 4.48]	1.20	0.229
	400	-2.42 [-5.19, 0.35]	-1.71	0.087	1.37 [-1.06, 3.80]	1.11	0.269

1.6 Discussion

The diversity of prey risk management strategies in a heterogeneous landscape needs to be considered to fully assess the ecological context of the landscape of fear (Gaynor et al., 2019).

Using high resolution arctic fox GPS data, behavioral observations and field experiments, we demonstrated that fine scale variation in space use of active predators accurately reflects spatial variation in predation risk, and explains anti-predator behavior of a main prey and nest distribution of some incidental prey species in an Arctic terrestrial community (Figure 1.4). More specifically, our results demonstrate how a main prey, which is easy to detect and cannot avoid predators in space, rely on reactive anti-predator behavior and show more intense nest defense in areas of highest risk. In contrast, we found that species of incidental prey that do not nest in refuges are located in areas of lowest fox utilization, while incidental prey that do nest in refuges may be found in areas of high risk because they avoid risk at finer spatial scales. This suggests that some incidental prey that are consumed only opportunistically may be able to win the predator-prey space race. Overall, our study examining predation-risk effects generated by predator activity on multiple prey species highlights the diversity of prey responses that occur at various spatial scales.

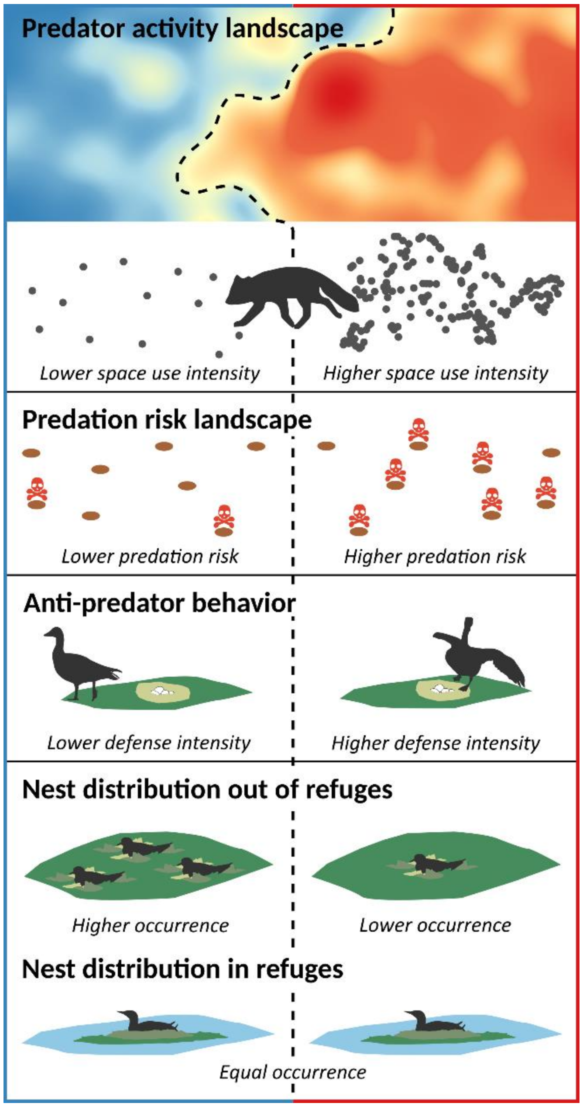

Figure 1. 4 Landscape of fear context in a terrestrial Arctic community. The predator activity landscape generates a landscape of predation risk and predicts anti-predator response and distribution of some prey species. The illustrated predator activity landscape shows the multiple spatial gradients of intensity in arctic fox space use (low in blue, high in red). The relationship between the predator activity landscape and the predation risk landscape is demonstrated by an artificial prey experiment. The predator activity landscape predicts anti-predator behavior of a main prey (here, snow goose) and nest distribution of incidental prey (here, a shorebird) nesting in habitats easily accessed by foxes. However, the nest distribution of incidental prey (here, a loon) nesting on small patches surrounded by water (i.e., islets acting as refuges) is independent of the predator activity landscape, which reflects fox utilization of the surrounding area rather than microhabitat use.

1.6.1 The predator activity landscape as a predation risk landscape

We obtained a predator activity landscape that robustly depicted fine scale variation in fox intensity of space use, thanks to the use of fox movement data collected at a high frequency in combination with the identification of active and resting behavioral states (see Grenier-Potvin et al. (2021) for what underlies variation in arctic fox space use). An artificial prey experiment using baits demonstrated that predation risk was highest in areas highly used by foxes, and therefore that predation risk for prey was related to spatial variation in fox space use. Our sensitivity analyses also confirmed the robustness of our results, which were consistent across our range of UD smoothing parameters (Tables 1.1, 1.2, 1.3).

Obtaining a good map of predation risk requires accurate spatial modeling of predator density, which is difficult to do from a limited number of predator locations or from proxies of predator space use, such as habitat features. Our study demonstrates the value of using fine scale predator movements to characterize the landscape of predation risk in landscape of fear studies. Also, multi-predator systems impose multiple and contrasting landscapes of risk to prey (Thaker et al., 2011; Gaynor et al., 2019). In this study, we were able to accurately depict spatial variation in predation risk because all foxes living in our study area were collared, and foxes are the main predators of nesting birds (McKinnon & Bêty, 2009; Gauthier et al., 2011).

1.6.2 The predator activity landscape explains goose nest defense intensity

Nesting snow geese can hardly use spatial avoidance to reduce predation risk, since active foxes select patches where goose nest density is highest (Grenier-Potvin et al., 2021). Geese nonetheless use nest defense when predation risk of their nest is imminent (Bêty et al., 2002; Lima, 2009). We found that this reactive risk management strategy was related to the level of risk, as snow geese nesting in areas highly used by foxes showed the highest level of nest defense. Indeed, geese nesting in high fox use areas face greater risks of nest predation when leaving their nest unattended (due to a greater density of foxes) and should thus defend their nest more intensely when approached by a potential predator (here a human). The relationship between goose nest defense and the predator activity landscape likely results from plastic adjustments of anti-predator behavior in response to variation in predation risk, as in female ungulates that are more vigilant where wolf presence is highest (Laundré et al., 2001). Assessing anti-predator behavior on the same individuals along a gradient of predation risk (Fontaine & Martin, 2006; Mathot et al., 2011) would however be required to fully understand the underlying mechanisms explaining the observed patterns. Nonetheless, our results suggest that predator space use influences prey behavior, with potential benefits to prey fitness (Cresswell, 2008).

The effect of local fox activity on goose flushing distance was moderate compared to the effect of the observer's starting distance, and model outputs slightly differed according to UD smoothing parameter (Table 1.2). Variables not considered may further explain variation in goose nest defense, like presence of conspecifics (Kazama et al., 2011), prey physiological state, or timing of breeding which affects the expected fitness value of the clutch (Bêty et al., 2003). Finally, nest visibility in the landscape may also affect perception of predation risk level and response to the predator activity landscape (Gaynor et al., 2019).

1.6.3 Microhabitats modulate the effect of the predator activity landscape on the distribution of incidental prey

We found that the physical landscape, along with the nesting behavior of prey, intervened in the ecological context of the landscape of fear. Microhabitats modulated the effects of the predator activity landscape on the distribution of incidental prey, as species proactively mitigated predation risk at different spatial scales, either by nesting in microhabitat refuges or by nesting in areas of low predator activity. Indeed, cackling geese, glaucous gulls and red-throated loons nest essentially on islets serving as refuges against fox predation (Gauthier et al., 2015). Accordingly, we found that the probability of nest occurrence of these birds was independent of the predator activity landscape, which at its measured spatial resolution reflected fox utilization of the surrounding area rather than the nest location per se. In fact, species using microhabitat refuges can likely better afford to have their nest surrounded by a relatively risky landscape, because they avoid predation risk at a finer spatial scale. On the contrary, species nesting in habitats easily accessible to foxes may perceive predation risk and avoid nesting in areas highly used by foxes, possibly by shifting location when encountering predators during nest building (Peluc et al., 2008). The ability to choose a safe nest location can also be adaptive, such as in shorebirds nesting strictly on stony shores (Léandri-Breton & Bêty, 2020), which are avoided by active foxes (Grenier-Potvin et al., 2021). However, nest distribution away from risky areas may also result from consumptive effects of predation, as nests located in areas highly used by foxes may have been preyed upon before we detected them. Monitoring fine-scale bird movements during nest establishment (Gilbert et al., 2016) and locating nests before any predation occurs would help investigating the ability of nesting birds to perceive and respond to predation risk, and thus win the predator-prey space race.

In this study, we assessed nest distribution of passerines, shorebirds, ducks, geese, and birds of prey, and grouped species according to whether they used microhabitat refuges or not. Although all species share arctic fox as their main predator and are thus functionally linked, they also differ in their nesting ecology and different variables may influence their nest distribution. It will thus be interesting to replicate our work with increased sample sizes to test hypotheses about potential differences in the way species respond to the predator activity landscape. Finally, animals face a variety of physiological, phylogenetic and ecological constraints that limit their ability to assess predation risk and respond to the landscape of fear (Jordan & Ryan, 2015; Gaynor et al., 2019). Directly measuring how prey perceive predation risk would increase our understanding of the complex relationships linking predation risk and prey responses, despite the challenges that this approach entails (Gaynor et al., 2019).

1.6.4 Conclusion

Our study demonstrates predation-risk effects resulting from the movements of an active predator shared by a community of nesting birds. We showed how prey that are searched for by predators and cannot avoid them in space mitigate risk reactively through anti-predator behavior, while prey that are consumed only opportunistically can win the space race by avoiding risk proactively through habitat selection occurring at different spatial scales.

Assessing the landscape of fear context in an animal community allows to better understand prey species behavior and distribution, thus clarifying key aspects of the structure and functioning of ecosystems.

1.7 Acknowledgments

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Author's contributions: J. Clermont, J. Bêty and D. Berteaux conceived the study with contribution from coauthors. All authors contributed to field planning or data acquisition. J. Clermont conducted statistical analyses, with significant help from A. Grenier-Potvin and contribution from coauthors. J. Clermont led the writing, with contribution from coauthors.

Data availability: Arctic fox GPS data are available from Movebank: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1241071371. Other data sets (artificial prey experiment, goose behavior and bird nest distribution) are available from Dryad: https://doi.org/10.5061/dryad.vdncjsxvd

1.8 Appendix S1 – Supplementary tables and figures

Table 1. 4 Number of GPS fixes obtained for 13 arctic foxes tracked during 10 days at the end of June 2019 on Bylot Island (Nunavut, Canada). The tag code, ID (also indicating sex, M: male, F: female) and territory color (see Figure 1.1) are given for each fox. GPS fixes were assigned an active or resting state using a hidden Markov model (HMM). Fixes with unknown location (time-outs) due to missing connection with satellites, which mostly occurred when foxes were inside their den, were excluded from analyses. The number of fixes per individual was nearly 3600 (10 days at a 4-min fix interval) for all foxes except F3 (due to a battery failure).

Fox			Number of GPS fixes			
Tag code	ID	Territory	Total	Active state	Resting state	Time-out
OBOB	M1	orange	3569	1484 (42%)	1886 (53%)	199 (5%)
JVOJ	F1	orange	3561	1096 (31%)	1006 (28%)	1459 (41%)
BORR	M2	gray	3562	1438 (40%)	1856 (52%)	268 (8%)
RMJJ	F2	gray	3572	1200 (33%)	2311 (65%)	61 (2%)
OBBB	M3	green	3550	1805 (51%)	1511 (42%)	234 (7%)
JMVJ	F3	green	2674	1021 (38%)	1485 (56%)	168 (6%)
VJOO	M4	pink	3567	1840 (51%)	1594 (45%)	133 (4%)
BVOB	F4	pink	3564	2087 (59%)	819 (23%)	658 (18%)
RVJO	M5	dark blue	3572	1994 (56%)	1554 (43%)	24 (1%)
OJOO	F5	dark blue	3240	1646 (51%)	966 (30%)	628 (19%)
ORRR	M6	light blue	3568	2136 (60%)	1430 (40%)	2 (0%)
RMBR	F6	light blue	3569	1637 (46%)	1694 (47%)	238 (7%)
BBJO	M7	red	3572	1577 (44%)	1946 (55%)	49 (1%)

Table 1. 5 Variance values for random effects of binomial mixed models testing the effect of fox UD score on the probability of predation of baits, with patch ID nested in territory ID fitted as random effects, for the 5 UDs with smoothing parameter ranging from 200 to 400 m (n = 428 baits).

UD smoothing parameter (m)	Random effect	Variance	SD
200	Patch: territory	0.40	0.63
	Territory	0.65	0.81
250	Patch: territory	0.39	0.63
	Territory	0.64	0.80
300	Patch: territory	0.38	0.62
	Territory	0.64	0.80
350	Patch: territory	0.37	0.61
	Territory	0.64	0.80
400	Patch: territory	0.37	0.61
	Territory	0.65	0.81

Table 1. 6 Variance values for random effects of linear mixed models testing the effect of fox UD score on goose flushing distance, with territory ID and observer ID fitted as random effects, for the 5 UDs with smoothing parameter ranging from 200 to 400 m (n = 458 goose nests).

UD smoothing parameter (m)	Random effect	Variance	SD
200	Territory	1.44	1.20
	Observer	0.10	0.32
	Residuals	3.78	1.94
250	Territory	1.44	1.20
	Observer	0.10	0.31
	Residuals	1.38	1.94
300	Territory	1.39	1.18
	Observer	0.10	0.31
	Residuals	3.79	1.95
350	Territory	1.34	1.16
	Observer	0.10	0.32
	Residuals	3.80	1.95
400	Territory	1.29	1.14
	Observer	0.10	0.32
	Residuals	3.81	1.95

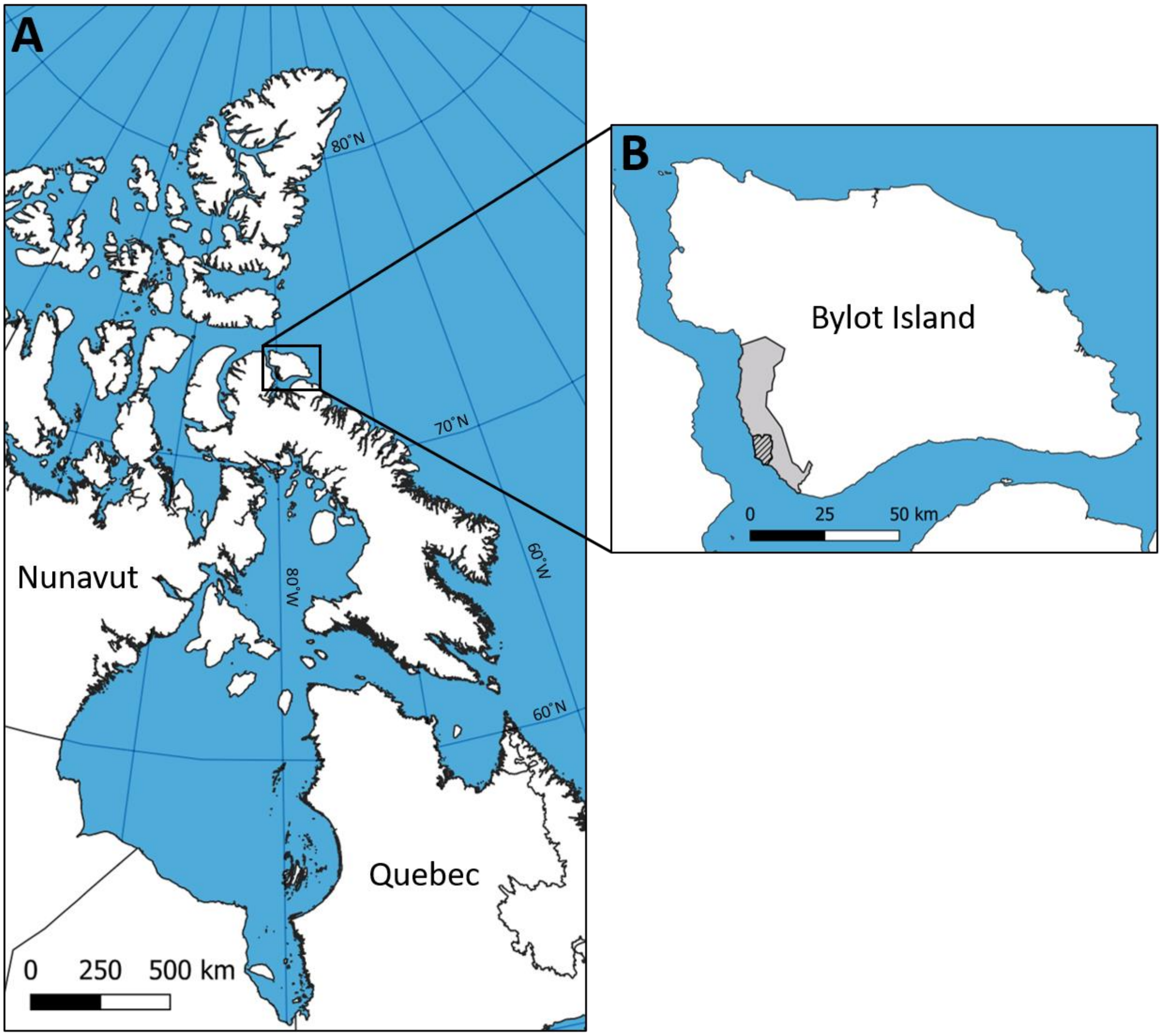

Figure 1. 5 Geographical context of the study area. Panel A locates Bylot Island (72°53' N, 79°54' W) in Nunavut, Canada. Panel B enlarges Bylot Island. The hatched area depicts our study area containing 6 arctic fox territories used by 6 fox pairs and one additional individual (Figure 1.1), while the larger gray area depicts the entire field site used during the last 30 years to study the ecosystem.

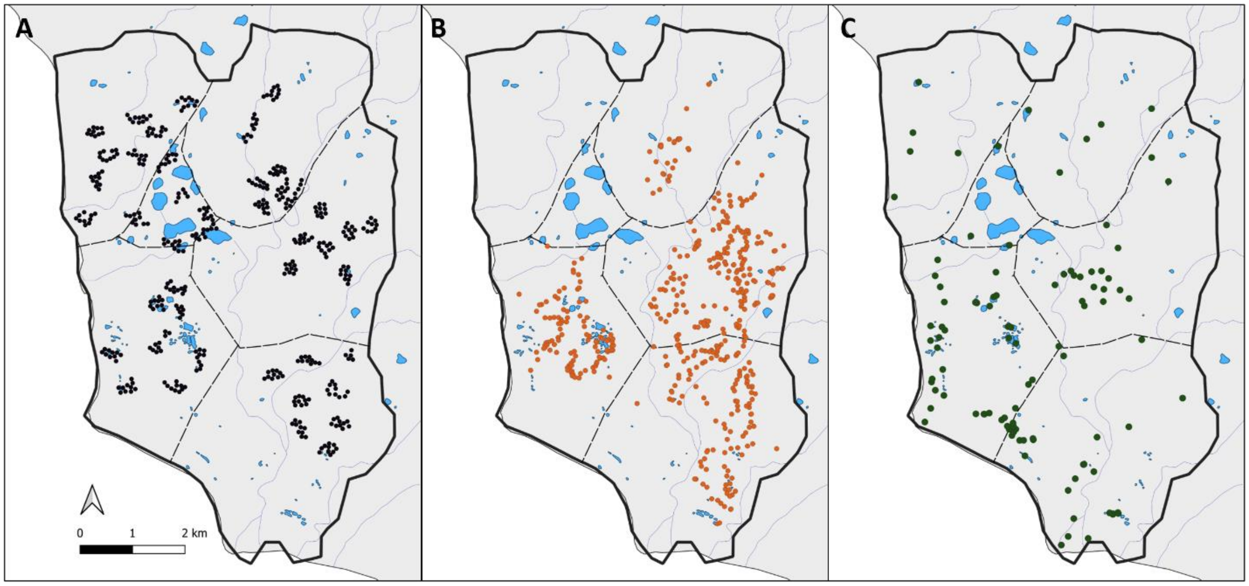

Figure 1. 6 Distribution of A) baits used in the artificial prey experiment (n = 428, black dots), B) nests used to evaluate snow goose anti-predator behavior (n = 458, orange dots), and C) nests of fox incidental prey, that is birds other than snow geese (n = 109, green dots). The dashed lines show the approximate boundaries of fox pair territories while the thick black line is the contour of the study area. Lakes and large ponds are in blue.

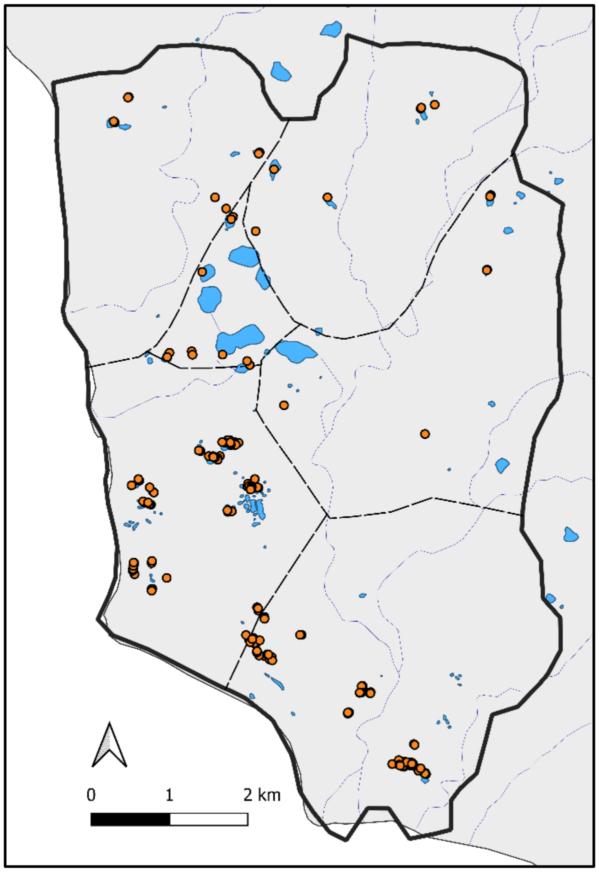

Figure 1. 7 Distribution of the 377 islets (orange dots) located in ponds, lakes and wetlands. Many dots are superimposed at this spatial scale. The dashed lines show the approximate boundaries of fox pair territories while the thick black line is the contour of the study area. Lakes and large ponds are in blue.

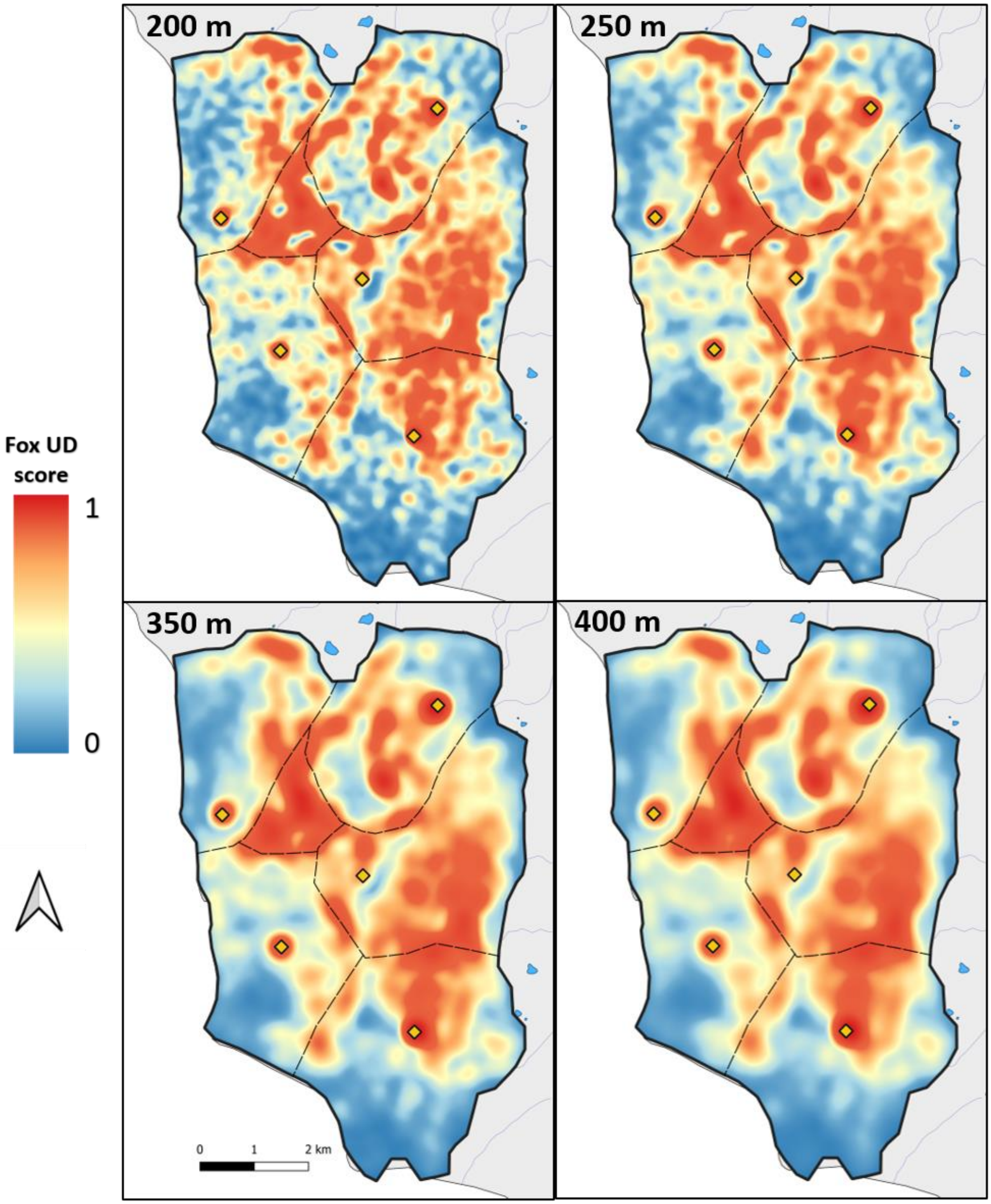

Figure 1. 8 Arctic fox activity landscapes generated from 20,961 GPS locations classified in the active state by a hidden Markov model, using UD smoothing parameters ranging from 200 to 400 m, as indicated on the top left corner of each map (see Figure 1.2 in the main text for activity landscape using the intermediate smoothing parameter of 300 m). The activity landscape reflects fox utilization distribution (UD) based on data from 13 individuals living

in 6 territories during 10 days at the end of June 2019 on Bylot Island. The color scale reflects fox UD score (from 0 to 1) and thus probability of presence of a fox. Yellow diamonds locate the 5 reproductive dens, dashed lines identify the approximate boundaries of fox pair territories, and the thick black line is the contour of the study area.

1.9 Appendix S2 – Complementary analyses for distribution of birds nesting in refuges

The number of available islets per nest varied according to the radius of the nest area, with 26 ± 12 (range 3–50) available islets for a radius of 1000 m, 40 ± 12 (3–50) for 1500 m, 46 ± 10 (3–50) for 2000 m, 47 ± 9 (9–50) for 1500 m and 48 ± 7 (10–50) for 3000 m. Results from these models are presented in Table 1.3 (main text).

We conducted two complementary analyses to verify whether using an unbalanced number of available locations affected results. First, we compared fox UD scores at bird nests to fox UD scores at available islets as described in Methods (3-Nest distribution of incidental prey/Second set of models), but using more balanced sample sizes of ≤ 10 islets instead of ≤ 50. We could not use a totally balanced design as the minimum number of islets was only 3. Obtained results (Table 1.7) did not differ from those presented in the main text (Table 1.3).

Second, we compared fox UD scores at bird nests to fox UD scores at available locations as described in Methods (3-Nest distribution of incidental prey/First set of models), thus comparing UD scores of used islets to 50 random locations picked anywhere in the nest area, excluding water bodies (this yielded a balanced design). An advantage of this approach is that it also allowed us to verify whether drawing available locations from georeferenced islets rather than anywhere in the nest area affected our conclusions. Results (Table 1.8) did not differ from those presented in the main text (Table 1.3).

Table 1. 7 Results from conditional logistic regressions with a use-available design testing the effect of fox UD score on the nest distribution of birds that nest in microhabitats providing refuge against foxes (n = 65 nests from 3 species). The fox UD score of each nest was compared to the fox UD score of ≤ 10 islets surrounding the nest within the nest area. Coefficient estimates are presented for 25 models, each reflecting a given size of the nest area (from 1000 to 3000 m) and UD smoothing parameter (from 200 to 400 m).

Radius of nest area (m)	UD smoothing parameter (m)	Coefficient [95% CI]	z value	p value
1000	200	0.41 [-7.95, 8.76]	0.10	0.924
	250	0.32 [-6.37, 7.01]	0.09	0.926
	300	0.18 [-5.47, 5.82]	0.06	0.952
	350	-0.02 [-4.97, 4.94]	-0.01	0.995
	400	-0.21 [-4.70, 4.27]	-0.09	0.926
1500	200	2.04 [-4.16, 8.24]	0.64	0.519
	250	1.41 [-3.40, 6.21]	0.57	0.566
	300	0.89 [-3.06, 4.85]	0.44	0.658
	350	0.50 [-2.87, 3.89]	0.29	0.771
	400	0.24 [-2.77, 3.24]	0.15	0.878
2000	200	4.12 [-1.67, 9.91]	1.40	0.163
	250	2.90 [-1.54, 7.33]	1.28	0.201
	300	2.06 [-1.59, 5.70]	1.11	0.269
	350	1.52 [-1.59, 4.63]	0.96	0.338
	400	1.20 [-1.53, 3.93]	0.86	0.390
2500	200	3.75 [-1.88, 9.39]	1.31	0.192
	250	2.74 [-1.56, 7.05]	1.25	0.211
	300	2.10 [-1.41, 5.62]	1.17	0.241
	350	1.66 [-1.34, 4.66]	1.08	0.278
	400	1.33 [-1.30, 3.98]	0.99	0.321
3000	200	3.04 [-2.35, 8.42]	1.11	0.269
	250	2.14 [-1.96, 6.23]	1.02	0.307
	300	1.49 [-1.87, 4.84]	0.87	0.385
	350	1.01 [-1.85, 3.86]	0.69	0.488
	400	0.69 [-1.81, 3.19]	0.54	0.589

Table 1. 8 Results from conditional logistic regressions with a use-available design testing the effect of fox UD score on the nest distribution of birds that nest in microhabitats providing refuge against foxes (n = 65 nests from 3 species). The fox UD score of each nest was compared to the fox UD scores of 50 random locations surrounding the nest within the nest area. Coefficient estimates are presented for 25 models, each reflecting a given size of the nest area (from 1000 to 3000 m) and UD smoothing parameter (from 200 to 400 m). Significant effects are in bold.

Radius of nest area (m)	UD smoothing parameter (m)	Coefficient [95% CI]	z value	p value
1000	200	2.91 [-0.83, 6.65]	1.52	0.128
	250	3.01 [-0.06, 6.09]	1.92	0.055
	300	**3.03 [0.33, 5.74]**	**2.20**	**0.028**
	350	**2.97 [0.51, 5.43]**	**2.36**	**0.018**
	400	**2.81 [0.50, 5.12]**	**2.39**	**0.017**
1500	200	2.56 [-1.05, 6.18]	1.39	0.165
	250	2.55 [-0.36, 5.47]	1.72	0.086
	300	2.48 [-0.05, 5.00]	1.92	0.054
	350	**2.32 [0.05, 4.58]**	**2.01**	**0.045**
	400	2.08 [-0.001, 4.17]	1.96	0.050
2000	200	-0.005 [-3.96, 3.95]	0.00	0.998
	250	0.17 [-2.90, 3.25]	0.11	0.912
	300	0.23 [-2.36, 2.82]	0.17	0.864
	350	0.19 [-2.10, 2.48]	0.16	0.870
	400	0.08 [-2.00, 2.16]	0.08	0.940
2500	200	-0.73 [-4.87, 3.42]	-0.34	0.731
	250	-0.39 [-3.64, 2.85]	-0.24	0.813
	300	-0.29 [-3.02, 2.45]	-0.21	0.836
	350	-0.31 [-2.71, 2.09]	-0.26	0.798
	400	-0.44 [-2.61, 1.73]	-0.40	0.690
3000	200	-2.61 [-7.21, 1.99]	-1.11	0.267
	250	-1.93 [-5.45, 1.58]	-1.08	0.281
	300	-1.61 [-4.49, 1.27]	-1.10	0.273
	350	-1.48 [-3.95, 0.99]	-1.17	0.241
	400	-1.48 [-3.67, 0.71]	-1.32	0.186

CHAPITRE II

DIGGING INTO THE BEHAVIOUR OF AN ACTIVE HUNTING PREDATOR: ARCTIC FOX CACHING EVENTS REVEALED BY ACCELEROMETRY

Jeanne Clermont, Sasha Woodward-Gagné & Dominique Berteaux

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2.1 Résumé

Mise en contexte

Les avancées en bio-télémétrie permettent de suivre les mouvements des animaux de manière détaillée, et génèrent de nouvelles connaissances en écologie comportementale. Particulièrement, l'utilisation de GPS et d'accéléromètres permet d'évaluer où les individus adoptent certains comportements, tels les évènements de prédation de grands prédateurs terrestres. Spécifiquement, l'identification de regroupements de localisations GPS résultant de la manipulation d'une proie permet l'identification de sites de capture. Cependant, pour les petits prédateurs qui manipulent leurs proies rapidement, il demeure difficile d'identifier les évènements de prédation à partir de données télémétriques. Une avenue prometteuse émerge quand le prédateur utilise des comportements alimentaires qui génèrent des patrons d'accélération spécifiques, comme les comportements de cache de proies du renard arctique (*Vulpes lagopus*), un prédateur actif qui dépend fortement de nourriture stockée lorsqu'il vit à proximité de colonies d'oiseaux.

