Use of space and resources by red foxes and Arctic foxes in a coastal tundra transitional ecosystem

by

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Abstract

Climate change and anthropogenic pressure can strongly impact food webs through modifications to species' ranges and population foraging strategies, notably altering their exposure to contaminants. In northern ecosystems, boreal-forest species have expanded onto the tundra, where they may disrupt food-web interactions through competition or predation. Their lack of adaptation to the harsh tundra conditions, however, may severely constrain individual behaviors, increasing survival and reproduction costs compared to tundra endemics. A red fox (*Vulpes vulpes*) population that recently settled onto the coastal tundra of western Hudson Bay, historically occupied by Arctic foxes (*Vulpes lagopus*), provides a useful model to study the mechanisms and impact of generalist species expansion in Arctic communities. I used satellite telemetry and stable isotope analysis to investigate red fox spatial and dietary response to food scarcity, dietary mercury exposure, and interaction with Arctic foxes. Red foxes did not exclude Arctic foxes by interference, and their movement strategies differed from Arctic foxes, reflecting poor adaptation to food scarcity on the tundra but high behavioral flexibility. Arctic and red foxes' diet tracked main prey densities. However, unlike Arctic foxes, which mostly consumed tundra rodents and switched to marine resources when rodent abundance decreased, red foxes consumed tundra, forest, and migratory prey in similar proportions. Those results suggested that the two species segregate resources to some extent and winter survival of red foxes relied on accessing forest prey. Both fox species consumed mostly terrestrial prey, explaining their generally low mercury intake, which increased with marine resource consumption. I also assessed the performance of keratinous tissues in predicting body-mercury burden, which despite being moderate at best, does not preclude using keratinous tissues to understand mercury intake while growing. Studying how expanding species respond to edge-habitat conditions and impact local communities will refine our capability to forecast future distribution and potential for adjustment of affected species. How climate change will affect wildlife exposure to mercury remains an open question: gathering empirical information using standardized protocols on wildlife responses to ongoing changes will help untangle the role of different ecological processes affecting population exposure to mercury.

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Dedication

To my aunt, Janice Rodrigues Ferreira, with whom I shared a love for working outdoors.

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Chapter 1: Introduction

Anthropogenic disturbances and range expansion of species in the Arctic

Ongoing climate-related changes have already generated substantial responses across species in diverse ecosystems at an unprecedented scale (Parmesan and Yohe 2003; Hampe and Petit 2005; Seabrook et al. 2014; Rehm et al. 2015). Extinction rates have been increasing, but some species have locally adapted through phenotypic plasticity and evolutionary adaptation (Chown et al. 2010; Hoffmann and Sgró 2011), and others have geographically tracked suitable conditions (Shoo et al. 2006; Rehm et al. 2015).

The Arctic, particularly, has been warming two to four times faster than the rest of the world (You et al. 2021). Among the most noticeable changes in tundra habitats: primary productivity has increased, winters have become warmer and shorter, and shrubs are encroaching onto the tundra (Henden et al. 2011; Elmhagen et al. 2015; Tape et al. 2016a). These changes have favored the expansion of species that were previously limited by cold temperatures, and shrub-dependent ones (Elmhagen et al. 2015; Tape et al. 2016a, 2016b). Boreal-forest herbivores, for example, like moose (*Alces alces*) and snowshoe hares (*Lepus americanus*), have followed the expansion of shrubs, which resulted from Arctic warming (Tape et al. 2016a, 2016b).

Although primary productivity has increased on the tundra, no evidence indicates that it was followed by increased secondary productivity. Changes in snow cover duration and quality, melt-freeze cycles, and frequency of extreme weather events are contributing to biodiversity loss (Bilodeau et al. 2013; Phoenix and Bjerke 2016; Berteaux et al. 2017). For example, small mammals — which are crucial to Arctic terrestrial food webs — may be more exposed to predation as snow duration decreases (Gilg et al. 2009), and may suffer from starvation when mild weather favors the formation of ice crust on the ground (Aars and Ims 2002; Berteaux et al. 2017); these processes contributed to the general decrease of rodent-density and longer cycle phases throughout the Arctic (Kausrud et al. 2008; Gilg et al. 2009). In turn, the damped rodent cycles could lead to local extinction of predators, which used to capitalize on rodent peak densities, especially if they cannot exploit alternative resources (Gilg et al. 2009). However, other anthropogenic activities may provide expanding species with food resources.

For example, lynx (*Lynx lynx*) have followed the northward expansion of agriculture in Norway by switching their diet from small game to ungulates, preying on livestock and roe deer (*Capreolus capreolus*), whose northward expansion has been induced by cultivated fields (Sunde et al. 2000). In northern Norway, herds of semi-domesticated reindeer (*Rangifer tarandus*) subsidize red foxes (*Vulpes vulpes*) in winter, and particularly when rodents are low (Killengreen et al. 2011), while in Prudhoe Bay, Alaska, near oil fields, about half of red foxes' diet comes from human food waste (Savory et al. 2014).

These diverse anthropogenic factors likely act in synergy to favor the geographic expansion and increased abundance of boreal-forest species (Henden et al. 2014; Elmhagen et al. 2015). Alternative resources to tundra prey could provide a buffer when tundra resource is low (Killengreen et al. 2011; Savory et al. 2014; Gomo et al. 2021), thereby allowing stable populations of these expanding species, which would in turn negatively affect native tundra species through competition (interference or exploitation), trophic cascades, and other predator-prey interactions (Henden et al. 2010; Rød-Eriksen et al. 2020; Gomo et al. 2021). Ongoing changes will thus likely induce dramatic shifts in Arctic communities.

Edge populations

Despite the complexity and large number of proximal causes shaping species distributions, species borders result from population demographic response to conditions in spatio-temporally heterogenous environments (Holt et al. 2005). Four main demography mechanisms — immigration, emigration, death, and birth rates — thus determine the local growth rate (and so persistence) of populations (Holt et al. 2005; Gaston 2009).

These demography mechanisms in turn occur in response to sets of abiotic conditions and interspecific interactions varying in relative importance along spatiotemporal gradients (Louthan et al. 2015). Immigration, for example, may be limited by impassable barriers or facilitated by the presence of alternative food subsidies, while emigration may be selected for when habitat quality varies spatiotemporally, or selected against in fragmented edge populations that represent demographic sinks (Holt 2003; Gaston 2009).

Diverse demographic parameters of importance for local persistence of populations (e.g., density, survival rate, recruitment, fecundity), may be lower at distribution edges compared to core areas because of the stress biotic and abiotic conditions exert on edge-population physiology (Brown 1984; Gilman 2006; Burgess et al. 2020). The stress caused by challenging abiotic conditions at distribution edges may negatively affect the competitive abilities of edge populations. Ecotones thus represent converging areas for diverse populations locally adapted to range edges, where exploitation and interference competition may be particularly high. As a result, abiotic stress and interspecific competition may synergistically limit edge populations (Louthan et al. 2015; Aguilera et al. 2019).

Competitive interactions in carnivores and coexistence

Interspecific competition is a major driver of the structure of carnivore communities (Palomares and Caro 1999; Ritchie 2002; Berger and Gese 2007). Competition is classically classified as exploitation, by which competitors negatively affect each other indirectly through depletion of limited shared resources, and interference, by which competitors directly prevent others from accessing resources along a behavioral continuum from passive blocking to interspecific killing (Case and Gilpin 1974; Schoener 1983; Vance 1984). While the intensity of exploitation competition depends on spatio-temporal patterns of resource abundance (Matassa and Trussell 2011; Holdridge et al. 2016), interference increases with competitor density and may not depend on resource availability (e.g., Amarasekare 2002; Holdridge et al. 2016). However, exploitation and interference competition typically increase together (Park 1954); as exploitation increases, encounter rates between predators also increase because the same movement mechanisms drive predator-prey and predator-predator encounters (Delong and Vasseur 2013).

Although interspecific competition is a frequent community feature, competitive exclusion remains rare, indicating the widespread occurrence of coexistence mechanisms (Schoener 1976; Ritchie 2002; Powell 2012). Coexistence mechanisms include temporal or spatial segregation to avoid interference (e.g., Andersen et al. 2020; Easter et al. 2020), habitat or food-resource partitioning to allow exclusive use of resources (Leal and Fleishman 2002;

Ramesh et al. 2012), or diverse levels of tolerance to abiotic factors that can lead to spatial interdependence of a species' population growth rate and a given resource threshold (Amarasekare 2003).

Carnivore interactions are often asymmetric and the likelihood of interference is maximal at intermediate body-size difference (*sensu* Donadio and Buskirk 2006), sometimes leading to interspecific killing, because overlap in resource use increases with body size similarity for ecologically similar species, and for equally sized species the risk of injury or death is high (Donadio and Buskirk 2006). A larger competitor may thus kill the smaller one without consuming it, possibly as a strategy to decrease the competition when resources are scarce (Palomares and Caro 1999; Donadio and Buskirk 2006). In canid species, competition has led to population decline, displacement, or extirpation of the lesser competitor (Ralls and White 1995; Linnell and Strand 2000; Kamler et al. 2003a). In some cases, spatial displacement arose because of killing by the dominant competitor rather than from avoidance behavior by the lesser competitor (Carbyn 1982; Kamler et al. 2003b, 2012).

Climate change likely will profoundly alter species relationships (Alexander et al. 2015). Relative abundance of competitors may shift in favor of expanding species through relaxing physiological stress imposed by abiotic conditions, which in turn may favor immigration, survival, and reproductive success of expanding species. These shift in community composition will likely change competitive interactions, which may affect some species' local persistence, and thus future distribution.

The long-term impact of climate change on tundra species may, however, be difficult to predict. In the short term, warmer temperatures could favor Arctic species when associated with an increased prey availability, and in the absence of larger competitors (e.g., Pálsson et al. 2016). In contrast, near treeline, warmer temperatures may support population growth of competitors to a point where the negative impact of interspecific competition outweighs possible positive effects (Hersteinsson and Macdonald 1992). Despite an initial greening of the Arctic, there has been a general browning trend (notably due to extreme events causing extensive vegetation damages), which may decrease the overall productivity of the Arctic tundra (Phoenix and Bjerke 2016). In the long term, consequences of climate warming on competition could thus go in either or both directions: favoring the shift of tundra communities into boreal forest communities, which could extirpate native tundra species through competition (e.g., Elmhagen et al. 2015), or a reduced productivity that negatively impacts both native tundra species and the currently expanding boreal forest species.

Feeding ecology and exposure to mercury

Anthropogenic activities (such as mining, smelting, coal combustion, waste burning or chemical industry) have generated considerable amounts of pollution by releasing contaminants in water, soil and air (Letcher et al. 2010; Hargreaves et al. 2011; Lavoie et al. 2013; Dietz et al. 2019). Mercury is of particular concern because methylation of inorganic mercury through microbial activity produces a highly toxic compound (methylmercury) that bioaccumulates in organisms and biomagnifies throughout both aquatic and terrestrial food webs (Rimmer et al. 2010; Lavoie et al. 2013; Li et al. 2021). Highest concentrations are thus often observed in top predators with established negative effects on reproduction, immune or neurological functions (e.g., Dietz et al. 2011; Bocharova et al. 2013; Peterson et al. 2015; Eccles et al. 2020).

Diet is a primary pathway of exposure to mercury (e.g., Bond et al. 2015; Gamberg et al. 2015; Chételat et al. 2020; Clatterbuck et al. 2021). Mercury concentration in individuals, thus, results from mercury dietary intake minus detoxification and excretion, for example in feces, keratinous tissues, milk, placenta, and eggs (Bond 2010; Chételat et al. 2020). In general, terrestrial wildlife in the Canadian Arctic have much lower levels of mercury than marine wildlife, although some species like caribou may show high levels due to a high consumption of lichen, or some Arctic fox (*Vulpes lagopus*) populations due to their opportunistic hunting or scavenging on marine species (Gamberg et al. 2015). The uncertainty associated with diet determination and mismatch between the patterns of integration of mercury and diet remain a complication when inferring contamination patterns and quantifying its transfer throughout food webs (Jardine et al. 2006; Bond 2010).

Projecting future effects of mercury on wildlife health may be challenging, since some climate-induced changes are projected to decrease, while others will increase mercury availability to Arctic biota (Stern et al. 2012). In the Arctic, wildlife exposure to mercury has increased considerably in comparison to the pre-industrial era (Dietz et al. 2009, 2011; Bond et al. 2015). However, recent temporal trends of Arctic wildlife exposure to mercury are not consistent (Rigét et al. 2011; Poste et al. 2018; Hallanger et al. 2019); tissue increases in mercury concentration mostly involve marine mammals and mammals feeding in the marine food web (Rigét et al. 2011; Hallanger et al. 2019), while terrestrial mammals showed either a decline or no variation in mercury concentration (Rigét et al. 2011). Predicting future levels of mercury in Arctic biota is complicated because multiple processes responsible for these levels interact and could lead to changes in either direction (Stern et al. 2012; Dietz et al. 2019; Hallanger et al. 2019). For example, sea-ice decline is associated with higher levels of mercury in many top predator tissues (Dietz et al. 2019, 2021), but, along with a projected increased in reindeer mortality due to rain-on-snow events, could promote a more terrestrial diet in opportunistic scavengers like the Arctic fox, thus overall reducing their exposure to mercury and some other contaminants (McKinney et al. 2015; Hallanger et al. 2019). Because of the complexity to infer the result of the interaction between all different processes that affect mercury contamination in Arctic wildlife, systematically measuring wildlife population exposure to contaminants would provide benchmarks against which to assess future studies, thus improving our understanding and predictive abilities (e.g., Dietz et al. 2019).

The red-Arctic fox model

The red fox (*Vulpes vulpes*) occupies a diversity of habitats across a wide latitude range in Eurasia and North America (e.g., Bartoń and Zalewski 2007; Elmhagen et al. 2017), while the Arctic fox (*Vulpes lagopus*) has a circumpolar distribution and is a tundra-adapted species of North America and Eurasia (Macpherson 1969). Those fox species overlap over a narrow area on alpine and Arctic tundra (Hersteinsson and Macdonald 1992).

Both species usually behave as opportunistic specialists: most populations prioritize microtine rodents even at low abundances, exhibit functional response to other prey, and broaden their diet when preferred prey is scarce (Englund 1980; Angerbjörn et al. 1999; Elmhagen et al. 2011). Arctic foxes may notably use marine resources in low rodent years (Roth

2002; Dudenhoeffer et al. 2021), likely increasing mercury intake when their preferred prey is scarce. Red foxes often consume ungulate carrion as alternative resource (e.g., Cavallini and Volpi 1996; Baltrūnaitė 2002, 2006; Kidawa and Kowalczyk 2011; Killengreen et al. 2011; Drygala et al. 2014), but can also make use of marine carrion washed on shore and on landfast ice, albeit rarely (Andriashek et al. 1985; Jung et al. 2020); one red fox was even observed to kill a seal pup (e.g., Andriashek and Spencer 1989). Although somewhat anecdotal, these events of red foxes using the sea ice denote the extreme adaptability of this species and its subsequent capability to colonize new habitats and use a wide range of food sources.

In some places, red foxes displaced Arctic fox populations, with interspecific killing events or Arctic foxes avoiding to breed in the vicinity of red foxes (Tannerfeldt et al. 2002; Rodnikova et al. 2011; Stickney et al. 2014), while in others they co-exist with Arctic foxes because they likely occur at densities too low to be a threat to Arctic foxes (Gallant et al. 2012; Elmhagen et al. 2017). The outcome of interspecific competition between red and Arctic foxes may depend on multiple factors, including the density and population stability of the red fox (Henden et al. 2010), relative abundance of the two species (Elmhagen et al. 2017) and possibly behavioral differences between different red fox populations (Berteaux et al. 2015). In Fennoscandia, red foxes are excluding Arctic foxes. The Fennoscandian Arctic fox was overharvested resulting in largely weakened populations, some close to extinction (Hersteinsson et al. 1989; Angerbjörn et al. 2013; Elmhagen et al. 2017), making them less likely to withstand competition with the dominant red fox, especially as red fox abundance increased throughout the overlap area following a higher availability of food (Selås et al. 2010; Killengreen et al. 2011; Elmhagen et al. 2017). In Prudhoe Bay, Alaska, red foxes excluded Arctic foxes from their vicinity, and their abundance increased concurrently to a decrease in abundance of Arctic foxes (Stickney et al. 2014). In this area, human food waste subsidized red foxes (Savory et al. 2014). Access to reliable subsidies likely increased their winter survival, thus promoting an increase in their abundance and stabilizing their population. Such a scenario is particularly detrimental to a sympatric Arctic fox population (Henden et al. 2010). In contrast, in Northern Yukon, red and Arctic fox coexistence likely resulted from continued food scarcity, and the lack of alternative stable food subsidies to red foxes (Gallant et al. 2012). Scenarios in which red fox populations cycle due to specializing on cyclic prey, like Arctic foxes, are the most favorable to coexistence (Henden et al. 2010).