Méthodes

Nous avons équipé 16 renards arctiques à l'île Bylot (Nunavut, Canada) d'un GPS et d'un accéléromètre, générant 23 étés-renard de données de mouvement. Les accéléromètres enregistraient l'accélération sur trois axes à 50 Hz, et pendant cet enregistrement, nous avons filmé les différents comportements des renards. Nous avons entraîné différents algorithmes d'apprentissage à classer les données d'accélérométrie en 4 comportements : l'immobilité, la course, la marche et le creusage, ce dernier comportement étant associé aux caches de proies. Finalement, nous avons évalué la concordance dans le temps et l'espace entre les évènements de creusage et la reproduction des grandes oies des neiges (*Anser caerulescens atlanticus*), afin de tester la pertinence écologique de notre classification comportementale dans un système où les forces descendantes sont dominantes au sein du réseau trophique.

Résultats

L’algorithme de forêt d’arbres décisionnels a généré la meilleure classification comportementale, avec une exactitude pour chaque comportement excédant 96%. Globalement, les renards ont passé 49% du temps à l’état immobile, 34% à la course, 9% à la marche, et 8% à creuser. La probabilité de creuser augmente avec la densité de nids d’oies, à la fois pendant la période d’incubation et d’élevage des oisons.

Conclusions

La combinaison de données d’accélérométrie et GPS nous a permis de suivre dans le temps et l’espace les comportements alimentaires d’un petit prédateur actif, nous informant sur la répartition spatio-temporelle du risque de prédation dans une communauté de vertébrés de l’Arctique. Notre étude ouvre de nouvelles possibilités pour l’étude des comportements de prédation de prédateurs terrestres, une étape essentielle pour mieux comprendre les mécanismes qui structurent les interactions prédateurs-proies et les réseaux trophiques.

Mots clés : bio-télémétrie, budget d’activité, cache de proies, classification comportementale, forêt d’arbres de décision, interactions prédateurs-proies, mise en réserve, prédation, taux d’acquisition, apprentissage supervisé

2.2 Abstract

Background

Biologging now allows detailed recording of animal movement, thus informing behavioural ecology in ways unthinkable just a few years ago. In particular, combining GPS and accelerometry allows spatially explicit tracking of various behaviours, including predation events in large terrestrial mammalian predators. Specifically, identification of location clusters resulting from prey handling allows efficient location of killing events. For small predators with short prey handling times, however, identifying predation events through technology remains unresolved. We propose that a promising avenue emerges when specific

foraging behaviours generate diagnostic acceleration patterns. One such example is the caching behaviour of the arctic fox (*Vulpes lagopus*), an active hunting predator strongly relying on food storage when living in proximity to bird colonies.

Methods

We equipped 16 Arctic foxes from Bylot Island (Nunavut, Canada) with GPS and accelerometers, yielding 23 fox-summers of movement data. Accelerometers recorded tri-axial acceleration at 50 Hz while we obtained a sample of simultaneous video recordings of fox behaviour. Multiple supervised machine learning algorithms were tested to classify accelerometry data into 4 behaviours: motionless, running, walking and digging, the latter being associated with food caching. Finally, we assessed the spatio-temporal concordance of fox digging and greater snow goose (*Anser caerulescens atlanticus*) nesting, to test the ecological relevance of our behavioural classification in a well-known study system dominated by top-down trophic interactions.

Results

The random forest model yielded the best behavioural classification, with accuracies for each behaviour over 96%. Overall, arctic foxes spent 49% of the time motionless, 34% running, 9% walking, and 8% digging. The probability of digging increased with goose nest density and this result held during both goose egg incubation and brooding periods.

Conclusions

Accelerometry combined with GPS allowed us to track across space and time a critical foraging behaviour from a small active hunting predator, informing on spatio-temporal distribution of predation risk in an Arctic vertebrate community. Our study opens new possibilities for assessing the foraging behaviour of terrestrial predators, a key step to disentangle the subtle mechanisms structuring many predator-prey interactions and trophic networks.

Keywords: acquisition rate, activity budget, behavioural classification, biologging, food caching, hoarding, predation, predator-prey interactions, random forest, supervised machine learning

2.3 Background

A critical question of predator-prey dynamics is when and where do predators catch prey. However, most predators are secretive, complicating detailed assessments of their hunting strategies. Recent technology may solve this problem by revealing the behaviour of even the most cryptic species, allowing important progress in behavioural and community ecology (Cagnacci et al., 2010; Wilmers et al., 2015; Studd et al., 2021).

With variable success, high precision GPS and accelerometers have been used to identify predation events, thus informing on the timing and location of kills as well as prey acquisition rate, a key metric to understand predator-prey relationships (Vucetich et al., 2011). Recently, predation events by seabirds (Watanabe & Takahashi, 2013; Carroll et al., 2017), fishes (Watanabe et al., 2019), marine (Viviant et al., 2010; Sweeney et al., 2019) and large terrestrial mammals (Wang et al., 2015; Petroelje et al., 2020) were identified through biologging. In large terrestrial mammals, killing events of large prey can be identified through the clusters of GPS locations resulting from prey handling, which includes prey consumption and sometimes food caching (Webb et al., 2008; Knopff et al., 2009; Wilmers et al., 2013). Although this approach, which often necessitates field confirmation of kills, works for large predators, it depends on long prey handling times (and thus large prey sizes) (Palacios & Mech, 2011; Petroelje et al., 2020) matched with adequate GPS fix frequency (Webb et al., 2008; Knopff et al., 2009).

Accelerometry can inform the predator’s behavioural state and thus confirm a killing event after a cluster of GPS locations is identified (Petroelje et al., 2020). Indeed, statistical tools like supervised machine learning can identify behavioural states (e.g., flying, travelling, resting, foraging) from tri-axial acceleration measurements (Nathan et al., 2012; Brown et al., 2013). Furthermore, accelerometry may also be used to directly identify killing events of ambush predators for which killing of large prey involves stalking and high acceleration attacks (Williams et al., 2014; Wang et al., 2015; Wilmers et al., 2017). Success of accelerometry in identifying predation events still depends on many factors like sampling regime, predator's hunting strategy, predator and prey body sizes, and prey handling time. This explains why most accelerometry-based studies identifying predation events by terrestrial mammals are restricted to large ambush predators feeding on large prey.

Using biologging to study hunting behaviour of small active hunting predators feeding on small prey and requiring short handling times cannot rest on the identification of clustered locations. Still, studying their hunting behaviour is critical to better understand trophic networks. Detailed behavioural classification obtained from accelerometry (Chimienti et al., 2017; Chakravarty et al., 2019) may offer avenues for progress, provided the foraging behaviour of the studied species contains diagnostic acceleration patterns. For example, the fast and sharp movements of foraging razorbills (*Alca torda*) and common guillemots (*Uria aalge*) allowed researchers to quantify prey pursuit and catching through accelerometry classification (Chimienti et al., 2017). Many other predators perform unique behavioural sequences potentially providing acceleration signatures of foraging events. Food caching (Masoero et al., 2018; Farhadinia et al., 2020; van der Veen et al., 2020) is one such sequence, as observed in many canids, which are active hunting predators storing food for later consumption (Macdonald, 1976). Canid caching behaviour generally follows a distinctive sequence of food carrying, digging with forepaws, tamping with muzzle to press food into the soil, and head scooping to cover food with substrate (Gadbois et al., 2015).

We tested the potential of accelerometry to inform the hunting behaviour of an active hunting predator with short prey handling times. We did so using the arctic fox (*Vulpes lagopus*) as study model, since this small canid (ca. 2.5 kg) is a key predator over its circumpolar range, where it has been thoroughly studied (Berteaux et al., 2017a, 2017b) and is well known to cache food (Careau et al., 2007, 2008b). Furthermore, predation by arctic foxes generates both important top-down effects on prey populations (Legagneux et al., 2012) and predator-mediated interactions among prey species (Bêty et al., 2002; McKinnon et al., 2013;

Duchesne et al., 2021), thus increasing the need to understand how arctic foxes' hunting behaviour generates a predation risk landscape (Clermont et al., 2021a). Due to harsh climatic conditions and the pulsed nature of rodent populations and migratory birds in many Arctic systems, arctic foxes highly depend on food caches during periods of food scarcities such as the winter season (Samelius & Alisauskas, 2000; Careau et al., 2007, 2008a). On Bylot Island (Nunavut, Canada), which is home to a large greater snow goose (*Anser caerulescens atlanticus*) colony composed of > 20,000 nesting pairs (Bêty et al., 2001), arctic fox summer diet is primarily composed of lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) and goose eggs (Bêty et al., 2001; Careau et al., 2007; Legagneux et al., 2012). They can cache up to 90% of the goose eggs they collect (Careau et al., 2007). They can also cache ca. 30% of collected goose goslings and lemmings (Careau et al., 2007). The caching rate of eggs collected from goose nests declines from laying to hatching, but foxes recache ca. 60% of the goose eggs recovered from initial caches (Careau et al., 2007, 2008b). Food caching thus represents a critical dimension of the foraging ecology of this predator. Given the stereotyped nature of food caching behaviour in canids, this behaviour could generate a spatially and temporally explicit signature of foraging events in individuals equipped with GPS and accelerometers.

Our first objective was to develop an algorithm allowing the behavioural classification of arctic fox accelerometry data and identifying prey caching events. Using in situ video calibration, we studied fox movements during two consecutive goose breeding seasons. Lemming density was low to moderate, thus most cached prey were goose eggs (see Methods for details). Our second objective was to assess whether fox digging events (the most conspicuous behaviour involved in food caching) and greater snow goose nesting were spatially and temporally congruent, as a way to test the ecological relevance of our behavioural classification. We predicted that digging should occur more frequently where nest density is highest (P1), digging should occur less frequently after egg hatching (P2), as eggs become goslings that gradually disperse, and the spatial correlation between digging frequency and goose nest density should hold even after eggs have hatched (P3), since foxes recover previously cached eggs for consumption or recaching in potentially safer sites

(Careau et al., 2007, 2008b). Lastly, we discuss the potential to gain information on prey acquisition rates of an active hunting predator from the behavioural classification of accelerometry data.

2.4 Methods

2.4.1 Study system

We worked in May-July 2018-2019 in the southwest plain of Bylot Island (72°53' N, 79°54' W), in Sirmilik National Park of Canada, Nunavut. The ecosystem is characterised primarily by mesic tundra and polygonal wetlands (Grenier-Potvin et al., 2021). Arctic foxes use dens to rear young and share a territory with their mating partner (Szor et al., 2008). In 2018 and 2019, there were 115 fox dens in the study area and all were georeferenced. On Bylot, arctic foxes rely mostly on small prey, such as lemmings (40-50 g), which show important annual density fluctuations (Gruyer et al., 2008). Lemming abundance was low (0.02 lemmings/km^2) in 2018 and moderate (137 lemmings/km^2) in 2019 as determined by capture-recapture methods (Fauteux et al., 2015; Duchesne et al., 2021). Foxes also collect snow goose eggs (100-150 g, Careau et al., 2008a) during the nesting period for immediate consumption or storage, as well as goslings after hatching (Bêty et al., 2001). The goose incubation period lasts 23 days from mid-June to early July, after which goose families disperse. Predation on goose nests by arctic foxes is greater when lemming abundance is low (Bêty et al., 2001, 2002; Lecomte et al., 2008a), as they then highly depend on this resource for reproduction (Giroux et al., 2012). Notably, from an isotopic analysis, Giroux et al. (2012) found that geese represented up to 97% of arctic fox cubs’ diet, depending on lemming abundance and distance from the center of the goose colony. Furthermore, based on 363 hours of observations inside the goose colony from June 8 to July 14 during a year of moderate lemming abundance, 75% of prey collected by foxes were goose eggs, 14% were lemmings and 11% were goslings (Careau et al., 2007).

Arctic foxes seem to cache food items individually (Samelius & Alisauskas, 2000), although more evidence is required on this matter regarding the smallest prey. Using radio-collared artificial eggs, Careau et al. (2007) found that eggs were cached 85 m (median) from the nest.

Median hoarding times (including carrying and caching times) are ca. 100 sec for eggs and ca. 60 sec for goslings and lemmings (Careau et al., 2007). Foxes also opportunistically prey upon nests of other ground nesting birds such as shorebirds, passerines, and ducks, and they are their main nest predator (McKinnon & Bêty, 2009; Gauthier et al., 2011). A simplified food web of the study system is available in Duchesne et al. (2021).

2.4.2 Fox captures, movement tracking and video observations

We captured 16 foxes using Softcatch #1 padded leghold traps (Oneida Victor Inc. Ltd., Cleveland, OH, USA), for a total of 23 fox-summers of movement data. Fox sex was determined at capture and reproductive status (yes/no) was based on whether automated cameras recorded cubs at the individual's den (Cameron et al., 2011). Each fox was marked with coloured ear tags allowing identification at a distance, and was fitted with a GPS-accelerometer collar (95 g, ca. 4% of body mass; Radio Tag-14, Milsar, Romania) equipped with rechargeable batteries, a solar panel, and UHF transmission allowing remote data download. We programmed collars to collect a GPS fix every 4 min and a 30-sec accelerometry burst every 4.5 min (we unintentionally set a 4-min rather than 3.5-min break between bursts). We collected triaxial accelerometry at 50 Hz on the vertical (heave), lateral (sway) and longitudinal (surge) axes. Table 2.5 in Additional file 1 describes sample sizes of accelerometry data for each fox and year considered in our study. After excluding data collected within two days of capture, we obtained 157,276 bursts totaling 4,718,280 sec of accelerometry, and collected 451,895 GPS locations (Figure 2.1: A).

We videotaped collared foxes at each encounter during June and July and managed to film 15 of the 16 foxes. We collected 2.42 hours of video (45 observations of 0.5-17 min) in 2018 and 6.48 hours (59 observations of 1-47 min) in 2019 (Figure 2.1: A). We filmed a handheld GPS at the end of each video observation to allow post-synchronisation of video and accelerometry sequences.

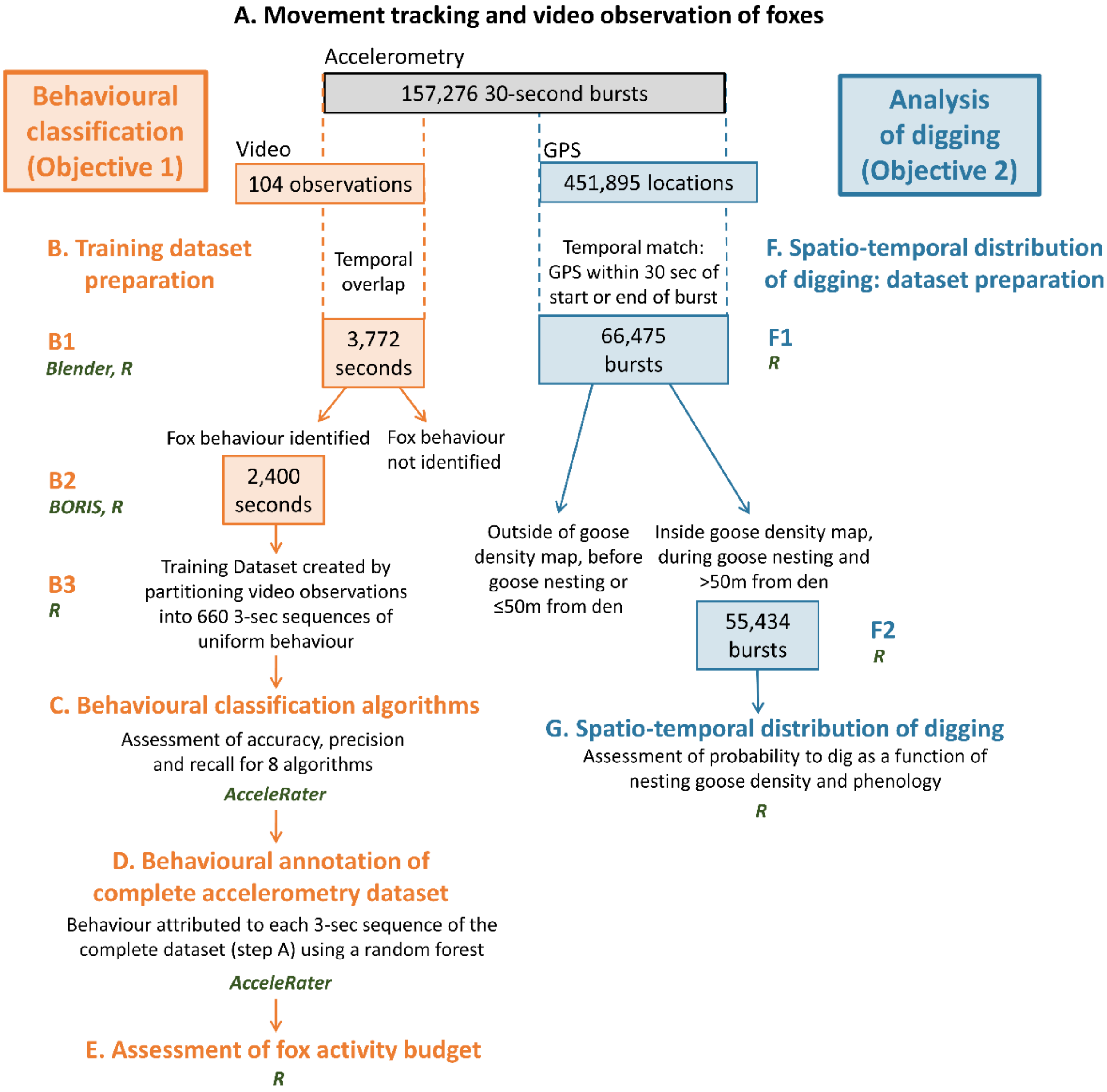

Figure 2. 1 Methodological workflow for the behavioural classification of accelerometry data and assessment of activity budget (objective 1, steps A-E), and the spatio-temporal distribution of digging events (objective 2, steps F-G) in arctic fox from Bylot Island (Nunavut, Canada). The software used for data handling and analysis are indicated in dark green below each step.

2.4.3 Objective 1: Behavioural classification from accelerometry data

1) Training dataset preparation

We first identified temporal overlaps between video and accelerometry sequences. To do so, we synchronised video times with GPS satellite time filmed at the end of the observation, using Blender video editing software (version 2.82.7, Blender Foundation, 2020). We then associated video observations to corresponding sequences of accelerometry data in R software (version 3.6.1, R Development Core Team, 2019). This yielded 3,772 seconds of video (from 12 foxes, both years combined) that were concurrent with accelerometry data (Figure 2.1: B1).

We then used BORIS software (version 7.9.7, Friard & Gamba, 2016) to annotate the video observations identified above, using the detailed ethogram from Table 2.6 in Additional file 1. We noted the start and end times of each behaviour. Rare behaviours were ignored, and similar behaviours were grouped (Additional file 1, Table 2.6), yielding 4 behaviour categories: running, walking, digging and motionless (Table 2.1, Figure 2.2). While running, walking, and motionless events are readily identified in canids (Tatler et al., 2021), digging is more context-specific. In all digging events, the fox had its head close to the ground and was handling a food item (Figure 2.2), mostly digging, usually tamping and scooping, and sometimes eating. The function of behavioural events grouped as digging could be identified on video observations as egg caching (44%), egg recovering (15%), or eating or recovering an unidentified food item from a ground cache (41%; Additional file 1, Table 2.6). Thus, during our observations, at least 59% of digging events involved a goose egg, and foxes were never seen handling a prey type other than a goose egg, suggesting that much more than 59% of digging events involved a goose egg. Movie clips are included as Additional file 2 (online only) to illustrate running, walking, digging and motionless behaviours as observed in arctic foxes from Bylot Island.

We could successfully identify fox behaviour in 2,400 (63.6%) of the 3,772 seconds of video observations that were concurrent with accelerometry data (Figure 2.1: B2). We prepared our training dataset by partitioning these data into 3-sec sequences that each contained a single, uninterrupted behaviour (thus excluding brief sequences of behaviours such as standing between two running sequences). This yielded 660 sequences representing 1,980 seconds of accelerometry (Table 2.1, Figure 2.1: B3). A training dataset composed of 5-sec sequences yielded similar model accuracies but lower precisions, so we used sequences of 3 sec to increase observation sample size and precision. Figure 2.2 presents an example of a 3-sec sequence of acceleration for each behaviour.

Table 2. 1 Description and function of four arctic fox behaviours used for accelerometry classification, and number of 3-sec sequences (N) obtained for each behaviour and used for training behavioural classification algorithms.

Behaviour	Description	Function	N
Running	Fast and long-distance movement	Travel between habitat patches	146
Walking	Slow movement of short duration	Transition between running and another behaviour	126
Digging	Head down, digging, usually tamping and scooping, sometimes eating. Individual remains at a fixed location	Cache or recovery of a food item	49
Motionless	Standing, sitting or lying down (most common), with head up or down	Resting or vigilance	339

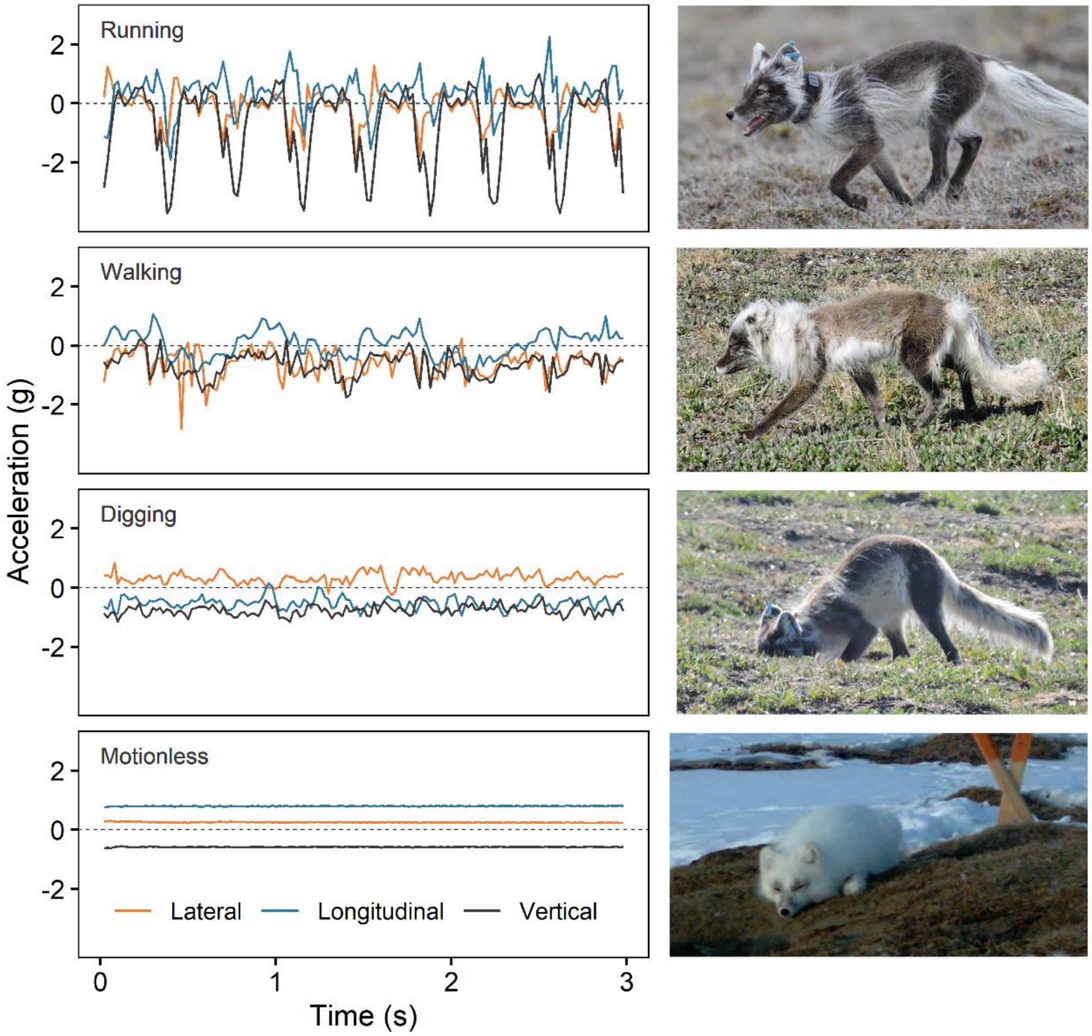

Figure 2. 2 Left column: Three-second acceleration bursts on the lateral (orange), longitudinal (blue), and vertical (black) axes, for the running, walking, digging and motionless behaviour categories considered in this study. Right column: Illustration of each behaviour category. Note the various molt stages observed in these arctic foxes photographed in May-July on Bylot Island (Nunavut, Canada).

2) Behavioural classification algorithms

We used the open-access web application AcceleRater (Resheff et al., 2014) to train behavioural classification algorithms based on our training dataset (Figure 2.1: C). We computed 52 summary statistics (Resheff et al., 2014) for each of the 660 3-sec sequences of the training dataset. Averages and standard deviations of the 52 summary statistics obtained for training sequences are presented for each behaviour category in Additional file 1 (Table 2.7), and among-behaviour differences in the summary statistics are also illustrated in Additional file 1 (Figure 2.4 Panels A-R).

We trained 8 algorithms, including a three nearest neighbours algorithm, a linear support-vector machine, a radial basis function kernel SVM, a decision tree, a random forest, a gaussian naïve Bayes, a linear discriminant analysis and an artificial neural network (Nathan et al., 2012; Resheff et al., 2014; Valletta et al., 2017). We used a five-fold cross-validation method to assess training accuracy, precision and recall for each behaviour. This method splits the dataset into 5 equal parts containing 20% of the dataset, uses 4 parts for training and the remaining one for validation. The cross-validation was repeated 5 times, with each part used once for validation.

To identify which algorithm performed the best at classifying our data, a confusion matrix was built in AcceleRater for each algorithm to represent correct and incorrect classifications, and count true positives (TP), true negatives (TN), false positives (FP), and false negatives (FN). Accuracy, precision and recall were calculated for each behaviour category to assess classification performance. Accuracy is the proportion of correct classifications either into or out of a given behaviour category:

$$accuracy = \frac{TP + TN}{TP + TN + FP + FN}$$

Precision is the proportion of classifications into a given behaviour category that were correct. Higher precision indicates fewer false positives:

$$precision = \frac{TP}{TP + FP}$$

Recall is the proportion of instances of a behaviour classified into the correct category. Higher recall indicates fewer false negatives:

$$recall = \frac{TP}{TP + FN}$$

Lastly, we used AcceleRater to annotate our complete accelerometry dataset (157,276 30-sec bursts) previously partitioned into 3-sec sequences in R (Figure 2.1: D). We used the random forest algorithm which showed the greatest performance for all metrics (see Results). We then determined fox activity budgets by calculating proportions of the dataset associated to each behaviour (Figure 2.1: E).

2.4.4 Objective 2: Spatio-temporal distribution of digging behaviour

1) Data preparation

To assess the spatio-temporal distribution of digging in relation to nesting goose density and phenology, each 30-sec accelerometry burst of the complete dataset (157,276 bursts) was associated to the closest GPS location, provided the time stamp of the GPS location was within 30 sec of the start or end of the burst, which was the case for 42.3% (66,475) of the bursts (Figure 2.1: F1). We then associated to each burst location the local nesting goose density (individual geese/ha), a proxy for nest density that was estimated from detailed field surveys performed in 2018 and 2019 (Grenier-Potvin et al., 2021). We also determined whether each burst occurred during the goose incubation or brooding (when goslings disperse) period, based on starting and ending dates of incubation and brooding for each year (incubation start dates: June 19 in 2018, June 12 in 2019; brooding start dates: July 12 in 2018, July 5 in 2019; brooding end dates: August 3 in 2018, July 27 in 2019), as provided in Grenier-Potvin et al. (2021). In addition, we calculated for each burst the distance to the nearest den (m). We then excluded from analyses 11,041 bursts (Figure 2.1: F2) that 1) were located outside of the snow goose density map (5,563 bursts), 2) were collected before the beginning of the goose nesting period (2,359 bursts; no bursts were collected after goose nesting), or 3) occurred within 50 m of a den, as digging may then be associated with den maintenance rather than foraging (3,119 bursts). This data preparation thus allowed us to assess whether digging events occurred during each of 55,434 30-sec bursts (35.2% of the complete dataset).

2) Statistical analysis

We used a generalised linear mixed model (R package lme4, Bates et al., 2015) with a binomial distribution and a cloglog-link function to predict the probability that a fox engaged in digging during a 30-sec acceleration burst (0 = no digging event, 1 = ≥ 1 digging event), with respect to nesting goose density (P1), goose reproduction period (P2) and their interaction (P3), all included as fixed effects (Figure 2.1: G). We also included sex, reproductive status, and their interaction as fixed effects, as these factors may affect fox behaviour and thus represent confounding variables. Fox ID and year were fitted as random effects. Nesting goose density was centered and standardised to facilitate interpretation of model estimates (Schielzeth, 2010). We used as reference values in the model period = incubation, sex = male, and reproductive status = reproductive.

2.5 Results

2.5.1 Behavioural classification of accelerometry data

The random forest model yielded the greatest average accuracy, precision and recall values compared to other algorithms, and it provided a good classification of the 4 behaviours, with accuracies > 96% (Table 2.2). Most importantly, it yielded by far the greatest precision for digging (92.5%, compared values are identified with an asterisk in Table 2.2) and thus the fewest number of false positives for this behaviour, which was required to address our second objective. The random forest however yielded a recall value that was lower for digging (75.5%, Table 2.2) than for the other behaviours, due to a greater proportion of digging false negatives (12 out of the 49 sequences of digging were false negatives, Table 2.3). Digging false negatives generated a small proportion of false positives in other behaviour categories, which were much more frequent in the data (Table 2.3). As a result, all behaviours were classified by the random forest with a precision > 90%.

Thus, we retained the random forest model to annotate our complete accelerometry dataset. Only 7.5% of the 3-sec sequences classified as digging by this algorithm were done so wrongly, while the random forest missed 24.5% of digging sequences. The random forest was therefore conservative when assigning digging to a given sequence.

Table 2. 2 Accuracy, precision and recall values obtained for the 4 behaviour categories, for each algorithm. Asterisks allow easy comparison of precision across algorithms for digging. The weighted average across behaviour categories is also given. The random forest model was retained and is in bold.

Algorithm	Classification performance	Running	Walking	Digging	Motionless	Weighted average
Three Nearest Neighbours	Accuracy	98.18	96.82	97.12	97.58	97.53
	Precision	95.27	91.34	*80.00	98.21	94.90
	Recall	96.58	92.06	81.63	97.05	94.85
Linear Support-Vector Machine	Accuracy	96.36	95.30	94.39	96.67	96.17
	Precision	93.57	87.40	*60.00	97.60	91.97
	Recall	89.73	88.10	73.47	95.87	91.36
Radial Basis Function Kernel SVM	Accuracy	97.12	96.82	96.67	96.97	96.95
	Precision	93.79	92.68	*75.47	97.05	93.89
	Recall	93.15	90.48	81.63	97.05	93.79
Decision Tree	Accuracy	97.27	96.21	95.15	97.42	96.99
	Precision	93.84	90.40	*64.41	98.79	93.54
	Recall	93.84	89.68	77.55	96.17	93.03
Random Forest	**Accuracy**	**97.58**	**96.67**	**97.73**	**98.03**	**97.65**
	Precision	**92.76**	**90.63**	***92.50**	**97.94**	**95.00**
	Recall	**96.58**	**92.06**	**75.51**	**98.23**	**95.00**
Gaussian Naïve Bayes	Accuracy	97.73	96.82	95.61	97.73	97.40
	Precision	93.38	98.17	*65.15	98.50	94.83
	Recall	96.58	84.92	87.76	97.05	93.94
Linear Discriminant Analysis	Accuracy	98.33	95.91	95.45	97.88	97.42
	Precision	97.20	88.37	*67.27	98.80	94.11
	Recall	95.21	90.48	75.51	97.05	93.79
Artificial Neural Network	Accuracy	97.42	96.52	96.82	97.42	97.21
	Precision	93.88	89.92	*81.82	97.35	94.01
	Recall	94.52	92.06	73.47	97.64	94.09

Table 2. 3 Random forest confusion matrix with actual and predicted number of observations for each behaviour category.

		Predicted category				
		Running	Walking	Digging	Motionless	Total
Actual category	Running	141	4	1	0	146
	Walking	5	116	2	3	126
	Digging	3	5	37	4	49
	Motionless	3	3	0	333	339
	Total	152	128	40	340	660

2.5.2 Arctic fox activity budget

Classification of our complete accelerometry dataset (Figure 2.1: E) confirmed that arctic foxes are active hunting predators, as 50.7% of their activity budget was devoted to active behaviours, specifically running (34.0%), walking (8.5%), and digging (8.2%). This left 49.3% of their activity budget devoted to motionless behaviours. These proportions may however be very slightly overestimated, as running, walking, digging and motionless composed ca. 97% of fox behaviours in the video observations used to create our training dataset (Table 2.6).

2.5.3 Spatio-temporal distribution of digging behaviour

Foxes engaged in digging in 31.1% of the 55,434 30-sec bursts retained for analysis of the spatio-temporal distribution of digging (Figure 2.1: G), justifying the use of the cloglog-link function in our binomial model since the ratio of 0:1 values was 69:31. Probability of digging increased with nesting goose density (P1 supported) and was slightly lower during brooding compared to incubation when nesting goose density was > ca. 12 ind/ha (P2 partly supported; Table 2.4, Figure 2.3A). The effect of nesting goose density on the probability of digging was consistent across goose reproduction periods (P3 supported; Table 2.4, Figure 2.3A). Probability of digging was the highest for reproductive females and the lowest for non-reproductive females, compared to reproductive and non-reproductive males who showed intermediate values (Table 2.4, Figure 2.3B).

Table 2. 4 Results of the generalised linear mixed model (on the cloglog-scale) explaining the probability of engaging in digging behaviour (binomial distribution), as a function of nesting goose density, goose reproduction period (incubation versus brooding), interaction between goose density and reproduction period, as well as fox sex, reproductive status and their interaction (n = 55,434 30-sec bursts of accelerometry collected on 23 fox-years). We used as reference values nesting goose density = average, period = incubation, sex = male, and reproductive status = reproductive. Nesting goose density, a proxy for goose nest density, was centered and standardised in the model. Variance and standard error were 0.21 and 0.46 for fox ID and 0.005 and 0.07 for year.

Fixed effect	Estimate [95% CI]	SE	z value	p value
Intercept	-1.35 [-1.68, -1.01]	0.16	-8.31	<0.001
Nesting goose density	0.16 [0.14, 0.18]	0.01	15.54	<0.001
Goose reproduction period	0.04 [0.01, 0.07]	0.02	2.50	0.01
Density : Period	-0.03 [-0.06, -0.01]	0.01	-2.38	0.02
Fox sex	0.59 [0.10, 1.07]	0.23	2.56	0.01
Fox reproductive status	0.03 [-0.07, 0.12]	0.05	0.55	0.59
Sex : Status	-1.05 [-1.16, -0.94]	0.06	-18.05	<0.001

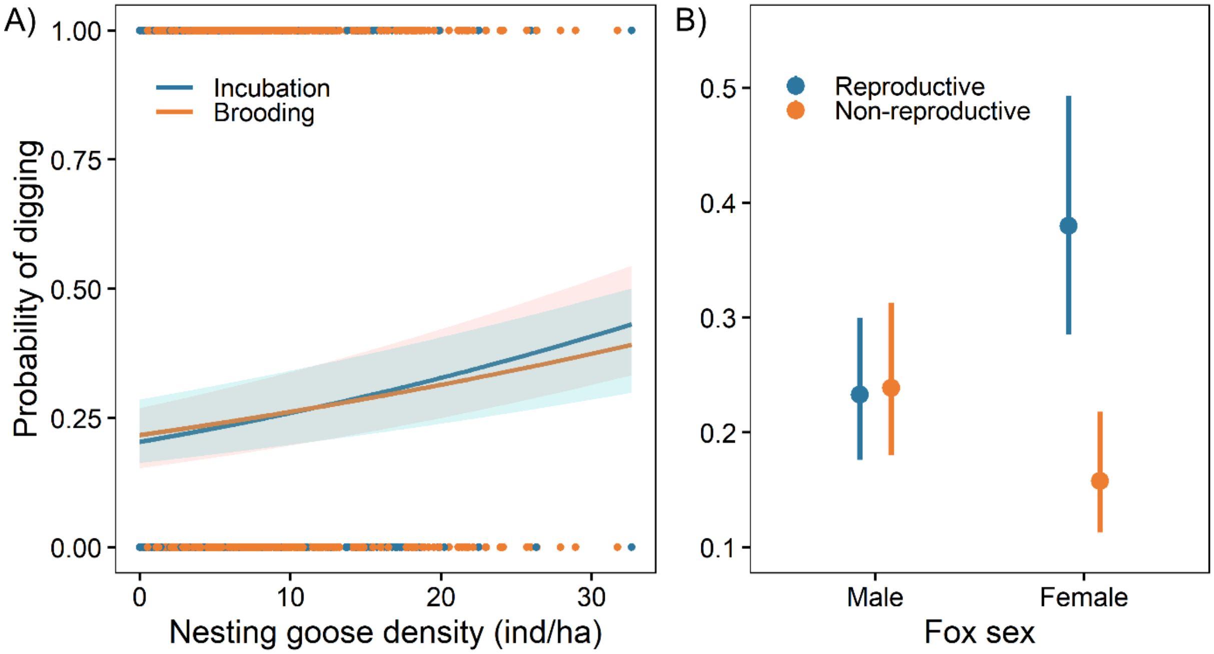

Figure 2. 3 Predicted probability of digging during a 30-sec acceleration burst (burst interval 4.5 min) as a function of A) nesting goose density (a proxy for goose nest density) and goose

reproduction period (incubation in blue, brooding in orange), and B) sex and reproductive status (reproductive in blue, non-reproductive in orange). Nesting goose density was centered and standardised in the model, then back-transformed before plotting. Model reference values are fox sex = male, fox reproductive status = reproductive, period = incubation and nesting goose density = average.

2.6 Discussion

We demonstrated that high precision movement data can indirectly inform hunting behaviour of a terrestrial, active hunting predator feeding on small prey requiring short handling times. Through the behavioural classification of accelerometry data, we detected events of digging, a behaviour that our detailed field observations associated with food caching. Our methodology should be applicable to other small carnivore species that cache their food, such as canids and felids (Macdonald, 1976), or more broadly to any predator using foraging behaviours resulting in diagnostic acceleration patterns. Furthermore, accelerometry combined with geolocation indicated when and where arctic foxes cached their prey, here goose eggs. This proved to have strong ecological relevance, since the spatial and temporal availability of goose eggs shaped the probability of digging. These findings open new opportunities for discovery. Most notably, predator hunting generates spatial variation in predation risk, which shapes prey behaviour and ultimately the structure of prey communities (Gaynor et al., 2019; Clermont et al., 2021a). Therefore, detailed assessments of predator activity budgets and identification of key hunting behaviours are important steps to decipher the mechanisms driving local biodiversity, at least in ecosystems strongly driven by top-down trophic interactions.

2.6.1 Accelerometry reveals prey caching events

Using a random forest, we classified accelerometry data into the four main behaviours composing ca. 97% (according to our training dataset) of an arctic fox activity budget: running, walking, digging and motionless. Our classification was 98% accurate, well in line with the performance reached with other predator species (Wang et al., 2015; Painter et al., 2016; Studd et al., 2021) although directly comparing studies is risky due to varying methods and studied behaviours. Our field observations show that digging behaviour can be mostly attributed to snow goose egg caching in our study system, and we know that foxes forage selectively in patches of high nesting goose density (Grenier-Potvin et al., 2021). In good agreement with the above, we found that the probability of digging increased with nesting goose density. However, the strength of the relationship between the probability to dig and nesting goose density may have been decreased by habitat characteristics and specificities of fox caching behaviour. First, patches of high goose nest density tend to occur in the most complex habitats, like polygonal wetlands (Lecomte et al., 2008b), in which fox attacks on goose nests are generally less successful, thus reducing egg acquisition and caching rates (Careau et al., 2008b; Lecomte et al., 2008a). Second, foxes cache eggs 85 m away (median) from predated nests (Careau et al., 2007) and goose nest density is rather patchy at this scale. Thus, nest density may differ between sites of egg collection and egg caching. Further research should seek to refine our understanding of the spatial distribution of fox digging in the greater snow goose colony of Bylot Island. More generally, our study should be considered as a first step in the use of accelerometry to model foraging behaviour of a small terrestrial carnivore.

We also found that the probability of digging by foxes was mostly similar between the goose incubation and brooding periods. This is counterintuitive since egg availability should obviously decrease after hatching. Yet, in our study system, the rate of egg recovery and recaching was shown to increase over the incubation period as foxes manage their stored food (Careau et al., 2008b). We could expect recovery rate to continue to increase after hatching, when food availability drops, thus reconciling apparently conflicting evidence. Moreover, our results show that after egg hatching, recoveries for consumption or recaching were more likely to occur in areas where goose nest density was highest, that is where a greater proportion of caches were initially made during the incubation period. Our results provide new insights on arctic fox foraging behaviour, but a finer classification of accelerometry data, with more detailed behaviours labeled, would strongly enlighten the complex dynamic of prey acquisition, caching, recovery, recaching, consumption, and even pilfering, in a predator-prey system characterized by pulsed resources, food storage, and delayed food consumption.

2.6.2 Prey caching events inform arctic fox foraging and predator-prey interactions

Our analysis of potentially confounding variables on the probability of digging suggested that reproductive females were more likely to dig (and thus perform egg caching or recovery) than males and non-reproductive females. If confirmed by larger sample sizes, such variation in the frequency of digging across sex and reproductive classes opens the door to productive tests of hypotheses. For example, more food caching by reproductive females than by males might indicate greater parental investment. Alternatively, reproductive males may prefer to bring food to the den to feed the female and the young, instead of caching it. Testing these hypotheses using accelerometry could quickly enhance our understanding of reproductive and movement ecology in arctic foxes and many other small to medium size predators.

Furthermore, as arctic foxes are territorial and tend to avoid territory borders (Grenier-Potvin et al., 2021), their territoriality could lead to non-random distribution of specific behaviours. For example, caches could be preferentially located away from territory edges to reduce pilferage, as observed in wolverines (*Gulo gulo*) that tend to cache food in sites less exposed to competitors (van der Veen et al., 2020). Another interesting avenue would be to directly assess arctic fox tendencies to do cache pilfering in neighbour territories or along overlapping areas. Interestingly, Samelius and Alisaukas (2000) observed on Banks Island (Canada) that during years where arctic foxes were very abundant, they recovered and moved cached eggs at a higher rate, potentially due to increased cache pilfering.

In our study area, foxes select habitats where lemmings and geese are most abundant (Grenier-Potvin et al., 2021). This generates spatial variation in predation risk, with cascading effects on nest site selection, anti-predator behaviour, or nesting success of multiple migrating birds (Lamarre et al., 2017; Clermont et al., 2021a; Duchesne et al., 2021). Differences in hunting behaviour among foxes, driven for example by female reproductive status, may lead to differences in predation risk among and within territories. Finer temporal and spatial scale analyses of predator hunting behaviour may help to better understand fine scale variation in prey distribution and behaviour.

Arctic fox activity budgets may vary on much larger temporal and spatial scales than considered above, due to changing prey availability across time and space. First (seasonal variation), foxes often forage on the sea ice, far away from their territory, to find food during winter (Lai et al., 2017). Yet, to our knowledge, no data exists on fox activity budgets in winter. Second (yearly variation), lemming abundance peaks every 3-4 years on Bylot (Gruyer et al., 2008) and this influences the intensity of food caching by foxes (Careau et al., 2008b), with likely effects on their activity budgets. Third (spatial variation within Bylot), how much a fox territory overlaps the greater snow goose colony should strongly influence fox activity budget (all foxes studied here lived in the colony), given that spatial heterogeneity of the prey base should induce among-individual differences in hunting behaviour. Fourth (spatial variation across the species distribution), we should expect the activity budget of foxes to strongly vary at the circumpolar scale given the many ecological conditions faced by the species (Berteaux et al., 2017b). Better understanding the determinants of fox activity budgets has direct ecological relevance. For example (yearly variations), predation risk on nests of many bird species decreases with lemming abundance on Bylot, likely due to changes in arctic fox behaviour, their shared main predator (McKinnon et al., 2014). Similarly (spatial variation within Bylot), fox predation on artificial nests decreases and shorebird nest abundance increases with distance from the goose colony, where arctic foxes aggregate (McKinnon et al., 2013; Lamarre et al., 2017). Thus, accelerometry data collected on small predators such as arctic foxes over multiple temporal and spatial scales creates new opportunities to shed light on the mechanisms through which predation shapes community structure and function.

2.6.3 What about acquisition rates and functional responses?

We have shown that quantifying behaviours indicative of foraging (and thus composing a predator's hunting strategy) offers opportunities to identify predation events. This was, to our knowledge, never achieved before in a small active predator feeding on small prey (50-100 g). Work is still needed, however, to fully estimate acquisition rates of small predators such as the arctic fox. In particular, not all prey items are cached after capture, caching rates can vary with prey availability, and some prey items can be cached and recovered several times. Thus, caching rates do not directly translate into acquisition rates. Future research should seek to differentiate digging events associated to caching of food items such as lemmings, large goose eggs, small passerine eggs, pieces of large mammal carcasses, etc., and differentiate among events of caching, cache recovery, recaching and eating. This will potentially be achieved using modelling techniques that identify microevents (Chakravarty et al., 2020), or other data sources such as video or audio recorders (Studd et al., 2021). At last, such a precise classification would allow the estimation of the predation metrics used to derive functional responses, which are central to predator-prey interactions as they determine links between trophic levels (Vucetich et al., 2011; Beardsell et al., 2021).

2.7 Conclusion

We developed a supervised-learning algorithm to classify arctic fox accelerometry data into four main behaviours. This allowed us to assess spatio-temporal variation in fox probability to dig, a behaviour associated with prey caching. In doing so we demonstrated that high precision movement data may be used to study the hunting behaviours of predators of small body size, as long as their foraging behaviours contain diagnostic acceleration patterns. Importantly, the identification of predation events from movement data opens the possibility to estimate predation metrics needed to disentangle the mechanisms structuring predator-prey relationships and trophic networks.

2.8 Declarations

Ethics approval and consent to participate: Arctic fox capture techniques and immobilization procedures were approved by the UQAR Animal Care Committee (CPA-64-16-169 R3) and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada (SIR-2018-28021).

Consent for publication: Not applicable.

Availability of data and materials: Arctic fox GPS data are available through the Movebank Data Repository at Berteaux, D. 2020, Arctic fox Bylot-GPS tracking, Movebank Study ID 1241071371 (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1241071371). The accelerometry and video datasets are available from the corresponding authors on reasonable request.

Competing interests: The authors declare that they have no competing interests.

Funding: Support was received from (alphabetical order) Canada Foundation for Innovation, Canada Research Chairs Program, Fonds de Recherche du Québec – Nature et technologies (FRQNT), Natural Sciences and Engineering Research Council of Canada (NSERC), Network of Centers of Excellence of Canada ArcticNet, Northern Scientific Training Program (Polar Knowledge Canada), Parks Canada Agency, Polar Continental Shelf Program (Natural Resources Canada), and Weston Family Foundation.

Author’s contributions: JC and DB designed the study and collected the data. JC and SWG analysed the data. JC wrote the manuscript, with help from DB. All authors read and approved the final manuscript.

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2.9 Additional File 1

Additional Tables

Table 2. 5 Sex (M: male, F: female), reproductive status (R: reproductive, NR: non-reproductive), period of accelerometry data collection, data collection duration, and number of 30-sec accelerometry bursts collected for each of 16 arctic foxes studied in 2018 and 2019 on Bylot Island (Nunavut, Canada). The last row provides summary information.

Unique ID	Colour code	Sex	Year	Reproductive status	Data collection period		Data collection duration (days)	Nb of 30-sec bursts
					Start	End		
718	OBBB	M	2018	R	2018-06-29	2018-07-20	22	6681
			2019	R	2019-05-30	2019-07-17	49	12950
746	BVOB	F	2018	NR	2018-07-04	2018-07-29	26	8106
			2019	R	2019-05-25	2019-07-21	58	8674
717	JVOJ	F	2018	R	2018-07-01	2018-07-28	28	8398
			2019	R	2019-06-20	2019-06-30	11	3323
737	RVJO	M	2018	R	2018-06-30	2018-07-16	17	5225
			2019	R	2019-06-14	2019-07-17	34	8445
722	OJOO	F	2018	R	2018-06-30	2018-07-19	20	5873
			2019	R	2019-06-17	2019-06-26	10	2856
376	JMVJ	F	2018	R	2018-06-27	2018-07-28	32	9769
			2019	R	2019-06-07	2019-07-14	38	5579
743	ORRR	M	2018	NR	2018-06-29	2018-07-27	29	8811
			2019	R	2019-06-21	2019-07-20	30	9214
747	JBOR	M	2018	NR	2018-07-04	2018-07-17	14	4411
758	BORR	M	2019	NR	2019-06-15	2019-07-12	28	5990
459	OBOB	M	2019	R	2019-06-20	2019-06-30	11	3401
759	RMJJ	F	2019	NR	2019-06-19	2019-07-22	34	8443
755	VJOO	M	2019	R	2019-06-05	2019-07-09	35	8154
757	BBJO	M	2019	NR	2019-06-12	2019-07-18	37	11516
405	RMBR	F	2019	R	2019-06-22	2019-07-20	29	9036
618	VORB	F	2019	R	2019-07-14	2019-07-19	6	1874
623	BOBB	M	2019	R	2019-07-18	2019-07-19	2	547
Summary information		Nb of M: 9 Nb of F: 7		Count of R: 17 Count of NR: 6			Average: 26	Average: 6838

Table 2. 6 Ethogram used to classify arctic fox behaviour in the video annotation software BORIS. The proportion of time represented by each behaviour within the 2,400-sec training dataset (before it was split into 3-sec sequences) is indicated. Also given is the 4-category behaviour grouping used for accelerometry classification in the web application AcceleRater, and the number of 3-sec sequences obtained for each behaviour category.

Behaviour	Description	Proportion of time in training dataset	Behaviour category	Nb of 3-sec sequences
Running	Form of locomotion used during fast and long-distance relocations	22.78%	Running	146
Walking	Form of locomotion used during slow relocations, usually during short transitions between running and another behaviour	19.13%	Walking	126
Trotting	Form of locomotion intermediate between running and walking	0.24%	(eliminated)	
Egg caching	Digging (usually with tamping and scooping) to cache an egg, fox is stationary and head is down	3.35%	Digging	49
Egg recovering	Digging to recover an egg previously cached by the same or another individual, fox is stationary and head is down	1.11%		
Other digging	Digging to cache or recover an item unseen by the observer, fox is stationary and sometimes eating, head is down	3.13%		
Standing	Body maintained still on four feet, often between running bouts as the fox stops and looks around	6.32%	Motionless	339
Sitting	Sitting with head up	7.80%		
Resting	Lying down, head either up or down	33.30%		
Sitting and scratching	Sitting while scratching with back paw	0.34%	(eliminated)	
Interacting with geese	Approaching a goose nest, often through a sequence of forward and backward movements adjusted to the goose defense behaviour, rapid reactions	1.68%	(eliminated)	
Interacting with another fox	Parent-offspring interactions at a den, rolling and playing	0.82%	(eliminated)	
Total		100.00%		660

Table 2. 7 Average and standard deviation (SD) for 52 statistics (centered and standardized) calculated for 4 behaviour categories across 660 3-sec sequences of the training dataset. X = lateral axis (sway), Y = longitudinal axis (surge), and Z = vertical axis (heave).

Statistic		Behaviour							
		Running		Walking		Digging		Motionless	
		Average	SD	Average	SD	Average	SD	Average	SD
Mean	MeanX	0.01	1.34	-0.75	0.50	0.37	1.33	0.22	0.74
	MeanY	-0.33	0.56	-0.71	0.35	-1.02	1.20	0.55	0.93
	MeanZ	0.40	0.97	0.19	0.48	0.58	0.96	-0.33	1.05
Standard deviation	stdX	1.37	0.92	0.32	0.37	0.06	0.61	-0.72	0.34
	stdY	1.33	0.90	0.37	0.27	0.16	0.46	-0.73	0.43
	stdZ	1.57	0.83	0.00	0.22	-0.07	0.38	-0.67	0.31
Skewness	SkX	-0.26	0.68	-0.04	0.48	-0.43	0.87	0.19	1.21
	SkY	-0.02	1.04	0.00	0.84	-0.05	0.78	0.02	1.07
	SxZ	-0.40	0.44	0.20	0.77	-0.19	0.74	0.12	1.21
Kurtosis	KuX	-0.39	0.22	-0.17	0.35	-0.01	1.19	0.23	1.25
	KuY	0.01	0.50	-0.13	1.20	-0.18	0.51	0.07	1.12
	KuZ	-0.43	0.15	-0.06	0.91	-0.04	0.64	0.21	1.21
Maximum	MaxX	0.90	1.05	0.24	0.80	0.22	0.58	-0.51	0.74
	MaxY	1.10	1.22	0.00	0.63	-0.27	0.76	-0.43	0.61
	MaxZ	1.21	0.68	0.37	0.54	0.23	0.49	-0.69	0.66
Minimum	MinX	-0.94	1.22	-0.58	0.50	-0.02	0.81	0.62	0.48
	MinY	-1.10	0.87	-0.51	0.44	-0.39	0.58	0.72	0.58
	MinZ	-1.36	1.10	0.03	0.27	0.07	0.41	0.56	0.51
Norm*	normX	1.03	0.99	0.54	0.44	0.07	0.76	-0.65	0.62
	normY	0.87	1.05	-0.23	0.31	0.38	0.56	-0.35	0.95
	normZ	0.80	1.20	-0.36	0.36	-0.65	0.70	-0.12	0.90
Cov*	cov(x,y)	-0.47	1.98	0.27	0.25	0.18	0.74	0.08	0.21
	cov(x,z)	1.05	1.72	-0.22	0.19	-0.14	0.58	-0.35	0.05
	cov(y,z)	0.20	2.03	0.11	0.15	-0.05	0.35	-0.12	0.35
r*	r(x,y)	-0.35	1.19	0.42	0.47	-0.17	0.81	0.02	1.02
	r(x,z)	0.54	1.41	0.17	0.50	0.18	0.69	-0.32	0.83
	r(y,z)	-0.04	1.12	0.39	0.44	-0.36	0.71	-0.08	1.09
DBA*	DBA_X	1.44	0.97	0.23	0.31	0.00	0.60	-0.71	0.21
	DBA_Y	1.47	0.87	0.24	0.28	0.14	0.48	-0.74	0.24
	DBA_Z	1.64	0.80	-0.06	0.21	-0.12	0.36	-0.67	0.17
ODBA*	ODBA	1.60	0.67	0.13	0.25	0.00	0.48	-0.74	0.21
Mean difference*	mean-diff_XY	0.26	1.06	0.01	0.47	1.08	1.63	-0.27	0.86
	mean-diff_XZ	-0.16	1.29	-0.62	0.52	0.03	1.29	0.30	0.81
	mean-diff_XZ	-0.49	0.76	-0.74	0.42	-1.22	1.17	0.67	0.69
Standard deviation difference*	std-diff_XY	1.42	0.92	0.23	0.26	0.09	0.38	-0.71	0.38
	std-diff_XZ	1.28	1.11	0.31	0.33	0.02	0.31	-0.67	0.43

	std-diff_YZ	1.39	1.05	0.12	0.22	0.11	0.37	-0.66	0.41
Wave amplitude*	wave amplitude X	1.38	0.86	0.40	0.38	0.07	0.56	-0.75	0.28
	wave amplitude Y	1.42	1.01	0.17	0.29	0.15	0.50	-0.70	0.30
	wave amplitude Z	1.56	0.88	0.02	0.26	-0.03	0.35	-0.67	0.27
Line crossings*	line crossings XY	0.91	0.79	0.74	0.56	0.08	1.11	-0.68	0.61
	line crossings XZ	0.76	0.57	1.17	0.77	0.09	1.00	-0.78	0.29
	line crossings YZ	1.19	0.79	0.24	0.66	0.91	1.17	-0.74	0.16
25 percentile	X 25%	-0.62	1.35	-0.67	0.46	0.28	1.15	0.48	0.58
	Y 25%	-0.70	0.62	-0.78	0.27	-0.89	0.91	0.72	0.75
	Z 25%	-1.11	1.23	0.18	0.33	0.54	0.62	0.33	0.72
50 percentile	X 50%	0.26	1.18	-0.87	0.54	0.38	1.35	0.16	0.79
	Y 50%	-0.29	0.64	-0.73	0.40	-0.98	1.20	0.54	0.92
	Z 50%	0.70	1.22	0.04	0.42	0.43	0.87	-0.38	0.87
75 percentile	X 75%	0.97	0.93	-0.68	0.46	0.42	1.24	-0.23	0.79
	Y 75%	0.24	0.65	-0.48	0.49	-0.98	1.44	0.22	1.04
	Z 75%	1.45	0.55	0.02	0.33	0.22	0.70	-0.67	0.59

* Description of statistics (Resheff et al., 2014):

Norm: The vector norm of the accelerometry sample.

Cov: Covariance between pairs of axes.

r: Pearson's correlation between every two axes.

DBA: Dynamic Body Acceleration by axis. The sum of acceleration values of the axis.

ODBA: Overall Dynamic Body Acceleration. The sum over the axes of the DBA.

Mean difference: The mean difference between every two axes.

Standard deviation difference: The standard deviation of the difference between every two axes.

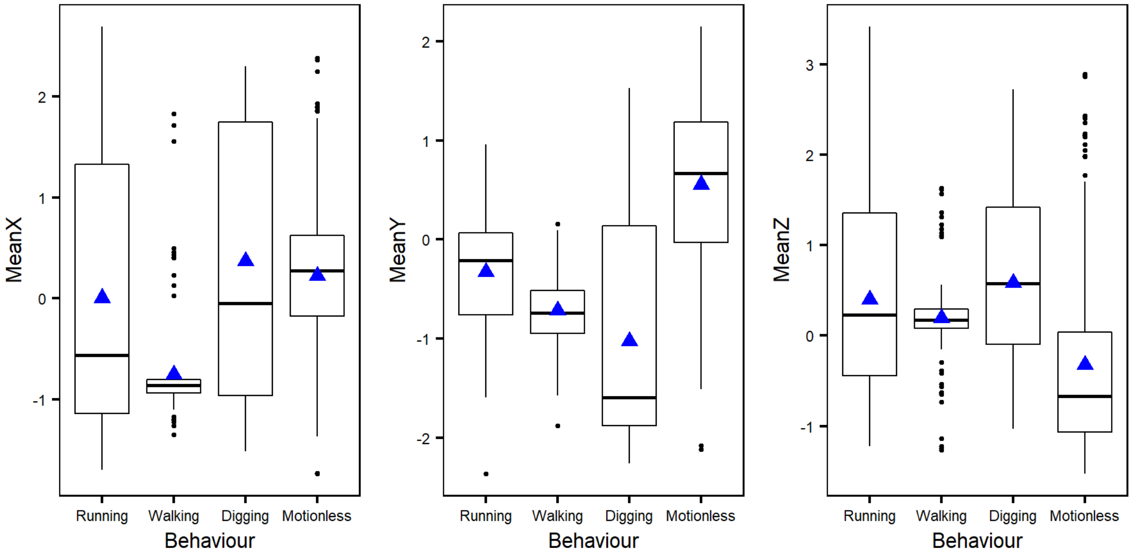
Wave amplitude: The average difference between consecutive local minima and maxima.

Line crossings: The number of times each two axes cross over each other.

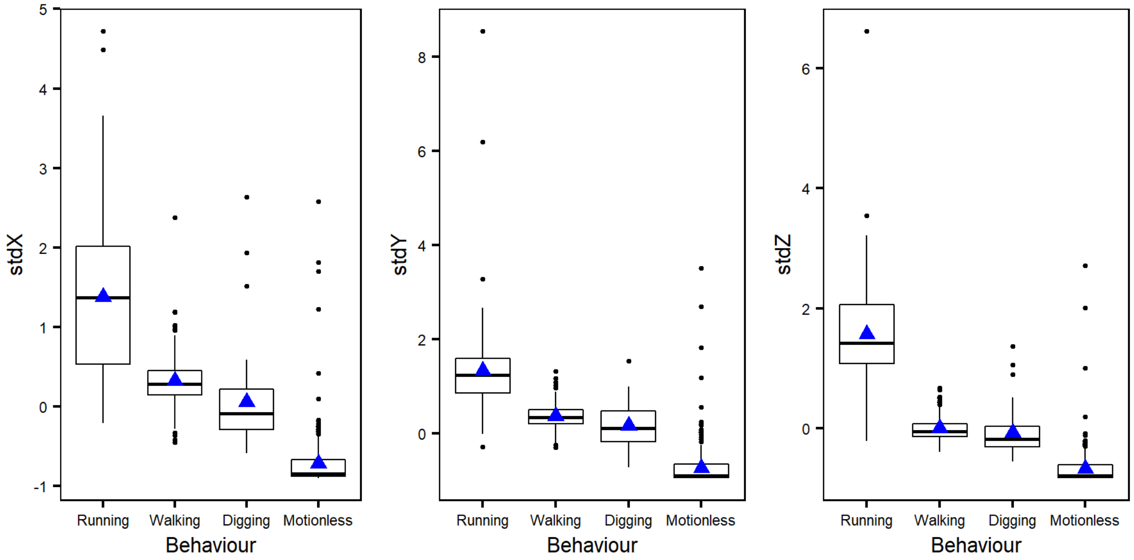
Additional Figures

Figure 2. 4 Panels A to R. Boxplots showing variation in the 52 summary statistics (described in Table S3) computed for each 3-sec sequence of the training dataset among the 4 behaviour categories. On all figures: X = lateral axis (sway), Y = longitudinal axis (surge), and Z = vertical axis (heave). Boxplots show first quartile, median, and third quartile. Lower and upper whiskers extend, respectively, to the lowest and highest value within the interquartile range multiplied by 1.5. Black dots represent values outside this range and blue triangles are mean values.