Although climate change did not induce secondary productivity on the tundra and reverse trends of decreased primary productivity are even observed (Phoenix and Bjerke 2016), in the long-term, it may ultimately favor the red fox. Through a shift in habitat, due to the advance of shrubs on the tundra, species like the snowshoe hare may increase in areas where red and Arctic foxes occur in sympatry, which could support larger populations of red foxes. In addition, other factors like a growing anthropogenic presence may subsidize red foxes, stabilizing their populations in places where they were disadvantaged by food scarcity, and thus change the balance of red-Arctic fox interactions, eventually resulting in Arctic fox extirpation.

Thesis objectives and structure

I have written my thesis in manuscript format, and my objective was to obtain an integrated understanding of diverse mechanisms that allow red foxes to survive on the tundra, determine the outcome of red-Arctic fox interactions, and how ongoing climate-related changes may affect the future of these species, including in terms of contaminant exposure. To achieve these objectives, I focused my work on a red fox population that has recently settled onto the coastal tundra of western Hudson Bay, in the Churchill region of Manitoba, near treeline. This population reproduces in sympatry with an Arctic fox population, using dens that were until about a decade ago only used by Arctic foxes. We know little about the mechanisms that allow red foxes to survive in this habitat over winter despite their lack of adaptations to food scarcity and extremely low temperatures. Most expanding red fox populations that have been studied had access to anthropogenic food subsidies, but it was not the case in the population examined in this thesis. Arctic and red foxes overlap over a narrow area, and most knowledge of the red-Arctic fox model comes from Fennoscandia, where environmental factors can differ substantially from the Nearctic. In the Churchill region, foxes live near treeline like in the Fennoscandian sites and thus both foxes occur as edge populations, but our Arctic fox population is larger (Elmhagen et al. 2017) and the lack of human-food subsidies likely hinders the red fox population from reaching the ecologically effective densities necessary to exclude Arctic foxes.

The species interaction-abiotic stress hypothesis proposes that abiotic stress mostly limits species distributions in areas where climate imposes stressful conditions (e.g., cold edge of a species range), while interaction with competitors dominate the causes limiting species distributions in milder areas (e.g., Louthan et al. 2015). Within that framework, Hersteinsson and Macdonald's (1992) hypothesis, refined by Elmhagen et al. (2017), proposed that food availability limits red foxes' northern distribution, while interspecific competition limits Arctic foxes' southern distribution. Instead, I hypothesized that in tundra areas where key prey species are particularly vulnerable to the effects of climate change, like rain on snow or melt-freeze cycles (Berteaux et al. 2017), both species are limited by climate-induced declines in rodent availability. I further propose that, in a context where human-food subsidies are limited, the landscape near treeline offers possibilities to relax interference competition through exclusive use of some resources, and that lemmings (*Dicrostonyx richardsoni*) and snowshoe hares as key prey in tundra and boreal forest food webs (Krebs 2011) drive fox diet and thus exposure to mercury, despite their low abundance.

I first quantified how seasonal fluctuation in resources and winter climate-related challenges of the tundra impacted red fox movements in comparison to the tundra-adapted Arctic fox in the Churchill area (chapter 2). Specifically, I hypothesized that movement strategy in both species is primarily driven by the temporal variability of food resources, but winter conditions are more limiting to red foxes. I then investigated the conditions of coexistence of the two fox species, with a specific emphasis on space-time and habitat use in the Churchill area (chapter 3). I hypothesized that the potential for exploitation competition when prey is scarcest (i.e., in winter) is substantial but habitat heterogeneity offers opportunities for the two species to partition resources, relaxing interference competition. In chapter 4, I compared winter diet between Arctic and red foxes and how it varies with important prey fluctuations and examined how diet variability, in turn, influenced mercury exposure in foxes. In that chapter, I hypothesized that red and Arctic foxes differ in their diet, and while population cycles of lemmings and voles generate annual variation in diet and mercury exposure of both foxes, snowshoe hares affect diet and mercury exposure in red fox only. Finally, in chapters 5 and 6, I addressed some methodological matters that arose when we were designing the methods for chapter 4. I assessed the usefulness of keratinous tissues in predicting body mercury burden and the relationship of mercury levels between internal organs using red fox data (chapter 5), and I examined how common practices of storage and sample treatment affected mercury concentration, and the possible impact on the resulting interpretation (chapter 6). Together, the first three chapters contribute to improve our understanding of climate-related changes in Arctic food webs using the Arctic-red fox model. The last two chapters jointly aim to contribute to best practices in toxicology studies.

A note on home range estimates and diet reconstruction

Much of my thesis relied on estimating space use and diet. Here, I provide some details on the home range and diet estimates used in this thesis, which are expanded on in the relevant chapters.

Home range, a widely used concept in spatial ecology (e.g., Powell 2000; Börger et al. 2008; Fieberg and Börger 2012; Powell and Mitchell 2012), has been defined as a cognitive map of resource dynamics an animal keeps updated for the area used to meet its needs (Powell and Mitchell 2012). A plethora of studies and reviews about the performance of home-range estimators are still being generated, as new methods are developed to answer the recurring question “what is the best estimator?”, with much emphasis put on data structure (e.g., sample size, autocorrelation, or homogeneity) (Walter et al. 2015; Stark et al. 2017; Baíllo and Chacón 2022). Although such studies provide crucial information, there is no single “best” estimator, and the selection of the ideal estimator should first consider the research question (Powell 2000; Fieberg and Börger 2012). My research questions required estimators that performed well in identifying boundaries (perceived or imposed by landscape features) and unused areas. Kernel density estimators are widely used, but perform poorly at detecting hard boundaries (e.g., Péron 2019; Silva et al. 2022). Among estimators capable of accurately detecting hard boundaries, I have selected Local Convex Hull methods because the resolution of my data was too coarse to consider methods using Biased random bridges (Benhamou 2011; Benhamou and

Cornélis 2011), and because Local convex hulls methods have been widely used and evaluated since they were first published (Getz and Wilmers 2004; Lyons et al. 2013).

A wide range of methods have been successfully used in ecology to estimate animal diet. A recent review by Nielsen at al. (2018) has highlighted the strength and limits of the most commonly used methods. Of these methods, stable isotope analysis could quantify the diet and dietary differences of red and Arctic foxes over the desired timeframe with lowest logistic costs. Although stable isotope analysis provides diet estimates with limited resolution, compared to DNA-based or visual methods, my goal was to quantify the contribution of the most likely prey available in the different habitats of our study area. I thus used Carbon (C) and Nitrogen (N) stable isotope ratios ($\delta^{13}C$ reflects $^{13}C/^{12}C$ and $\delta^{15}N$ reflects $^{15}N/^{14}N$) in muscle to estimate the foxes' diet. Stable-isotope ratio in muscle provides an integrated dietary estimate of approximately two months before sample collection (Vander Zanden et al. 2015) and thus, in the foxes captured during the winter fur harvest, reflected a late-fall and winter diet. The probabilistic contribution of the different sources to the mixture is then estimated using Bayesian mixing models, that typically require data on chemical tracers characterizing both the sources and the consumers (mixture). Major advantages of the Bayesian approach over frequentist mixing models lie in the opportunity to incorporate prior information, uncertainty in the parameters estimates, covariates (as both fixed and random effects), and variability in the consumer population (e.g., Stock and Semmens 2016; Stock et al. 2018).

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Prelude to Chapter 2

Climate warming and anthropogenic pressure have prompted many species from the boreal forest to expand onto the tundra (Tape et al. 2016a, 2016b; Gallant et al. 2020). Some herbivore species have followed the expansion of shrubs, like moose (*Alces alces*) or snowshoe hares (*Lepus americanus*) (Tape et al. 2016a, 2016b), and red foxes may heavily rely on anthropogenic subsidies and are thus often present near human settlements (Killengreen et al. 2011; Gallant et al. 2020). However, human-induced subsidies do not occur within Wapusk National Park, but a red fox population is nonetheless continuously present within park boundaries, i.e., red foxes remain resident during the period of food scarcity. The next chapter will thus explore from a spatial ecology perspective the mechanisms that allow that red fox population to survive on the low-Arctic tundra over winter, and how their coping strategies compare with those of Arctic foxes. Specifically, I am addressing the first part of the overarching hypothesis, i.e., that in a southern Arctic region although resource scarcity challenges both species, it affects the red fox more strongly.

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Chapter 2: Seasonal shift in space use in red foxes on their expanding front in the low Arctic tundra, compared to Arctic foxes

Abstract

Resource fluctuation is a major driver of animal movement, influencing strategic choices such as residency vs nomadism, or social dynamics. The Arctic tundra is characterized by strong seasonality: resources are abundant during the short summers but scarce in winters. Therefore, expansion of boreal-forest species onto the tundra raises questions on how they cope with winter-resource scarcity. We examined a recent incursion by red foxes (*Vulpes vulpes*) onto the coastal tundra of western Hudson Bay, an area historically occupied by Arctic foxes (*Vulpes lagopus*) that lacks access to anthropogenic foods, and compared seasonal shifts in space use of the two species. We used 4 years of telemetry data following 8 red foxes and 11 Arctic foxes to test the hypothesis that the movement tactics of both species are primarily driven by temporal variability of resources. We also predicted that the harsh tundra conditions in winter would drive red foxes to disperse more often and maintain larger home ranges year-round than Arctic foxes, which are adapted to this environment. Dispersal was the most frequent winter movement tactic in both fox species, despite its association with high mortality (winter mortality was 9.4 times higher in dispersers than residents). Red foxes consistently dispersed towards the boreal forest, whereas Arctic foxes primarily used sea ice to disperse. Home range size of red and Arctic foxes did not differ in summer, but resident red foxes substantially increased their home range size in winter, whereas home range size of resident Arctic foxes did not change seasonally. As climate changes, abiotic constraints on some species may relax, but associated declines in prey communities may lead to local extirpation of many predators, notably by favoring dispersal during resource scarcity.

Introduction

Species' range expansions rank among the preeminent ecological consequences of Arctic warming and anthropogenic pressure (McCarty 2001). For example, species that primarily inhabit the boreal forest have settled onto the tundra due to milder winters, longer productive periods, and increased availability of anthropogenic subsidies (Hersteinsson and Macdonald 1992; Tape et al. 2016; Gallant et al. 2020). However, at the edge of its distribution, a species also reaches the limits of its environmental tolerances (biotic and abiotic). Scarce patches of preferred habitat, lower resource availability, and harsh winters may challenge the survival of peripheral individuals and force them to adjust their behavior, including ranging behavior (e.g., Niedzielski and Bowman 2016; Linnell et al. 2021).

Movement tactics are driven by ecological, social, and morpho-physiological factors acting in synergy, such as resource availability, body size, seasonality, or the distribution of prey or competitors (Macdonald and Johnson 2015). Although most individuals restrict their ranging behavior to familiar areas to meet their needs efficiently, some can disperse if the cost of staying in an area exceeds the benefits (e.g., Avgar et al. 2014). Individuals usually favor residency when they find abundant and predictable resources and can avoid competitors or predators (Jonzén et al. 2011; Marneweck et al. 2019). Residents' successive maintenance movements (i.e., movements performed within the context of necessary activities to survive and reproduce; Roshier and Reid 2003), as measured over short time periods, typically occur over relatively short distances and do not produce a net displacement along a movement vector over a longer time period. The succession of these maintenance movements thus perpetuates a home range (or a territory if actively defended) (e.g., Powell 2000). In contrast, individuals may engage in long-range movements when they cannot predict resource availability, nor avoid adverse weather conditions, competitors or predators (Jonzén et al. 2011; Hsiung et al. 2018). Long-range movements occur on a continuum. Unlike migrations, nomadic movements lack directionality and regular timing: the animal leaves its former range permanently, and may wander over long time periods (Roshier and Reid 2003). Although carnivores typically exhibit residency, they may engage in long-range movements to reproduce or settle in more suitable habitat, resulting in dispersal (Roshier and Reid 2003).

Resource availability influences not only movement tactic and ranging behavior (and hence home range sizes), but also the degree to which competitors tolerate each other (Maher and Lott 2000; Mcloughlin et al. 2000; Eide et al. 2004). The resource dispersion hypothesis predicts that home range size increases with increased resource dispersion, while territoriality decreases with increased food abundance. When resources are highly unpredictable, an individual (or breeding pair) will likely maintain a home range large enough to meet its needs during times of scarcity (Macdonald 1983). Furthermore, Maher and Lott (2000) hypothesized that as resource predictability decreases, so does the net benefit of territoriality, except in food-caching species, which still benefit from being territorial. This territorial benefit was empirically corroborated in fieldfares (*Turdus pilaris*), which defend stored food in anticipation of food scarcity, and in Arctic foxes (*Vulpes lagopus*), which defend food caches and exhibit the lowest home range overlap in areas where prey are unpredictable (Maher and Lott 2000; Eide et al. 2004).

Arctic ecosystems are characterized by marked seasonality and interannual resource fluctuation (Korpimäki and Hongell 1986; Jonzén et al. 2011). Low availability of resources in winter contrasts with a summer resource burst; geese, seabirds, and shorebirds reproduce every summer in the Arctic, offering an abundant and predictable food source to predators, if only for a limited period (Tannerfeldt and Angerbjörn 1998; Eide et al. 2004; McDonald et al. 2017). Many Arctic predators primarily rely on arvicoline rodents (lemmings and voles) that are present year-round but whose fluctuating populations peak every 3-4 years (Krebs et al. 2002; Fauteux et al. 2015). Together, rodent-abundance fluctuations and the relatively short lifespan of mammalian predators make rodents an unpredictable resource (Tannerfeldt and Angerbjörn 1998; Krebs et al. 2002; Bilodeau et al. 2013).

Predators may thus migrate or disperse, either to track their preferred prey (Korpimäki and Hongell 1986; Jonzén et al. 2011) or because peaks of rodent abundance have favored a higher consumer density, which reduces *per capita* energy intake (Mysterud et al. 2011) when rodent abundance decreases again (Avgar et al. 2014; Robillard et al. 2016). In that context, long-range movement may be an adaptive tactic to reduce competition between consumers or alleviate the negative effects of food scarcity on survival and reproduction. However, such movements are often associated with high rates of mortality because individuals lack familiarity with or adaptation to the landscapes they cross (Korpimäki and Hongell 1986; Roth 2003; Powell and Mitchell 2012). Therefore, terrestrial predators typically favor residency (Powell 2012; Lai et al. 2017), and develop strategies to cope with prey scarcity while retaining their home ranges. Examples of such strategies include demographic lability (Barraquand and Benhamou 2008), food caching (Sklepkovych and Montevecchi 1996), larger home range maintenance to cope with prey scarcity (Eide et al. 2004), and increased frequency of short extraterritorial trips (excursions) to exploit alternative resources (Messier 1985; Lai et al. 2017).

The harsh Arctic conditions historically limited the northern distribution of red foxes (*Vulpes vulpes*) (Hersteinsson and Macdonald 1992; Bartoń and Zalewski 2007; Gallant et al. 2020), but during the 20th century, red foxes considerably extended their range into the Arctic due to increased availability of anthropogenic subsidies that buffered winter-food scarcity in many Arctic areas (Gallant et al. 2020). Red and Arctic foxes are ecologically similar: they use dens to reproduce and raise their young, beginning shortly before migratory birds arrive, and although they depend strongly on arvicoline rodents, they forage opportunistically and cache food (Roth 2002; Careau et al. 2007a; McDonald et al. 2017). However, red foxes are larger than Arctic foxes, which increases their food requirements (Carbone et al. 2007), and are less adapted than Arctic foxes to prey scarcity during the harsh Arctic winters (Fuglesteg et al. 2006; Careau et al. 2007b).