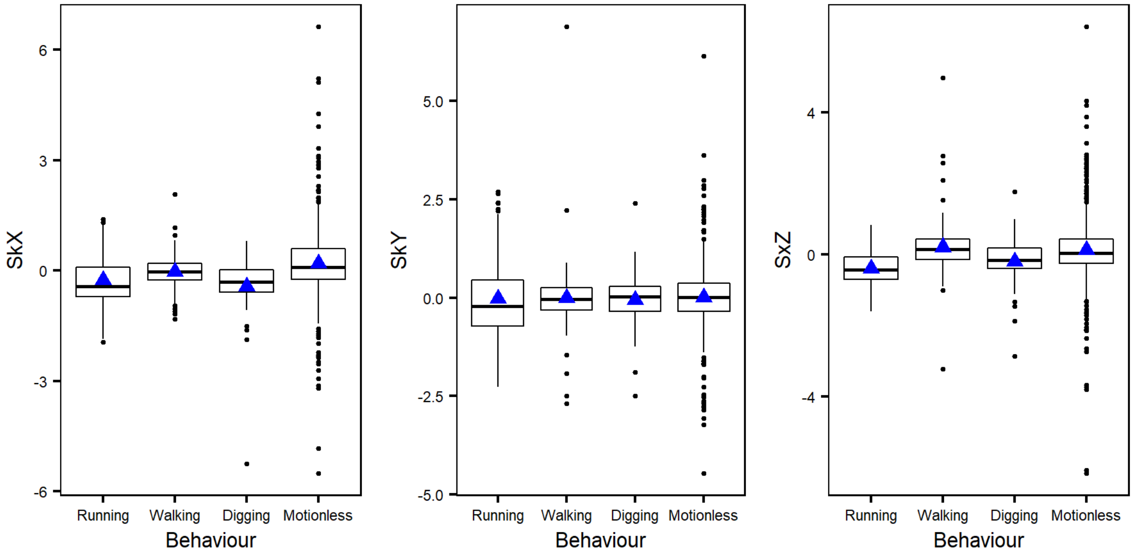
A. Mean



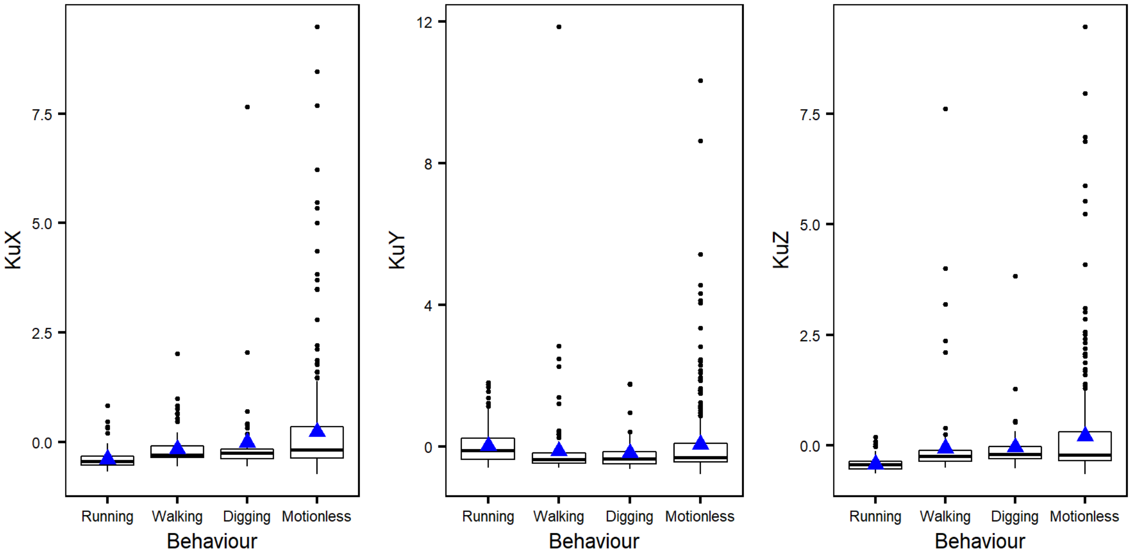
B. Standard deviation



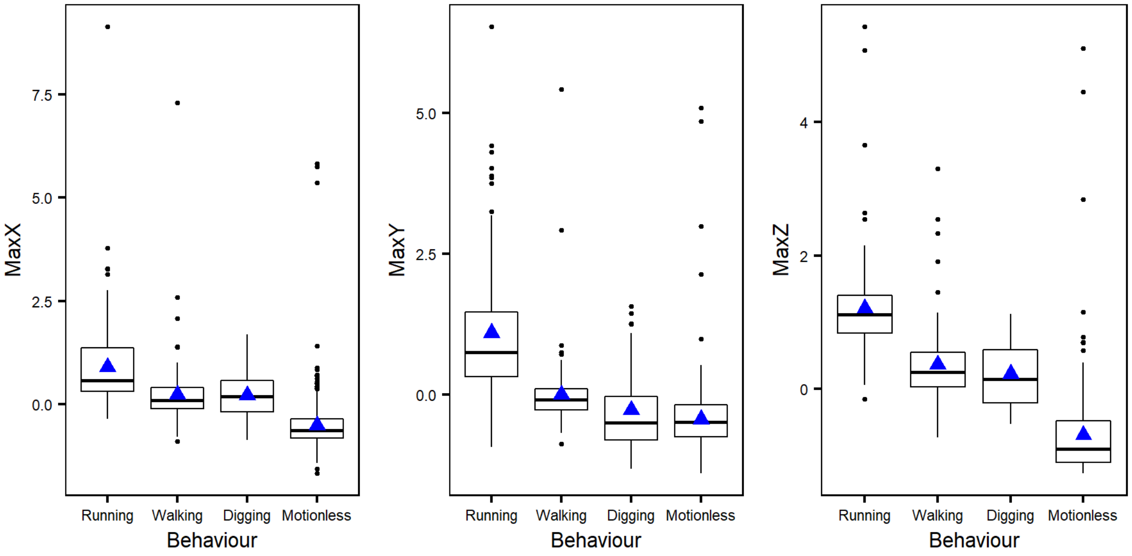
C. Skewness



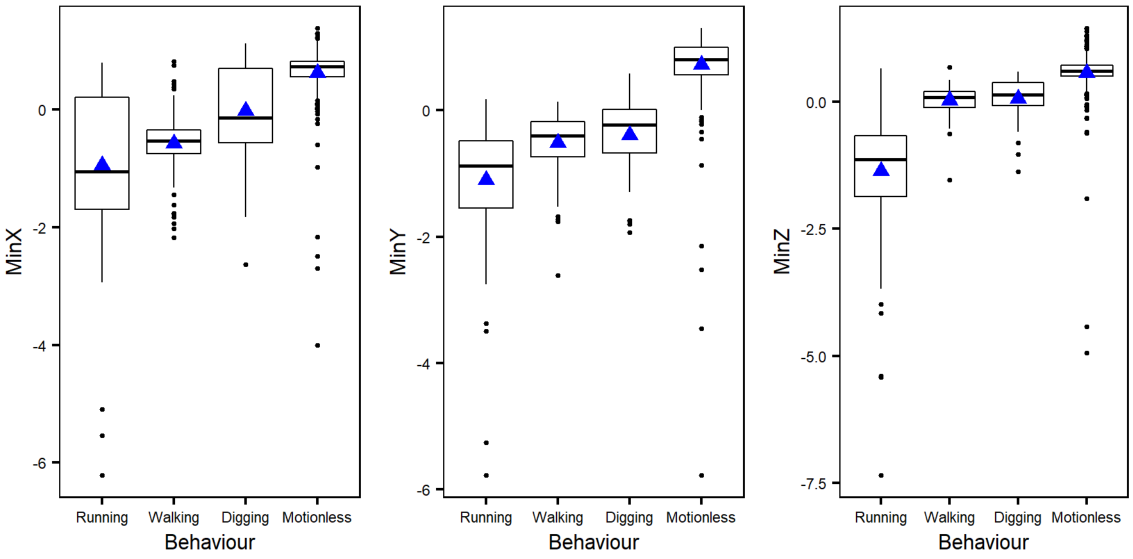
D. Kurtosis



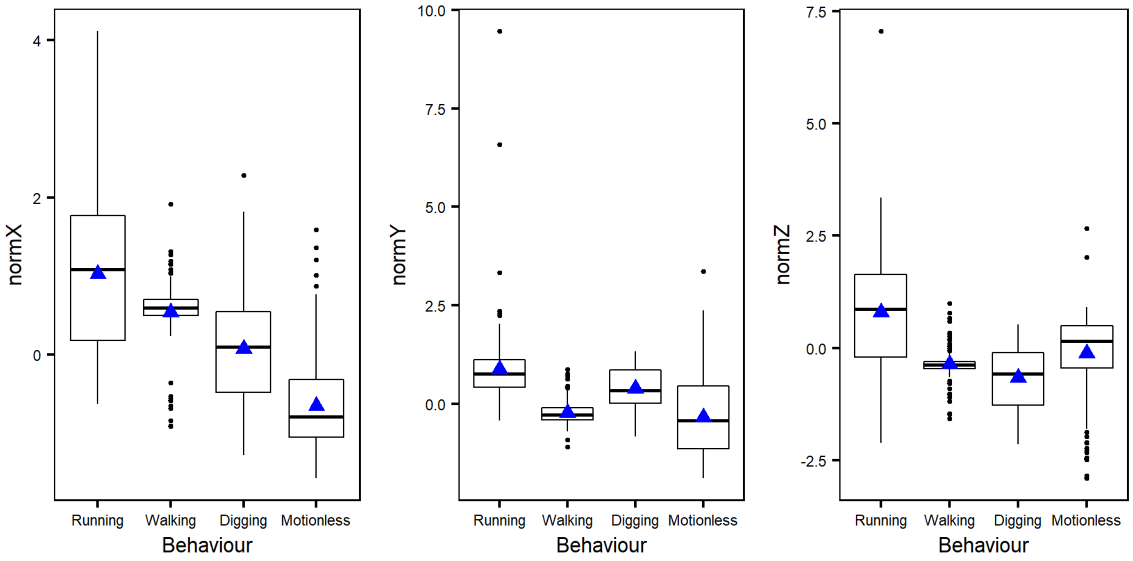
E. Maximum



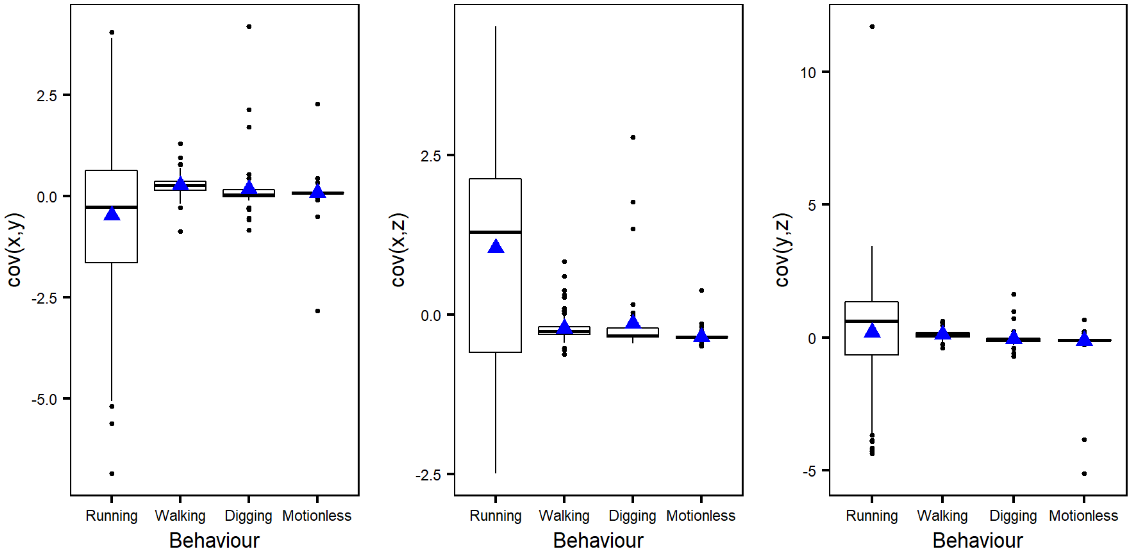
F. Minimum



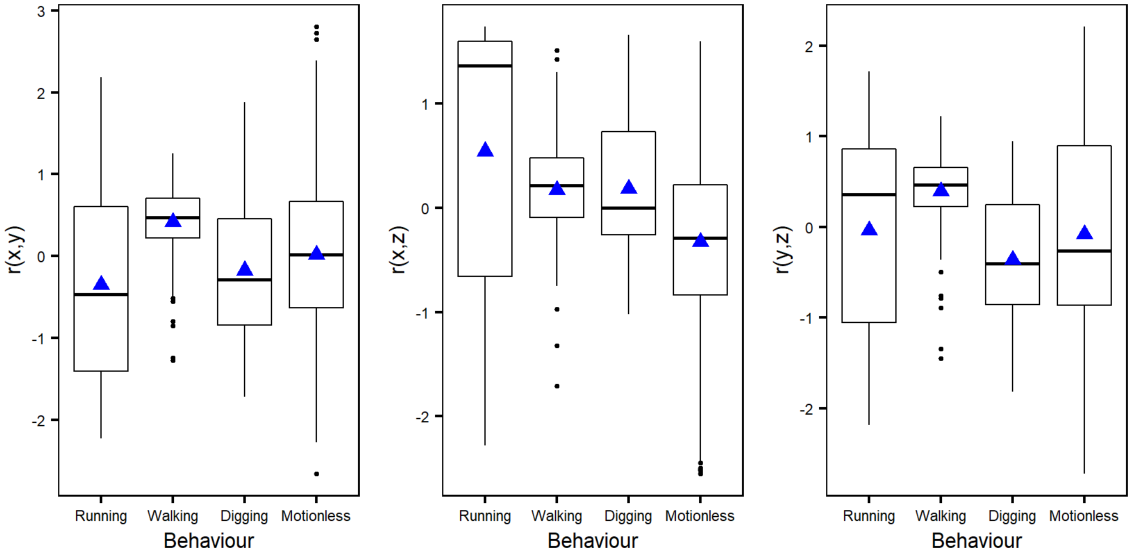
G. Norm



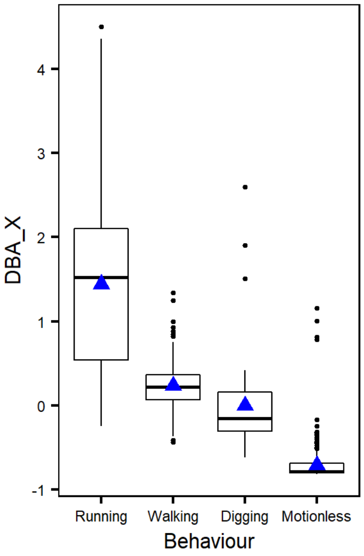
H. Cov

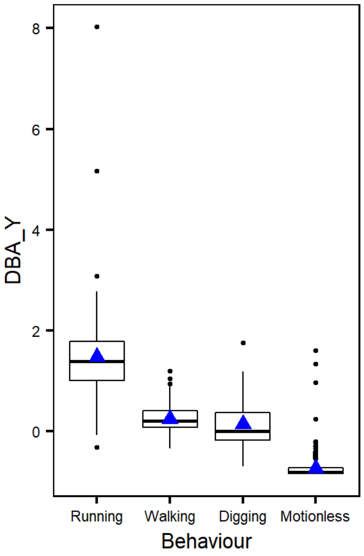

cov(x,y)
2.5
0.0
-2.5
-5.0
Running
Walking
Digging
Motionless
Behaviour
cov(x,z)
2.5
0.0
-2.5
Running
Walking
Digging
Motionless
Behaviour
cov(y,z)
10
5
0
-5
Running
Walking
Digging
Motionless
Behaviour

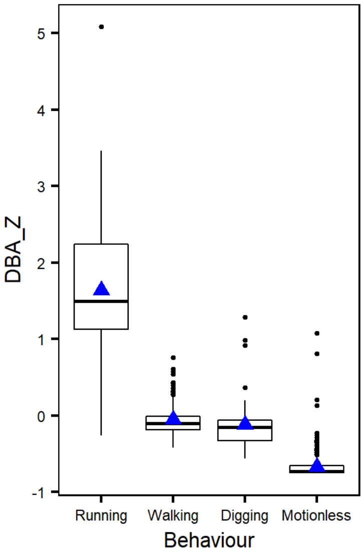
I. r


r(x,y)
3
2
1
0
-1
-2
Running
Walking
Digging
Motionless
Behaviour
r(x,z)
1
0
-1
-2
Running
Walking
Digging
Motionless
Behaviour
r(y,z)
2
1
0
-1
-2
Running
Walking
Digging
Motionless
Behaviour

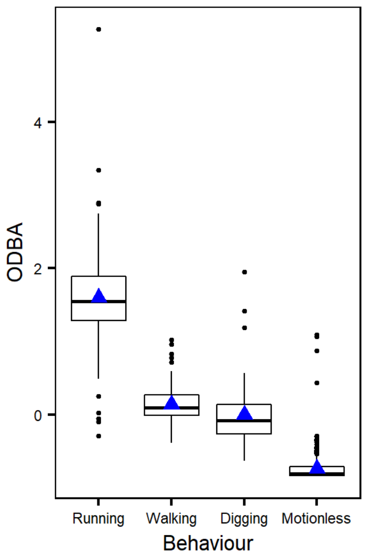
J. DBA


DBA_X
4
3
2
1
0
-1
Running
Walking
Digging
Motionless
Behaviour

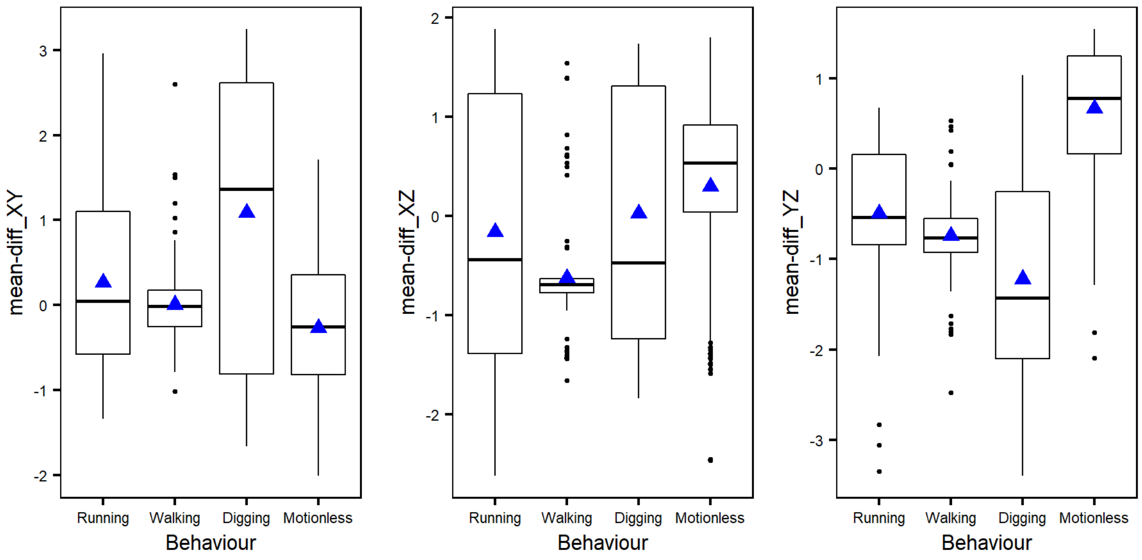

DBA_Y
8
6
4
2
0
Running
Walking
Digging
Motionless
Behaviour


DBA_Z
5
4
3
2
1
0
-1
Running
Walking
Digging
Motionless
Behaviour

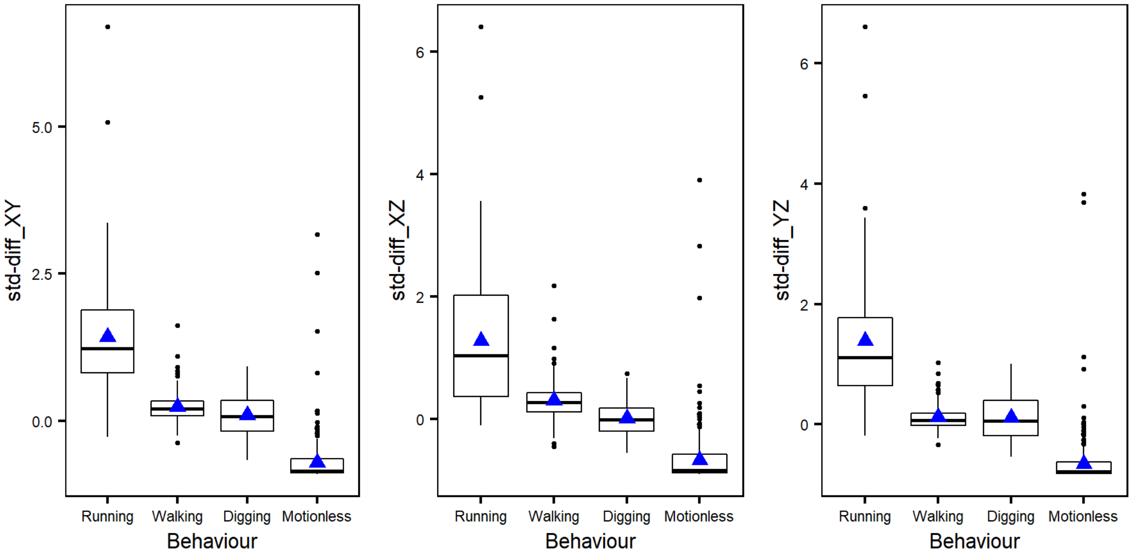
K. ODBA



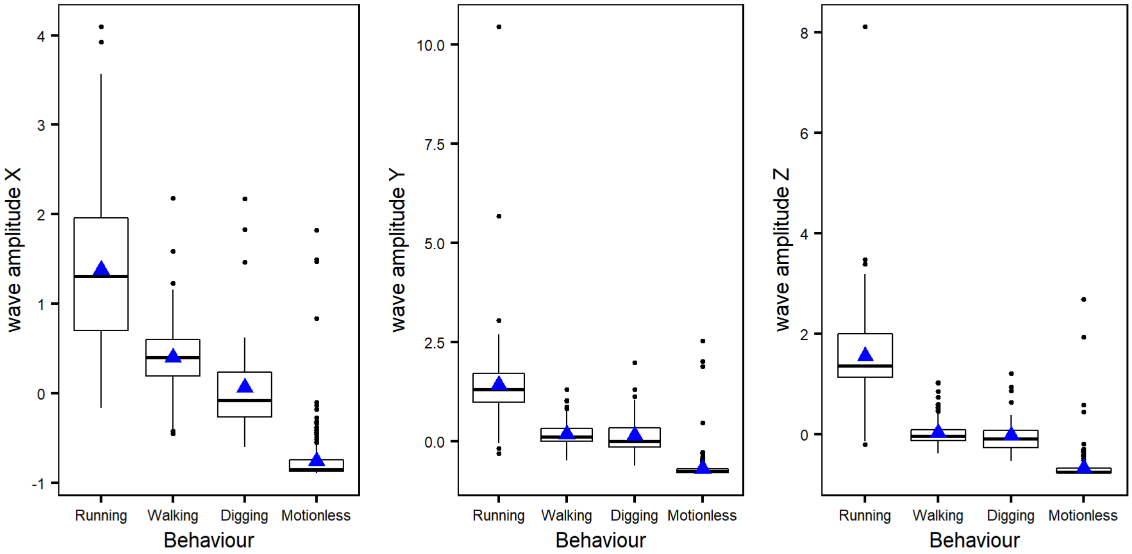
L. Mean difference



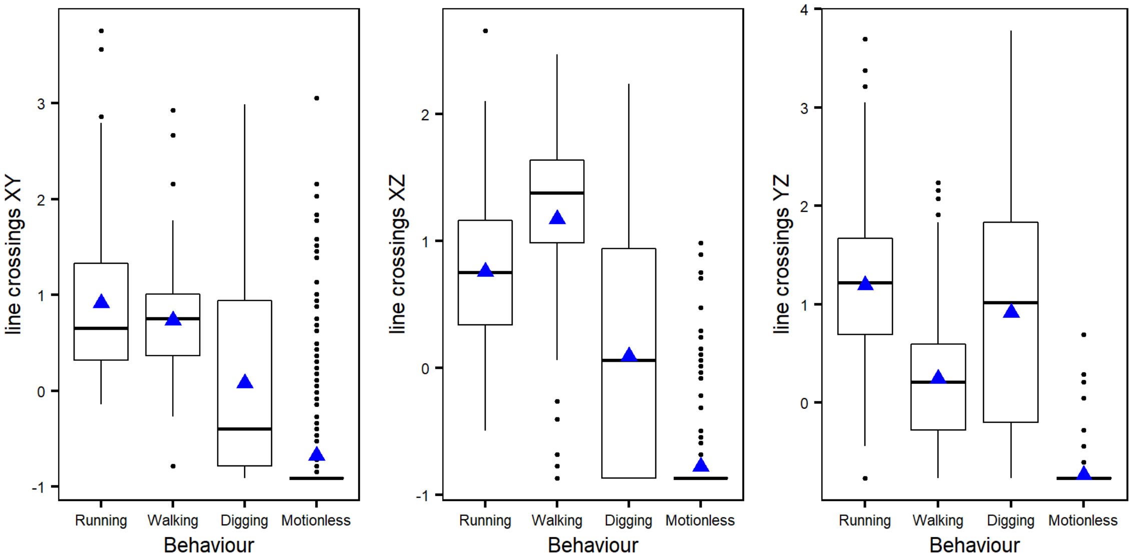
M. Standard deviation difference



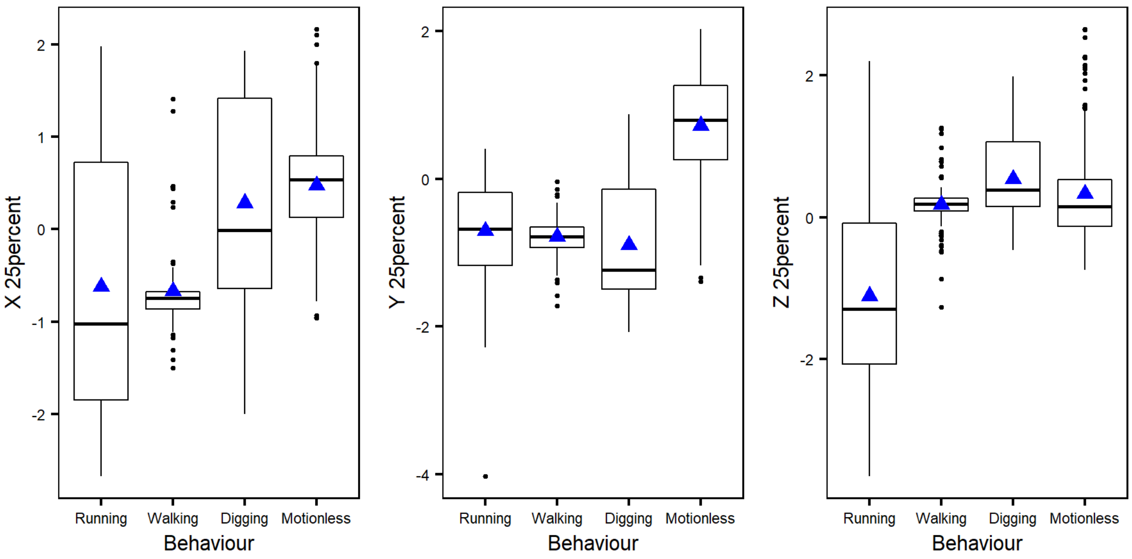
N. Wave amplitude



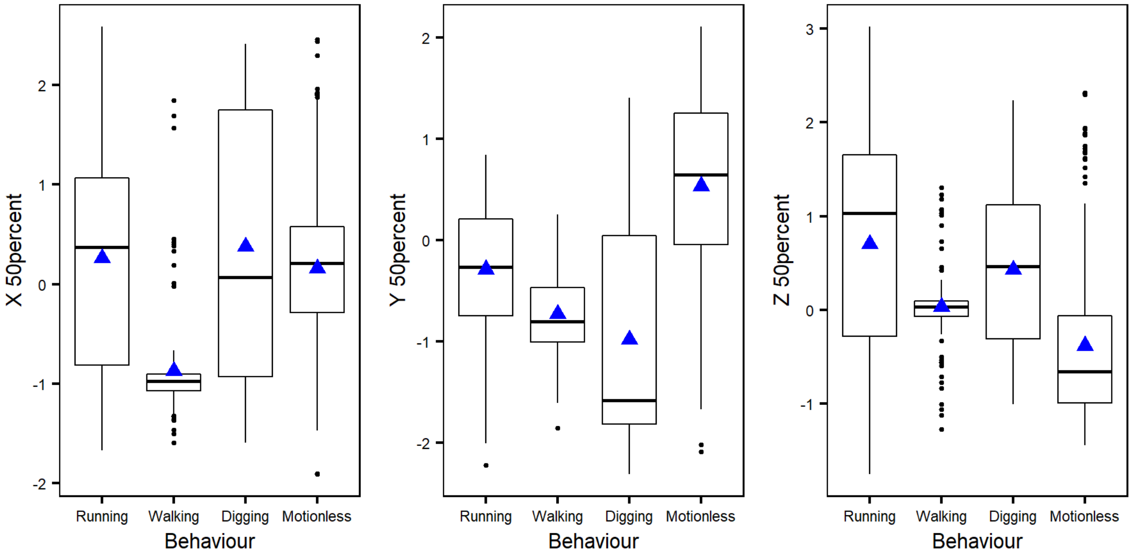
O. Line crossings



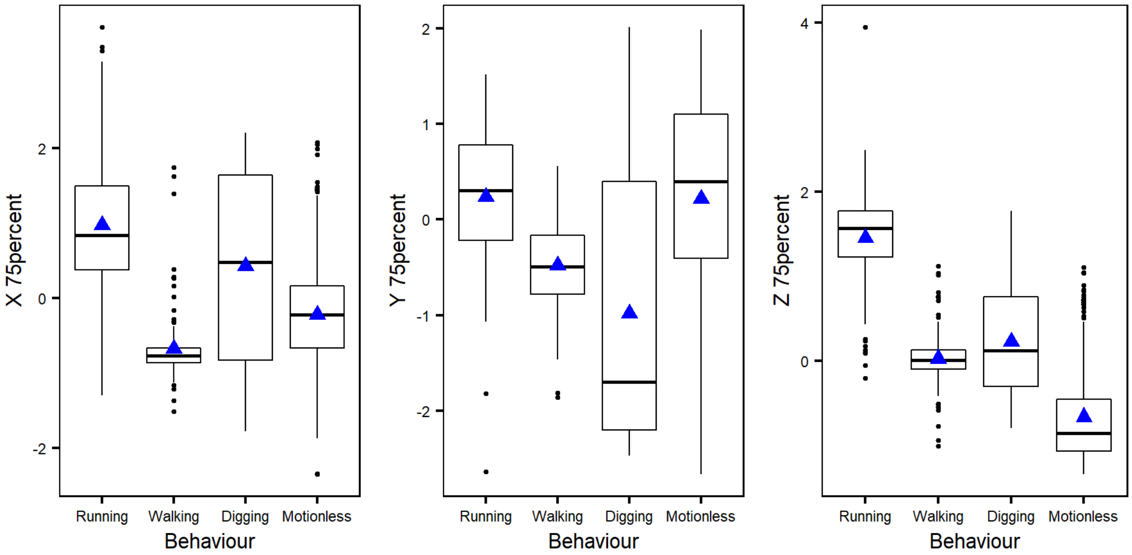
P. 25 percentile



Q. 50 percentile



R. 75 percentile



CHAPITRE III

TERRITORIALITY MODULATES THE EFFECT OF CONSPECIFIC ENCOUNTERS ON THE FORAGING BEHAVIOURS OF A MAMMALIAN PREDATOR

Jeanne Clermont, Frédéric Dulude-de Broin, Marie-Pier Poulin & Dominique Berteaux

Manuscrit en préparation pour publication.

3.1 Résumé

La probabilité de rencontrer un conspécifique, c'est-à-dire qu'un individu se retrouve à la même place et au même moment qu'un autre individu de son espèce, influence de multiples dimensions des comportements animaux. Par exemple, les individus territoriaux augmentent leur vigilance, leur taux de marquage et d'émission de cris d'alarme lorsqu'ils se rapprochent des frontières de leur domaine vital. Cependant, on ne sait toujours pas si les prédateurs modifient leurs comportements de prédation en fonction de la probabilité de rencontrer un voisin. Pourtant, ceci pourrait fortement influencer la répartition du risque de prédation et ainsi moduler les interactions prédateurs-proies. Nous avons étudié les mouvements et comportements de 13 renards arctiques résidents, qui occupaient des domaines vitaux voisins en 2019 à l'île Bylot, Nunavut, Canada. Grâce au suivi GPS simultané des individus, nous avons estimé la répartition spatiale des probabilités de rencontre entre voisins. Nous avons d'abord déterminé si les individus occupaient un territoire (un espace exclusif) en évaluant la répartition des probabilités de rencontre avec un voisin dans les domaines vitaux. Seulement les individus plus âgés et reproducteurs ont exclu les autres renards d'une partie de leur domaine vital et pouvaient donc être considérés comme territoriaux. En utilisant les données GPS et d'accélérométrie pour identifier les évènements de recherche et de cache de nourriture, nous avons ensuite évalué comment la probabilité de rencontrer un voisin influence la répartition spatiale des comportements de prédation, et si cette relation diffère entre les individus territoriaux et non territoriaux. Nous avons trouvé que seulement les individus non territoriaux répondent à la variation dans la probabilité de rencontrer un voisin dans leur domaine vital. Ils étaient moins actifs dans les endroits où la probabilité de rencontre était grande, suggérant qu'ils recherchent leurs proies moins intensément et sont plus vigilants dans ces zones. Les individus non territoriaux faisaient également moins de caches de proies dans les zones où la probabilité de rencontre était grande, diminuant possiblement le risque de chapardage des caches. Nos résultats suggèrent que les individus territoriaux et non territoriaux utilisent différentes tactiques pour sécuriser des ressources, les non territoriaux ajustant leurs comportements de prédation à la probabilité de rencontrer un voisin. Finalement, nous soulignons comment la présence d'individus résidents mais non territoriaux, dont les domaines vitaux chevauchent ceux de leurs voisins territoriaux, pourrait influencer la répartition du risque de prédation en créant des zones ou la densité de prédateurs est plus élevée, ce qui pourrait ultimement influencer les interactions prédateurs-proies.

Mots clés : domaine vital, interaction intraspécifique, mouvement, prédation, recherche de nourriture, rencontre, territorialité, utilisation de l’espace, *Vulpes lagopus*

3.2 Abstract

The probability of encountering conspecifics, that is being at the same place at the same time as other individuals of the same species, shapes multiple dimensions of animal behaviour. For example, territorial individuals increase vigilance, scent marking and alarm calling when approaching home range boundaries. Whether territorial predators modify their foraging behaviors with respect to the probability of encountering neighbouring territory owners is poorly understood. However, this could strongly influence the distribution of predation risk and therefore modulate predator-prey interactions. We studied the movements and behaviours of 13 resident Arctic foxes occupying neighbouring home ranges in 2019 on Bylot Island, Nunavut, Canada. Based on simultaneous GPS tracking of individuals, we estimated the spatial distribution of the probability of encounter among neighbours. We first established which individuals used a territory (an exclusive area) by looking at the distribution of the probability of encountering a neighbour within their home range. Only the oldest and reproductive individuals excluded other foxes from a part of their home range and could thus be considered territorial. Using GPS and accelerometry data to identify prey searching and caching events, we then evaluated if the probability of encountering a neighbour influenced the spatial distribution of foraging behaviours, and whether this relationship differed between territorial and non-territorial individuals. Only non-territorial individuals responded to variation in the probability of encountering a neighbour in their home range. They were less active in areas with a high probability of encounter, suggesting they searched prey less intensively and engaged in more vigilance in these areas. Non-territorial individuals also performed less prey caching in areas with a high probability of encounter, possibly reducing the risk of cache pilfering. Our results suggest that territorial and non-territorial Arctic foxes use different tactics to secure resources, the latter adjusting their foraging behaviours to the probability of encountering neighbours. Lastly, we highlight how the presence of resident, but non-territorial predators, whom home ranges overlap those of their territorial neighbours, may influence the distribution of predation risk by creating zones where predator density is high, potentially influencing predator-prey interactions.

Keywords: encounter, foraging, home range, intraspecific interactions, movement, predation, space use, territoriality, *Vulpes lagopus*

3.3 Background

The ability of animals to manage encounters with other individuals is key to all social and interspecific interactions, thus directly influencing reproduction, survival, and ultimately fitness (Silk et al., 2003; Cresswell, 2008; Wey et al., 2008). Consequently, many animal behaviours have evolved to modulate the probability of encountering other individuals. One well known example is how predators and prey modify their habitat use to either find or avoid each other (Sih, 1984; Smith et al., 2019a). Similarly, individuals may avoid conspecifics to decrease resource competition. Individuals may for example secure limited resources by becoming territorial, thus signalling space ownership and aggressing intruders (Sillero-Zubiri & Macdonald, 1998; Giuggioli et al., 2011; Tórrez-Herrera et al., 2020), given the benefits outweigh the costs (Maher & Lott, 2000; Ord, 2021). A territory represents the area of a home range that is successfully defended by one or several individuals, resulting in the territory owners having exclusive access to the defended area (Brown & Orians, 1970; Powell, 2000; Hinsch & Komdeur, 2017).

The intensity of territoriality is often assessed by measuring the amount of overlapping area between neighbouring home ranges (Persson et al., 2010), or the frequency to which individuals adopt territorial behaviours such as scent marking (Fawcett et al., 2013). Furthermore, the degree to which individuals of a given species are territorial can vary among and within populations (Macdonald et al., 1999; McLoughlin et al., 2000; Eide et al., 2004). Ecological variables such as the abundance, predictability and distribution of food resources influence the costs and benefits of territoriality, and therefore partly explain the degree of territoriality (Maher & Lott, 2000; Sells & Mitchell, 2020). Notably, a cost-benefit model developed by Maher and Lott (2000) suggests that individuals should be territorial when food abundance and predictability are intermediate, but non-territorial when food abundance and predictability are below or above some thresholds, which was supported by McLoughlin et al. (2000) who studied variation in home range overlap across brown bear (*Ursus arctos*) populations. Costs and benefits of territoriality may also vary according to predator and competitor densities (Maher & Lott, 2000; Webber et al., 2023), individual characteristics such as sex (Rosell & Thomsen, 2006; Fawcett et al., 2013), or other variables such as the degree of relatedness among neighbours (Persson et al., 2010; Humphries et al., 2021).

The probability of encountering neighbours varies spatially in the home range of territorial animals, being higher near boundaries. Where the probability of encountering a competitor is high, individuals should modify their behaviour to avoid potentially costly physical encounters while still signaling territory ownership more intensively (Schlägel et al., 2017). For example, when located near boundaries, white-faced capuchins (*Cebus capucinus*), which defend group territories, tend to socialise less with each other (Tórrez-Herrera et al., 2020) and travel at lower speed (Noonan et al., 2021), suggesting more vigilance. Also, Ethiopian wolves (*Canis simensis*) and grey wolves (*Canis lupus*) increase scent-marking near boundaries (Sillero-Zubiri & Macdonald, 1998; Zub et al., 2003), while red foxes (*Vulpes vulpes*) spend more time patrolling where artificial scent marks are deposited (Arnold et al., 2011). The probability of encountering neighbours may further affect behaviours not linked to territory defence, such as foraging. For example, in food caching animals that are territorial, such as many canids, felids and mustelids, it may be beneficial to cache food away from competitors to reduce cache pilfering (van der Veen et al., 2020).

Identifying the determinants of foraging patterns is particularly important for predators, as they generate predation risk landscapes that influence the dynamics of prey populations and the functioning of communities (Lima, 2002; Gaynor et al., 2019; Clermont et al., 2021a). The probability of encounter among neighbours of a territorial predator may indeed strongly affect space use. For example, in systems where the predator is highly territorial and avoids encountering conspecifics, buffer zones between territories may serve as refuge for prey. For example, Lewis and Murray (1993) mathematically showed that predation risk is reduced in areas between wolf pack territories, where white-tailed deer (*Odocoileus virginianus*) were indeed found to be more abundant (Mech, 1977). Anderson et al. (2005) further found that reintroduced elks (*Cervus elaphus*) established their home ranges in the periphery of wolf territories and selected areas within their home ranges that were further from wolf territory centers. In contrast, if predator territoriality is low and home ranges are small, the risk of predation could be increased where home ranges overlap and predator density is highest, but this remains to be tested. Better understanding how intraspecific interactions and territoriality shape the distribution of predator foraging, and thus predation risk, would also better inform predator-prey interactions.

Modern tracking techniques can locate animals at high frequencies while producing detailed behavioural classification (Nathan et al., 2012; Wilmers et al., 2015). For example, activity level can be identified using GPS data (Patterson et al., 2017), and scent marking (Bidder et al., 2020), killing of prey (Studd et al., 2021) and food caching (Clermont et al., 2021b) may be identified using accelerometry. Estimating where encounters between individuals occur is challenging, however, limiting our ability to assess how such probabilities of encounter affect behaviours (Noonan et al., 2021). So far, most research has compared how animal behave in and out of overlapping areas or with respect to the distance to territory borders (assuming these variables are good surrogates for encounter probability), instead of directly estimating the spatial distribution of encounter probabilities (Rosell & Thomsen, 2006; Tórrez-Herrera et al., 2020). To address this methodological gap, Noonan et al. (2021) recently proposed a statistical framework using tracking data and home range estimation to evaluate the spatial distribution of the probability of encounter, termed the conditional distribution of encounters. Combining behavioural classifications to an estimation of where encounters are most likely to occur should allow to better understand how interactions with neighbours affect behaviours of territorial animals, further improving our understanding of important ecological processes.

We used GPS tracking and accelerometry to monitor the movements and behaviours of Arctic foxes living in a large Greater snow goose (*Anser caerulescens atlanticus*) colony on Bylot Island (Nunavut, Canada) (Clermont et al., 2021a, 2021b). At this site, foxes are socially monogamous, offer biparental care, and most home ranges are occupied by a mated pair (Cameron et al., 2011). Our first objective was to quantify among-individual differences in the degree of territoriality, by mapping the probability of encountering foxes other than the mate within the home range. Our second objective was to test the hypothesis that the probability of encountering a neighbour influences the spatial distribution of foraging behaviours within home ranges, including prey searching and prey caching. We predicted (P1) that foxes should spend less time searching prey in areas associated to a high probability of encounter with neighbours to avoid costly encounters that may lead to the loss of foraging opportunities or even aggressive interactions. As Arctic foxes may perform cache pilfering (Samelius & Alisauskas, 2000; Careau et al., 2007), we also predicted (P2) that foxes should avoid caching prey where the probability of encountering a neighbour, and thus the risk of cache pilfering, is high. A third objective was to test the hypothesis that the relationship between the probability of encountering a neighbour and the spatial distribution of foraging behaviours differs between territorial and non-territorial foxes. We predicted (P3) that the effect of the probability of encountering a neighbour on the spatial distribution of foraging behaviours should be more important in non-territorial than in territorial foxes, since the latter individuals are free from encounters in large fractions of their home range.

3.4 Methods

3.4.1 Study system

We worked in 2019 in the southwest plain of Bylot Island (72°53′ N, 79°54′ W) in Sirmilik National Park of Canada (Nunavut), where the Arctic fox is the main terrestrial predator. Arctic foxes at this site are highly range resident (i.e., they use a stable home range), and most individuals show low home range overlap with their neighbours (Grenier-Potvin et al., 2021). They bark and scent mark to indicate territory ownership, and they chase intruders (Eberhardt et al., 1982). In addition to selecting habitats suitable to their main prey, they avoid home range borders, potentially to minimise interactions with their neighbours (Grenier-Potvin et al., 2021).

On Bylot, Arctic foxes rely mostly on small prey, such as lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*). They also feed on the eggs of the greater snow goose when their home range overlaps Bylot's large colony of more than 20,000 nesting pairs (Bêty et al., 2001). They also opportunistically prey on the nests of other ground nesting birds (Duchesne et al., 2021). Lemming density fluctuates cyclically (Gruyer et al., 2008), and was moderate in 2019 as determined by capture-recapture methods (Fauteux et al., 2015; Duchesne et al., 2021). The snow goose incubation period lasts 23 days from mid-June to early July, during which foxes collect eggs for later consumption (Samelius et al., 2007). In years of low to moderate lemming densities, goose eggs represent the majority of prey collected by foxes during the goose incubation period (Careau et al., 2007). Foxes cache up to 90% of the goose eggs they collect, and caches are located 85 m (median) from the nest (Careau et al., 2007). They also recache ca. 60% of the goose eggs, and recovery rate (for recaching or consumption) is highest at the end and after the goose incubation period (Careau et al., 2008b). Furthermore, access to the snow goose colony influences fox probability of reproduction (Chevallier et al., 2020). Despite interindividual variation, the phenology of fox reproduction largely coincides with that of geese, with cubs remaining in the den during the goose egg incubation period, and progressively emerging and becoming independent from the den during goose brooding (Grenier-Potvin et al., 2021).

3.4.2 Arctic fox tracking

In May and June 2019, 13 foxes were captured in the snow goose colony using Softcatch #1 padded leghold traps (Oneida Victor Inc. Ltd., Cleveland, OH, USA). During each capture, we determined the individual's sex from genitalia characteristics, took pictures of full dentition to estimate age from visual analysis of tooth wear (Chevallier et al., 2017), and fitted the individual with 4 coloured-ear tags and a GPS-accelerometer collar (95 g, ca. 4% of body mass; Radio Tag-14, Milsar, Romania) for subsequent identification and tracking. The 13 foxes consisted of 6 neighbouring pairs plus one individual, and their home ranges formed our study area (Figure 3.1). We determined reproductive status of each individual based on whether automated cameras recorded cubs at the individual's den (Cameron et al., 2011). Daily observations and automated cameras at fox dens also showed that we tracked all foxes using the study area. We collected one GPS location every 4 minutes and one 30-sec burst of accelerometry (50 Hz) every 4.5 minutes (Clermont et al., 2021b). The 30-sec bursts of accelerometry were divided into ten 3-sec sequences and, using a random forest algorithm, we associated each sequence to one of four behaviours: Running, Walking, Digging and Motionless (see analytical details in Clermont et al., 2021b). During the goose incubation period, digging behaviour of foxes is mainly associated with goose egg caching (Clermont et al., 2021b).

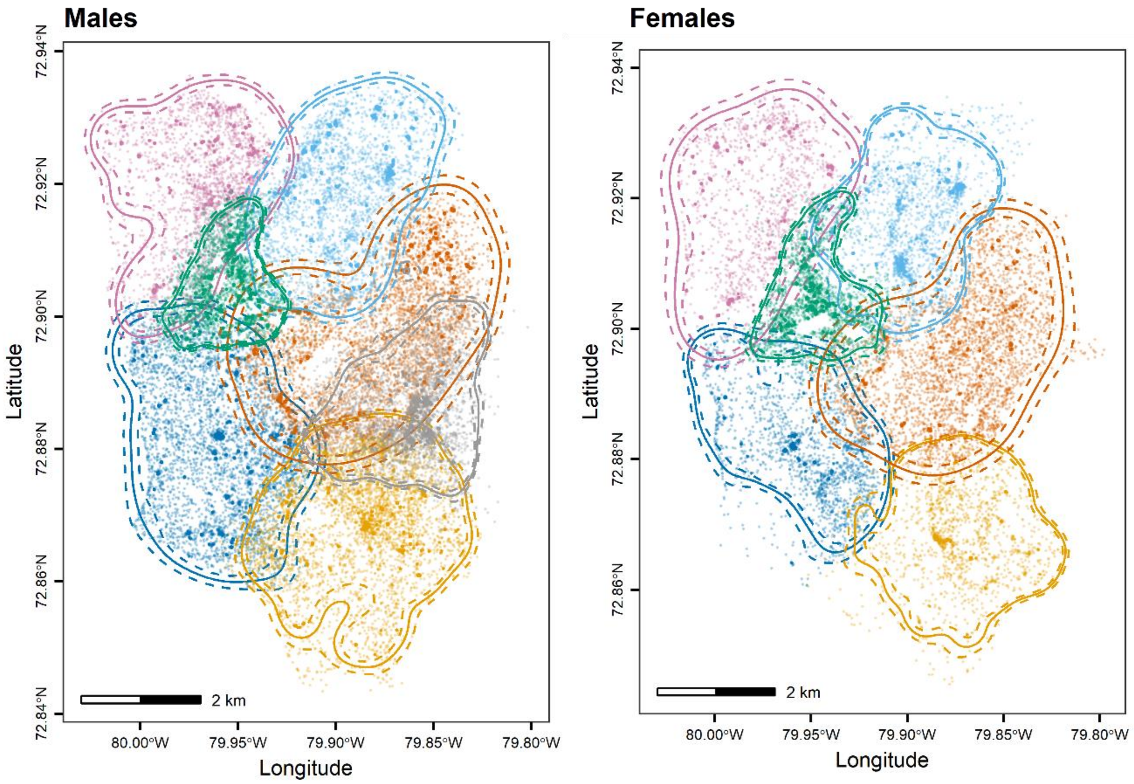


Figure 3. 1 GPS locations (dots) of 13 Arctic foxes (left: males, right: females) tracked from June 12th to July 4th 2019 on Bylot Island, Nunavut, Canada. GPS data (n = 67,109) were obtained using a 4-min fix interval. Solid lines are 95% home range contours obtained through auto-correlated kernel density estimation and dashed lines are 95% confidence intervals. The same colours are used across panels for members of a given fox pair.

3.4.3 Data analysis

1) Estimation of homes ranges

We used GPS data collected from June 12th to July 4th 2019, corresponding to the goose egg incubation period in 2019, to define Arctic fox summer home ranges. Prior to home range estimation, we confirmed home range residency for each individual using variogram analysis (Fleming et al., 2014), and excluded location data resulting from extra-territorial trips as it affects home range estimation (Calabrese et al., 2016). Indeed, during the study period, some individuals made a few extra-territorial trips going up to 15 km away from the center of the home range. These "outliers" were identified by evaluating distances between points and home range core, and a cut-off distance was determined visually for each individual (see Appendix A for further details). We excluded 9%, 6% and 4% of datapoints for three individuals that performed extra-territorial trips. The remaining 10 individuals showed high range residency and we excluded < 1% of their GPS locations.

We then fitted range-resident continuous-time movement models to the data of each individual (model selection resulted in the Ornstein-Uhlenbeck Foraging (OUF) process used for each individual), to control for autocorrelation in both speed and location (Fleming et al., 2014; Calabrese et al., 2016). Then, we estimated home range areas using auto-correlated kernel density estimation (AKDE; Fleming et al., 2015). AKDE performs better and is more accurate than other home range estimators for autocorrelated location data, and also allows to measure uncertainty in home range estimations (Noonan et al., 2019). The complete workflow we used is detailed in Silva et al. (2021), and was performed using the package ctmm (version 0.6.2, Calabrese et al., 2016) in R 4.1.0 (R Development Core Team, 2021).

2) Estimation of probability of encounter among neighbours

Following Noonan et al. (2021), we then estimated the conditional distribution of encounters (CDE) from tracking data and AKDE home range estimates, using the package ctmm. In short, the CDE estimates the spatial distribution of the probability of encounter between individuals based on their occurrence distribution. Since we were interested in encounters among neighbours, we excluded interactions between mates within their shared home range.

Therefore, the CDE is an estimation of the distribution of the probability that neighbours encounter each other. A CDE value of 1 indicates that neighbours should always be in contact with each other at that location, and a value of 0 that neighbours should never encounter each other at that location. We then determined the degree of territoriality of each fox (objective 1) through a visual analysis of the distribution of the probability of encounter within each home range (Figures 3.2 and 3.3). Individuals were classified as territorial if the probability of encountering a fox other than their mate was null in a portion of their home range.

3) Arctic fox foraging behaviours: prey searching and prey caching

The Arctic fox is a cursorial, active hunting predator for which most active periods are associated with prey searching (Schmitz et al., 2004; Poulin et al., 2021). We therefore determined whether foxes were searching prey by assigning to each GPS location an active or inactive state. To do so we fitted a hidden Markov model (HMM) using the R package moveHMM (version 1.7, Michelot et al., 2016). The active state is characterised by long step lengths and small turning angles, and the inactive state by short step lengths and large turning angles. HMM construction and model selection are detailed in Grenier-Potvin et al., 2021). HMM behavioural states were well correlated with an accelerometry behavioural classification, where the active state was mostly associated with running sequences, and the inactive state with motionless sequences (Appendix B).

We described how to identify prey caching events in Clermont et al. (2021b). We used the accelerometry classification described above to determine whether individuals engaged in digging during each 30-sec accelerometry burst. At least one out of the ten 3-sec accelerometry sequences had to be assigned to the Digging behaviour to consider that the fox engaged in digging in that burst. Each 30-sec burst was then associated to the closest GPS location, provided the time stamp of the GPS location was within 30 sec of the start or end of the burst. Bursts occurring at less than 50 m of a den were excluded as digging may then reflect den maintenance.

We excluded from analyses all GPS locations or accelerometry bursts occurring within 500 m of the study area boundary, since interactions with unknown foxes may occur at the edge of the study area (details in Appendix C), leading to an underestimation of CDE. We repeated our analyses using a 1 km buffer to ensure that buffer size did not affect results (Appendix D).

4) Effect of the probability of encountering a neighbour on fox behaviours

To test P1 and P2 (objective 2), we used generalised linear mixed models (R package lme4, version 1.1-27.1, Bates et al., 2015) with a binomial distribution to model fox probability of being active (P1) and engaging in digging (P2) with respect to the probability of encountering a neighbour. We used a logit link function for the model with fox activity (0 = inactive, 1 = active) as the response variable, and a cloglog-link function for the model with digging (0 = no digging, 1= digging) as the response variable. As not all foxes experienced the same range of probability of encounter (see Results), we centered the probability of encounter values to a mean of 0 within each fox home range. We added to the models a categorical variable representing whether the fox was territorial (yes/no), which we included in interaction with the probability of encountering a neighbour, to test P3 (objective 3). In both models, we also controlled for nesting goose density (individual geese/ha, a proxy for nest density estimated from detailed field surveys, Grenier-Potvin et al., 2021), as it affects fox habitat selection during active and inactive periods (Grenier-Potvin et al., 2021) and fox probability to dig (Clermont et al., 2021b). We included as random effects the ID of the fox and the ID of the pair. Pair ID however led to a singular fit (variance estimated at zero, Bolker et al., 2009) for probability of being active and was thus excluded from the model. All continuous covariates were centered and standardised to facilitate the interpretation of model estimates (Schielzeth, 2010). We validated model assumptions and independence of residuals using the R package DHARMa (version 0.4.3, Hartig, 2021). We initially found autocorrelation among the residuals of both models when using the complete dataset. Therefore, we ensured our results were robust and solved autocorrelation issues by fitting models on 10 different subsamples of our dataset. For both probability of being active and probability of digging, subsamples were composed of 6 daily observations (either GPS locations or accelerometry bursts) by individual (Appendix D). Results are expressed using an evidence-based language following Muff et al. (2021).

3.5 Results

3.5.1 The degree of territoriality varies across foxes

Home range areas averaged 9.03 ± 3.12 (SD) km^2 (Figure 3.1). We found no evidence that home ranges differed between sexes within pairs (paired t-test: $t = 1.85$, $p = 0.12$, average male home range area = 9.41 ± 3.52 (SD) km^2, average female home range area = 8.58 ± 2.83 (SD) km^2, for 6 Arctic fox pairs). The resulting CDE shows areas where neighbours have a higher probability of encountering each other, and as expected higher CDE values occur where home ranges of tracked neighbours overlap (Figure 3.2). The CDE distribution differs among home ranges, with three individuals (green and grey) having overall high probabilities of encounter with neighbours within their home range, with no or virtually no part of their home range with a null probability of encountering a neighbour (Figure 3.3). On the contrary, all other 10 individuals used a territory, having a considerable area in their home range where the probability of encounter with a neighbour is null (Figures 3.2, 3.3). Some interactions inevitably occurred at home range boundaries located at the edge of the study area (Figure 3.10, Appendix C), where neighbouring foxes were not tracked, but the limited size of these areas compared to the size of home ranges ensured that identification of territorial and non-territorial foxes was robust.

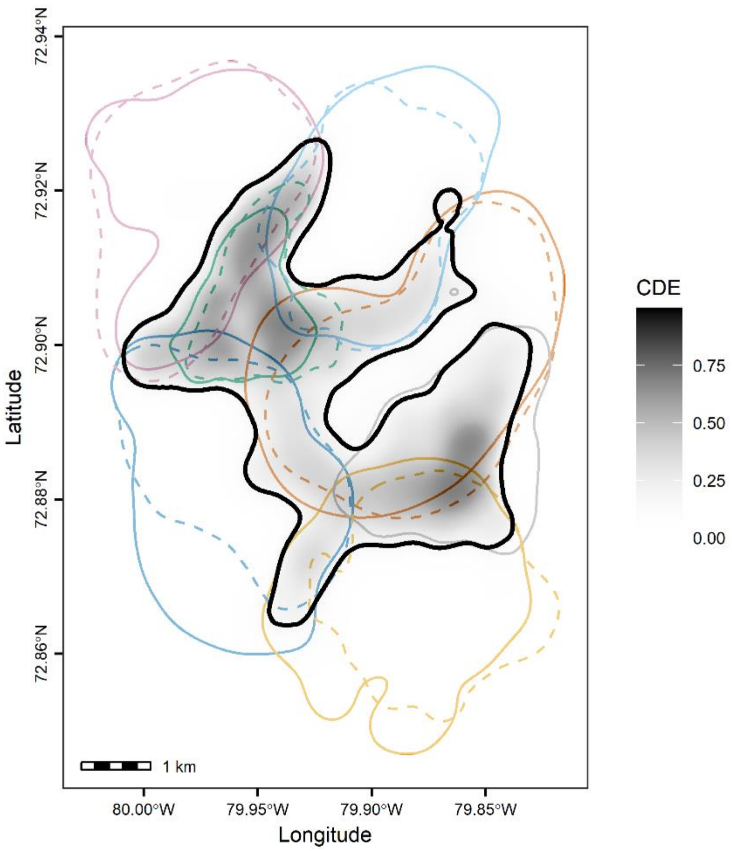


Figure 3. 2 Conditional distribution of encounters (CDE) among 13 Arctic fox neighbours tracked with GPS, excluding interactions between pair members. The thick black line is the 95% CDE contour and coloured lines are 95% AKDE contours. Males and females are represented by solid and dashed lines, respectively, and members of a given pair are identified by the same colour. Confidence intervals are not shown.

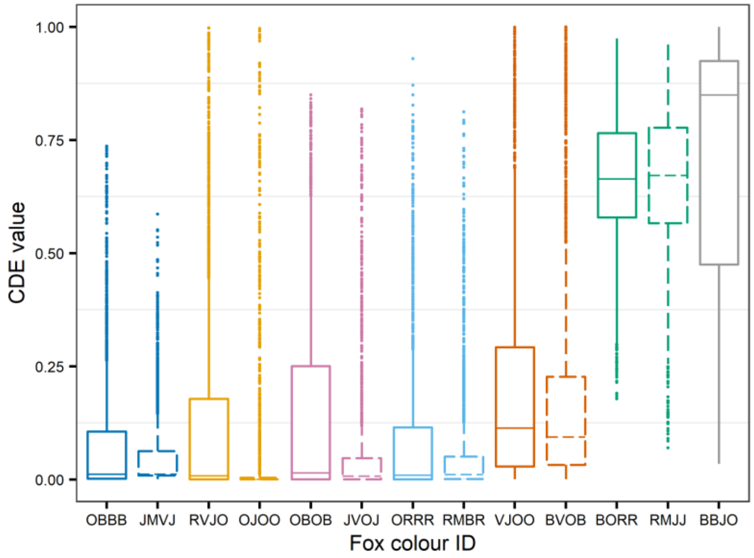


Figure 3. 3 CDE values (probability of encountering a neighbour) observed at each GPS location from Figure 3.1 (n = 67,109), for each fox. Fox IDs reflect the unique combinations of colours of the 4 ear tags (e.g., OBBB: orange-blue-blue-blue). Boxplot colours used for each individual are the same as in Figures 3.1 and 3.2. Males and females are represented by solid and dashed lines, respectively, and members of a given pair are identified by the same colour. Boxplots show first quartile, median, and third quartile. Lower and upper whiskers extend, respectively, to the lowest and highest values within the interquartile range multiplied by 1.5. Points represent values outside this range.

3.5.2 The probability of encountering a neighbour affects fox behaviour only when they are not territorial

We found strong evidence that non-territorial foxes (individuals in green and grey in Figures 3.1 to 3.3) were more active and engaged in more digging where they were less likely to encounter a neighbour, thus supporting P1 and P2 (Table 3.1; Figure 3.4). On the contrary, we found no evidence that territorial foxes modified their level of activity and propensity to dig with changes in the probability of encounter, contradicting P1 and P2 (Table 3.1; Figure 3.4). In good agreement with P3, we found strong evidence that the probability of encountering a neighbour constrains fox behaviour differently whether they were territorial or not, as shown by p values of interaction terms in Table 3.1. We also found that nesting goose density had a positive effect on the level of activity and propensity to dig of foxes

(Table 3.1). Repeating models on different subsamples of the dataset or after excluding locations within 1 km of the study area boundary did not change the results (Appendix D).

Table 3. 1 Results of generalised mixed models predicting A. probability of fox being active (n = 1,368 GPS locations) and B. probability of fox digging (n = 1,218 accelerometry bursts), using a binomial distribution with logit-link and cloglog-link functions, respectively. Bolded characters indicate coefficients with 95% confidence intervals that do not overlap 0.

A. Probability of fox being active

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	0.20	-0.03	0.44	0.11	1.80	0.07
Probability of encountering a neighbour	0.11	-0.06	0.29	0.09	1.24	0.21
Territorial yes/no [no]	-0.05	-0.56	0.44	0.24	-0.23	0.82
Goose nest density	**0.50**	**0.37**	**0.64**	**0.07**	**7.17**	**<0.001**
Prob encounter: Territorial yes/no [no]	**-0.73**	**-1.03**	**-0.45**	**0.15**	**-4.95**	**<0.001**

B. Probability of fox digging

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	**-1.11**	**-1.54**	**-0.71**	**0.18**	**-6.11**	**<0.001**
Probability of encountering a neighbour	0.03	-0.11	0.17	0.07	0.45	0.653
Territorial yes/no [no]	-0.24	-1.04	0.62	0.38	-0.63	0.531
Goose nest density	**0.21**	**0.10**	**0.32**	**0.06**	**3.79**	**<0.001**
Prob encounter: Territorial yes/no [no]	**-0.38**	**-0.67**	**-0.09**	**0.15**	**-2.62**	**0.009**

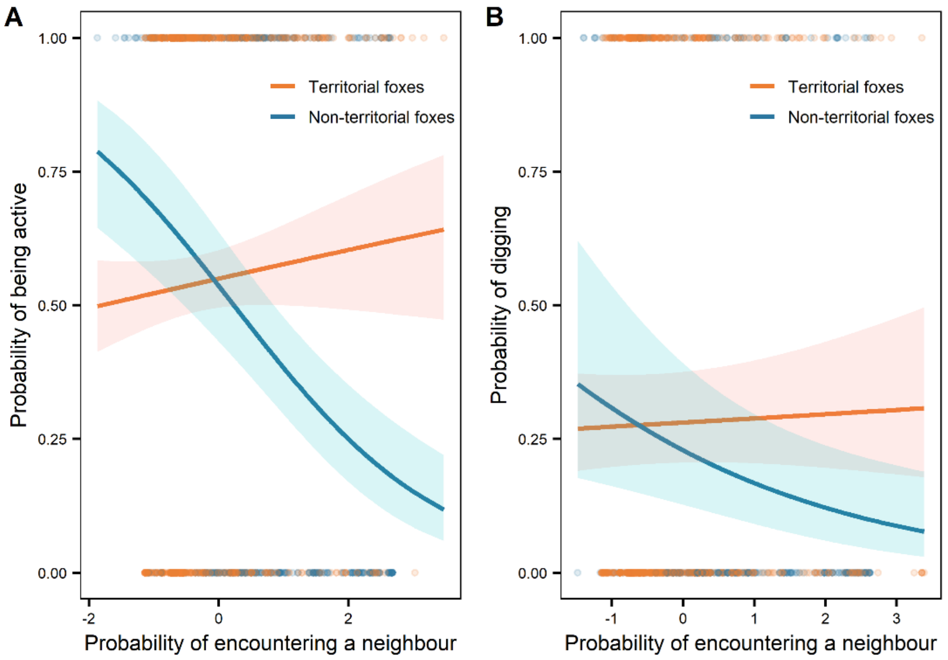


Figure 3. 4 Predicted effects of the probability of encountering a neighbour on A. probability of fox being active (0 = inactive, 1 = active, n = 1,368 GPS locations) and B. probability of fox digging (0 = no digging, 1= digging, n = 1,218 accelerometry bursts). The probability of encountering a neighbour was obtained from the conditional distribution of encounters (Figure 3.2). Orange dots and lines refer to territorial individuals (n = 10 foxes), and blue dots and lines refer to non-territorial individuals (n = 3 foxes). The blue and orange shaded areas represents 95% confidence intervals.

3.6 Discussion

Using high throughput tracking technologies, we estimated the spatial distribution of the probability of encounter among 13 Arctic foxes using neighbouring home ranges. We benefited from a natural situation where most, but not all individuals were territorial, thus enabling us to evaluate the effect of territoriality on the spatial distribution of foraging behaviour. Non-territorial foxes had some probability of encountering neighbours throughout their entire home range. Those individuals, contrary to territorial ones, responded to the variation in the probability of encountering a neighbour by shifting the distribution of prey searching and food caching away from the places where encounters were most likely to occur.

Given the challenges of documenting the movements and foraging behaviours of many neighbouring vertebrate predators 24 hours a day during several weeks, our sample of 13 individuals tracked for 23 days remains limited, and we recognise that our findings need to be confirmed with a larger sample size. Yet, our study informs on how intraspecific interactions may influence the spatial distribution of predator foraging. More specifically, our results suggest that in predators characterised by territoriality, those individuals unable to establish a territory may adjust their foraging behaviours to the probability of encountering neighbours. We develop this idea in the following sections.

3.6.1 Among-individual differences in territoriality

Three individuals were non-territorial and thus always faced a relatively high probability of encountering other foxes in their home range. Interestingly, these three individuals were also those that performed extra-territorial trips and were thus the least resident (Annexe A). Variation in the distribution, abundance and predictability of resources often explains among-individual differences in territoriality (Maher & Lott, 2000). For example, Eide et al. (2004) observed that in Arctic foxes of Svalbard, high home range overlap occurred near the coast where seabird colonies are concentrated. On the other hand, little home range overlap occurred inland where reindeer (*Rangifer tarandus*) carcasses are scattered and unpredictable. In our study area, we do not suspect that variation in prey distribution, abundance or predictability explains among-individual differences in territoriality, as all 13 foxes lived near the center of the goose colony where nests were abundant and habitats favourable to lemmings.

We identified individual characteristics that may differentiate territorial from non-territorial individuals, although larger sample sizes are required to confirm this result. Both non-territorial males BORR and BBJO were only one year old (the age of non-territorial female RMJJ is unknown), while the 10 territorial individuals were all at least three years old (average ± SD of 5.7 ± 2.6 years old). Since age impacts behavioural traits such as boldness (Bubac et al., 2018), we suspect that age influences the ability of an individual to defend a territory. Being older may indeed favour dominance over younger conspecifics, as was observed in pack living canids such as free-ranging domestic dogs (*Canis lupus familiaris*) and Arctic wolves (*Canis lupus arctos*) (Mech, 1999; Bonanni et al., 2017). Age also determines the probability to reproduce in Arctic foxes, since reproductive success initially increases with age before declining with senescence (Di Bernardi et al., 2021), and the three non-territorial individuals were the only studied foxes that did not reproduce in 2019. Using a territory may in fact be necessary to secure enough resources to reproduce and ensure the survival of young.

3.6.2 Effect of the probability of encountering a neighbour on Arctic fox behaviours

Being territorial or not determined how Arctic foxes responded to variation in the probability of encountering a neighbour. Territorial individuals searched and cached prey independently of the CDE, which overall tended to be low in their home range, likely because there was no benefit of modulating the distribution of foraging behaviours according to potential encounters in an area that was used exclusively. On the other hand, the three non-territorial individuals responded to the CDE, as they were less active in areas where the probability of encounter with neighbours was highest. As they had no exclusive use in their home range, those Arctic foxes may have increased foraging efficiency by searching prey more intensely where the risk of encounter with other foxes was the lowest. Also, inactive periods indicated that the fox was stationary, which might reflect periods of resting or vigilance, as we observed in the field. A hypothesis is that non-territorial foxes were more vigilant when using areas with a high probability of encounter, to avoid interactions with dominant neighbours, as observed with white-faced capuchins (Tórrez-Herrera et al., 2020; Noonan et al., 2021).

We also found that the probability of encountering neighbours explained the probability of non-territorial foxes to engage in digging. A greater probability of encounter with another fox may generate a greater risk of cache pilfering, and we hypothesise that this could explain why non-territorial foxes tended to dig less where the probability of encounter with another fox was higher. Furthermore, although during the goose incubation period, digging events should mostly reflect prey caching, we cannot differentiate caching events from prey captures, cache recoveries and recaching events (Clermont et al., 2021b), which may affect our results and interpretations. For example, our results could also indicate that non-territorial individuals favour recaching away from high CDE values, in safer sites. Caching and recaching prey in "out of view" sites are in fact common cache protection strategies in other species such as corvids (Dally et al., 2006). Careau et al. (2007) also showed that Arctic fox recaches of goose eggs were made further from the nest compared to initial caches, potentially to secure eggs in sites where chances of pilfering are lower (e.g., closer to the den).

3.6.3 Implications for predator-prey interactions

Arctic fox predation has important top-down effects in the tundra and generates multiple predator-mediated interactions among prey (Bêty et al., 2002; Legagneux et al., 2012; Duchesne et al., 2021). At fine spatial scales, Arctic fox movements generate a predation risk landscape influencing the behaviour and nest distribution of several migratory birds (Clermont et al., 2021a). It is therefore of strong interest to identify the factors explaining where Arctic foxes choose to forage. We found that three out of 13 foxes adjust their foraging behaviours to the probability of encountering neighbours. Therefore, and given our low sample size, we cannot conclude that interactions among neighbouring foxes influence predation risk distribution. However, although most Arctic foxes are territorial, there are no unused areas between home ranges, which overlap (Figures 3.1 and 3.2). As such, the spatial configuration of fox home ranges does not lead to buffer zones of low predation risk between territories as observed in some wolf-ungulate systems (Mech, 1977; Anderson et al., 2005). Conversely, the presence of non-territorial individuals, whom home ranges overlap those of their territorial neighbours, creates zones where fox density is high, which may increase the risk of predation (Clermont et al. 2021a). As such, we hypothesise that the greatest risk of predation should be located within the home range of non-territorial individuals, while the lowest predation risk should be found in defended territories, where probability of encounter among neighbouring foxes is null.

3.6.4 Conclusion

In this study, we found that not all Arctic foxes from Bylot Island used a territory. We highlight that because costs and benefits of territoriality may differ among individuals in a population, alternative behavioural tactics may emerge from non-territorial individuals to secure resources. Including the conditional distribution of encounters into habitat selection analyses would further help to better understand how different individuals deal with both the physical and social environments when using their habitat, and how they compromise between the needs to acquire valuable resources and avoid competitors. Finally, a spatial configuration in which the home ranges of non-territorial individual predators overlap those of their territorial neighbours may influence the distribution of predation risk, with could modulate the distribution and behaviour of prey and the structure of communities.

3.7 Acknowledgements

We thank A. Grenier-Potvin, R. Gravel, and G. Roy for field work, M. Noonan for advice on spatial analyses, and the community of Mittimatalik for support. Funding was received from (alphabetical order) Canada Foundation for Innovation, Canada Research Chairs Program, Fonds de Recherche du Québec – Nature et technologies (FRQNT), Natural Sciences and Engineering Research Council of Canada (NSERC), Network of Centers of Excellence of Canada ArcticNet, Northern Scientific Training Program (Polar Knowledge Canada), Parks Canada Agency, Polar Continental Shelf Program (Natural Resources Canada), and Weston Family Foundation.