We examined movement tactics and space use by red and Arctic foxes on the low Arctic tundra in northern Manitoba, Canada, where red foxes recently expanded from the adjacent boreal forest and now reproduce in sympatry with Arctic foxes (Moizan et al. *submitted*; Zhao et al. 2022). Seasonal variability of resources likely drives movement tactics in both red and Arctic foxes. In that context, we hypothesized that winter conditions are limiting for red foxes, in contrast to Arctic foxes and compared to summer. Specifically, red foxes are evolutionarily rooted in the boreal forest (Kamler and Ballard 2002; Wells and Aubry 2011) and, thus, lack adaptations to exploit the sea ice (Klein and Sowls 2015; Colson et al. 2017). In addition, their increased energetic requirements during winter (Fuglesteg et al. 2006) will likely constrain their ranging behavior. We thus predicted that long-range movements are primarily initiated during winter (P1), red foxes are more likely to disperse in search of better conditions instead of commuting to the sea ice and back like Arctic foxes do (P2), due to their larger size and higher energetic needs, red foxes always maintain larger home ranges than Arctic foxes (P3), extra-territorial excursions are more frequent in winter in both species (P4), and extra-territorial excursions occur more frequently for resident red foxes than for Arctic foxes (P5).

Methods

Study area and species. – Our study area near Churchill, Manitoba (Fig. 2.1; 58°N, 94°W), is part of the Hudson Bay Lowlands, a uniformly flat (<200m elevation) wetland bordering the south-western shore of Hudson Bay (Brook and Kenkel 2002). This wet tundra ecosystem lies between the boreal forest to the south and west, and the marine ecosystem to the north and east. The three biomes thus transition in our study area. In fall, this part of Hudson Bay freezes as early as the first week of November, and the ice along the northern and western coasts of the Bay is typically consolidated by December 2, providing a platform for fox movements and opportunities to forage on marine resources. Sea ice in the area breaks up around mid-June, and the area is typically free of ice by the first week of July (Hochheim et al. 2010), thus limiting access to marine resources on the sea ice until the ocean freezes again. We considered that the sea ice starts at the low tideline (Ponomarenko et al. 2014).

Lemmings are available year-round, but their peak abundance has dramatically declined throughout the Arctic (e.g., Bilodeau et al. 2013), particularly for low Arctic populations that are sympatric with voles (Ehrich et al. 2020). Abundant populations of Canada geese (*Branta canadensis*) and lesser snow geese (*Anser caerulescens*) nest each year in the study area, providing an important food source to predators (McDonald et al. 2017). Canada goose nests are distributed throughout the entire area along with some snow goose nests, and two major snow goose colonies (>20,000 nesting pairs) occur near the coast (Fig. 2.1) (Andersen et al. 2010; McDonald et al. 2017). Peak arrival of snow geese occurs during the first week of May (Cargill and Jefferies 1984) and >95% of Canada goose nests are initiated before the last week of May, with a median hatch date during the 3rd week of June (Andersen et al. 2010). Geese remain abundant throughout fall and may be present until late October—the latest observation of snow or Canada geese in the Churchill area based on band recoveries for the 2017-2019 period was on October 16 (Celis-Murillo et al. 2020).

Capture and satellite telemetry. – Between 2017 and 2019 we captured 10 red foxes and 13 Arctic foxes using Tomahawk (Model 208, Tomahawk Live Trap Co., WI) and padded leghold traps (Softcatch # 1.5, Oneida Victor Ltd, USA). Traps were placed on active dens or by protruding features (e.g., driftwood or spruce islets) and remained open continuously for up to one week. We checked the traps every 4-6 hours and closed them during extreme weather conditions (e.g., blizzard or temperatures below -25°C). We captured adult foxes from March to May when snow still covered the ground and facilitated travel over large distances, except for two adult foxes caught near our field camps in June 2018. We did not anesthetize the foxes, which were easily handled without chemical restraint. Foxes were first wrapped in a blanket and released from the traps, then we assessed sex and body condition, deployed an Iridium satellite collar (#4170 or 4270, Telonics, Mesa, Arizona, USA; ~100g, i.e., 2-4% of a fox body mass), and released them at the site of capture. All handling procedures were approved by the University of Manitoba Animal Care Committee (Protocol F17-012), and the research was conducted under Parks Canada Research and Collection Permits WAP-2017-25781 and WAP-2018-27938, and Manitoba Wildlife Scientific Permits WB20226 and WB21856.

Movement analysis. – Our GPS collars used different schedules throughout the year (see Table S1), so we thinned all the tracks by randomly selecting 1 location per day (the lowest fix frequency) to obtain independent successive locations. We defined two relevant contrasting periods based on goose phenology. The season of abundant resources (hereafter summer) thus extended from May 15, the approximate date of nest initiation, to the end of October, the last month during which geese can be considered alternative prey for the foxes of this area (Andersen et al. 2010; McDonald et al. 2017). The resource-scarcity period (hereafter winter) extended from November 1 to May 14, when geese are absent and foxes mostly rely on arvicoline rodents.

We plotted all fox tracks in ArcGIS 10.3 (ESRI 2017, Redland, CA, USA) to remove possible major erroneous locations and identify movement strategies: residency and long-range movements. We labelled a fox as a resident only if it maintained a home range (i.e., showed non-directional movements within a geographically circumscribed area) from the start of a given season until the end of that season or until its death, if it occurred after the area resulting from movement analysis had reached an asymptote (i.e., we did not include the season of capture in movement tactic and home range comparisons). Using a subset of 16 individuals with 111 to 187 locations each, we determined that home range areas reached an asymptote with 38 locations on average. All our resident foxes exceeded this threshold with at least 61 locations. All foxes that underwent long-range movements (hereafter dispersals) were considered dispersers, since none returned to their departure area (they either died dispersing or settled elsewhere). The dispersal events we used to compare movement tactics were not natal dispersal because we only included adults (at least 1.5 years old), unlike the track descriptions, which included all available tracks.

For each dispersal (including those initiated during the season of capture) we calculated the cumulative distance travelled (i.e., sum of straight-line distances between successive daily relocations), the duration (starting with the last position within the home range boundaries), the cumulative to straight-line distance ratio (a proxy for fox behavior during dispersal), the cardinal direction (the angle of the vector between first and last locations, degrees from due North), the main substrate used for movement (sea ice or land), and the average daily speed. We considered that the dispersal started with the last location in a home range prior to dispersal initiation, or at the point of capture if a fox did not exhibit residency prior to dispersal (and thus was likely captured while already dispersing), and ended with the first location associated with a settlement of >7 days in a new delimited ranging area (on land, not ice) or with the death of the fox. Although foxes can exhibit staged dispersal, exploring delimited areas for a temporary period ranging from a few days up to a few weeks (e.g., Walton et al. 2018), we never observed clear staging behavior.

We estimated residents’ home ranges and core areas, defined as the 95% and the 50% utilization distribution isopleths, respectively, with local convex hulls (LoCoH) using the package T-LoCoH v.1.40.07 in R (Lyons et al. 2013). LoCoH are nonparametric estimates of utilization distributions and perform better than parametric kernel methods to identify boundaries (such as coastlines) and unused areas (Getz et al. 2007; Stark et al. 2017). As such, they are well-suited for our main objective to determine if red foxes were using the sea ice. We were not specifically interested in the temporal partition of space within seasons since we modelled space use using only one location per day. We, therefore, set the user-defined parameter s to 0, which entailed that the time-scaled distance was equivalent to the Euclidian distance. Due to heterogeneous location densities, we used the adaptive method (a-LoCoH). We selected the a value for each animal using the graph tools provided in the T-LoCoH package and following the recommendations to minimize the risks of both excluding used areas and including unused areas. All home ranges and core areas are displayed in Supplemental File 2.1. Based on the same dataset, we also estimated home ranges (95% utilization distribution) using a classic bivariate kernel density estimator (KDE) with a reference bandwidth, with R package adehabitatHR v.0.4.20 (Calenge 2006). Although we decided not to use kernel density methods in this study, we provide the areas resulting from the KDE in Table S5, for comparison purposes.

To estimate seasonal home-range shifts in each fox, we measured summer and winter home range overlaps using the package T-LoCoH.dev v. 1.34.00/r12 and the distance between their centroids estimated in ArcGIS 10.3 (ESRI 2017).

Many residents undertook short-distance and short-duration trips outside the boundaries of their home range, either on land or on the sea ice. We defined excursions as any exploratory movement <7 days unusually far away from the current center of activity followed by a return to the home range (most foxes left their home ranges for up to 7 days before returning to it, or over 3 weeks with only occasional visit to the former area defined as home range; we considered the latter a shift of the center of activity and not an excursion). Home-range borders include areas that are already peripheral to the center of activity. Therefore, to avoid making arbitrary decisions on a distance threshold to the border, we differentiated excursions from other movements near the home range border, based on the distribution of the distances between a location and the home-range centroid. Locations that appeared to be outliers using a one-sided Hampel filter:

(1) upper bound = median (Tukey-transformed distance) + 3 median absolute deviations)

were considered excursions. If a trip outside the boundaries of the LoCoH home range estimate consisted of multiple consecutive locations, we used the farthest away of the consecutive locations to determine if that trip was an excursion. Finally, we called “commuting trip” (i.e., a trip in a different habitat) any excursion on the sea ice (Lai et al. 2017).

Statistical analyses. – We performed all statistical analyses in R software (R Core Team, 2020). To compare the frequency of dispersal events (P1, P2) and home-range size (P3) between species and between seasons, we used generalized linear mixed-effect models (GLMM), family binomial (link logit) and gaussian (link identity) respectively, using the lme4 package v.1.1-25 (Bates et al. 2015). We included species, season and their interaction term, and controlled for fox ID as a random effect. Two of the collared red foxes were a mated pair and like fox pairs elsewhere in the Arctic (Rioux et al. 2017, Lai et al. 2022), their home range sizes were similar (paired permutation t-tests, home range: $t = 9.78$, $P = 0.25$; core area: $t = 11.00$, $P = 0.25$, n = 3). We reviewed 3 potential outlier foxes with leverage higher than 0.5 (Cooks' distance) individually to decide whether they should be removed. Two red foxes settled in forest habitat after dispersing and therefore were excluded. We found no valid ecological or methodological reason to remove the outlying Arctic fox, and thus retained that estimate in the data set. We assessed if dispersal track parameters differed between species using two-sided permutation tests based on the t statistics ($n_{perm} = 9999$) in library RVAideMemoire v. 0.9-79 (Hervé 2021). We assessed the impact of dispersing on winter survival and annual survival using a right-censored Cox mixed effect model from the coxme library (Therneau 2020), controlling for fox ID as a random effect, and with time-to-event as the number of days since the start of a given winter (1 November). We then tested if land excursions by resident foxes were more likely in winter and in red foxes (P4 and P5) using GLMMs to control for fox ID as a random effect: we transformed the raw number of excursions into a frequency of excursions per week, due to substantial inter-individual variation in tracking period length. We checked our models' assumption by plotting residuals versus fitted values, and we report no problem during model validation. All summary statistics are presented as mean ± SE and/or mean [range] unless stated otherwise. Given our low sample size and individual heterogeneity in spatial behavior, we used an alpha threshold at 0.1 to lower the risk of evidence minimization (e.g., Knaub 1987; Altman and Bland 1995).

Results

We tracked 13 Arctic foxes and 10 red foxes between May 2017 and August 2020 (see Table 2.S2 for capture details), which yielded a total of 6159 locations after thinning their tracks to one daily location, with 10 Arctic and 7 red foxes yielding enough data to perform home-range analyses and assess seasonal shifts in space use. Since we followed 7 individuals for more than one year, we obtained 8 Arctic and 9 red fox home ranges over 3 winters, and 13 Arctic and 12 red fox home ranges over 4 summers.

Dispersal events. – We recorded 14 dispersal events overall: 9 by Arctic foxes (8 individuals, since one fox dispersed twice) and 5 by red foxes (see Tables S2 and S3). One Arctic fox and one red fox were captured while dispersing (i.e., they were not using a home range at the time of capture) and 11 of the other 12 dispersals were initiated during winter (specifically between November 14 and May 10), while one was initiated on September 15 by an Arctic fox. Six of the eight Arctic and three of the five red foxes settled in a new area (at least temporarily, red foxes in forest and Arctic foxes in tundra habitats) after the dispersal events, but four Arctic foxes died 11 days to four months after dispersing (at least one Arctic fox was caught by a fur trapper) and the three red foxes died 19 days to 2 months after dispersing. Two red and two Arctic foxes died while dispersing. The two red foxes were caught by fur trappers, but we have no information on the cause of death for the two Arctic foxes.

All red foxes dispersed toward forested areas, and all but one in a southwestern direction, whereas Arctic foxes moved towards other tundra habitats, 8 to the northeast and northwest, and 1 to the southeast (but still in the Hudson Bay Lowlands) (Fig. 2.2). Of the 9 Arctic foxes that dispersed, 3 used sea ice exclusively until they died or reached a new delimited ranging area, 3 navigated between sea ice and land, and 3 used land exclusively. No red foxes dispersed using sea ice. The mean length, duration, speed and cumulative-distance to straight-line ratio of dispersal tracks were all smaller in red foxes, indicating they dispersed a shorter distance (permutation test: $t = 1.44$, $P = 0.002$, $n_{\text{Arctic}} = 9$, $n_{\text{red}} = 5$), over less time ($t = 1.55$, $P = 0.036$), with a slower speed ($t = 1.78$, $P = 0.043$), and more directly ($t = 1.08$, $P = 0.020$) than Arctic foxes (Table 1).

Of the 16 fox observations over 3 winters, 56% dispersed (5/9 red foxes and 5/7 Arctic foxes), but red foxes did not disperse more often than Arctic foxes (GLMM: z = -1.06, P = 0.29, n = 16). Dispersals were associated with higher mortality than residency: mortality risk was 9.4 times higher for dispersing foxes in the short-term (i.e., during the same winter: z = -1.99, P = 0.046; $n_{disperse}$ = 14, $n_{resident}$ = 7) and 6.5 times higher in the long-term (i.e., within a year of dispersing: z = -1.95, *P* = 0.051). However, mortality risk did not differ by species in the winter of dispersal (z = 1.29, *P* = 0.20; n_{red} = 10, n_{Arctic} = 11) or the following year (z = 0.42, *P* = 0.67).

Seasonal home ranges. – Resident fox space-use patterns differed between species (Table 2). While summer home ranges and core areas of red foxes and Arctic foxes were similar, red foxes drastically increased the size of their home range in winter (Fig. 3; GLMM: t_{season} = 0.72, *P* = 0.48, n_{summer} = 24, n_{winter} = 12; $t_{species}$ = 0.14, *P* = 0.89, n_{red} = 19, n_{Arctic} = 17; $t_{species*season}$ = 3.06, *P* = 0.006, n_{total} = 36). Winter home range and core areas of red foxes were 1.9 and 2.7 times larger than their summer home ranges and core areas, respectively.

Individuals' summer and winter home ranges overlapped moderately in both species, although the seasonal change in home-range geometry was small for some (red foxes: 55.8±11.9% [33.2-70.7%], n = 7; Arctic foxes: 62.3±12.3% [45.9-75.4%], n = 4). The distance between winter and summer home range centroids was also relatively short (red foxes: 0.9±0.6 km [0.4-2.0 km], n = 7; Arctic foxes: 0.8±0.4km [0.3-1.1km], n = 4). Core areas, however, generally overlapped only slightly to moderately between seasons (red foxes: 21.4±20.2% [0-55.7%], n = 7; Arctic foxes: 29.9±29.3% [1.5-70.7%], n = 4), and so the seasonal shift of core area centroids was often sizeable (red foxes: 3.5±2.2 km [0.6-7.4 km], n = 7; Arctic foxes: 1.6±1.1 km [0.4-3.3 km], n = 4).

Excursions and commuting trips. — In winter, all resident Arctic foxes used the sea ice, commuting at least once and up to 7 times, although their commuting trips never lasted more than three days. However, no red foxes commuted to the sea ice. We found no overall difference in land excursion frequency between seasons or species (GLMM: $t_{species}$ = -0.859, *P* = 0.397; t_{season} = -0.539, *P* = 0.593; $t_{season*species}$ = 1.650, *P* = 0.109, n = 36). Weekly frequency of land excursion in red foxes increased from 0.05 [0-0.25] in summer to 0.13 [0-0.32] in winter, while Arctic fox land excursion frequency was 0.08 [0-0.21] in summer and 0.06 [0-0.13] in winter. Pooling together excursions and commuting trips, we found that these extraterritorial exploratory trips were more frequent in winter (GLMM: $t_{season} = 3.113$, $P = 0.004$, $n = 36$) but occurred at a similar frequency in both species ($t_{species} = -1.547$, $P = 0.131$).Table S4 provides all parameters from all GLMMs performed in this study.

Discussion

Both red and Arctic foxes showed mixed movement tactics in our study area, some remaining resident and others engaging in long-range movements, which denotes flexibility in both species' spatial behavior. However, although resident red foxes used space similarly to resident Arctic foxes during summer, their winter strategy differed markedly. While home-range or core-area sizes did not differ between species during summer, when food is plentiful and the climate mild, red foxes substantially increased their ranging behavior in winter, whereas Arctic foxes did not. The harshness of winter abiotic conditions (i.e., duration of snow cover and low temperatures) is the main limitation to red fox distribution (Bartoń and Zalewski 2007), while the availability of stable anthropogenic food sources was the main driver of their expansion across the Arctic (Gallant et al. 2020). Red foxes in the Arctic benefit from a high mass-adjusted basal metabolic rate, which likely lowers the range of cold temperatures they can face, but also increases their food requirements (Fuglesteg et al. 2006; Careau et al. 2007). This increase in food requirements occurs when food is scarce, most prey having migrated back South, and the rodents sheltered by a hard snow cover (Jędrzejewski and Jędrzejewska 1992). Thus, this large seasonal increase in home-range size likely reflected red foxes' lack of adaptation to prey scarcity and the harsh conditions of the tundra during winter.

As predicted (P1), foxes did not disperse in summer while prey was abundant. During summer, foxes raising their young are constrained to remaining around breeding dens. However, the proportion of foxes raising a litter largely depends on spring resources (McDonald et al. 2017) and even in years when spring resources were at the lowest, no foxes dispersed the following summer. We also have indirect evidence that some foxes of this study did not breed (e.g., established in areas with no breeding dens, center of activity shifting often during summer), yet they still maintained a home range over the summer. The high dispersal rate in winter contrasted with the usually low proportion of dispersing adults found in both red and Arctic fox populations elsewhere (e.g., Storm et al. 1976; Lai et al. 2017; Walton et al. 2018), and other carnivores in general (e.g., Ferreras et al. 2004), suggesting that overwinter survival near the treeline was particularly difficult for both species. The higher dispersal rate in our study area could be due to low rodent densities compared to elsewhere, notably the Canadian High Arctic (Ehrich et al. 2020; Lai et al. 2022), and scarce access to anthropogenic subsidies unlike other areas of sympatry (Killengreen et al. 2011; Rød-Eriksen et al. 2020). This high rate of dispersal could further indicate that foxes in our study area were less likely than other populations (such as Bylot Island Arctic foxes living near a snow goose colony that is much larger than those in Churchill) to capitalize on summer-abundant resources, caching items to survive winters as residents (Rioux et al. 2017). Notably, although foxes in Bylot did not select caching sites according to depth to permafrost, the maximum depth recorded was 46.5 cm (Juhasz et al. 2018), thus closer to the surface than in Churchill; in Churchill, depth to permafrost can reach 95 cm (Sjögersten et al. 2016), possibly rendering caching prey less effective. In the case of Arctic foxes, it is also possible that the Hudson Bay sea ice is more productive than elsewhere.

Dispersal can incur high fitness costs, with higher mortality or missed opportunities to reproduce following dispersal (e.g., Ferreras et al. 2004; Soulsbury et al. 2008; Lai et al. 2017). As expected, the survival cost of dispersal was high in our population, with 11 of 13 dispersers suffering mortality within 4 months of starting dispersal. Our results are consistent with observations from the Canadian High Arctic. While foxes of Bylot Island remained resident and were able to survive over multiple winters, on Herschel Island both red foxes dispersed and died (Lai et al. 2022). Mortality during dispersal may occur because dispersers must cross unfamiliar areas (e.g., Storm et al. 1976; Ferreras et al. 2004) and, in leaving our remote study area, may come into greater contact with humans (e.g., Ferreras et al. 2004). The cost of dispersal on reproduction was also likely high, as only three of our 13 dispersed foxes survived long enough through the subsequent breeding season to have successfully raised pups, whereas all but one of twelve residents survived long enough to raise pups successfully. However, remaining resident during prey scarcity may compromise reproduction too, as resources may be allocated to winter survival at the cost of next-season reproduction (Löfgren et al. 1986). Although each tactic may have a cost, our results suggest that dispersing is risky for both red and Arctic foxes, and may be a desperate tactic to cope with local prey scarcity.

Arctic foxes are well-known for their long-range movements, specifically using the sea ice (Lai et al. 2017; Fuglei and Tarroux 2019; Pamperin et al. 2008; Tarroux et al. 2010). Two-thirds of our Arctic foxes indeed dispersed using the sea ice as a platform, whereas red foxes never did. Instead, red foxes in our study dispersed inland, towards the boreal forest. The dispersal distances of red foxes, despite being shorter than those of Arctic foxes, were particularly large for this species. Only two studies have reported similar dispersal distances, one in Sweden and one the Canadian High Arctic (Walton et al. 2018; Lai et al. 2022). The low cumulative to straight-line dispersal distance ratio of these red foxes suggests straight relocation until finding suitable habitat. Arctic foxes, in contrast, seemed more prone to exploration during dispersal, suggesting they primarily use the sea ice for foraging (as suggested by diet studies; Roth 2003), and not just as a dispersal platform. When rodent abundance is low, Arctic foxes respond numerically to marine resources, suggesting that exploiting the sea ice in winter is a well-established strategy for responding to prey scarcity (Roth 2003).

Further highlighting that sea ice is a key habitat for Arctic foxes and in partial agreement with P3, all Arctic foxes commuted to the sea ice. Anecdotally, one Arctic fox even had 76.7% of her winter home range on the sea ice, yet she still took five exploratory trips even farther onto the sea ice (Fig. S1). Red foxes, however, never commuted to the sea ice, further suggesting they generally avoid this habitat, like on St. Matthews island where red foxes hunt inland while Arctic foxes used the coast (e.g., Klein and Sowls 2015). Yet, direct and indirect evidence suggest that red foxes use sea ice occasionally, either to travel — red foxes are found on offshore islands sometimes quite far from the mainland, which suggest they use seasonal ice to disperse there (Andriashek et al. 1985; Klein and Sowls 2015; Lai et al. 2022) — or to forage (Andriashek and Spencer 1989; Jung et al. 2020) — interestingly, both reports of red foxes foraging on sea ice come from the same area in Yukon, Canada. Although these observations are not unique, they remain rare. While on Herschel Island (where winter food is scarce) a pair of red foxes left their summer home range and ventured on the sea ice (including intertidal ice), where they died relatively quickly (Lai et al. 2022), the red fox pair on Bylot Island (where food is less scarce) remained resident for multiple winters and never went to the sea ice, only relying on inland resources (Lai et al. 2022). On Herschel Island, red foxes were far from the boreal forest, while red foxes in our study area were close to the treeline, and thus had alternative habitats other than the sea ice. Whilst sea ice may offer alternative resources when terrestrial prey is scarce, our red fox population did not exploit this habitat, likely due to their lack of adaptation to that particularly unpredictable and harsh environment (Klein and Sowls 2015).

Red foxes' difficulty to overwinter on the tundra is further reflected in the seasonal change in home-range size of residents. This winter expansion of home range may originate from both a decrease in prey abundance and an increase of red foxes' energetic requirements. Arctic foxes adapt to the harsh winter climate with a low resting metabolic rate (likely to conserve energy) and exceptional insulation (Prestrud 1991; Fuglei and Øritsland 1999; Fuglesteg et al. 2006). They also show metabolic depression (i.e., a significant decrease in the resting metabolic rate) in response to starvation, indicating an adaptation to food scarcity (Fuglei and Øritsland 1999). Red foxes in the Arctic compensate for their poorer insulation with a higher basal metabolic rate, which benefits them by expanding their thermoneutral zone (Careau et al. 2007b), but which also increases their energetic requirements (Fuglesteg et al. 2006). Yet, red foxes did not engage more often in dispersal or excursions than Arctic foxes, nor did their excursion rate increase in winter. Expanding their home range during winter may have been sufficient for residents to obtain enough prey.

The Obstinate Strategy hypothesis states that animals may not adjust their ranging behavior to the fluctuation of resources because fighting competitors to expand a home range is costly (von Schantz 1984). Our red fox population instead behaved as flexible strategists, unlike many other carnivore populations (Meia and Weber 1995; Eide et al. 2004; López-Bao et al. 2019). Winter home ranges of these red foxes averaged ~35 km^2 (up to 56 km^2), among the largest reported for this species (Goszczyński 2002; Walton et al. 2017; Lai et al. 2022), unlike Arctic foxes which maintained home ranges twice smaller than in the high Arctic (home ranges estimated with the same method; Lai et al. 2022). Large home ranges suggest a low fox density in our area (Trewhella et al. 1988), which may decrease the cost of expanding the home range in winter, compared to maintaining such a large home range during summer. Anecdotally, one red fox captured on the tundra relocated to the boreal forest long enough during winter to calculate two core areas and home ranges (tundra and forest): her forest home range was 25% the size of her tundra home range (only 14% for core areas), suggesting that forest habitat had higher prey density and milder abiotic conditions than the tundra.

We found low seasonal overlap of individual core areas and large distances between core-area centroids, indicating relatively low site fidelity, and thus quite high spatial flexibility in both species. The flexible and the obstinate strategies are two ends of a continuum that depend on the amplitude of resource fluctuation and the species' life span relative to the periodicity of resource fluctuation. In the Canadian High Arctic, Arctic foxes behaved as flexible strategists, unlike in the European Arctic (e.g., Eide et al. 2004), adjusting the size of their home range yearly to lemming density (Tarroux 2011). Hyenas (*Crocuta Crocuta*) have also shown mixed strategies at the species level, some clans behaving as obstinate and other clans as flexible strategists in response to resource fluctuation (Maude et al. 2019). That behavioral plasticity in carnivores may allow them to adapt to future changes in prey abundance and distribution linked to climate change (Nater et al. 2021).

Although current conditions of food scarcity during winter may limit red fox density (Gallant et al. 2012, 2020), resident red foxes were able to overwinter without relying on anthropogenic subsidies and they did not engage in risky dispersal more often than their congeners. The hindrance to overwinter survival imposed by their lack of adaptation to food scarcity and the harsh conditions of the tundra seem therefore limited at the treeline, where they may be able to use sparse forest patches to buffer the tundra's low food availability.

Our study generally supports the idea that movement strategies in both red and Arctic foxes are mostly driven by seasonal fluctuations of resources, and that both species are highly flexible. Current winter conditions seem limiting to the Churchill red fox population: most individuals dispersed, and the residents needed to increase their home range to find enough resources to survive winter, suggesting that food scarcity during winter may limit red fox density (Gallant et al. 2012, 2020). However, Arctic regions are warming up to four times faster than the rest of the globe (You et al. 2021), and due to climate-induced variability in environmental conditions, Arctic ecosystems are not at equilibrium. The red fox is among the most adaptable mammals (Wells and Aubry 2011), and as such may adapt to new conditions and change its behavior in the future.

Arctic foxes foraged on the sea ice instead of expanding their home ranges. Sea-ice dependent predators may lose opportunities to cope with terrestrial food scarcity, as sea ice will be negatively impacted as the Arctic warms. However, although the negative impact of Arctic warming on most native Arctic wildlife is widely recognized (e.g., Post et al. 2009; Molnár et al. 2010; Descamps et al. 2017), the direction of these changes may be more difficult to predict for expanding species. Some effects may benefit these boreal-forest species. For example, milder winters may lower the costs associated with thermoregulation (Pálsson et al. 2016; Nater et al. 2021), and changing tundra communities will provide expanding species with increased foraging opportunities (Post et al. 2009; Tape et al. 2016), favoring boreal-forest species' persistence in this environment (Callaghan et al. 2004). The species interaction-abiotic stress hypothesis indeed proposes that abiotic stress mostly limits a species' distribution in areas where climate imposes stressful conditions (e.g., cold edge of a species' range), while interactions with heterospecific competitors likely limits species distributions in milder areas (e.g., Louthan et al. 2015). But climate-induced changes in the Arctic are also having dire consequences (such as rain-on-snow events and melt-freeze cycles) on the persistence of many herbivorous species (Stien et al. 2010; Forbes et al. 2016; Berteaux et al. 2017). For example, such dramatic declines in some crucial prey may reach critical winter thresholds that trigger important dispersal in highly mobile predators, or prevent newcomers from becoming established, which could lead to local extirpation of both expanding and native predator species. In a warming Arctic, we propose that both leading- and trailing-edge predator populations may, thus, also become directly limited by climate-induced declines in prey availability. The persistence of expanding population and the outcome of their competition with tundra-native species will likely vary greatly spatiotemporally based on current local conditions.

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Tables

Table 2.1. Dispersal track parameters for red and Arctic fox between 2017 and 2020, indicating different behaviors while dispersing. Sampling schedule is thinned to 1 location per day.

species	parameter	mean	se	median	min	max	n
Red fox	**Duration[1] (days)**	15.40	2.94	15	8	23	5
	Distance[2] (km)	200.80	28.81	167.90	144.80	280.60	5
	CSL distance[3] (km)	1.50	0.16	1.31	1.17	2.03	5
	Speed[4] (km/day)	15.24	3.74	12.38	7.30	28.06	5
Arctic fox	**Duration[1] (days)**	43.11	12.96	29	6	135	9
	Distance[2] (km)	1243.00	529.60	781.70	216.30	5197.27	9
	CSL distance[3] (km)	4.36	1.95	1.90	1.26	19.62	9
	Speed[4] (km/day)	27.96	4.83	28.69	9.63	55.58	9

[1] days between start and end points of dispersal

[2] sum of distances between successive relocations of dispersal track (cumulative, in km)

[3] ratio of cumulative to straight-line distance (distance between start and end points of dispersal)

[4] average daily speed (km/day).