3.8 Appendix A: Workflow to exclude GPS locations associated to extra-territorial trips for home range estimation

Some individuals performed extra-territorial trips (Figure 3.5), which affected home range estimation. We considered these GPS locations associated to extra-territorial trips as outliers, and identified them by calculating the distance between the core of the home range and each GPS location in the R package ctmm with the function ‘outlie’ (Calabrese et al., 2016). Figure 3.6 shows distance values for the individual BORR (green male on Figure 3.1 of the main text). Zooming in on lower distance values helped to determine cut-offs for individuals travelling far from their home range core, as did BORR (Figure 3.7). For BORR, we removed GPS locations >1700 m from the home range core, which removed 9% of its original dataset. The 1700 m cut-off threshold was determined visually so that extra-territorial trips disappeared from the spatial representation of the individual’s movements (Figure 3.8). BORR was the most drastic case. We removed 4% of GPS locations for RMJJ (green female on Figure 3.1), 6% for BBJO (grey male on Figure 3.1), and < 1% for all others.

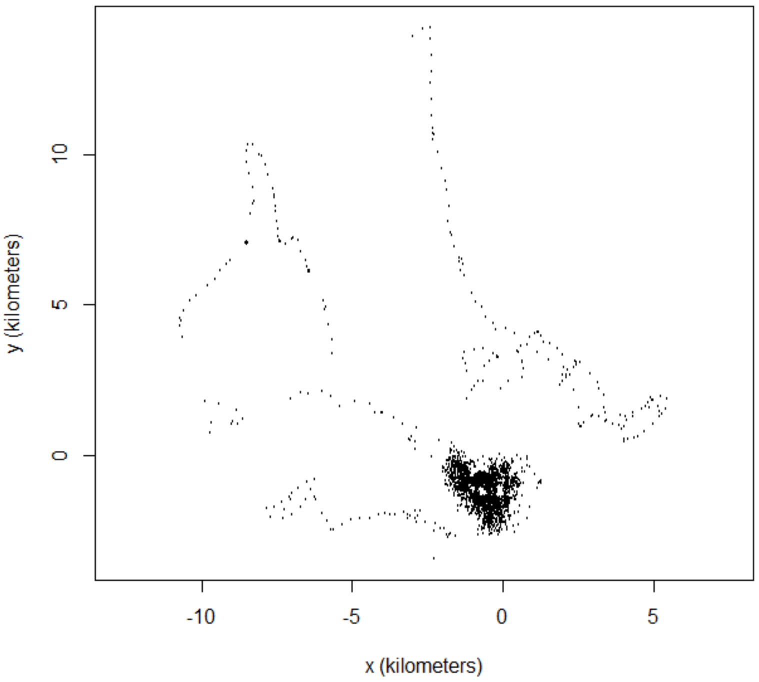


Figure 3. 5 GPS locations for individual BORR, that performed a few extra-territorial trips during the study period. X and Y axis show distance from home range core.

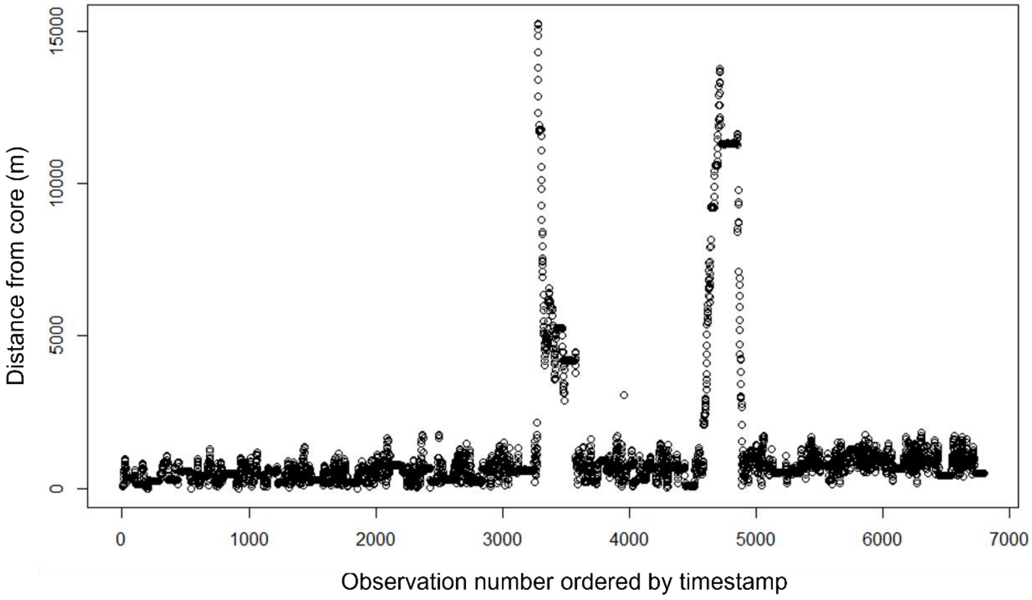


Figure 3. 6 Distances between GPS locations and the core of the home range for individual BORR.

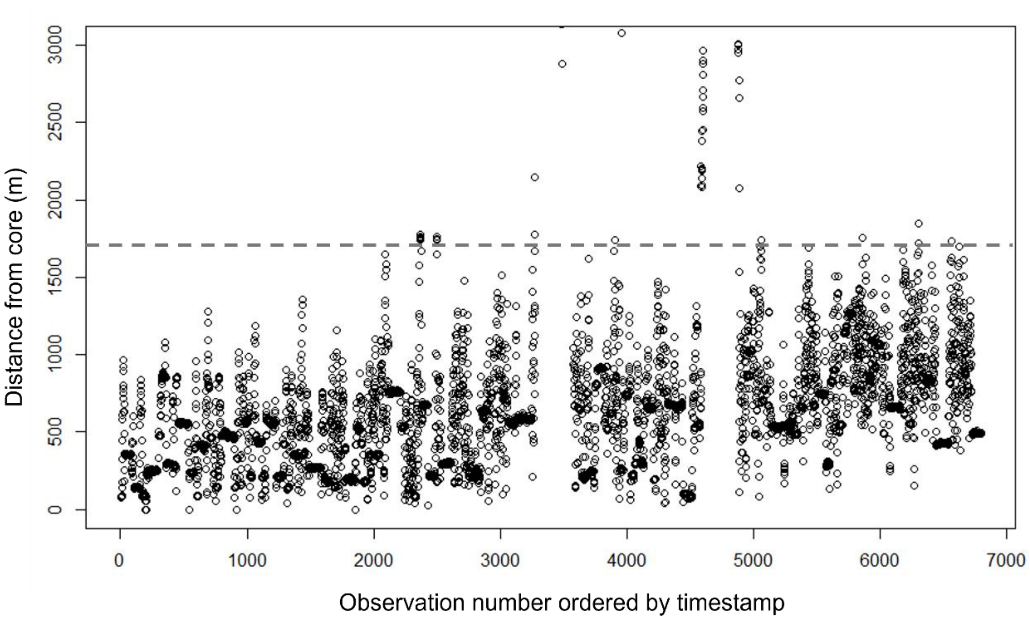


Figure 3. 7 Distances between GPS locations and the core of the home range for individual BORR, for distances ranging from 0 to 3000 m. The dashed-line shows the 1700 m cu-toff.

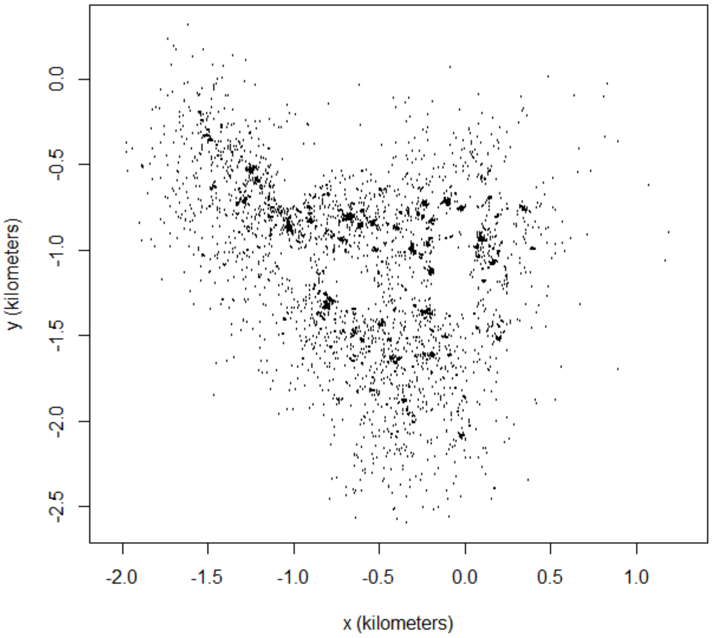


Figure 3. 8 GPS locations for individual BORR after the removal of extra-territorial trips.

3.9 Appendix B: Relation between behavioural state and accelerometry classification

30-sec accelerometry bursts are composed of 10 3-sec sequences which were attributed to a behaviour (Motionless, Walking, Digging or Running) through a machine learning classification (see the main text and Clermont et al., 2021). Behavioural states (active or inactive) were attributed to each GPS location through a hidden Markov model (HMM, see main text and Grenier-Potvin et al., 2021 for the details). To evaluate the relation between behavioural states and the accelerometry classification, we first associated each 30-sec burst of accelerometry data to the closest GPS location (provided the time stamp of the GPS location was within 30 sec of the start or end of the burst). We found Running was the most common behaviour for the active state, while Motionless was the most common behaviour for the inactive state (Figure 3.9).

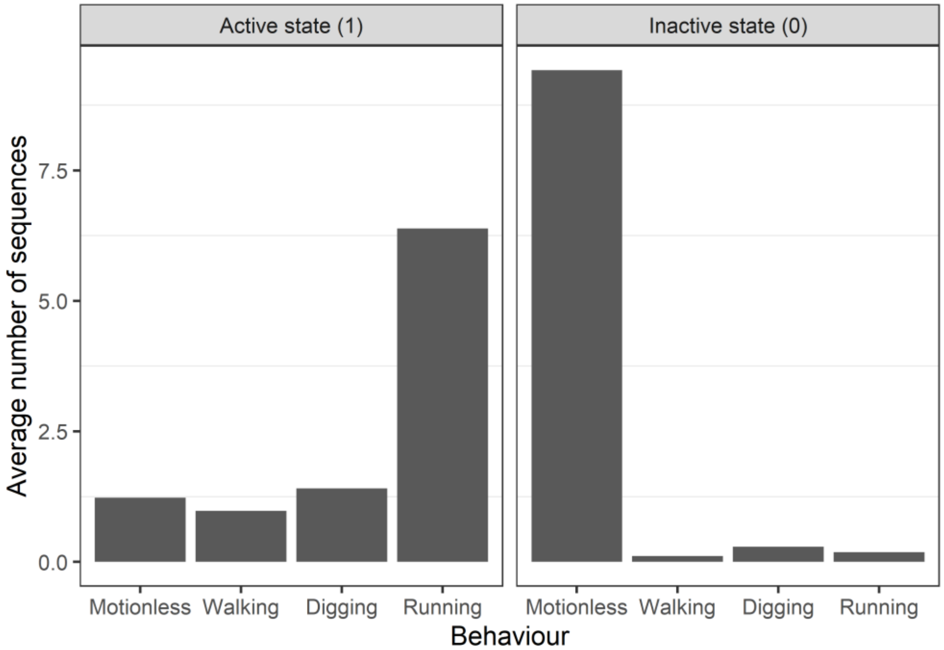


Figure 3. 9 Average number of 3-sec sequences attributed to each behaviour for both behavioural states.

3.10 Appendix C: Exclusion of datapoints near study area boundaries

Interactions with foxes that were not tracked occurred on the outer margin of our study area, thus biasing negatively our CDE estimates. To remove this bias, we excluded from our dataset all locations within a 500 m inner buffer of the study area before the analyses described in the main text Methods section 3.6.2 Effect of the probability of encountering a neighbour on Arctic fox behaviours. Details are described in Figure 3.10.

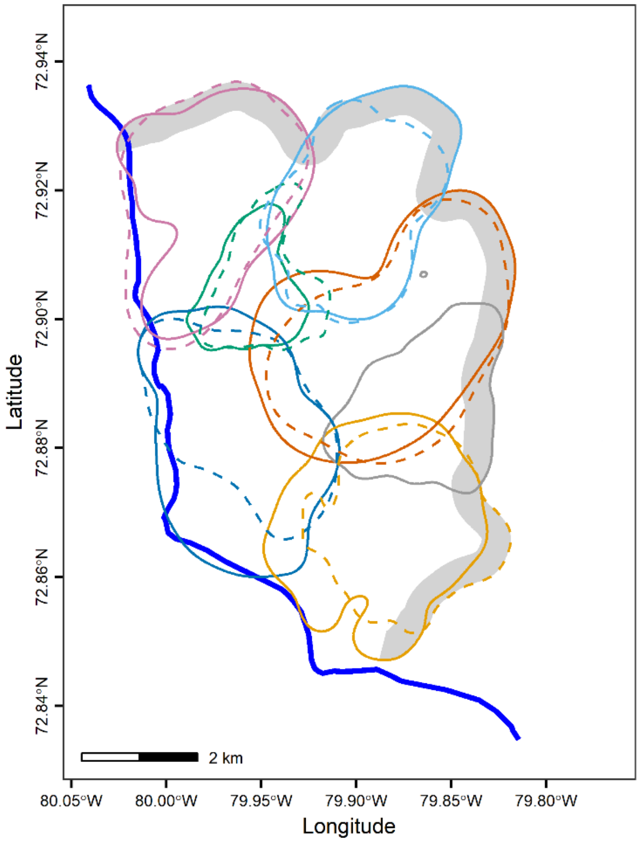


Figure 3. 10 Study area with 95% auto-correlated kernel density estimation contours for 7 male (solid-coloured lines) and 6 female (dashed-coloured lines) arctic foxes. The grey shaded area represents a 500 m inner buffer where observations were excluded. The thick blue line shows the coastline where interactions with neighbouring foxes could not occur.

3.11 Appendix D: Validation of model results using different subsamples

To validate the results of our models (Table 3.1 of the main text), we fitted 10 models for probability of being active and 10 models for probability of digging, each using a different subsample of data. Subsamples were composed of 6 daily observations for each individual, reaching a sample size of 1,368 GPS locations for probability of being active, and 1,218 accelerometry bursts for probability of digging. Results of models using the first subsamples are shown in the main text in Table 3.1. Table 3.2 and 3.3 below show the results of the 9 other models for probability of being active and probability of digging respectively.

For probability of being active, model results were highly similar across subsamples. For probability of digging, model results were similar across subsamples, except for sample 4 where we found no evidence of an interaction between the probability of encounter among neighbours and whether the fox was territorial (territorial yes/no). As it was the only case where this occurred, we believe that the results presented in the main text are robust.

Interactions with foxes not equipped with a GPS may occur at home range boundaries. As explained in Appendix C, we therefore excluded GPS locations and accelerometry bursts falling inside a 500 m inner buffer of our study area in all models presented in Table 3.1 of the main text and Tables 3.2 and 3.3 below. We validated that our choice of buffer size did not affect our results by repeating models using a buffer size of 1 km. Model results were similar (Table 3.4).

Table 3. 2 Results of generalised mixed models for probability of fox being active, using a binomial distribution with logit-link function, for subsamples 2 to 10 (n = 1,368 in each model).

Subsample 2

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	0.22	-0.09	0.53	0.15	1.47	0.14
Probability of encountering a neighbour	0.28	0.10	0.46	0.09	3.03	0.002
Territorial yes/no [no]	-0.30	-0.97	0.37	0.32	-0.95	0.34
Goose nest density	0.37	0.24	0.51	0.07	5.50	<0.001
Prob encounter: Territorial yes/no [no]	-1.18	-1.51	-0.86	0.16	-7.17	<0.001

Subsample 3

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	0.18	-0.07	0.42	0.12	1.50	0.13
Probability of encountering a neighbour	0.15	-0.01	0.32	0.08	1.79	0.07
Territorial yes/no [no]	-0.27	-0.80	0.27	0.26	-1.06	0.29
Goose nest density	0.49	0.35	0.63	0.07	6.99	<0.001
Prob encounter: Territorial yes/no [no]	-1.02	-1.35	-0.70	0.16	-6.20	<0.001

Subsample 4

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	0.15	-0.05	0.34	0.09	1.59	0.11
Probability of encountering a neighbour	0.08	-0.09	0.24	0.08	0.90	0.37
Territorial yes/no [no]	0.22	-0.21	0.67	0.21	1.03	0.31
Goose nest density	0.40	0.27	0.53	0.07	6.09	<0.001
Prob encounter: Territorial yes/no [no]	-0.99	-1.32	-0.68	0.16	-6.13	<0.001

Subsample 5

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	0.09	-0.10	0.28	0.09	1.02	0.31
Probability of encountering a neighbour	0.08	-0.08	0.25	0.08	1.01	0.31
Territorial yes/no [no]	0.50	0.08	0.94	0.21	2.40	0.02
Goose nest density	0.48	0.35	0.61	0.07	7.07	<0.001
Prob encounter: Territorial yes/no [no]	-1.13	-1.45	-0.82	0.16	-7.03	<0.001

Subsample 6

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	0.12	-0.10	0.34	0.10	1.18	0.24
Probability of encountering a neighbour	0.24	0.08	0.42	0.09	2.78	0.01
Territorial yes/no [no]	-0.21	-0.68	0.25	0.22	-0.96	0.34
Goose nest density	0.37	0.25	0.51	0.07	5.73	<0.001
Prob encounter: Territorial yes/no [no]	-0.76	-1.05	-0.47	0.15	-5.16	<0.001

Subsample 7

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	0.19	-0.01	0.38	0.09	2.05	0.04
Probability of encountering a neighbour	0.13	-0.04	0.31	0.09	1.47	0.14
Territorial yes/no [no]	0.01	-0.41	0.44	0.21	0.04	0.96
Goose nest density	0.42	0.30	0.56	0.07	6.47	<0.001
Prob encounter: Territorial yes/no [no]	-0.89	-1.20	-0.59	0.16	-5.75	<0.001

Subsample 8

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	0.03	-0.21	0.28	0.12	0.28	0.78
Probability of encountering a neighbour	0.13	-0.03	0.30	0.08	1.60	0.11
Territorial yes/no [no]	0.14	-0.39	0.68	0.25	0.55	0.59
Goose nest density	0.36	0.23	0.49	0.07	5.43	<0.001
Prob encounter: Territorial yes/no [no]	-1.05	-1.37	-0.74	0.16	-6.57	<0.001

Subsample 9

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	0.15	-0.05	0.35	0.10	1.56	0.12
Probability of encountering a neighbour	0.09	-0.07	0.26	0.08	1.13	0.26
Territorial yes/no [no]	0.04	-0.39	0.49	0.21	0.20	0.84
Goose nest density	0.54	0.41	0.68	0.07	7.72	<0.001
Prob encounter: Territorial yes/no [no]	-0.75	-1.04	-0.47	0.15	-5.15	<0.001

Subsample 10

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	0.09	-0.16	0.33	0.11	0.75	0.46
Probability of encountering a neighbour	0.01	-0.16	0.19	0.09	0.15	0.88
Territorial yes/no [no]	0.07	-0.44	0.61	0.25	0.29	0.77
Goose nest density	0.46	0.33	0.60	0.07	6.65	<0.001
Prob encounter: Territorial yes/no [no]	-0.78	-1.09	-0.48	0.16	-5.01	<0.001

Table 3. 3 Results of generalised mixed models for probability of fox digging, using a binomial distribution with cloglog-link function, for subsamples 2 to 10 (n = 1,218 in each model).

Subsample 2

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	-1.03	-1.45	-0.63	0.18	-5.82	<0.001
Probability of encountering a neighbour	0.11	-0.03	0.24	0.07	1.55	0.122
Territorial yes/no [no]	-0.25	-1.03	0.59	0.36	-0.68	0.494
Goose nest density	0.11	-0.004	0.22	0.06	1.94	0.05
Prob encounter: Territorial yes/no [no]	-0.32	-0.58	-0.06	0.13	-2.49	0.01

Subsample 3

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	-0.97	-1.47	-0.49	0.21	-4.56	<0.001
Probability of encountering a neighbour	-0.06	-0.20	0.08	0.07	-0.78	0.43
Territorial yes/no [no]	-0.35	-1.27	0.61	0.42	-0.83	0.40
Goose nest density	0.15	0.04	0.25	0.05	2.74	0.01
Prob encounter: Territorial yes/no [no]	-0.31	-0.60	-0.03	0.14	-2.17	0.03

Subsample 4

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	-1.03	-1.38	-0.72	0.15	-7.05	<0.001
Probability of encountering a neighbour	0.02	-0.13	0.16	0.07	0.29	0.77
Territorial yes/no [no]	-0.48	-1.14	0.22	0.32	-1.51	0.13
Goose nest density	0.24	0.13	0.34	0.05	4.43	<0.001
Prob encounter: Territorial yes/no [no]	-0.12	-0.41	0.18	0.15	-0.77	0.44

Subsample 5

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	-1.05	-1.53	-0.60	0.20	-5.13	<0.001
Probability of encountering a neighbour	0.15	0.004	0.29	0.07	2.09	0.04
Territorial yes/no [no]	-0.32	-1.22	0.61	0.41	-0.77	0.44
Goose nest density	0.15	0.04	0.26	0.06	2.63	0.01
Prob encounter: Territorial yes/no [no]	-0.33	-0.61	-0.05	0.14	-2.38	0.02

Subsample 6

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	-1.02	-1.47	-0.59	0.19	-5.31	<0.001
Probability of encountering a neighbour	0.004	-0.14	0.14	0.07	0.06	0.96
Territorial yes/no [no]	-0.11	-0.94	0.77	0.38	-0.29	0.77
Goose nest density	0.13	0.02	0.24	0.06	2.42	0.02
Prob encounter: Territorial yes/no [no]	-0.48	-0.75	-0.21	0.14	-3.50	<0.001

Subsample 7

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	-1.25	-1.91	-0.63	0.28	-4.51	<0.001
Probability of encountering a neighbour	0.02	-0.14	0.16	0.08	0.22	0.82
Territorial yes/no [no]	-0.04	-1.22	1.20	0.53	-0.07	0.94
Goose nest density	0.14	0.02	0.25	0.06	2.37	0.02
Prob encounter: Territorial yes/no [no]	-0.35	-0.61	-0.09	0.13	-2.65	0.01

Subsample 8

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	-1.07	-1.47	-0.69	0.17	-6.19	<0.001
Probability of encountering a neighbour	-0.13	-0.29	0.02	0.08	-1.61	0.11
Territorial yes/no [no]	-0.24	-1.02	0.57	0.36	-0.65	0.51
Goose nest density	0.23	0.12	0.33	0.05	4.26	<0.001
Prob encounter: Territorial yes/no [no]	-0.38	-0.67	-0.09	0.15	-2.55	0.01

Subsample 9

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	-1.04	-1.49	-0.63	0.19	-5.53	<0.001
Probability of encountering a neighbour	0.10	-0.04	0.24	0.07	1.46	0.14
Territorial yes/no [no]	-0.23	-1.04	0.63	0.38	-0.60	0.55
Goose nest density	0.15	0.03	0.25	0.06	2.60	0.01
Prob encounter: Territorial yes/no [no]	-0.48	-0.75	-0.21	0.14	-3.49	<0.001

Subsample 10

Fixed effect	Estimate	Lower 95% CI	Upper 95% CI	SE	z value	p value
Intercept	-1.06	-1.54	-0.61	0.20	-5.18	<0.001
Probability of encountering a neighbour	0.02	-0.14	0.17	0.08	0.28	0.78
Territorial yes/no [no]	-0.26	-1.15	0.67	0.41	-0.64	0.52
Goose nest density	0.12	0.004	0.23	0.06	2.08	0.04
Prob encounter: Territorial yes/no [no]	-0.30	-0.58	-0.02	0.14	-2.11	0.03

Table 3. 4 Results of generalised mixed models predicting A. fox probability of being active (n = 1,368 GPS locations) and B. probability of digging (n = 1,218 accelerometry bursts), using a binomial distribution with logit-link and cloglog-link functions respectively. We excluded datapoints falling inside a 1000 m inner buffer of the study area.

A. Probability of fox being active

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	0.40	0.05	0.76	0.17	2.39	0.02
Probability of encountering a neighbour	-0.06	-0.22	0.11	0.08	-0.68	0.50
Territorial yes/no [no]	0.35	-0.41	1.13	0.36	0.95	0.34
Goose nest density	0.62	0.47	0.78	0.08	7.73	<0.001
Prob encounter: Territorial yes/no [no]	-0.88	-1.22	-0.57	0.16	-5.35	<0.001

B. Probability of fox digging

Fixed effect	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**SE**	**z value**	**p value**
Intercept	-0.98	-1.39	-0.60	0.17	-5.78	<0.001
Probability of encountering a neighbour	0.005	-0.14	0.14	0.07	0.07	0.95
Territorial yes/no [no]	-0.15	-0.91	0.68	0.36	-0.43	0.67
Goose nest density	0.06	-0.05	0.17	0.05	1.15	0.25
Prob encounter: Territorial yes/no [no]	-0.39	-0.66	-0.13	0.13	-2.95	0.003

CHAPITRE IV

PREY AVAILABILITY INFLUENCES THE EFFECT OF BOLDNESS ON REPRODUCTIVE SUCCESS IN A MAMMALIAN PREDATOR

Jeanne Clermont, Charline Couchoux, Sandra Lai & Dominique Berteaux

Manuscrit soumis à *Behavioral Ecology and Sociobiology*.

4.1 Résumé

Les individus au sein des populations montrent souvent des différences constantes dans leur niveau de témérité, qui explique le succès reproducteur. La force et la direction de la relation entre les comportements et les traits d'histoire de vie varient cependant en fonction des conditions environnementales, et une sélection fluctuante agissant sur les traits comportementaux pourrait contribuer au maintien des différences de personnalité. Nous avons exploré les sources de variation dans la témérité du renard arctique (*Vulpes lagopus*) et investigué comment la variation temporelle dans l'abondance d'une proie principale (lemmings) influence la relation entre la témérité et le succès reproducteur des renards. Lors du relâché après une capture, nous avons mesuré les réactions comportementales des individus comme indicateur de leur témérité. Nous avons obtenu 70 mesures chez 42 individus lors de deux années à faible abondance en lemmings et deux années à forte abondance de lemmings, et nous avons estimé la taille de portée des renards comme indicateur de leur succès reproducteur. Tout d'abord, les caractéristiques individuelles (âge, sexe, masse) n'ont pas expliqué de variation dans la témérité des renards, contrairement à l'identité de l'individu. Ensuite, nous avons trouvé que durant les années à faible abondance en lemmings, les individus montrant des comportements téméraires ont produit un plus grand nombre de jeunes que les individus ayant agi plus prudemment, suggérant que la témérité est avantageuse quand les lemmings sont rares en augmentant le succès de chasse ou en permettant l'accès à des ressources alternatives. Cependant, tous les individus tendaient à agir de manière téméraire lorsque les lemmings étaient abondants, et tous ont produit plusieurs jeunes. La variation temporelle dans l'abondance d'une proie principale pourrait ainsi influencer la relation entre la témérité et le succès reproducteur d'un prédateur. Si les différences interindividuelles de témérité sont constantes, une sélection fluctuante pourrait contribuer au maintien de différences de personnalité.

Mots clés : abondance des ressources, personnalité, prédation, renard arctique, taille de portée, témérité

4.2 Abstract

Individuals within animal populations often consistently differ in their level of boldness, which relates to fitness. The strength and direction of relationships between behavioral and life-history traits may however vary according to environmental conditions, where fluctuating selection acting on behavioral traits contributes to the maintenance of personality differences. We explored sources of variation in Arctic fox (*Vulpes lagopus*) boldness and investigated how temporal variation in the abundance of a main prey (lemmings) influences the relationship between fox boldness and reproductive success. We measured the behavioral reaction of individuals when escaping after handling, as an indicator of their boldness. We obtained 70 measurements from 42 individuals during two years of low lemming abundance and two years of high lemming abundance, and assessed fox litter size as an indicator of reproductive success. First, individual characteristics (age, sex, mass) did not affect Arctic fox boldness, while individual identity generated variation in boldness. Next, we found that during years of low lemming density, individuals behaving boldly had more pups than those behaving less boldly, suggesting boldness may provide an advantage when lemmings are scarce by increasing hunting success or allowing access to alternative resources. However, all individuals tended to show high levels of boldness when lemming density was high, and all produced large litters. Temporal variation in the abundance of a main prey might therefore influence the relation between boldness and reproductive success of a predator, and if individuals consistently differ in their level of boldness, fluctuating selection could contribute to the maintenance of personality.

Keywords: Arctic fox, boldness, litter size, personality, predation, resource abundance

4.3 Significance statement

Effects of boldness on Arctic fox reproductive success: lemming abundance matters! When lemmings are scarce, foxes showing bold behavior have more pups than foxes showing less bold behavior. This highlights that under low prey availability, boldness may bring short-term benefits to predators, potentially because it allows to acquire more food. When lemmings are abundant, however, all foxes produce as many pups. This shows that environmental conditions such as prey abundance can influence the relation between behavior and reproductive success in a predator. Studying the context-dependency of relationships between behavior and reproductive success is critical to better understand ecological and evolutionary consequences of environmental change.

4.4 Introduction

Individuals within populations of many species differ consistently in behavioral traits such as boldness (i.e., an individual’s willingness to take risks, measured on a bold–shy continuum), both over time and across contexts (Réale et al., 2007, 2009; Carter et al., 2013). Consistent among-individual differences (or personality) have also been highlighted for other behavioral traits such as exploration of novel environments, activity, aggressiveness, and sociality (Réale et al., 2007). Those behavioral traits may covary and form a behavioral syndrome (Sih et al., 2004). Personality traits have important evolutionary implications as they can explain fitness variation (Dingemanse & Réale, 2005; Smith & Blumstein, 2008; Réale et al., 2009). Bolder and more aggressive individuals usually grow faster and are more fecund, since they tend to maximize foraging and reproduction opportunities (Biro & Stamps, 2008; Smith & Blumstein, 2008). For example, bolder female grey seals (*Halichoerus grypus*) produce heavier pups than shyer ones (Bubac et al., 2018). However, boldness is also associated with a reduction in lifespan, potentially because bolder individuals engage in more risky situations that increase mortality risk (e.g., through predation), but also because boldness incurs physiological costs such as higher metabolic rates and thus greater costs of living (Wolf et al., 2007; Smith & Blumstein, 2008; Réale et al., 2010). Individuals of different behavioral types therefore resolve life-history trade-offs in alternative ways, favoring either current or future reproduction but reaching an equivalent lifetime reproductive success, which should contribute to maintain personality differences in populations (Wolf et al., 2007; Réale et al., 2010; but see Montiglio et al., 2018).

Trade-offs between current and future reproduction may thus lead to consistent among-individual differences in personality traits, but they can also lead to within-individual variation in behavior (e.g., through phenotypic plasticity). First, residual reproductive value varies with individual traits such as age and body condition. As younger individuals have more reproductive opportunities ahead of them, they should act less boldly compared to older individuals that should favor current reproduction (Dammhahn, 2012; Bubac et al., 2018). Similarly, individuals in good body condition should be less bold as they have a greater potential for future reproduction, compared to individuals in poor condition (Moran et al., 2021). Therefore, individuals may become bolder as they age, and boldness could be adjusted throughout an individual's life according to body condition (Dammhahn, 2012; Moran et al., 2021). Females and males may also differ in their expression of some behavioral traits and in their degree of behavioral consistency, and these differences may result from sexual selection where selection pressures differ between males and females (Schuett et al., 2010).

The life-history trade-off hypothesis thus predicts that bolder, more aggressive individuals will favor current reproduction and live shorter lives. However, empirical studies show that the strength and direction of relationships between behavioral and life-history traits can vary. For example, Bridger et al. (2015) found that in male hermit crabs (*Pagurus bernhardus*), shy individuals were more fecund than bold ones. Moreover, in female great tits (*Parus major*) the relationship between exploration and reproductive success varied according to food availability (Dingemanse et al., 2004). In fact, fluctuating environments, especially fluctuating food resources, may influence the strength and direction of relationships between behavioral and life-history traits, where bolder individuals are favored over shyer ones, or vice versa, depending on environmental conditions. For example, in Siberian chipmunks (*Tamias sibiricus*), the boldest individuals have the greatest annual reproductive success during years of low food availability, but the opposite is true when food is abundant (Le Cœur et al., 2015). Furthermore, female wild boars (*Sus scrofa*) that are the least aggressive and that show the lowest exploratory tendencies have the greatest reproductive success, but only when their main food is abundant (Vetter et al., 2016). In female American red squirrels (*Tamiasciurus hudsonicus*), the effects of activity level on offspring growth rate, and of aggressiveness on offspring survival, vary in magnitude and direction according to food abundance (Boon et al., 2007). Fluctuating selection acting on behavioral traits is another potential mechanism explaining the maintenance of personality differences in wild animal populations (Dingemanse et al., 2004; Wolf & Weissing, 2010; Le Cœur et al., 2015;

Mouchet et al., 2021), where various ecological variables may influence associations between behavior and life-history traits (Smith & Blumstein, 2008; Adriaenssens & Johnsson, 2009; Montiglio et al., 2018). Still, only a handful of studies have assessed such context-dependent relationships, using as model species insectivorous birds (Dingemanse et al., 2004; Quinn et al., 2009), rodents (Boon et al., 2007; Bergeron et al., 2013; Le Cœur et al., 2015) and other herbivores (Vetter et al., 2016). Studying those relationships is critical to better understand how personality differences may be maintained in animal populations, and more broadly to inform on ecological and evolutionary consequences of environmental change.