Table 2.2. Minimum, maximum, and average home range (95% Utilization Distribution; UD95) and core area (UD50) sizes (km^2) per season (summer: May 15 – Oct. 31 – and winter: Nov. 1 – May 14) and species (red and Arctic fox) between 2017 and 2020.

season	species	UD	mean	se	min	max	n
summer	**Arctic fox**	**95**	15.86	2.65	0.94*	33.91	12
winter	**Arctic fox**	**95**	19.81	6.47	8.59	44.32	5
summer	**Red fox**	**95**	18.06	1.77	9.84	28.61	12
winter	**Red fox**	**95**	34.72	4.17	23.90	56.58	7
summer	**Arctic fox**	**50**	4.03	0.68	0.22*	8.27	12
winter	**Arctic fox**	**50**	3.70	0.54	2.44	5.42	5
summer	**Red fox**	**50**	3.80	0.64	1.55	9.61	12
winter	**Red fox**	**50**	10.18	1.61	6.51	18.91	7

***This fox had settled in a snow-goose colony.**

Figures

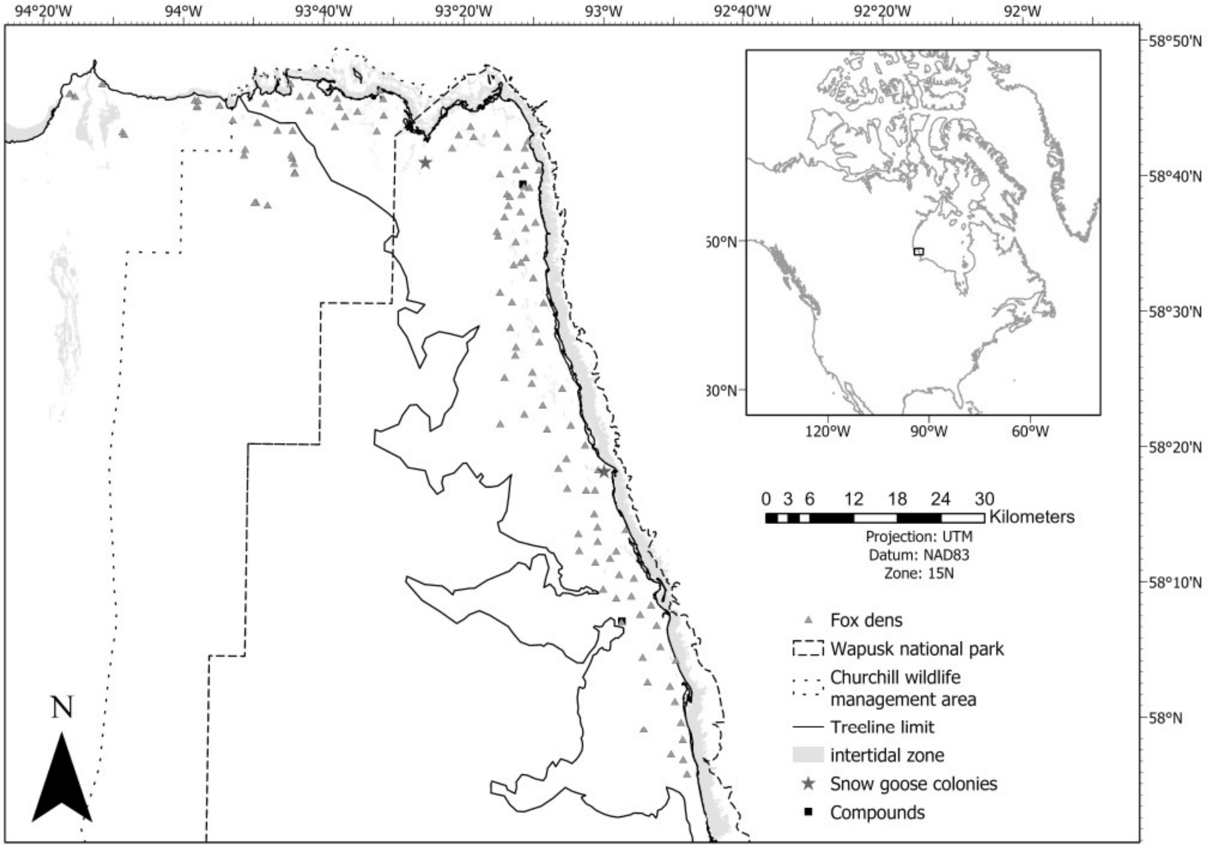


Fig. 2.1. Map of our study area on the southwestern shores of the Hudson Bay, in northern Manitoba, Canada. The area includes Wapusk National Park, the wildlife management area of Churchill, and Churchill and its surroundings.

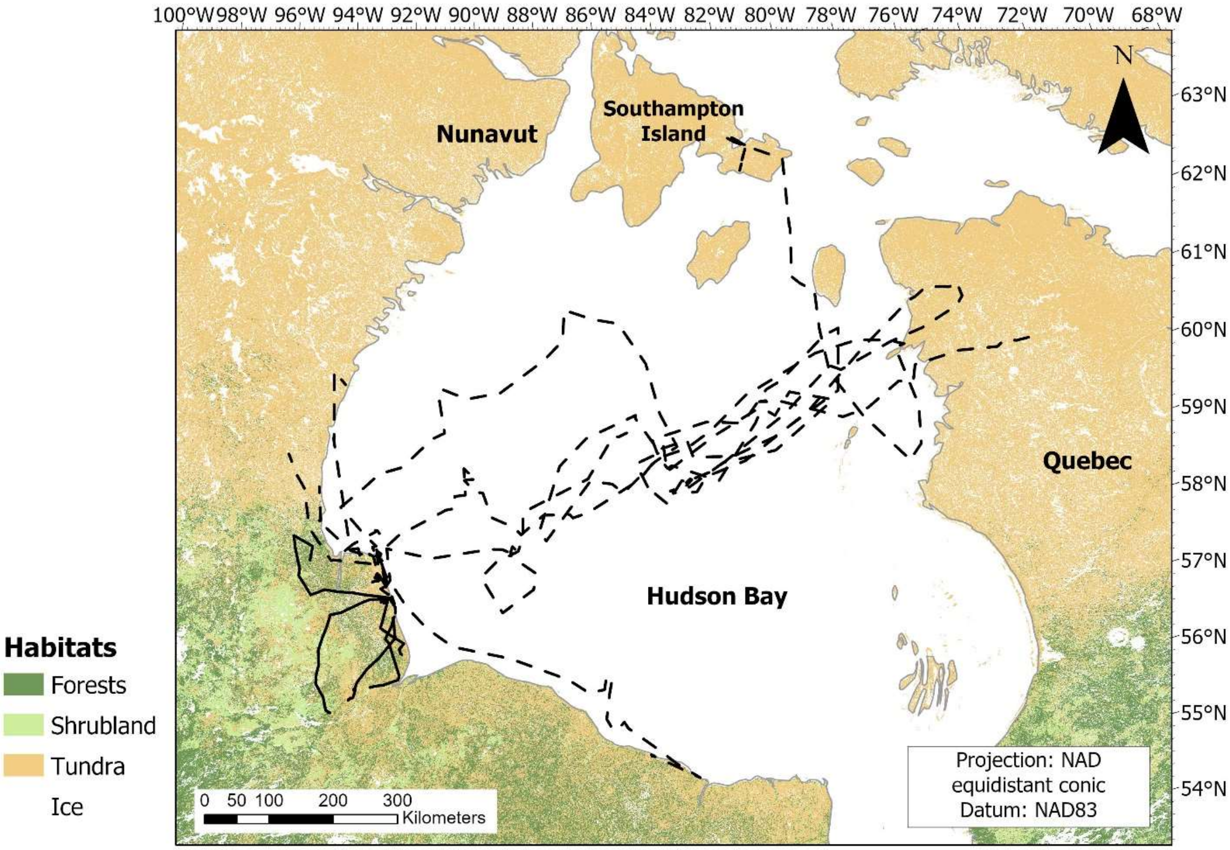


Fig. 2.2. Dispersal tracks of red (solid lines) and Arctic (dashed lines) foxes fitted with a satellite collar in the Churchill area, in all years (2017 – 2020). Sampling schedule is standardized to 1 location per day.

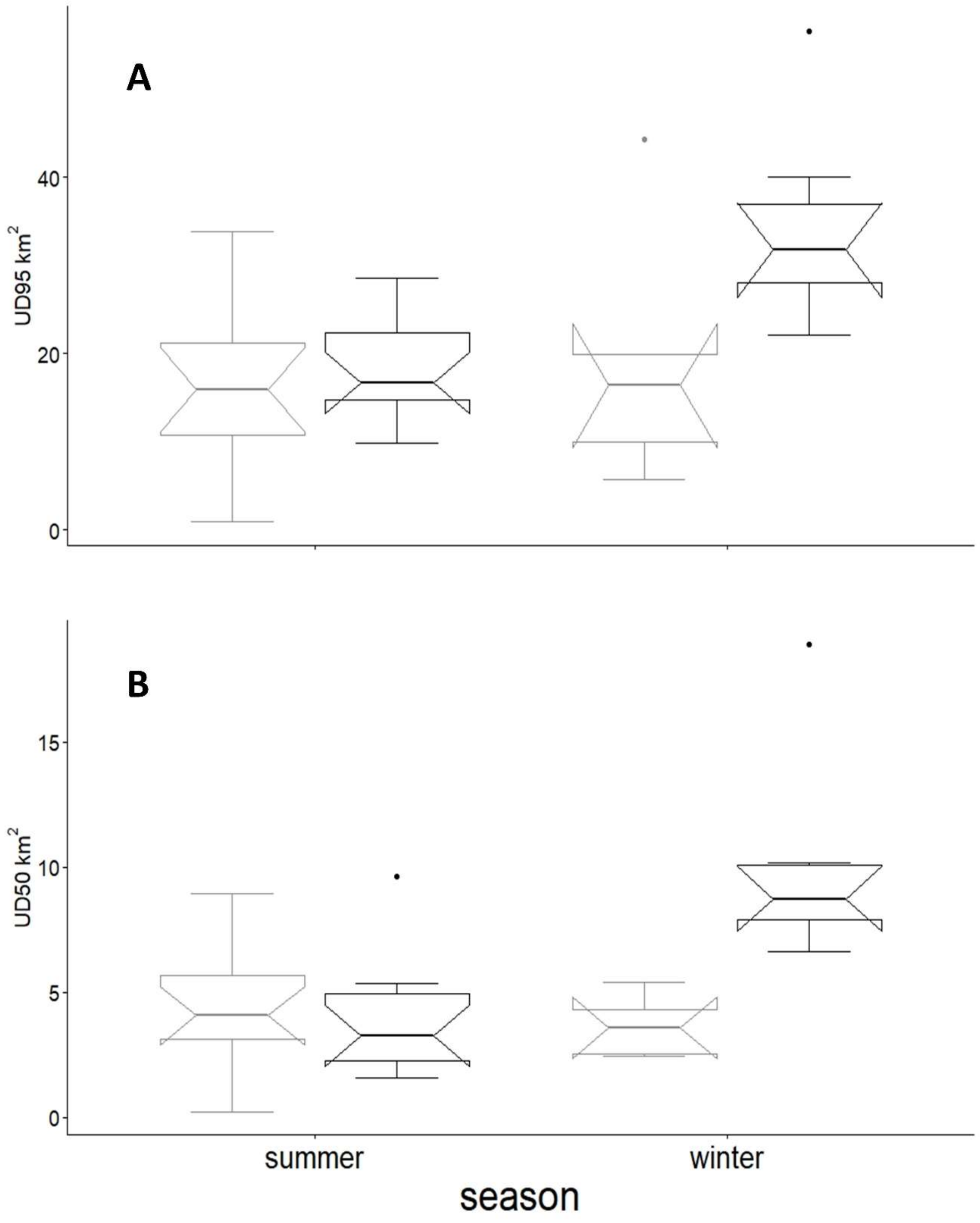


Fig. 2.3. Home range size (A:UD95) and core area size (B:UD50) of red (in black) and Arctic (in grey) foxes in summer (n_{red} = 12, n_{Arctic} = 12) and winter (n_{red} = 7, n_{Arctic} = 5). The notch on each box represents the 95% confidence interval of the median, while the box itself represent the interquartile (IQR), i.e, 50% of the data from 1st to 3rd quartile. The whiskers extend from the greater of 25th percentile - 1.5IQR to the smaller 75th percentile + 1.5IQR. Home range and core area sizes are considered different when the notches do not overlap.

Supplementary data

Table 2.S1. Fix schedule of our different satellite collars (purchased in 2 batches, in 2017 and 2018).

Number of collars	Year	Dates	Update period (hours)
5	2017	10 April-30 June	2
5	2017	1 July-30 August	4
5	2017	1 September-31 December	24
5	2018	1 January-9 April	24
3	2018	10 April-30 June	2
2	2018	1 July-30 August	4
2	2018	1 September-31 December	24
1	2019	1 January-9 April	24
5	2018	10 April-14 June	1.5
4	2018	15 June-14 August	6
4	2018	15 August-14 December	24
2	2018	15 December-31 December	6
2	2019	1 January-14 March	6
13	2019	15 March-14 June	1.5
10	2019	15 June-30 September	6
9	2019	1 October-14 December	24
7	2019	15 December-31 December	6
6	2020	1 January-14 March	6
6	2020	15 March-14 June	1.5
4	2020	15 June-30 September	6
1	2020	1 October-31 December	24
1	2021	1 January-3 February*	24

* The last collar's battery died on February 3, 2021. We retrieved the collar from the fox in April.

Table 2.S2. History of each fox of our project from capture to loss of contact with their collar. We included the fate, i.e., the reason why we lost the signal from collars, and the number of home ranges we obtained from an individual fox (per season; "winter" and "summer") and dispersal track each animal provided. RF: red fox, AF: Arctic fox.

Fox	species	Capture date	start track	end track	Fate	winter	summer	dispersal
LR	RF	2017-05-07	2017-05-08	2018-05-28	unit damaged	1	1	0
U	AF	2017-05-08	2017-05-08	2018-02-06	died on sea ice	1	1	1
FJ	RF	2017-05-09	2017-05-09	2018-02-01	died on land	0	1	1
MM	AF	2017-05-09	2017-05-09	2018-10-07	died on land (at den)	1	2	0
AB	RF	2017-05-09	2017-05-09	2019-01-21	died on land	2	2	1
W	RF	2018-04-14	2018-04-18	2018-06-07	malfunction	0	0	0
GH	AF	2018-04-14	2018-04-18	2018-05-21	died on intertidal ice	0	0	0
GI	AF	2018-04-15	2018-04-15	2018-06-03	died on land (at den)	0	0	0
MJ	AF	2018-04-20	2018-04-20	2018-09-22	died on land	0	1	1
GK	AF	2018-04-21	2018-04-21	2018-12-13	died on land	0	1	1
SH	AF	2018-06-15	2018-06-15	2019-11-20	battery expired	1	2	2
LB	RF	2018-06-18	2018-06-18	2019-02-08	died on land	0	1	1
BG	RF	2019-03-20	2019-03-20	2019-04-12	died on land	0	0	1
BR	RF	2019-04-06	2019-04-06	2019-05-23	died on land (at den)	0	0	0
LR*	RF	2019-04-09	2019-04-09	2021-02-03	battery expired	1	2	0
CN	AF	2019-04-07	2019-04-07	2019-05-04	died on land	0	0	1
A	RF	2019-04-09	2019-04-09	2020-07-29	battery expired	1	2	0
B	AF	2019-04-09	2019-04-09	2019-11-23	died on land (at den)	0	1	0
MP	AF	2019-04-09	2019-04-09	2019-07-08	died on land	0	1	1
S	RF	2019-04-09	2019-04-09	2020-04-18	died on land	1	1	1
I	RF	2019-04-10	2019-04-10	2020-08-10	battery expired	1	2	0
M	AF	2019-04-17	2019-04-17	2020-03-22	died on land	1	1	1
DL	AF	2019-04-30	2019-04-30	2019-12-30	died on sea ice	1	1	0
T	AF	2019-05-02	2019-05-02	2020-07-30	battery expired	0	2	1

*This fox was captured a second time and fitted with a new collar

Table 2.S3. Detailed parameters of the dispersal tracks of Arctic and red foxes captured between 2017 and 2019 in the Churchill area, that left their home range (on start date) and their fate.

Fox ID	species	start date (d/m/y)	end date (d/m/y)	duration (d)	total distance (km)	speed (km/d)	track direction (deg. from N)	habitat used for dispersal	survival time after dispersal (d)	survived into next reproductive season
SH	Arctic fox	15-Sep-18	8-Nov-18	54	781.73	14.48	183.5	land	> 377	Yes
SH	Arctic fox	3-Mar-19	2-May-19	60	2133.31	35.56	77.8	sea ice	> 202	Yes
U	Arctic fox	9-Jan-18	4-Feb-18	26	841.55	32.37	81.0	sea ice	0	No
MJ	Arctic fox	1-May-18	20-May-18	19	426.35	22.44	324.9	land	125	Yes
MP	Arctic fox	10-Apr-19	24-May-19	44	423.86	9.63	338.2	land	45	Yes
GK	Arctic fox	14-Nov-18	13-Dec-18	29	832.05	28.69	115.6	both	0	No
CN*	Arctic fox	8-Apr-19	23-Apr-19	15	216.30	14.42	258.9	both	11	No
T	Arctic fox	18-Nov-19	1-Apr-20	135	5197.27	38.50	79.5	sea ice	> 120	Yes
M	Arctic fox	23-Feb-20	29-Feb-20	6	333.45	55.58	353.1	both	18	No
FJ	Red fox	3-Jan-18	13-Jan-18	10	280.62	28.06	294.0	land	19	No
AB	Red fox	26-Dec-18	18-Jan-19	23	167.92	7.30	208.5	land	0	No
LB	Red fox	24-Nov-18	15-Dec-18	21	259.92	12.38	193.3	land	55	No
BG*	Red fox	28-Mar-19	12-Apr-19	15	144.81	9.65	185.3	land	0	No
S	Red fox	20-Jan-20	28-Jan-20	8	150.58	18.82	210.3	land	81	No

* Fox was captured while dispersing. All parameters were thus estimated from the point and date of capture.

**measured in June of the year the dispersal started.

Table 2.S4. Parameters (β coefficient, 95% confidence interval [2.50%-97.50%], df = degree of freedom, Z or t ratio, associated p-value and n = sample size) of all GLMMs (full and null versions) to fit the home range and core area size of red and Arctic foxes in northeastern Manitoba, Canada.

model	Covariate	Estimate	Confidence intervals 2.50%	97.50%	df	Z or t ratio	P value
UD95 ~ Species*Season + Species + Season + (1|fox ID)	Intercept	16.93	11.55	23.05	16.97	5.170	< 0.001
n = 36	Species	0.69	-8.95	9.73	15.78	0.143	0.888
	Season	2.65	-4.40	9.79	20.46	0.718	0.481
	Species*Season	14.88	5.11	25.52	19.84	3.060	< 0.001
dispersal~Species + (1|fox ID)	Intercept	0.92	-0.66	14.66		1.095	0.273
n = 16	Species	-1.14	-23.92	2.93		-1.063	0.288
land excursions~Species*Season + (1|fox ID)	Intercept	0.08	0.03	0.14	32.00	3.135	0.004
n = 36	Species	-0.03	-0.12	0.05	32.00	-0.859	0.397
	Season	-0.03	-0.14	0.07	32.00	-0.539	0.594
	Species*Season	0.11	-0.02	0.25	32.00	1.650	0.109

Table 2.S5. Winter (Nov. 1 – May 14) and summer (May 15 – Oct. 31) home-range areas (km^2) of individuals fitted with Telonics satellite collars in northern Manitoba, Canada, between 2017 and 2020. Home ranges were estimated based on one location per day using an *a*-Local Convex Hull (LoCoH) and a classic bivariate kernel density estimator (KDE). LoCoH estimates were used in this study, and KDE are provided for purpose of comparison.

Fox ID	species	sex	Period	Area UD95	
				LoCoH	KDE
MM	Arctic fox	M	repro 2017	16.48	47.20
U	Arctic fox	M	repro 2017	15.35	25.99
GK	Arctic fox	M	repro 2018	6.30	13.19
MJ	Arctic fox	F	repro 2018	26.67	63.67
MM	Arctic fox	M	repro 2018	4.37	9.69
SH	Arctic fox	F	repro 2018	0.94	31.52
B	Arctic fox	F	repro 2019	20.82	38.00
DL	Arctic fox	M	repro 2019	12.17	32.53
M	Arctic fox	M	repro 2019	33.91	71.93
SH	Arctic fox	F	repro 2019	22.06	75.14
T	Arctic fox	F	repro 2019	18.79	33.59
T	Arctic fox	F	repro 2020	14.99	155.95
AB	Red fox	F	repro 2017	17.08	35.94
FJ	Red fox	M	repro 2017	28.61	188.41
LR	Red fox	M	repro 2017	15.49	34.00
AB	Red fox	F	repro 2018	16.54	51.04
LB	Red fox	F	repro 2018	10.30	39.30
A	Red fox	F	repro 2019	24.04	78.32
I	Red fox	F	repro 2019	12.44	54.70
LR	Red fox	M	repro 2019	16.76	57.96
S	Red fox	F	repro 2019	9.84	31.69
A	Red fox	F	repro 2020	27.08	60.72
I	Red fox	F	repro 2020	16.67	54.43
LR	Red fox	M	repro 2020	21.88	57.69
MM	Arctic fox	M	winter 2018	19.86	90.19
U	Arctic fox	M	winter 2018	9.94	32.79
SH	Arctic fox	F	winter 2019	5.65	33.45
DL	Arctic fox	M	winter 2020	16.35	58.89
M	Arctic fox	M	winter 2020	44.32	305.39

AB	Red fox	F	winter 2018	31.56	61.70
LR	Red fox	M	winter 2018	31.76	78.85
AB	Red fox	F	winter 2019	22.13	101.99
A	Red fox	F	winter 2020	56.58	104.77
I	Red fox	F	winter 2020	33.90	63.50
LR	Red fox	M	winter 2020	40.08	78.98
S	Red fox	F	winter 2020	24.43	89.46

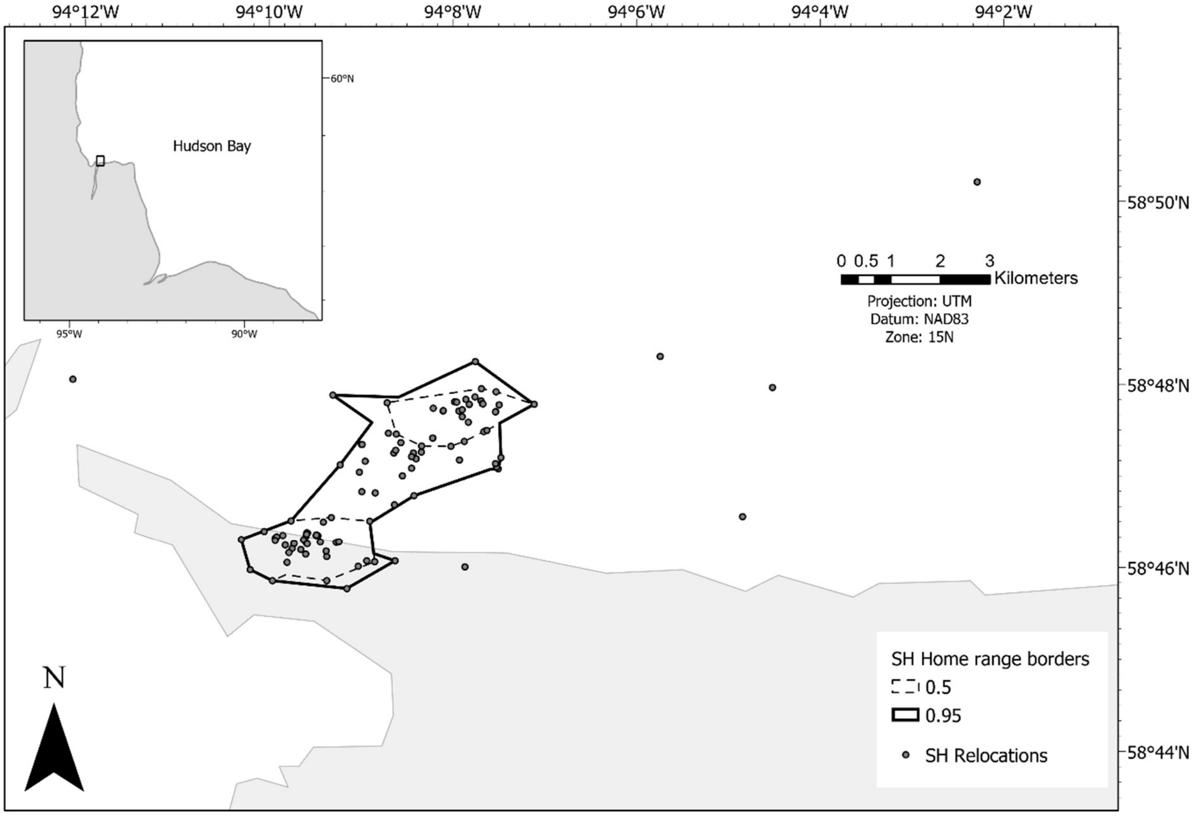
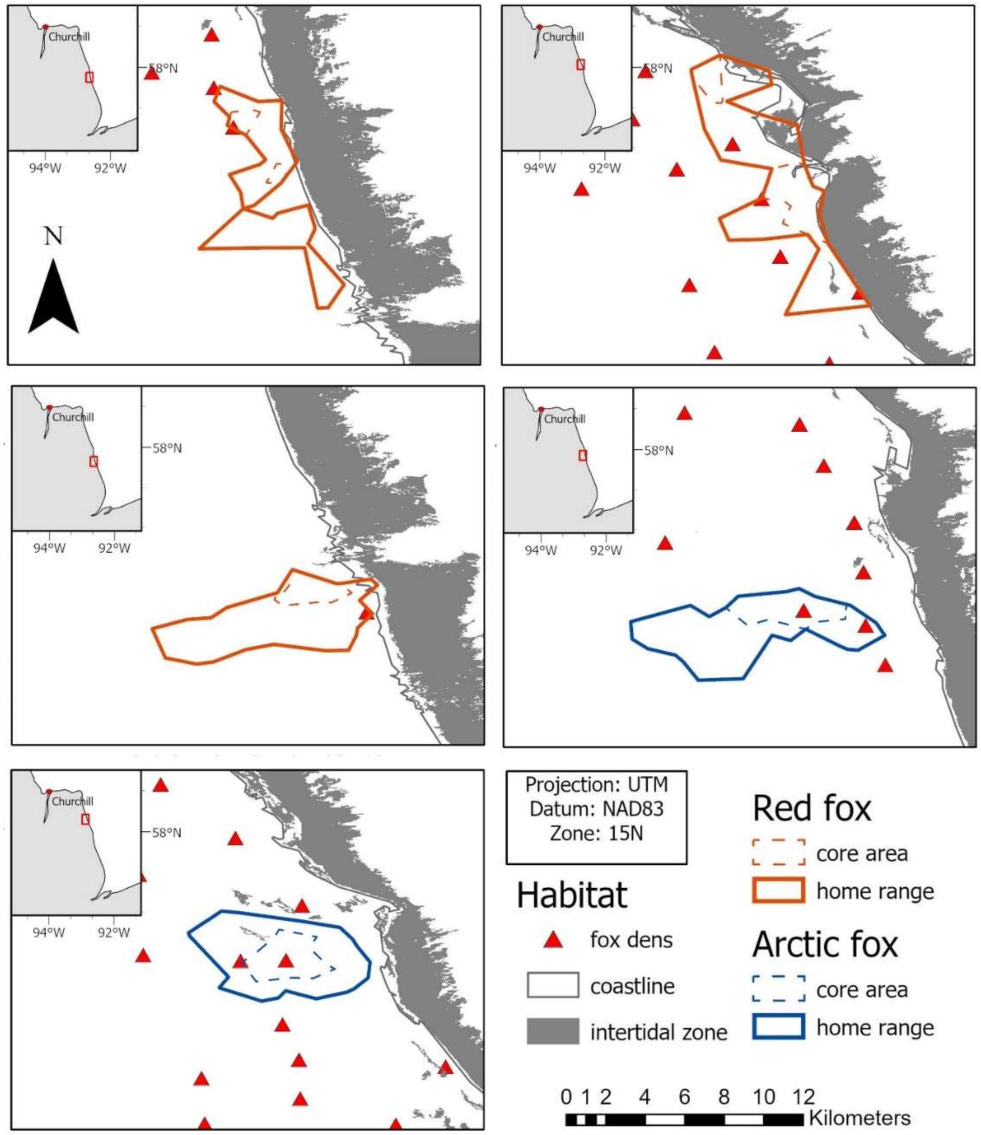
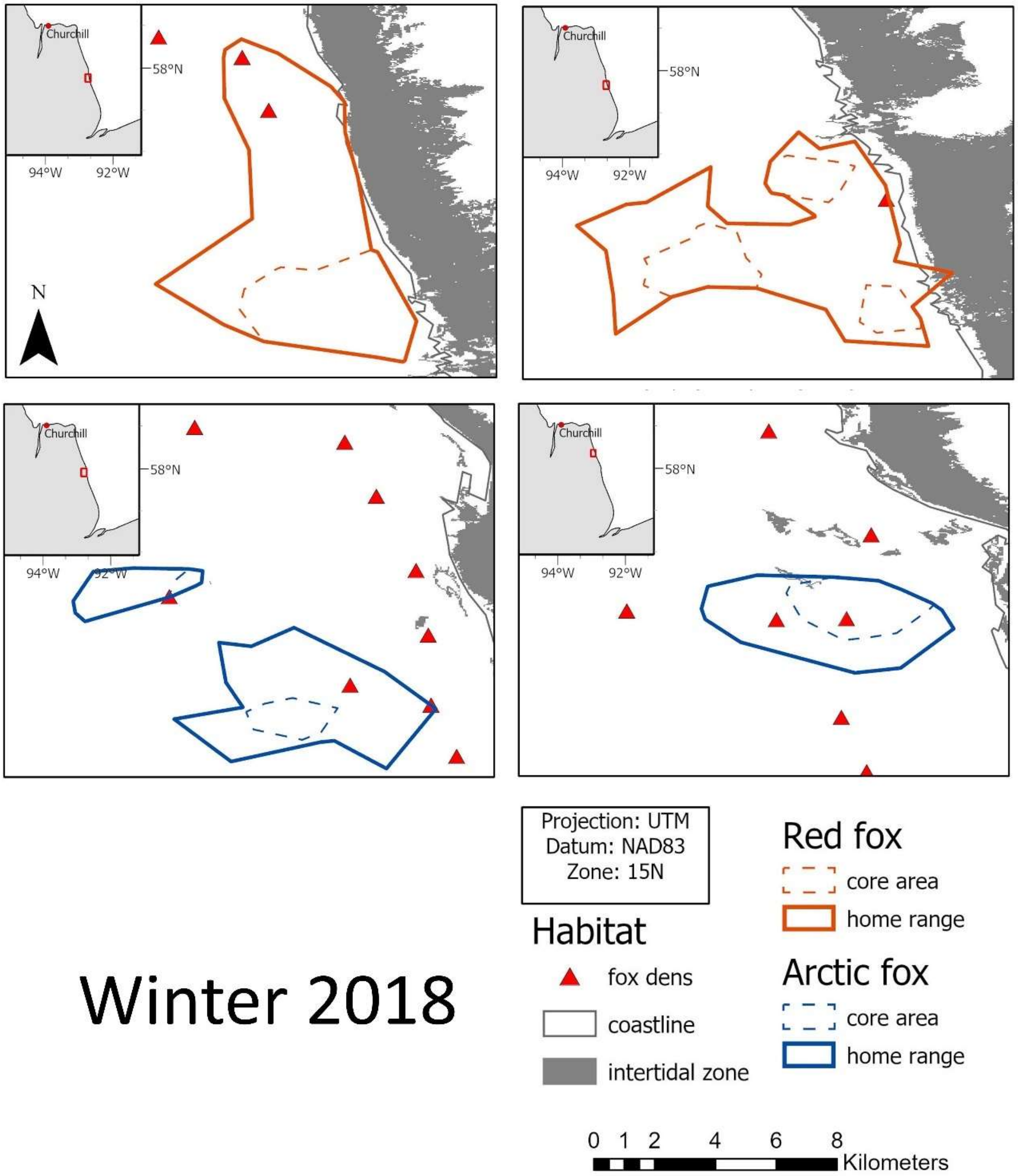