In this study, we assessed how the boldness of a predator predicts its reproductive success across variable prey abundances. We studied the Arctic fox (*Vulpes lagopus*), a predator showing consistent among-individual differences in boldness within years (Choi et al., 2019), and subjected to cyclic variation in the abundance of its main prey (lemmings, *Lemmus* and *Dicrostonyx* spp.) across most of its circumpolar distribution (Audet et al., 2002; Angerbjörn et al., 2004). While it is clear that the abundance of lemmings influences Arctic fox probability to reproduce (Chevallier et al., 2020; Juhasz et al., 2020) and litter size (Tannerfeldt & Angerbjörn, 1998), the role of boldness in explaining these relationships is unknown. The general aim of this study was thus to evaluate whether prey abundance affected the relationship between boldness and reproductive success in the Arctic fox. The fitness of predators being highly dependent on prey availability (Salamolard et al., 2000; Terraube et al., 2015), their reproductive success under low prey availability should depend on their capacity to obtain valuable food resources. Boldness, which could relate to hunting strategies (Patrick et al., 2014; Chang et al., 2017), could therefore be advantageous under low prey availability. However, as boldness incurs costs, acting boldly may be less beneficial when prey are abundant.

We estimated the litter size and boldness of Arctic fox parents by counting their pups at dens and observing their escape behavior after handling. We did so during two years of low lemming abundance and two years of high lemming abundance in Nunavut, Canada. We first explored sources of variation in Arctic fox boldness, by evaluating how individual characteristics (age, sex and mass) and consistent among-individual differences influenced fox behavioral reaction to a risky situation, that is the handling environment from which they were escaping. Second, we tested the hypothesis that the effect of boldness on litter size depends on lemming density. We predicted that 1) when lemmings are scarce, individuals behaving boldly would have larger litter sizes than individuals behaving less boldly, since bold individuals may be more efficient at acquiring resources, but 2) when lemmings are abundant, individuals behaving boldly would have similar or smaller litter sizes as those behaving less boldly, since shy individuals may be just as efficient at acquiring resources in such conditions and behaving boldly may incur additional costs.

4.5 Methods

4.5.1 Study system

We conducted fieldwork from 2016 to 2019 in the southwest plain of Bylot Island (73° N, 80° W), in Sirmilik National Park of Canada, Nunavut, where the Arctic fox is the main terrestrial predator. At Bylot Island, fox probability of reproduction is highly dependent on the abundance of brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), and on the access to a large greater snow goose (*Anser caerulescens atlanticus*) colony (Chevallier et al., 2020; Juhasz et al., 2020). Lemmings follow a 3–4-year cycle in abundance, but fluctuations are much stronger for brown lemmings, the most abundant species (from < 1 to 10 individual/ha for brown lemmings and always < 1 individual/ha for collared lemmings; Gruyer et al., 2008; Gauthier et al., 2013; Fauteux et al., 2015). The snow goose colony (> 20,000 nesting pairs, Bêty et al., 2001) is restricted to a ca. 60 km^2 area in the southern portion of the study area. The goose colony provides an alternative food resource during summer and foxes may take and cache goose eggs for consumption during the rest of the year (Careau et al., 2008b). In years of low lemming abundance, foxes with access to the snow goose colony have a higher probability of reproducing than those without access (Giroux et al., 2012; Chevallier et al., 2020). The greater snow goose is a relatively large bird, with a wingspan of ca. 1.5 m and weighing up to 3.5 kg. Small Arctic foxes (ca. 3 kg) that attempt to take goose eggs from nesting pairs are faced with aggressive defense behaviors from both parents (Bêty et al., 2002).

4.5.2 Fox captures and behavioral measurements

We captured Arctic foxes using Tomahawk cage traps #205 (Tomahawk Live Trap Company) or Softcatch #1 padded leg-hold traps (Oneida Victor Inc. Ltd.). At each capture, we marked individuals with 4 colored ear tags allowing identification at a distance, weighed them to the nearest g, determined their sex from genitalia characteristics, and assessed whether females were lactating. We also took pictures of full dentition to estimate age from visual analysis of tooth wear (Chevallier et al., 2017). Foxes were sometimes anesthetized if they were too aggressive to be handled. We used a combination of medetomidine (0.05 ml/kg) and ketamine (0.025 ml/kg), and then atipamezole (0.05 ml/kg) as a reversal agent, before releasing foxes at the capture site.

Different measurements may be used to assess the boldness of wild animals, such as the latency to emerge from a refuge, flight initiation distance, or reaction towards a novel object (Réale et al., 2007; Carter et al., 2013). We measured foxes' level of boldness by assessing their reaction when released after the manipulations described above. Escape behavior after handling has also been used to evaluate boldness in other species (Jornod & Roche, 2015; DeRango et al., 2019). More specifically, once released, a fox escapes the danger represented by the observers handling them by running away, and its behavior should reflect its willingness to take risk. At some point, the fox stops and turns its body and head to look back at the observers (hereafter referred as a turnaround), potentially to re-assess the danger. At each release, we thus measured to the nearest meter the distance at first turnaround, using a telemeter or counting 1-m steps between the release point and the location at which the fox first stopped and looked back at the observers. We also noted the general pace of the fox when escaping, which was scored as slow, intermediate and fast pace. As much as possible, we released individuals in flat areas free of obstacles. Video examples of releases are included as Supplementary Material to demonstrate the variability in both distance at first turnaround and pace when escaping (this will be made available in the online, published version). It was not possible to record data blind because our study involved focal animals in the field.

Our measure of fox escape behavior also has similarities with the flight initiation distance from an approaching human, which is commonly recorded to assess boldness or fear towards humans (Cooper & Blumstein, 2015; Sih et al., 2022). As the smallest flight initiation distances indicate the boldest reaction and lower fear level (Blumstein, 2003; Sih et al., 2022), so would the smallest distances at first turnaround after release, as foxes stay near humans, which represent a threat, rather than rapidly fleeing away. A fox that stopped and turned around at a small distance from observers, escaping at a slow pace, thus displayed a bold behavior (low fear level), while a fox that turned around at a large distance from observers, escaping at a fast pace, showed a shy behavior (high fear level). The level of fear experienced by individuals should correlate across contexts, such as the fear from humans, predators or competitors (Sih et al., 2022). Therefore, we expect that the reaction of individuals towards a human threat should reflect their reaction towards a variety of other threats.

We excluded from analyses all assessments of behavioral reactions from foxes anesthetized during capture (12 observations from 9 foxes, all years combined), as the anesthesia affected their behavior at release. Furthermore, in 2016, when our study was first implemented, we only assessed fox pace and did not measure distance at first turnaround ($n = 16$). We however found that pace and distance at first turnaround were positively associated in 2017-2019, with individuals using a faster pace being located at a greater distance from the release point at their first turnaround (ANOVA: $SS = 2448$, $F = 8.55$, $p < 0.001$, $n = 55$; Figure 4.1; Tukey HSD post-hoc comparisons: fast pace differs from slow and intermediate paces, $p < 0.01$ and $p = 0.02$ respectively, but slow and intermediate paces do not differ statistically, $p = 0.42$). To avoid losing valuable information, we attributed to the 16 observations that lacked the distance at first turnaround the median distance associated to each pace score, calculated from the 55 observations for which both distance and pace had been assessed (i.e., slow = 3 m, intermediate = 6.5 m, fast = 12 m). Distance at first turnaround was the main behavioral trait analysed statistically, since a quantitative variable allows easier interpretation of interaction terms and uses less degrees of freedom. We thus obtained 71 measurements of distance at first turnaround (but see section *Fox reproduction monitoring* for final sample size), from 42 captured foxes observed on average (± SD) 1.7 ± 1.1 times. Twenty-five observations were obtained from 25 individuals observed once, while 46 observations came from 17 individuals with at least two observations (10 individuals observed twice, 3 observed thrice, 3 observed 4 times and 1 observed 5 times). For the latter we thus obtained 29 observations considered as replicated measurements, with 8 that were within-year and 21 that were among-year replicates.

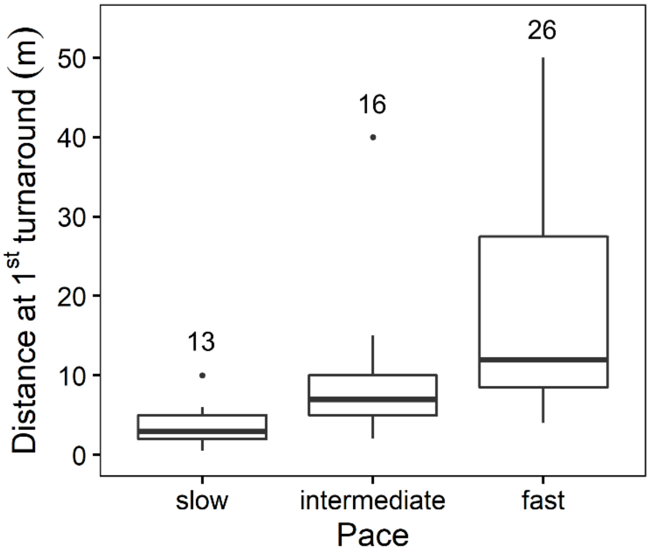


Figure 4. 1 Fox distance at first turnaround (m) as a function of its pace (n = 55) when escaping after handling. Boxplots show first quartile, median, and third quartile. Lower and upper whiskers extend, respectively, to the lowest and highest values within the interquartile range multiplied by 1.5. Points represent values outside this range. Numbers on top of boxes are number of observations for each category.

4.5.3 Fox reproduction monitoring

Arctic foxes live as territorial pairs and use dens for reproduction. Arctic fox pups first emerge from their natal den when about 3-weeks-old (Tannerfeldt & Angerbjörn, 1998). The 115 dens located in our study area were visited at least twice in May-August. During the first visit in May, we installed automated cameras (RapidFire Professional PC85 and HyperFire PC800, Reconyx, Holmen, WI, USA) on all dens showing signs of recent activity (digging, hair, tracks, prey remains, presence of adults or pups). Cameras were retrieved in late July-early August, at the end of the field season. Analysis of pictures from cameras and visual observations at dens allowed us to determine the identity and estimate the litter size of foxes using each den. Following the first observation of pups on the den, we counted the maximum number of pups observed on pictures. Picture analysis showed that the maximum number of pups for a litter is typically recorded 6 days after pup first den emergence (Morin, 2015). It is always possible that some pups die before emergence or do not appear on pictures, so the maximum number of observed pups represents the minimum litter size. We used this to quantify reproductive success, but note that this may not reflect precisely annual fitness since pups can die later in the breeding season and extra-pair paternity occurs in our study area (Cameron et al., 2011). In addition, we could not separate foxes producing no pup from those producing pups who died before emergence from the den.

Individuals were considered non-breeders (litter size = 0) when they used no den with pups, did not lactate (for females), and when we could ascertain that they did not reproduce outside of the study area. We excluded from analyses one male without known pups and that had a territory outside the study area, for a final sample size of 70 behavioral observations associated with a litter size.

4.5.4 Lemming density and access to the snow goose colony

Lemming density was estimated each year using live-trapping in July and a capture-mark-recapture method (Fauteux et al., 2015; Duchesne et al., 2021). We pooled densities of brown and collared lemmings and used two density categories (low/high) following Duchesne et al. (2021). Densities were low in 2017 and 2018 with < 0.3 lemming/ha, while they were high in 2016 and 2019 with > 1.3 lemming/ha.

For each fox-year, we determined whether the fox territory overlapped the snow goose colony, thus giving access to goose eggs. To do so, the boundaries of the colony were determined annually in late June with a GPS and helicopter (Duchesne et al., 2021). Then, we determined whether the locations of the fox captures, dens and field observations fell within the colony, adding a 1.75-km buffer outside the colony boundaries to account for short extra-territorial excursions (Chevallier et al., 2020).

4.5.5 Statistical analyses

1) Determinants of fox boldness

Statistical analyses were performed using R version 3.6.1 (R Development Team, 2019). To evaluate causes of variation in Arctic fox boldness, we used a linear mixed model (LMM), using the package glmmTMB (version 1.1.1; Brooks et al., 2017), modelling variation in distance at first turnaround (response variable) according to fixed and random effects. We log-transformed the distance at first turnaround to respect the assumption of normality and homoscedasticity in the model's residuals. We included as fixed effects the individual characteristics sex, age, and mass, the latter indicating body condition despite being confounded by body size. We also controlled for habituation to capture by including the number of times the individual was captured throughout its life at the time of the behavioral assessment, including the captures allowing our tests (hereafter capture number). Fox ID was fitted as a random effect to evaluate individual consistency in boldness. We estimated repeatability of boldness as the proportion of variance in that behavior attributed to differences among individuals (Bell et al., 2009; Nakagawa & Schielzeth, 2010), using the R package rptR (version 0.9.22; Stoffel et al., 2017). We estimated both adjusted repeatability using a model including fixed effects, and un-adjusted repeatability using a model only containing the overall intercept and ID as random effect. Confidence intervals (CI) were estimated by parametric bootstrapping. Our repeatability estimates mostly reflect among-year individual consistency in boldness, as behavioral tests were mostly replicated in different years for each individual (21 of 29 replicates are among-year replicates). Note that rptR fits a model using the lme4 package (Bates et al., 2015), rather than glmmTMB. We also included year as a random effect to control for variation among years, but then excluded this variable from analyses as this led to a singular fit (variance estimated at zero, see Bolker et al., 2009).

2) Litter size as a function of boldness and resource abundance

We modeled litter size (response variable) using a zero-inflated Poisson (ZIP) generalized linear mixed model (GLMM), again using glmmTMB, to solve overdispersion and zero-inflation problems observed in exploratory analyses using regular Poisson or negative binomial GLMMs. Zero-inflated models allow to properly model count data that include more zeros than expected by a Poisson or negative binomial distributions. Specifically, the ZIP GLMM models the response variable as a mixture of two probability distributions: 1) the zero-inflated part which models binary data, here fox probability to reproduce (0 = no pup observed, 1 = at least 1 pup observed), with a logit-link binomial distribution, and 2) the count part which models the count data, here litter size, with a Poisson distribution (see Zuur et al., 2009; Blasco-Moreno et al., 2019). Each model part may include different fixed and random effects. We were specifically interested in the count part of the model to better understand how lemming density and boldness interacted to determine litter size.

On the zero-inflated part of the ZIP GLMM, we included as fixed effects lemming density (low/high) and whether the fox had access to the goose colony (yes/no), as both variables affect fox probability to reproduce (Chevallier et al., 2020; Juhasz et al., 2020). We kept the zero-inflated part of the model as simple as possible because preliminary models including more fixed and random effects (see below other effects included on the count part) led to convergence issues and underdispersion.

On the count part of the ZIP GLMM, we included as fixed effects lemming density (low/high), the distance at first turnaround as indicator of fox boldness, and their interaction. We also included confounding variables potentially affecting litter size: whether the fox had access to the goose colony (yes/no), fox age (litter size increases with age in some Arctic fox populations, Di Bernardi et al., 2021), and age^2 representing non-linear age effects related to senescence. We fitted as random effects year and fox ID as some measures were repeated. All continuous variables were centered and standardized (Schielzeth, 2010). Overdispersion, zero-inflation and residuals diagnostics were assessed using simulation-based tests in the R package DHARMa (version 0.4.3; Hartig, 2021).

4.6 Results

4.6.1 Determinants of fox boldness

We found no evidence that the fixed effects included in the LMM (sex, mass, age, capture number) had an effect on distance at first turnaround (n = 68 due to missing values of fixed effects, Table 4.1). Adjusted repeatability in fox log-distance at the first turnaround was of 0.19 CI: [0, 0.62], whereas un-adjusted repeatability was 0.14 CI: [0, 0.47] (n = 71). Figure 4.2 represents individual differences in distance at first turnaround, for the 17 individuals that were observed more than once.

Table 4. 1 Results from a linear mixed model with log-distance at the first turnaround as the response variable (n = 68 due to missing fixed effect values). Model reference value is sex = F.

Fixed effect	Estimate [95% CI]	SE	z value	p value
(Intercept)	2.05 [1.67, 2.42]	0.19	10.81	<0.001
sex	0.07 [-0.49, 0.64]	0.29	0.25	0.80
mass	-0.18 [-0.46, 0.10]	0.14	-1.25	0.21
age	-0.17 [-0.41, 0.08]	0.12	-1.35	0.18
capture No	0.05 [-0.21, 0.31]	0.13	0.39	0.69

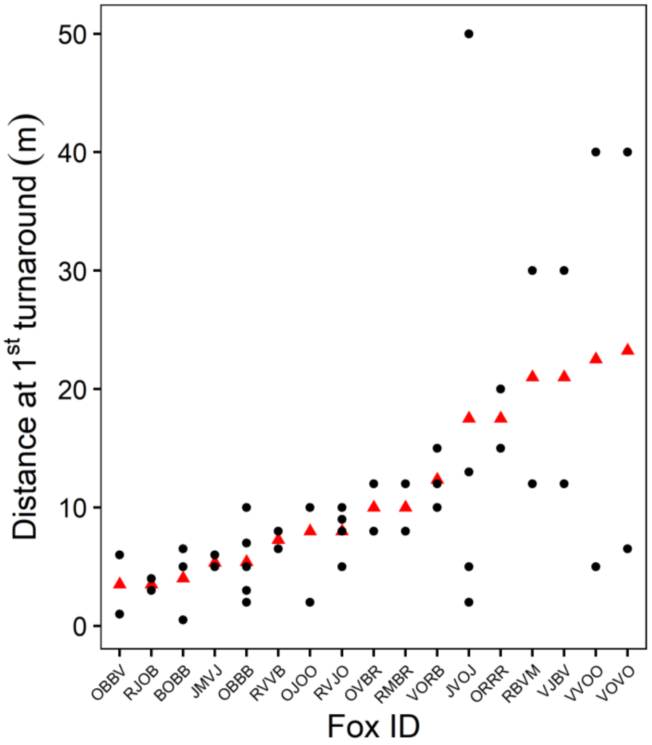


Figure 4. 2 Distance at first turnaround (black dots), for the 17 individuals with more than one behavioral observation (n = 46). Red triangles are mean values. Fox IDs reflect the unique combinations of colors of the 4 ear tags (e.g., OBBV = orange-blue-blue-violet).

4.6.2 Litter size as a function of boldness and resource abundance

Average (± SD) litter size was 3.8 ± 4.3 pups, with a minimum of 0 (31 out of 70 observations) and a maximum of 14 pups produced. On the zero-inflated part of the ZIP GLMM, we found that lemming density influenced fox probability to reproduce (thus generating the large number of zeros in the dataset). Specifically, in years of low lemming density, few individuals reproduced (Table 4.2). However, we found weak evidence of a positive effect of the access to the snow goose colony on the probability to reproduce (Table 4.2). Then, on the count part of the model, which evaluated determinants of fox litter size, we found strong evidence of an effect of lemming density, with high densities leading to larger litter sizes (Table 4.2). We further found that distance at first turnaround influenced litter size when considered in interaction with lemming density (Table 4.2). In years of low lemming density, individuals turning at short distances (i.e., individuals exhibiting bold behavior) produced more pups than individuals turning at large distances (i.e., individuals exhibiting shy behavior) (Table 4.2; Figure 4.3). In years of high lemming density, we found no evidence that litter size varied with distance at first turnaround (Table 4.2; Figure 4.3). However, when lemming density was high, most observations yielded lower distances at first turnaround (Figure 4.3), which probably reduced our ability to estimate an effect. Regarding the tested confounding effects, as expected, age and age^2 both had an effect on litter size (Table 4.2), where litter size increased with age until approximately age 5. We however found no evidence that access to the snow goose colony influenced litter size (Table 4.2). The dataset contained one apparent outlier, as shown on the right side of the orange area of Figure 4.3. Testing the ZIP GLMM without this observation yielded similar results. Excluding observations from year 2016, when we inferred distance at first turnaround from pace, yielded similar results.

Table 4. 2 Results from a zero-inflated Poisson generalized linear mixed model (ZIP GLMM) with litter size as the response variable. The zero-inflated part models probability to reproduce with a logit-link binomial distribution, while the count part models litter size with a Poisson distribution. Fox ID and year were fitted as random effects on the count part of the model. Fixed effects fitted for each part are shown within the table (n = 70). Model reference values are lemming density = high and access to colony = yes.

Model part	Fixed effect	Estimate [95% CI]	SE	z value	p value
zero-inflated	(Intercept)	-2.32 [-3.63, -1.01]	0.67	-3.47	<0.001
zero-inflated	lemming density	2.25 [0.87, 3.64]	0.71	3.18	<0.001
zero-inflated	colony	1.16 [-0.15, 2.47]	0.67	1.73	0.08
count	(Intercept)	1.90 [1.67, 2.14]	0.12	15.96	<0.001
count	lemming density	-0.86 [-1.34, -0.38]	0.24	-3.53	<0.001
count	distance first turnaround	0.07 [-0.11, 0.26]	0.09	0.80	0.43
count	lemming density: distance first turnaround	-1.20 [-1.96, -0.44]	0.39	-3.09	0.002
count	colony	0.16 [-0.19, 0.50]	0.17	0.89	0.37
count	age	0.99 [0.28, 1.69]	0.36	2.74	0.006
count	age^2	-1.05 [-1.72, -0.38]	0.34	-3.08	0.002

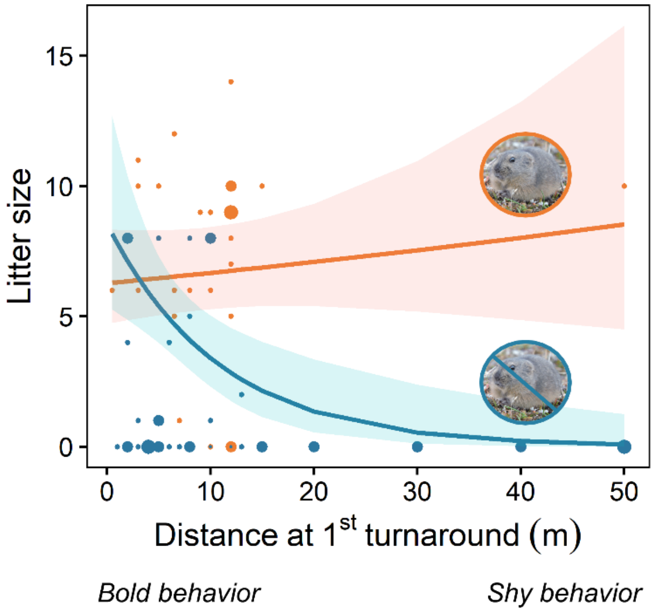


Figure 4. 3 Arctic fox litter size as a function of distance at first turnaround (m) and lemming density (orange = high density, blue = low density), as estimated by the zero-inflated Poisson GLMM (n = 70). Levels of boldness (from bold to shy behavior) associated to distances at first turnaround are indicated in italics below the x axis. The size of points indicates the number of observations (1, 2 or 3 observations).

4.7 Discussion

Boldness in animals is often advantageous on the short term as it increases annual reproductive success (Smith & Blumstein, 2008). Temporal variation in environmental conditions may however affect the strength and direction of relationships between behavioral and life-history traits. We indeed found a positive effect of boldness on the litter size of Arctic foxes, but most importantly, this effect depended on the availability of a main prey. When lemmings were scarce, foxes behaving boldly had larger litter sizes than foxes behaving less boldly, but this positive effect of boldness disappeared when lemmings were abundant, when foxes overall tented to produce larger litters and to exhibit bold behavior. In agreement with Choi et al. (2019), our data also pointed to among-individual differences in boldness in Arctic fox, but our small sample size did not allow to statistically demonstrate that foxes differed consistently in their boldness through time. We also found no effect of individual characteristics on boldness, such as sex, age and mass, which stresses the need to identify the sources of variation in the boldness of predators.

4.7.1 Weak evidence for consistent among-individual differences in boldness among years

Although males are sometimes bolder than females (Schuett et al., 2010; DeRango et al., 2019), this difference may be more pronounced in sexually dimorphic species compared to monomorphic ones such as the Arctic fox, where sex did not explain variation in boldness after handling. Furthermore, although older individuals are usually bolder than younger individuals, which have a higher residual reproduction value (Dammhahn, 2012; Bubac et al., 2018), this effect may be more evident when comparing juveniles to adults than when comparing adults of various ages. We also did not observe any effect of body mass on escape behavior after handling, suggesting body size and condition may not influence boldness in Arctic foxes. However, we could not distinguish the effects of size and condition, and body condition alone could be a better predictor of boldness (Moiron et al., 2019; Moran et al., 2021). Lastly, the number of times individuals were captured did not explain boldness, suggesting that foxes did not habituate to captures and manipulations, which is not surprising given that recaptures were rare and mostly occurred among years. The lack of effect of sex, age, mass and capture number on Arctic fox boldness should however be confirmed using larger sample sizes.

Choi et al. (2019) observed important within-year among-individual differences in the boldness of Arctic fox, estimating a repeatability of 0.66 CI: [0.19, 0.86]. In our study, among-individual variation explained 19% of the variation (adjusted repeatability) in Arctic fox boldness after handling, but the confidence interval was large and included zero. Whether Arctic foxes from our population show consistent among-individual differences in boldness among and within years should therefore be confirmed using larger sample sizes. The first possible explanation as to why we observed a low repeatability in boldness is that we replicated measures mostly among years (21 of 29 replicates), and personality traits such as boldness are expected to be less repeatable between than within years (Araya-Ajoy et al., 2015). More replicate measures of fox boldness within the same year might yield repeatability estimates equivalent to those found for Arctic foxes by Choi et al. (2019) and also for kit foxes (*Vulpes macrotis mutica*) by Bremner-Harrison et al. (2018). Second, measures obtained upon capture, although useful when studying species hard to observe, may be prone to sampling biases that can reduce the range of possible behaviors and thus among-individual variation and repeatability estimates (Biro & Dingemanse, 2009; Biro, 2013). For example, the shyest individuals are usually less likely to be trapped than the boldest ones (Réale et al., 2000). In addition, if a boldness-aggressiveness behavioral syndrome was present in the population (Sih et al., 2004), we may have excluded the boldest foxes from the study, as they were possibly the most aggressive and thus the most likely to be anesthetized. Finally, as illustrated in Figure 4.2, only some individuals seemed consistent in their distance at first turnaround. Individuals with the shiest reactions overall showed more variation in their escape behavior, suggesting a correlation between behavioral type and level of consistency (shy individuals being more plastic) (Dingemanse et al., 2010). Nevertheless, our results represent an important step forward as very few studies have evaluated the effect of individual characteristics and consistent among-individual differences on the boldness of canid species or other high-trophic level predators, possibly because they are so difficult to observe and capture in large numbers.

4.7.2 Prey availability determines the effect of boldness on reproductive success

Variation in prey abundance strongly influenced the relation between boldness and litter size. When lemming density was low, foxes showing shy reactions produced no pup whereas foxes showing bold reactions had up to 8 pups. Our measure of boldness could relate to risk-taking while foraging (e.g., Dammhahn & Almeling, 2012), where boldness may facilitate energy acquisition during reproduction, but this remains to be tested. Acting boldly may allow foxes to acquire lemmings, birds, and eggs at higher rates, for example by hunting lemmings closer to territory edges or by attacking more often adult geese despite their aggressive nest defense (Bêty et al., 2002). Our model predicted a positive effect of the access to the goose colony on the probability to reproduce but the evidence was weak ($p = 0.08$, Table 4.1), probably because of our low sample size compared to the study of Chevallier et al. (2020). Our results further suggest that access to the goose colony does not affect litter size. However, such an effect on litter size may depend on lemming density, and we did not test the interaction between lemming density and the access to the colony to avoid using more degrees of freedom. Based on our work, further investigations with larger sample sizes will allow the robust test of clear predictions regarding how the access to the goose colony interacts with lemming density and fox boldness to determine fox litter sizes.

Bold foxes may also be the most active and the ones with higher exploratory tendencies (Sih et al., 2004; Mazué et al., 2015). Greater activity and exploration levels may allow foxes to find alternative types of food when lemmings are scarce, thus increasing food intake. Importantly, exploration on the sea ice allows foxes to find alternative prey such as marine mammals (Gagnon & Berteaux, 2009; Tarroux et al., 2012; Lai et al., 2015). In contrast, foxes showing a low level of boldness may not be able to access such alternative resources and may thus not be able to reproduce when lemmings are scarce. So far, only a handful of studies have associated predator behavioral types to their foraging performances, using laboratory or mesocosm experiments (e.g., Ioannou et al., 2008; Chang et al., 2017).

Furthermore, how hunting abilities explain reproductive success of high-trophic level predators is also largely unknown (but see Jeanniard-du-Dot et al., 2017). For species occupying lower trophic levels, such as insectivorous birds, parental food provisioning mediates the relationship between personality and reproductive success (Mutzel et al., 2013; Thys et al., 2021). A better understanding of how predator behavioral types affect prey capture rates in the wild is required to identify pathways linking behavioral and life-history traits, thus enlightening ecological and evolutionary consequences of variation in the behaviors of predators. This may become possible using sophisticated technologies, such as GPS combined with accelerometers, which might allow detailed assessments of predator behaviors (Hertel et al., 2020; Clermont et al., 2021b) and estimation of kill rates (Studd et al., 2021), combined with detailed monitoring of individuals' life-history.

We found no evidence for reproductive benefits of higher boldness level under high food abundance. This underlines the importance of lemmings for the successful reproduction of (all) Arctic foxes. We should however be cautious in interpreting the lack of relation between boldness and litter size during years of high lemming density, as during those years, all observations but one showed bold behavior, thus resulting in a large confidence interval for large distances to first turnaround values (Figure 4.3, right part of the orange area). Again, a larger sample size would be necessary to confirm that litter size does not vary with boldness under high prey abundance. The fact that most foxes exhibited bold behavior when resources were abundant is also interesting in itself as it suggests that 1) foxes may have responded to the high lemming abundance by adopting bolder behaviors, or 2) boldness is state-dependent. Future studies should investigate whether predators show plastic responses and adjust their boldness with environmental conditions such as prey availability, or if boldness actually depends on reproductive output (i.e., the state) and not the other way around as we assume in this manuscript.

Overall, our results suggest that temporal environmental variation determines the relationship between a behavioral and life-history trait of a predator. Assuming Arctic fox level of boldness is repeatable within years (Choi et al., 2019), boldness brings reproductive advantages to Arctic foxes under low prey availability, potentially because it allows them to acquire more food or alternative resources when their main prey is scarce. Given our results, we could expect positive selection on Arctic fox boldness, with selection strength fluctuating in time. However, bolder Arctic foxes may suffer survival costs, while shyer foxes may save energy by skipping reproduction during years of low food abundance, which could increase their lifespan and lifetime reproductive success. Testing this hypothesis will be challenging as it requires repeated measures of multiple traits for many individuals, ideally over their entire lifespan. However, such a test would greatly increase our understanding of the mechanisms leading to the maintenance of personality differences in animal populations.

4.8 Declarations

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Conflict of interest: The authors declare no conflict of interest.

Ethical approval: Capture techniques and immobilisation procedures were approved by the UQAR Animal Care Committee (CPA-64-16-169), and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada (SIR-2018-28021).

Data Availability: The dataset will be made available upon acceptance on Dryad repository at https://doi.org/10.5061/dryad.zcrjdfngj. It is temporarily available for review at https://datadryad.org/stash/share/pV2S8Tg6WqU7AOI-PIkrCfLRJoAkI_OSEvPEvvdSS38

4.9 Acknowledgments

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CONCLUSION

La prédation joue un rôle central dans les processus écologiques en affectant la dynamique et la croissance des populations de proies (Menge & Sutherland, 1976). En plus des effets létaux de la prédation, le paysage du risque de prédation résultant du paysage physique et de l'activité des prédateurs engendre des changements phénotypiques chez les proies, qui modifient leurs comportements afin d'éviter la prédation (Fortin et al., 2005; Valeix et al., 2009; Laundré et al., 2010; Gaynor et al., 2019). Ces réponses comportementales des proies au risque de prédation peuvent être coûteuses et générer des effets non létaux en affectant l'aptitude phénotypique des individus et la dynamique des populations (Cresswell, 2008; Teckentrup et al., 2018; Peacor et al., 2022). Les mécanismes qui génèrent les effets non létaux sont cependant moins bien compris que ceux générant les effets létaux (Gaynor et al., 2019; Peacor et al., 2020, 2022), c'est pourquoi il demeure essentiel d'étudier les effets du risque de prédation au sein des communautés animales. Les résultats du Chapitre 1 de cette thèse montrent notamment comment les patrons de mouvement d'un prédateur actif, le renard arctique, génèrent un paysage du risque de prédation, et influencent les comportements anti-prédateurs et la répartition d'espèces aviaires nichant à l'île Bylot au Nunavut.

Identifier ce qui génère la variation dans les comportements des prédateurs, comme le degré de territorialité (Lewis & Murray, 1993) et la personnalité (Sih et al., 2012), permet également de mieux comprendre comment ceux-ci influencent le paysage du risque de prédation qui affecte les proies. Cependant, les méthodes pour étudier les comportements de prédateurs cryptiques sont limitées. Une solution réside dans l'analyse de données de mouvement récoltées à fine échelle spatiale et temporelle, qui permet d'identifier des comportements clés liés à la prédation (Knopff et al., 2009; Wang et al., 2015; Studd et al., 2021). Au Chapitre 2, je montre comment la classification de données d'accélérométrie a permis l'identification de comportements alimentaires des renards arctiques, et je discute également du potentiel de notre classification pour étudier les effets du risque de prédation. Le Chapitre 3 a ensuite permis d'explorer le rôle de la territorialité au sein du contexte écologique du paysage de la peur. Nous avons notamment trouvé que les individus non territoriaux ajustent leurs comportements de prédation dans leur domaine vital, en évitant de rechercher et de cacher leurs proies dans les zones où la probabilité de rencontrer un voisin est élevée. Finalement, au Chapitre 4, nous trouvons que la témérité des renards arctiques influence leur succès reproducteur lorsque leurs proies principales sont peu abondantes. Cette étude montre l'importance écologique et évolutive de la témérité chez ce prédateur actif, une étape permettant d'éventuellement mesurer l'effet de la personnalité des prédateurs au sein du contexte écologique du paysage de la peur.