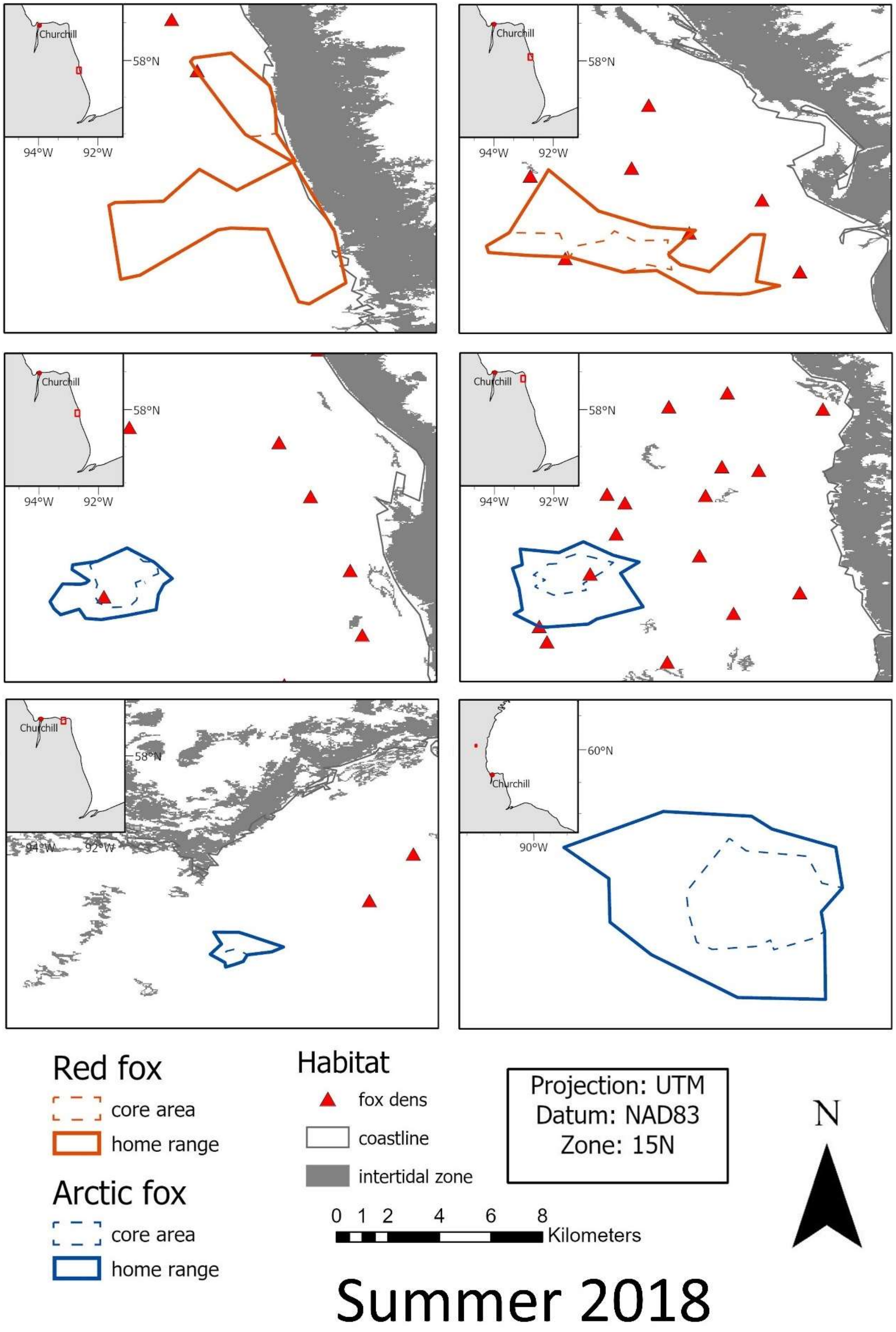
Fig. 2.S1. Relocations, home range (iso level 0.95) and core area (iso level 0.5) of the Arctic fox SH during winter 2019. The female fox was fitted with a Telonics satellite collar (Telonics, Mesa, Arizona, USA) in June 2018, left her summer home range on September 15, 2018, established a winter home range on November 9, 2018 including part of the town of Churchill (Manitoba, Canada) and nearby sea ice, until she dispersed in March 2019. Her home range was estimated based on one location per day using an *α*-Local Convex Hull (LoCoH). Ice (sea and Churchill River estuary) is in white and land in grey.

Supplemental file 2.1. Series of maps displaying individual home ranges of all red and Arctic foxes fitted with satellite collars in the Churchill area (Manitoba, Canada) that remained resident on the tundra over a season. Seasonal home ranges (Utilization Distribution 95) were estimated based on one location per day using an *α*-Local Convex Hull (LoCoH). Each map cluster groups all foxes resident during one season of each year (summer 2019 was split by species, for legibility).



Summer 2017


Churchill
58°N
94°W
92°W
N
Projection: UTM
Datum: NAD83
Zone: 15N
Red fox
core area
home range
Arctic fox
core area
home range
Habitat
fox dens
coastline
intertidal zone
Winter 2018
0 1 2 4 6 8
Kilometers


Churchill
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Red fox
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Habitat
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Projection: UTM
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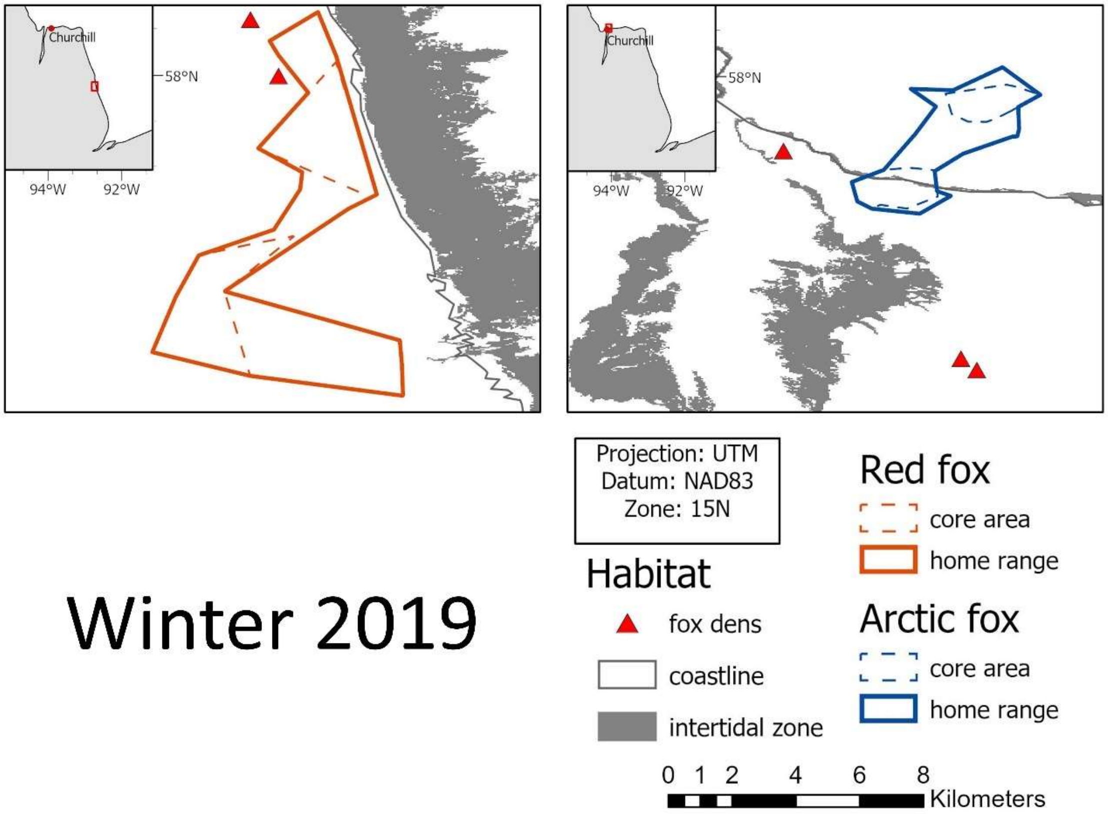
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fox dens
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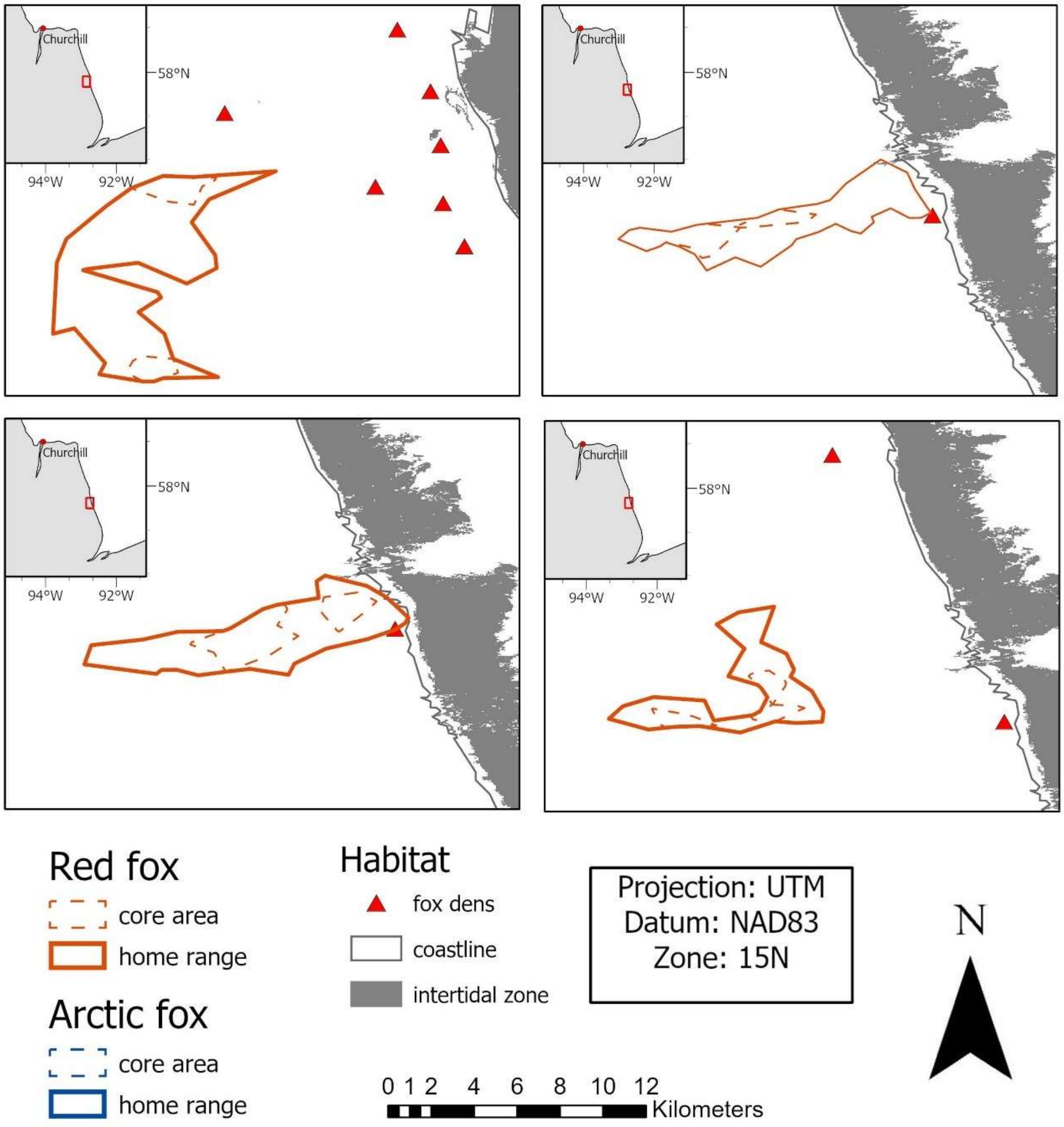
Churchill
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Red fox
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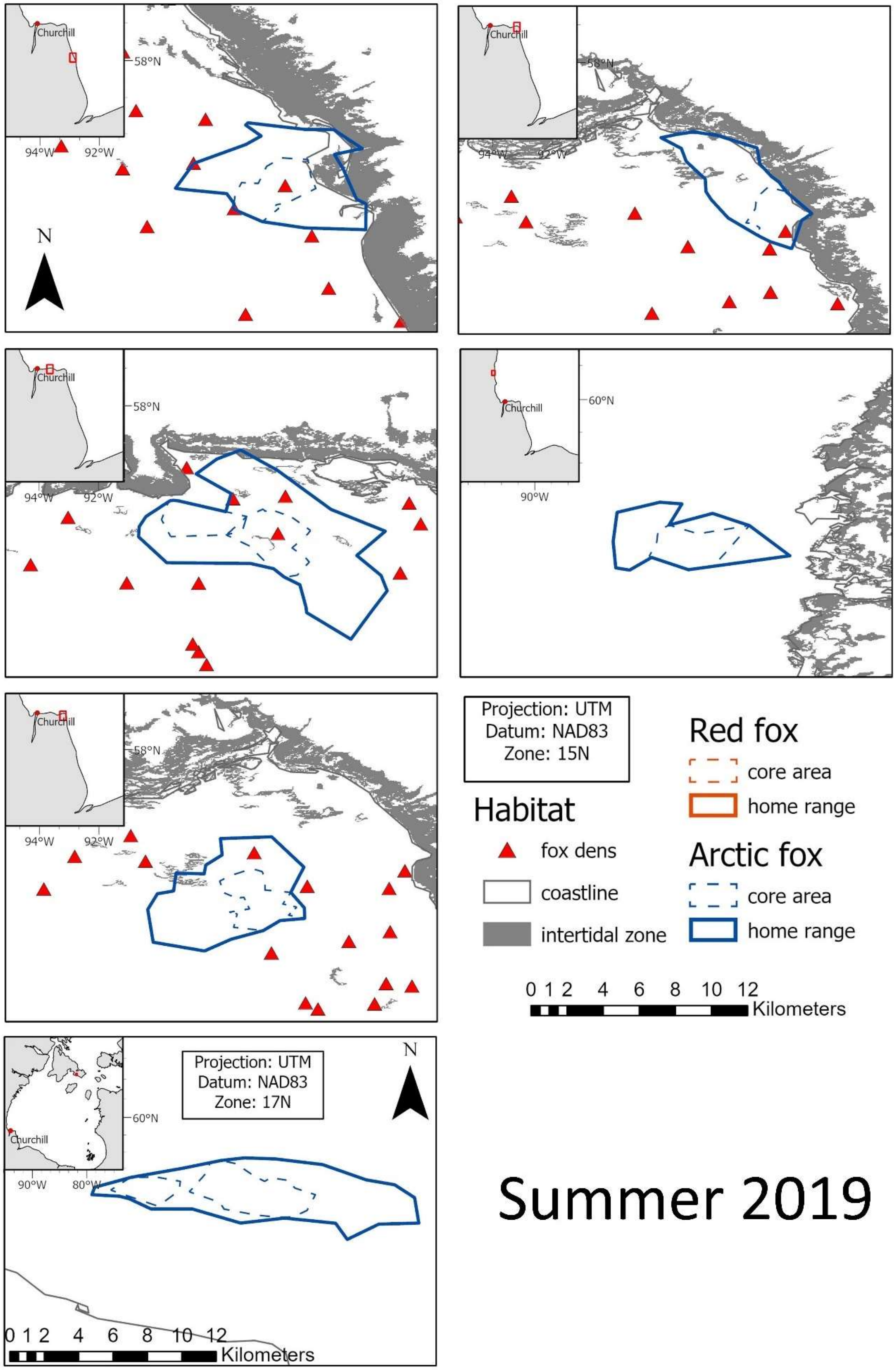
Summer 2019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Habitat
fox dens
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intertidal zone
Red fox
core area
home range
Arctic fox
core area
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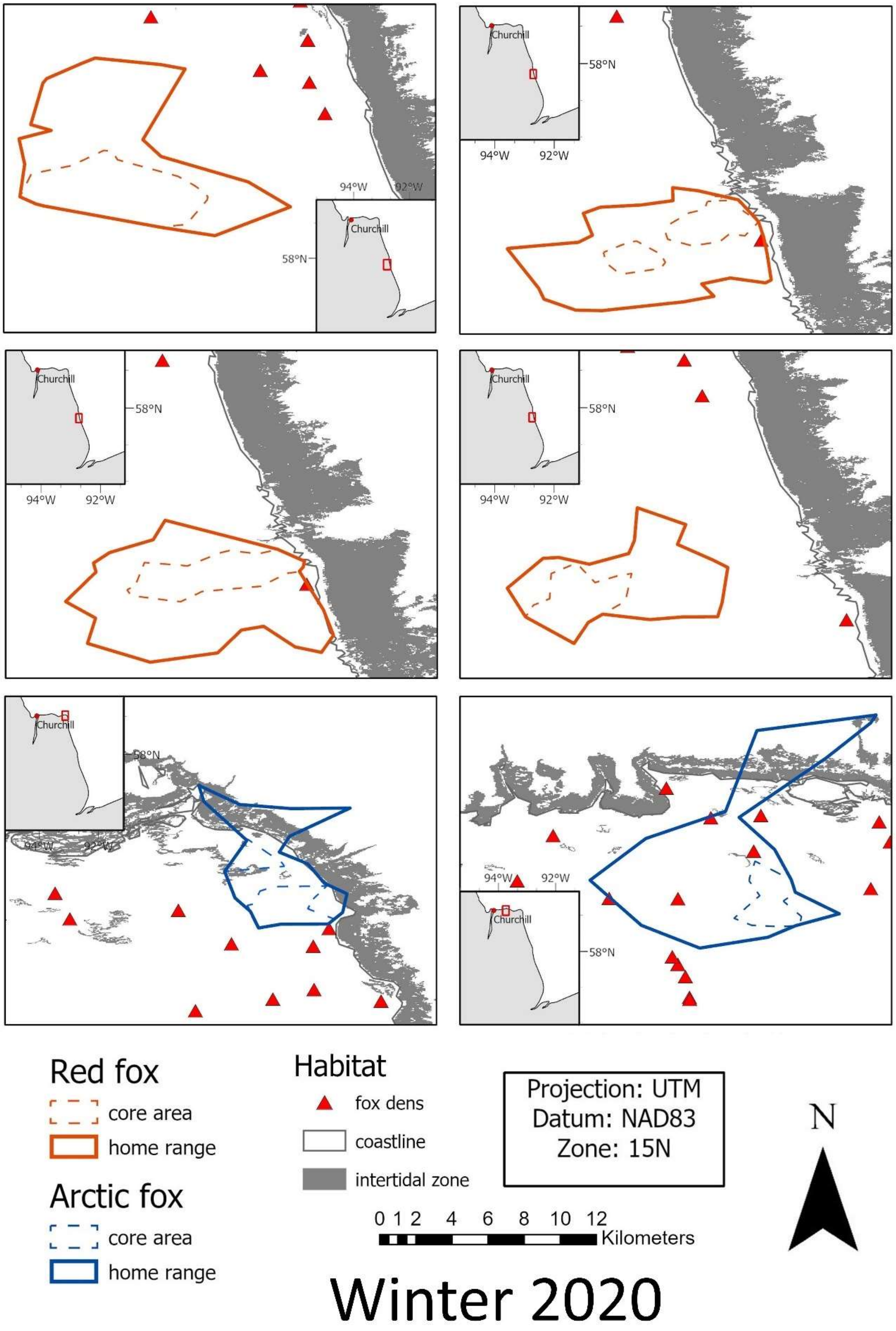
Kilometers
Summer 2019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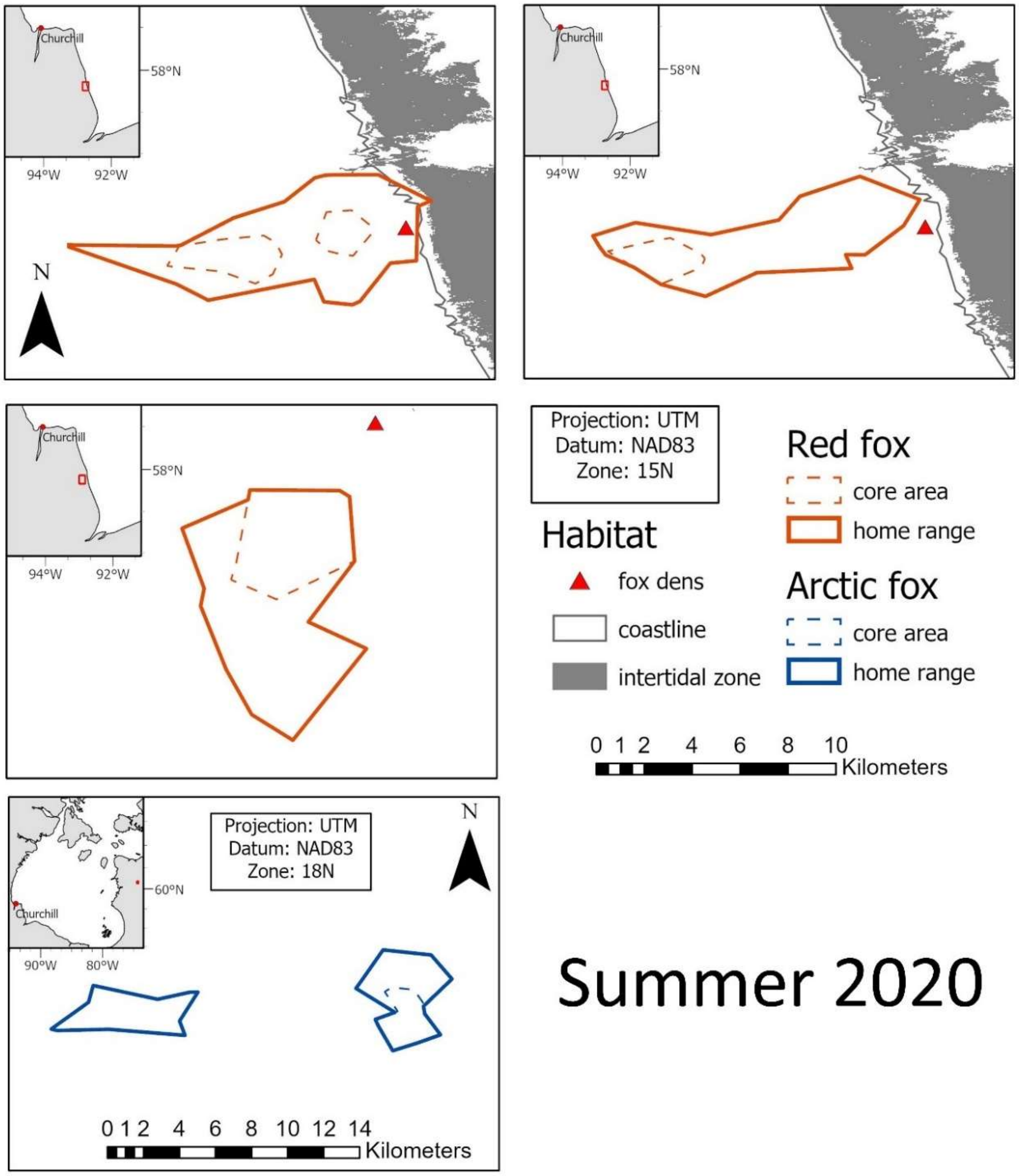
Winter 2020