5.1 Contributions principales

Au Chapitre 1, nous avons montré que la variation spatiale dans l'intensité d'utilisation de l'espace d'un prédateur actif détermine le paysage du risque de prédation, et structure une communauté de proies en influençant les comportements et la répartition des oiseaux nicheurs. L'utilisation de données de mouvement récoltées à haute fréquence a permis de caractériser un paysage de l'activité des prédateurs à fine échelle spatiale. Nous avons ensuite montré à l'aide d'une expérience de proies artificielles que l'intensité de l'utilisation de l'espace par un prédateur actif, le renard arctique, était reliée au risque de prédation. Nous avons donc pu estimer précisément la répartition du risque de prédation dans notre aire d'étude, ce qui est essentiel pour mesurer les effets du risque sur les comportements des proies. Dans cette évaluation du contexte écologique du paysage de la peur, nous avons également bénéficié d'un système d'étude simple où le renard arctique est le prédateur principal de la grande majorité des proies (McKinnon & Bêty, 2009; Gauthier et al., 2011). En effet, les liens unissant les paysages physique, de l'activité des prédateurs, du risque de prédation, et des réponses comportementales des proies peuvent être plus complexes et difficiles à identifier dans des systèmes où les proies ont plusieurs prédateurs principaux qui génèrent des paysages du risque contrastés (Thaker et al., 2011; Cresswell & Quinn, 2013; Lone et al., 2014).

Globalement, nos résultats illustrent comment l'effet des prédateurs sur les populations de proies dépassent ceux résultant de la prédation d'individus, puisque les mouvements des prédateurs influencent également comment les proies se comportent et utilisent leur habitat. Le Chapitre 1 s'ajoute ainsi aux nombreuses études montrant les effets du risque de prédation sur les comportements des proies (Laundré et al., 2001; Valeix et al., 2009; Arias-Del Razo et al., 2012; Kohl et al., 2018). Cependant, les études ayant évalué les effets du paysage de la peur en le considérant dans son contexte écologique sont rares (mais voir Suraci et al., 2019), bien qu'elles permettent une meilleure compréhension des mécanismes qui expliquent les effets du risque de prédation sur les proies (Gaynor et al., 2019). En effet, en plus de considérer l'importance des mouvements des prédateurs, nous avons considéré dans cette étude comment le paysage physique influence la répartition du risque de prédation, notamment par la création de micro-habitats refuges. Nos résultats suggèrent que les individus d'espèces aviaires de Bylot qui nichent sur des îlots peuvent ignorer le risque de prédation qui entoure l'îlot lorsqu'ils sélectionnent ce dernier pour nicher, puisqu'ils évitent déjà le risque de prédation à l'échelle du micro-habitat. À l'opposé, nos résultats suggèrent que les oiseaux nichant en milieu facilement accessible aux renards considèrent le risque de prédation dans l'ensemble de l'habitat qui entoure le nid lors de la sélection du site de nidification. En effet, l'utilisation de tactiques pour éviter la prédation (par ex. fuite, défense, utilisation de refuge) permet aux proies d'occuper des habitats qui sont fortement utilisés par leurs prédateurs, alors que les proies n'utilisant pas ces tactiques et qui sont donc plus vulnérables à la prédation devraient tendre à éviter les zones les plus utilisées par leurs prédateurs (Wirsing et al., 2010). Notre considération des micro-habitats dans le paysage physique met également en évidence que les proies peuvent répondre au risque de prédation en sélectionnant des habitats à différentes échelles spatiales (Suraci et al., 2022). Finalement, nous avons également considéré la diversité des réponses comportementales des proies face au risque de prédation en évaluant une réponse réactive, la défense du nid à l'approche d'un prédateur potentiel, et une réponse proactive, le choix de site de nidification. En effet, peu d'études ont considéré ces différents types de réponses dans une seule et même étude (mais voir aussi Creel et al., 2014; Gehr et al., 2018), une approche qui permet pourtant de mettre en valeur la diversité des effets du risque de prédation sur les proies. Il faut cependant noter qu’en plus du paysage du risque de prédation, la prédation elle-même a pu influencer la répartition des nids au moment où nous l’avons évaluée, puisque les nids situés dans des zones très fréquentées par les renards peuvent avoir été prédatés avant que nous ne les ayons détectés.

En plus de la considération des patrons de mouvements des prédateurs actifs, l’identification des évènements de prédation des prédateurs permettrait de mieux définir le paysage du risque de prédation. Par contre, les méthodes couramment utilisées pour identifier et quantifier les évènements de prédation sont difficilement applicables aux prédateurs actifs qui se nourrissent de petites proies (Petroelje et al., 2020), comme le renard arctique. Au Chapitre 2, bien que nous n’ayons pas réussi à identifier directement les évènements de prédation des renards, nous avons montré qu’il était possible d’identifier des comportements associés à la prédation chez ce prédateur à partir d’une classification comportementale de données d’accélérométrie, puisque certains comportements de prédation des renards génèrent un patron d’accélération distinct. Plus spécifiquement, nous avons identifié les évènements de creusage, qui sont principalement associés aux caches de proies. En effet, l’utilisation d’un algorithme d’apprentissage supervisé (Resheff et al., 2014), entraîné pour reconnaître des comportements d’une durée minimale de 3 secondes dans notre cas, a limité notre capacité à identifier des comportements très courts (moins de 3 secondes) et difficilement observables (voir Wang (2019) et Chakravarty et al. (2020) pour une discussion sur les limites de cette méthode), tels les évènements de prédation de lemmings ou de capture d’œufs. Cependant, puisque les renards cachent la majorité des œufs d’oies qu’ils capturent durant l’été (Careau et al., 2007, 2008b), notre classification pourrait éventuellement permettre d’estimer l’intensité de la prédation effectuée par les renards dans différentes zones du site d’étude en quantifiant le nombre d’évènements de cache de proies effectués par les renards. Globalement, notre classification montre le potentiel de l’accélérométrie pour l’identification de comportements de prédation, et représente un progrès pour l’identification directe des évènements de prédation à partir de données de mouvement chez une grande diversité de prédateurs.

La classification comportementale des données d'accélérométrie a également servi à évaluer au Chapitre 3 l'effet des interactions intraspécifiques sur les comportements de quête alimentaire des renards. En suivant les mouvements et les comportements d'individus voisins, et grâce à une méthode statistique développée récemment (Noonan et al., 2021), nous avons pu définir la répartition des probabilités de rencontrer des voisins au sein des domaines vitaux. Nous avons trouvé que la répartition des comportements de prédation des renards dépendait de celle des probabilités de rencontrer un voisin, mais seulement chez les individus non territoriaux, qui recherchent et cachent leurs proies plus fréquemment lorsqu'ils se trouvent dans des zones où la probabilité de rencontrer un voisin est faible. Contrairement aux individus territoriaux qui sécurisent des ressources en excluant les autres individus d'une partie de leur domaine vital, nous suggérons que les individus non territoriaux pourraient utiliser une tactique alternative pour sécuriser des ressources en ajustant leurs comportements de quête alimentaire à leur environnement social. Notre étude ne comprenant que 13 individus, ces résultats devront être validés avec un plus grand échantillon de renards.

À ce jour, peu d'études se sont intéressées à comment la territorialité et les interactions intraspécifiques influencent les comportements alimentaires des prédateurs (mais voir Kauffman et al., 2007). Pourtant, identifier les déterminants des comportements des prédateurs est essentiel pour définir le paysage du risque de prédation et ultimement mieux comprendre les effets du paysage de la peur sur la dynamique des populations de proies. En effet, le risque de prédation pourrait varier au sein des domaines vitaux des prédateurs. Puisque nous trouvons que seulement les renards arctiques non territoriaux modifient leurs comportements alimentaires en fonction de la probabilité de rencontrer un voisin, et que seulement 3 sur 13 individus étudiés étaient non territoriaux, on ne peut conclure sur l'importance générale de nos résultats pour notre compréhension des interactions trophiques à Bylot. En revanche, nos résultats montrent que la variation dans le degré de territorialité des prédateurs peut influencer la répartition du risque de prédation à une échelle spatiale un peu plus grande que celle d'un domaine vital, soit au niveau de plusieurs domaines vitaux adjacents. En effet, la présence d'individus non territoriaux dont les domaines vitaux chevauchent ceux de leurs voisins territoriaux augmente la densité locale de prédateurs, et donc potentiellement le risque local de prédation (Chapitre 1). Des études effectuées à Bylot expliquent que la prédation d’espèces de proies accidentelles est plus grande dans la colonie d’oies des neiges qu’à l’extérieur de celle-ci, car les renards sont présents en plus grande densité dans la colonie qu’à l’extérieur, du fait qu’ils utilisent des domaines vitaux plus petits et qui se chevauchent davantage (Lai 2017; Duchesne et al., 2021; Beardsell et al., 2022a). À cette explication pourrait s’ajouter le fait qu’un plus grand nombre d’individus non territoriaux sont présents dans la colonie, mais ceci reste à démontrer.

En plus de son degré de territorialité, la personnalité d’un prédateur pourrait avoir un impact sur les interactions prédateurs-proies puisqu’elle pourrait influencer sa capacité à obtenir des proies (Sih et al., 2012), et donc moduler la répartition du risque de prédation. Pour cette raison, nous avons tenté d’évaluer la présence de différences interindividuelles dans la témérité des renards arctiques au Chapitre 4, et d’identifier les variables écologiques qui pourraient favoriser le maintien de ces différences. Nous avons évalué l’importance adaptative de la témérité chez les renards en mesurant l’effet de ce trait sur la taille de portée, tout en considérant les variations temporelles dans l’abondance en lemmings, la proie principale des renards. Les résultats du Chapitre 4 montrent que la témérité serait avantageuse pour les renards arctiques lorsque les ressources sont peu abondantes, puisqu’elle est associée à un plus grand succès reproducteur. Ceci suggère que la témérité chez le renard arctique pourrait donner accès à des ressources alternatives qui assurent le succès de la reproduction. Cependant, quand les ressources sont abondantes, tous les renards produisent un grand nombre de jeunes. Ces résultats sont importants puisqu’ils montrent que la fluctuation temporelle dans l’abondance des ressources influence l’effet de la témérité sur le succès reproducteur. La force de la sélection qui agit sur la témérité pourrait donc dépendre de l’abondance en lemmings. Notre étude s’ajoute ainsi à quelques autres ayant évalué comment la relation entre un trait de personnalité et un trait d’histoire de vie fluctue selon le contexte environnemental (Boon et al., 2007; Dingemanse et al., 2004; Le Cœur et al., 2015; Mouchet et al., 2021).

Nous avons également observé que les renards arctiques de Bylot montraient différents niveaux de témérité lorsque relâchés à la suite d’une capture et des manipulations associées. Bien que notre taille d’échantillon ne fût pas suffisante pour évaluer si ces différences interindividuelles étaient constantes entre les années, notre étude constitue une avancée intéressante, puisque les traits de personnalité des mammifères prédateurs terrestres ont encore été très peu évaluées en milieu naturel (Yoshida et al., 2016; Bremner-Harrison et al., 2018), surtout en lien avec le succès reproducteur. En effet, les prédateurs sont souvent cryptiques et vivent à faible densité, limitant notre capacité à observer les comportements de plusieurs individus à plusieurs reprises, ou d’estimer précisément des traits d’histoire de vie comme la fécondité. Les recherches liant la personnalité des prédateurs à leur valeur sélective ont donc un fort potentiel scientifique. De plus, la difficulté d’observer les prédateurs nous oblige à évaluer le degré de témérité des individus en contexte peu naturel, par exemple lors de tests à la suite d’une capture (Bremner-Harrison et al., 2018; Choi et al., 2019). Malheureusement, les comportements qui sont alors mesurés peuvent ne pas correspondre à des comportements naturels chez l’espèce (Carter et al., 2013, mais voir Dammhahn & Almeling, 2012). Dans le cas de notre étude, mesurer l’association entre les mesures de témérité post-capture des renards arctiques et leur prise de risque en milieu naturel permettrait une interprétation plus claire de nos résultats.

5.2 Perspectives de recherche

Je présente ici quatre suites possibles à ce projet de thèse qui offrent un fort potentiel d’avancement des connaissances. Dans chacun des cas, je propose comment les recherches pourraient être appliquées au système d’étude de l’île Bylot.

5.2.1 Modèles mécanistiques des interactions entre prédateurs et proies

Les données d’accélérométrie récoltées à haute fréquence et de manière régulière permettent d’établir des budgets d’activité détaillés (Nathan et al., 2012; Wang et al., 2015). L’identification directe des évènements de prédation à partir de données de mouvement permettent aussi de mesurer des métriques telles que le taux d’acquisition de proies, qui sont essentielles pour mieux établir les relations prédateurs-proies et comprendre la structure des réseaux trophiques (Vucetich et al., 2011; Studd et al., 2021). En effet, les données résultant de suivis de mouvement à fine échelle spatiale et temporelle apportent des informations précises sur les comportements des prédateurs, et ces données empiriques peuvent notamment être utilisées pour développer des modèles mécanistiques des interactions prédateurs-proies. Dans le système d'étude de l'île Bylot, des progrès ont déjà été réalisés dans cette direction. En effet, en plus d'apporter des informations nouvelles sur les patrons d'activité des renards, les budgets d'activité que j'ai générés au Chapitre 2 ont permis de paramétrer des modèles mécanistiques de la réponse fonctionnelle (soit le taux d'acquisition de la proie par le prédateur selon la densité de la proie) entre le renard arctique et diverses espèces de proies à Bylot (PhD Andréanne Beardsell, UQAR). Ces modèles ont notamment montré que les changements comportementaux des renards pouvaient expliquer une partie de l'effet positif de la densité de lemmings sur les oiseaux nicheurs, en plus d'aider plus globalement à mieux comprendre les interactions indirectes qui unissent les espèces de proies qui partagent le renard arctique comme prédateur principal (Beardsell et al., 2022a, 2022b). Afin de pousser nos recherches encore plus loin, il sera essentiel de continuer de développer la classification des données d'accélérométrie en comportements plus fins, et d'identifier directement les évènements de capture de différents types de proies (lemmings, œufs d'oies ou de d'autres espèces d'oiseaux) par les renards. Ceci permettra d'estimer plus précisément les métriques qui définissent la prédation des renards sur différentes espèces de proies dans la communauté de l'île Bylot, et d'en apprendre davantage sur la manière dont la prédation structure les communautés animales.

5.2.2 Effets du risque de pédation sur l'aptitude phénotypique et la dynamique des populations de proies

Les effets de la prédation sur les populations de proies dépassent ceux qui résultent de la mortalité par prédation. En effet, le risque de prédation généré par le paysage physique et les comportements des prédateurs influencent aussi comment les proies se répartissent dans l'espace et se comportent (Figure 0.1, Gaynor et al., 2019). De même, ils influencent également d'autres traits physiologiques, morphologiques et d'histoire de vie des proies (Zanette et al., 2006; Dunn et al., 2010). Comme pour les effets létaux, ces modifications phénotypiques peuvent influencer la survie et la reproduction des proies et leur dynamique de population (Figure 5.1, Sheriff et al., 2020). Certains soutiennent même que les effets non létaux de la prédation sur les dynamiques de populations de proies sont plus importants que les effets létaux (Preisser et al., 2005). Cette affirmation est couramment répétée dans la littérature (Sheriff et al., 2020). Pourtant, très peu d'études ont mesuré l'effet des réponses des proies au risque de prédation sur l'aptitude phénotypique des individus proies, ainsi que le taux de croissance ou l'abondance de leurs populations (Sheriff et al., 2020; Peacor et al., 2022). Peacor et al. (2022) ont révisé près de 4000 études publiées entre 1990 et 2018 qui traitent des effets du risque de prédation, et ont trouvé que 81% d'entre elles évaluaient seulement les effets du risque sur les réponses phénotypiques des proies (lien A de la Figure 5.1). C'est notamment le cas de mon étude présentée au Chapitre 1. Ensuite, seulement 19% des études ont évalué l'effet de ces changements phénotypiques sur une mesure de l'aptitude phénotypique des proies (lien B) ou sur la croissance ou abondance de la population de proies (liens C et D), et seulement 7% de ces études ont mesuré ces processus dans une population exempte de manipulations en milieu naturel. Les auteurs arrivent donc à la conclusion que les évidences actuelles ne permettent pas de soutenir que les effets non létaux de la prédation sur la dynamique des populations de proies sont répandus et ont une grande importance écologique et évolutive (Peacor et al., 2022).

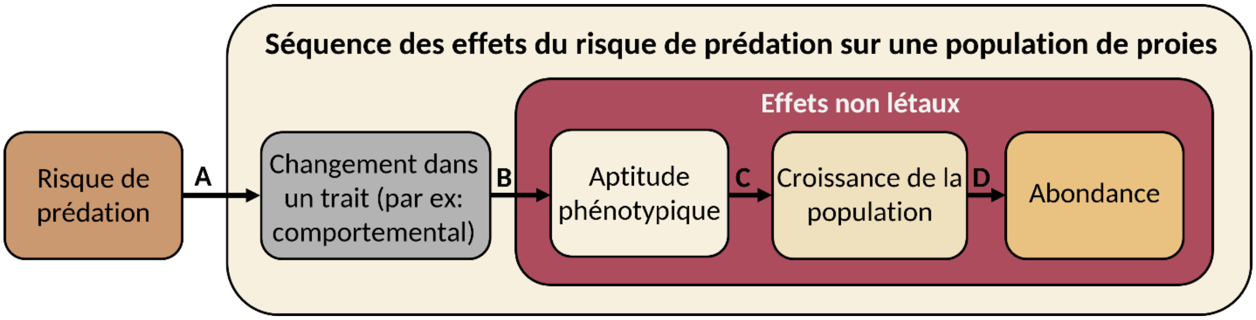

Figure 5. 1 Séquence des effets du risque de prédation sur une population de proies. Le risque de prédation résulte en un changement phénotypique chez les proies, qui modifient par exemple leurs comportements (lien A). Ces changements phénotypiques peuvent générer des effets non létaux de la prédation, en affectant des composantes de l'aptitude phénotypique des proies comme leur survie et leur reproduction (lien B), la croissance de leurs populations (lien C) ou leur abondance (lien D). Figure modifiée de Peacor et al. (2022).

Mesurer les effets du risque de prédation jusqu'aux changements dans les paramètres démographiques des populations permettrait de mieux évaluer l'importance des effets du risque de prédation sur la structure et le fonctionnement des communautés. Par exemple, les wapitis (*Cervus elaphus*) qui partagent leur habitat avec des loups répondent à la présence de ce prédateur entres autres en augmentant le temps passé en vigilance, en diminuant le temps passé à s'alimenter et en utilisant des habitats moins favorables (résultats d'études révisées dans Creel et al., 2009). Creel et al. (2009) ont par la suite montré que ces changements comportementaux entraînent une réduction du succès producteur et de la taille de population de wapitis qui cohabitent avec les loups, et donc des effets non létaux. Møller et al. (2016) ont quant à eux trouvé qu'une augmentation de la taille d'une population d'autour des palombes (*Accipiter gentilis*) avait des effets non létaux sur une population de pigeon colombin (*Columba oenas*). Spécifiquement, les dates de ponte plus retardées et une plus grande proportion d'œufs ne se rendaient pas à l'éclosion, suggérant une plus basse fertilité, et diminuant ainsi le taux de recrutement dans la population. À l'île Bylot, une diminution proactive du risque de prédation par les oiseaux, qui établissent leur nid là où les renards sont les moins présents, serait en effet bénéfique à court terme en réduisant le risque de prédation du nid. Cette réponse comportementale pourrait cependant engendrer des coûts à plus long terme (effets non létaux) notamment si les individus modifient aussi leurs comportements de reproduction. Pour vérifier cette hypothèse, on pourrait suivre les nids d'oiseaux nichant dans des endroits plus ou moins utilisés par les renards arctiques, qui sont associés à des risques de prédation plus ou moins élevés (Chapitre 1), et évaluer l'effet de l'intensité de l'utilisation de l'espace par les renards au site de nidification sur des traits qui affectent le succès reproducteur des oiseaux, comme la date de ponte, tout en considérant les variables confondantes dans un modèle multivarié. On pourrait ensuite vérifier si cette baisse du succès reproducteur affecte le taux de recrutement dans la population.

5.2.3 Variation temporelle du paysage de la peur

Tel que présenté dans le cadre conceptuel du contexte écologique du paysage de la peur, le risque de prédation varie spatialement et influence la répartition et les comportements des proies qui naviguent dans le paysage (Gaynor et al., 2019). En plus de varier dans l'espace, le risque de prédation peut varier temporellement et générer un paysage de la peur dynamique, par exemple lorsque les prédateurs ont un cycle d'activité journalier, ou changent de façon saisonnière ou intra-saisonnière l'intensité de leurs activités de prédation (Palmer et al., 2017, 2022). Ignorer la dimension temporelle du paysage de la peur peut limiter notre capacité à mesurer les effets du risque de prédation (Suraci et al., 2022). Les proies peuvent en effet répondre au paysage de la peur dynamique en ajustant leurs activités à celles des prédateurs, et utiliser les zones où les ressources qu'elles recherchent sont abondantes, mais où le risque de prédation est élevé, aux périodes où les prédateurs sont les moins actifs (Kohl et al., 2018; Smith et al., 2019b). Les ajustements comportementaux temporels des proies pourraient même expliquer l'absence d'effets non létaux de la prédation, puisque les proies pourraient parvenir à utiliser les habitats les plus favorables à leur alimentation lors de périodes où le risque de prédation est temporairement diminué (Palmer et al., 2022). La variation temporelle du risque de prédation et des réponses des proies n'a que rarement été considérée dans les études traitant des effets du paysage de la peur, qui considèrent généralement le paysage du risque de prédation comme temporellement statique pendant la période étudiée (Palmer et al., 2022). La prise en compte des aspects temporels ouvre donc une piste de recherche qui pourrait être très productive.

Le risque de prédation peut varier au courant de la journée, entre le jour et la nuit, selon le cycle lunaire, entre les saisons, ou au long du cycle vital du prédateur, et influencer les patrons de mouvement des proies (Palmer et al., 2017, 2022). Pour les espèces aviaires qui viennent nicher à l'île Bylot l'été, la variation spatiale du risque de prédation pourrait influencer la sélection du site de nidification (Chapitre 1). Une fois le site de nidification sélectionné, les individus de certaines espèces, comme l'oie des neiges, demeurent relativement immobiles à proximité de leur nid, mis à part lors de courtes excursions pour s'alimenter et s'abreuver (Poussart et al., 2001). Ces oiseaux pourraient potentiellement répondre au paysage de la peur dynamique en synchronisant les moments où ils quittent le nid avec les périodes où les renards sont les moins actifs. De plus, le risque de prédation pourrait varier sur une plus grande échelle temporelle, soit entre les années, selon les phases du cycle d'abondance des lemmings. En effet, la pression de prédation exercée par le renard sur les espèces aviaires de Bylot est supérieure quand les lemmings sont peu abondants (Bêty et al., 2002; McKinnon et al., 2013; Lamarre et al., 2017). Les oiseaux pourraient percevoir la variation interannuelle du risque de prédation associée au cycle d'abondance des lemmings. Au Chapitre 1, nous avons mesuré l'effet du paysage de l'activité des prédateurs sur les comportements anti-prédateurs et la répartition des proies lors d'une seule année, pendant laquelle les lemmings étaient modérément abondants (137 lemmings/km^2 en 2019). Nous pourrions tester l'hypothèse selon laquelle l'intensité des réponses comportementales des proies varie selon l'abondance annuelle en lemmings en répétant l'étude du Chapitre 1 lors d'années à faible et forte abondance de lemmings. Lorsque les lemmings sont en faible abondance, et que la prédation exercée sur les oiseaux est la plus forte, on pourrait s'attendre à ce que les effets observés au Chapitre 1 soient plus importants. Notamment, quand il y a peu de lemmings, les oies des neiges qui nichent dans une zone fortement utilisée par les renards pourraient défendre leur nid de façon encore plus intense qu'observé en 2019, puisqu'un nid laissé sans surveillance aurait d'encore plus fortes chances de se faire prédater par un renard. L'évitement proactif du risque pourrait aussi être plus important, et les nids d'oiseaux pourraient donc être encore plus abondants qu'en 2019 dans les zones moins utilisées par les renards.

5.2.4 Personnalité spatiale et effets sur le risque de prédation

De plus en plus d'études montrent qu'il existe des spécialisations individuelles dans les mouvements au sein des populations de différentes espèces de vertébrés, suggérant que des composantes du mouvement pourraient représenter une facette de la personnalité animale (Spiegel et al., 2017; Hertel et al., 2020; Stuber et al., 2022). Les individus montreraient différentes personnalités spatiales (en anglais *spatial personality*, introduit par Stuber et al., 2022), par exemple lorsqu'ils diffèrent dans leur taux de mouvement (Hertel et al., 2019), dans leur patron d'activité journalier (Hertel et al., 2017), dans les ressources qu'ils sélectionnent (Leclerc et al., 2016) ou dans des comportements liés à la quête alimentaire (Patrick et al., 2014). Stuber et al. (2022) soutiennent que de considérer les personnalités spatiales des individus étudiés, plutôt que de considérer ces derniers interchangeables, change notre compréhension de processus écologiques comme la transmission de pathogènes ou les interactions interspécifiques. Chez les renards arctiques de l'île Bylot, on observe notamment des différences interindividuelles importantes dans les distances parcourues par jour pendant l'été 2019, telles que montrées à la Figure 5.2 (n = 303 jours, pour 14 individus avec 22 ± 9 (SD) jours par individu). J'obtiens également une forte répétabilité de 0.74 CI : [0.50, 0.85] pour ce jeu de données (calculée selon Stoffel et al., 2017). Certains individus ont parcouru dans une journée plus du double de la distance parcourue par d'autres renards. La manière dont un individu se déplace et utilise l'habitat peut également dépendre de traits de personnalité indépendants du mouvement, comme la témérité ou l'agressivité (Chapman et al., 2011; Patrick & Weimerskirch, 2014; Spiegel et al., 2015). Des différences de personnalité dans la témérité (Chapitre 4) pourraient notamment expliquer les fortes différences interindividuelles dans les distances journalières parcourues par les renards, en plus d'autres facteurs comme la taille du territoire, la qualité de l'habitat, le sexe et le statut reproducteur. Ceci fera l'objet d'une analyse future incluant des données de mouvements pour plus de 40 individus pendant 4 étés.

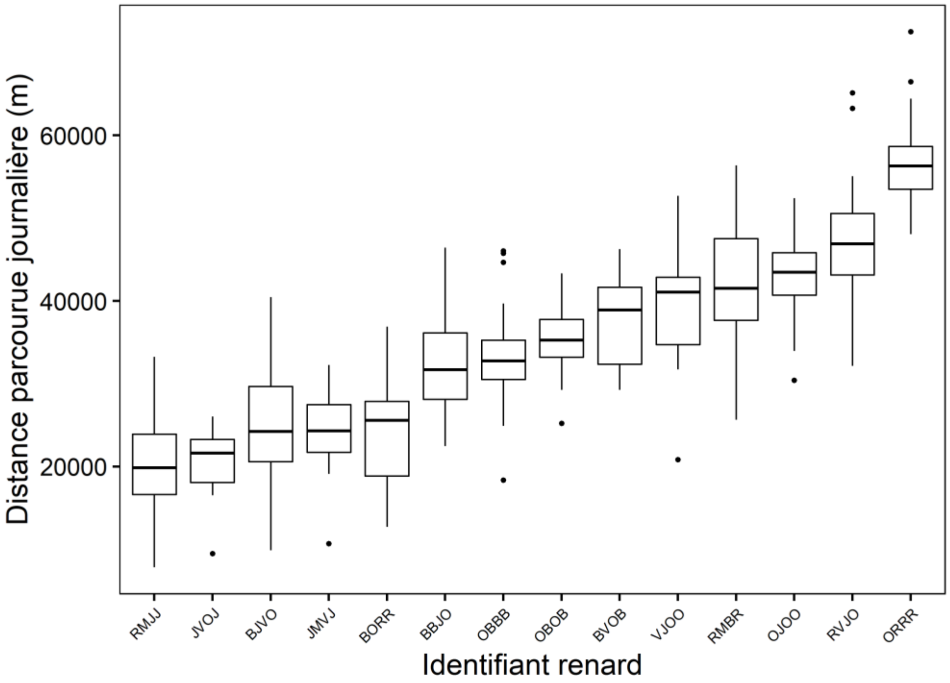

Figure 5. 2 Distances journalières parcourues par 14 renards arctiques, mesurées du 1er juin au 1er août 2019 à l'île Bylot au Nunavut à partir de localisations GPS programmées pour

être récoltées aux 4 minutes (n = 303 jours). Seulement les journées où au moins 75% des localisations GPS (sur un potentiel de 360 localisations étant donné l’intervalle d’échantillonnage de 4 minutes) programmées ont été obtenues sont considérées.

Tel qu’évoqué dans l’introduction générale (pages 12-13), des différences interindividuelles de témérité chez des espèces de prédateurs pourraient intervenir dans les interactions prédateurs-proies, notamment si la témérité d’un prédateur influence sa capacité à acquérir des proies (Ioannou et al., 2008). En effet, les individus les plus téméraires et les plus actifs pourraient générer une plus grande pression de prédation sur les populations de proies (Sih et al., 2012; Toscano & Griffen, 2014). Étant donné les fortes différences interindividuelles dans les distances parcourues par les renards, on pourrait également s’attendre à des différences interindividuelles dans le taux d’acquisition de proies, puisque la distance parcourue par un prédateur actif est corrélée à l’intensité de sa recherche de nourriture et influence son taux d’acquisition de proies (Merrill et al., 2010). À ma connaissance, aucune étude n’a à ce jour relié la personnalité du prédateur à la pression de prédation qu’il exerce sur des proies en milieu naturel. Cette relation pourrait être testée chez les renards arctiques de Bylot. Tout d’abord, il faudrait continuer de développer l’algorithme de classification des données d’accélérométrie (Chapitre 2) pour identifier directement les évènements de prédation et mesurer des taux d’acquisition de proies pour chaque individu prédateur (Studd et al., 2021). Les taux d’acquisition de proies pourraient être mis en relation avec différents traits comportementaux pouvant refléter la personnalité des renards, comme la témérité (Chapitre 4) et différentes métriques du mouvement obtenues grâce au suivi GPS.

Ainsi, le risque de prédation pourrait varier entre les domaines vitaux des individus d’une espèce prédatrice en fonction de la témérité ou de la personnalité spatiale des individus. Cette hypothèse pourrait être confirmée dans la communauté animale de l’île Bylot à l’aide d’expériences de proies artificielles telles qu’utilisées au Chapitre 1, ou en mesurant la survie de nids dans plusieurs territoires. De plus, si 1) la témérité et les capacités de chasse sont reliées chez le renard arctique et donc que 2) le risque de prédation est plus grand dans les territoires des renards les plus téméraires, les proies alternatives des renards, qui ne sont pas recherchées de façon active par ces derniers, pourraient répondre à la variation du risque en évitant de nicher dans les territoires de renards téméraires ou qui parcourent de grandes distances par jour. En effet, tel que proposé par quelques auteurs, considérer les différences de personnalité des prédateurs et des proies permettrait de mieux comprendre certaines interactions trophiques (Sih et al., 2012; Kalinkat, 2014), ce que soutiennent les quelques études effectuées dans des milieux contrôlés (Ioannou et al., 2008; Belgrad & Griffen, 2016; Sommer & Schmitz, 2020), sans pour autant avoir été appuyé en milieu naturel.

5.3 Conclusion générale

Les suivis à fine échelle spatiale et temporelle des mouvements d'individus, soit la télémétrie à haut débit, génèrent de grandes quantités de données permettant parfois de mieux comprendre certains processus écologiques (Nathan et al., 2022). De telles données de mouvements récoltées chez les renards arctiques ont permis de développer le paysage de l'activité des prédateurs à l'île Bylot, et d'évaluer comment les mouvements d'un prédateur actif génèrent un paysage du risque de prédation qui structure les comportements anti-prédateurs et la répartition des proies. Cet exemple empirique du contexte écologique du paysage de la peur illustre les mécanismes via lesquels les prédateurs influencent la dynamique des populations de proies. La classification de données d'accélérométrie couplée aux données GPS a également permis de rendre spatialement explicites certains comportements de prédation des renards. Cette avancée méthodologique est prometteuse et permettra ultimement de mieux définir le paysage du risque de prédation. La classification des données de mouvement en comportements spécifiques a par la suite mené à des découvertes sur l'écologie comportementale des renards arctiques. Notamment, nous avons montré que les renards arctiques utilisent différentes tactiques comportementales pour sécuriser des ressources, soit la territorialité ou l'ajustement des comportements de prédation à la probabilité de rencontrer un voisin. Cette thèse montre également que considérer les variations temporelles dans l'abondance des proies principales permet de mieux comprendre comment la témérité d'un prédateur affecte son succès reproducteur. En effet, une grande témérité pourrait permettre d'accéder à des ressources alternatives lorsque les ressources principales sont peu abondantes, permettant aux prédateurs de se reproduire. En somme, cette thèse permet de mieux comprendre des mécanismes qui régissent les effets de la prédation sur la biodiversité locale, en plus d'apporter des connaissances nouvelles sur les comportements des prédateurs.

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