Churchill
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Projection: UTM
Datum: NAD83
Zone: 15N
Red fox
core area
home range
Habitat
fox dens
coastline
intertidal zone
Arctic fox
core area
home range
0 1 2 4 6 8 10
Kilometers
Churchill
60°N
90°W
80°W
Projection: UTM
Datum: NAD83
Zone: 18N
N
0 1 2 4 6 8 10 12 14
Kilometers

Summer 2020

Prelude to Chapter 3

The high proportion of both red and Arctic foxes that dispersed in Chapter 2 may be indicative of particularly harsh winter conditions on the low-Arctic tundra compared to other areas (Lai et al. 2017). In addition, resident red foxes in Wapusk National Park had to range over substantially larger areas in winter compared to summer. Arctic foxes, however, remained resident in winter without increasing the size of their home range, which suggests that they were better adapted than red foxes to resource scarcity during winter.

Reproduction in foxes starts towards the end of winter and constrains their movements because both species are central-place foragers that depend on dens to protect their young (Careau et al. 2007; Potts et al. 2012). When reproduction starts in the Churchill area, food resources are still scarce and may be limiting, which suggests that interspecific competition may be maximal at that time of the year. Chapter 3 examines the spatial ecology of the interactions between these two predators at a time of the year when exploitative and interference competition should be maximized. Therefore, I address the second part of the overarching hypothesis, i.e., that although the potential for exploitation is high at the end of the winter, the heterogeneity of the landscape near treeline allows the two fox species to relax competition.

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Lai, S., Bêty, J., and Berteaux, D. 2017. Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic. Oikos **126**(7): 937–947. doi:10.1111/oik.03948.

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Chapter 3: Coexistence of two sympatric predators at the edge of Arctic under constraining environmental conditions

Abstract

Range expansion of boreal-forest species onto the tundra is a major consequence of Arctic warming and may cause substantial changes in Arctic tundra communities due to competition with tundra dwellers. We studied competitive interactions between red (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) using satellite telemetry to assess the potential for endemic tundra species to coexist with expanding boreal-forest competitors. We targeted the beginning of the reproductive period (March – May) because resource scarcity, increased food requirements and spatial constraints of the foxes likely exacerbate the potential for competition. The strong territoriality of our 17 collared foxes suggested substantial exploitation competition for space, with no obvious differential use of the areas shared by heterospecific neighbors. Despite the scarcity of resources, red foxes did not exclude Arctic foxes by interference. If anything, intraspecific competition in red foxes may be stronger than both interspecific and intraspecific competition in Arctic foxes, thus creating the potential for self-limitation of the red fox population, which should advantage the Arctic fox. In addition, our results suggest that differential tolerance for the tundra environmental conditions may be a better axis for niche separation, and thus promotes coexistence. The heterogeneity of the landscape near the tree line may release competitive pressure between boreal-forest and endemic tundra species by allowing the exclusive use of some resources. Thus, at low density, expanding boreal-forest species may coexist with native tundra dwellers under current environmental conditions: lesser adaptations of forest species to abiotic conditions of the tundra environment may create asymmetric competitive interactions, where the dominant competitor benefits from interference and the subordinate has superior exploitation capabilities, thus promoting coexistence.

Introduction

Interspecific competition is a structuring force of carnivore communities (Palomares and Caro 1999; Ritchie 2002; Berger and Gese 2007). Wherever ecologically similar species are sympatric, competition can occur over limited shared resources with varied intensity levels (Case and Gilpin 1974; Schoener 1976; Connell 1983), depending on the similarity of the competitors' ecological niches (Vandermeer 1972; Donadio and Buskirk 2006; Polechová and Storch 2008). Two forms of competition are classically described (e.g., Case and Gilpin 1974). Exploitation competition is indirect, as competitors negatively affect each other by depleting a resource; its strength thus depends on spatio-temporal patterns of resource abundance (Matassa and Trussell 2011; Holdridge et al. 2016). Interference competition can be indirect when the simple presence of a competitor leads to prey hiding or relocating, or direct, as individuals prevent others from accessing resources along a behavioral continuum from passive blocking to interspecific killing (e.g., Amarasekare 2002); its strength thus increases with competitor density and may not depend on resource availability (e.g., Amarasekare 2002; Holdridge et al. 2016). Exploitation and interference competition typically increase together (Park 1954), likely because the rate of encounter of consumers with both competitors and their prey are driven by movement patterns (Delong and Vasseur 2013).

Niche theory forecasts niche optima separation as a condition for similar species to coexist (Hutchinson 1959; Polechová and Storch 2008). Hence, although interspecific competition is a frequent community feature, it seldom leads to competitive exclusion, indicating coexistence mechanisms must be widespread (Schoener 1976; Ritchie 2002; Powell 2012). Examples of coexistence mechanisms include 1) differential tolerance to abiotic factors that can lead to spatial interdependence between the population growth rate of a species and a given resource threshold (Amarasekare 2003), 2) temporal or spatial segregation to avoid interference (e.g., Andersen et al. 2020; Easter et al. 2020), 3) habitat or food-resource partitioning to allow exclusive use of resources (Leal and Fleishman 2002; Ramesh et al. 2012) — and thus the persistence of a given density of each competitor based on those resource dynamics. Niche partitioning is, therefore, contingent on heterogeneity along the niche axes (Amarasekare 2003).

Furthermore, when ecologically similar species have similar body sizes, the likelihood of using the same resources increases, thereby increasing the chances of encounter and thus of agonistic interactions (Palomares and Caro 1999). Carnivore interactions are usually asymmetric and the likelihood of interference is highest at intermediate body-size differences, because at large differences dietary overlap is usually reduced, and at small differences the risk of injury or death from interference encounters is too high, even for the dominant competitor (Donadio and Buskirk 2006). The subordinate species may thus shift their realized niche in response to a dominant competitor (Polechová and Storch 2008). Empirical examples included generalist subordinate species that altered their resource selection (American mink (*Neovison vison*), Harrington et al. 2009; Arctic foxes (*Vulpes lagopus*), Gallant et al. 2014), habitat or space use (cheetahs (*Acinonyx jubatus*) Durant 1998; lions (*Panthera leo*), Schuette et al. 2013), or activity peaks (mountain gazelle (*Gazella gazella*), golden jackals (*Canis aureus*), crested porcupine (*Hystrix indica*), red fox (*Vulpes vulpes*) and wild boar (*Sus scrofa*) - Shamoon et al. 2018).

Arctic warming and other anthropogenic influences have permitted boreal forest species to expand their range onto the Arctic tundra, where they may compete with native species (Hersteinsson and Macdonald 1992; Tape et al. 2016; Gallant et al. 2020). In particular, harsh winter conditions historically prevented red foxes from becoming established on the tundra, but during the twentieth century, their northern range limit expanded >1,700km towards the North pole (Gallant et al. 2020). The presence of red foxes within the distribution of Arctic foxes, which range throughout the circumpolar Arctic, may thus elicit competitive interactions between the two foxes, given their ecological similarities. Both species are central-place foragers (Careau et al. 2007a; Potts et al. 2012), specifically when they reproduce, because they depend on dens for shelter and to protect their offspring from predators (Gallant et al. 2013). They feed preferentially on arvicoline rodents (lemmings and voles) year-round (Jędrzejewski and Jędrzejewska 1992; Roth 2002), but are also opportunists and use alternative resources if the preferred prey is less available or if an alternative prey becomes particularly abundant (Roth 2003; Dell'Arte et al. 2007; Lai et al. 2017). Geese (*Branta canadensis* and *Anser caerulescens*), for example, provide an abundant source of food for tundra predators throughout summer (McDonald et al. 2017), and in winter, the sea ice may provide foxes with alternative resources to terrestrial prey (Roth 2002, 2003).

We examined the potential for competition and segregation between red foxes and Arctic foxes in and near Wapusk National Park, in northern Manitoba, where red foxes recently became established on the thin band of coastal Arctic tundra between tree line and Hudson Bay and now reproduce in sympatry with the endemic Arctic foxes (Moizan et al. *submitted*; Chapter 2). We focused this study on the period during which foxes settle to reproduce and before the pups emerge (mid-March to mid-June during gestation and lactation) because it is a critical period in terms of resources. Foxes may compete for pre-existing dens as the ground is still frozen and they cannot excavate new ones. Food resources slowly increase throughout this period, but geese only start to arrive during the first week of May (Cargill and Jefferies 1984), and the median hatch date of Canada goose eggs occurs during the 3rd week of June (Andersen et al. 2010). This timeframe thus represents a period of higher resource requirements to support reproduction, while food is still scarce. Competition over food resources may thus be strong during this period, exacerbated by the fact that fox movements are constrained to remain near their reproductive dens.

We hypothesized that the potential for exploitation competition during this critical period is substantial (see Appendix 3.A), but habitat heterogeneity offers opportunities for the two species to partition resources, thus relaxing a high potential for a red-fox-dominated interference competition driven by intermediate body size difference. We consequently predicted that during this time period, P1) red foxes have larger home ranges than Arctic foxes, reflecting their difference in body size, P2) resource scarcity exacerbates competition, so little home-range overlap occurs (Eide et al. 2004), P3) risks of interference induce asymmetric spatiotemporal use of the shared area between heterospecific neighbors, in favor of the red fox, and P4) Arctic and red foxes partition habitat and time use of the shared areas.

Methods

Study area. – We studied the spatiotemporal interactions of red and Arctic foxes in Wapusk National Park and the Churchill Wildlife Management Area (58°N, 94°W) (Fig. 3.1). This area is part of the Hudson Bay lowlands, a uniformly flat (<200m elevation) wetland bordering the south-western shore of Hudson Bay to the western shore of James Bay (Brook and Kenkel 2002). Hudson Bay exerts a strong cooling effect on the area. Onshore winds from the Bay dominate during most of the growing season, and are an important factor limiting tree growth (Rouse 1991; Mamet and Kershaw 2011). The interchanging influence of the offshore and onshore winds favors abrupt and sometimes important changes in air temperature (Rouse 1991).

Three biomes merge in this area: the tundra and marine ecosystem of Hudson Bay to the north and east, and the boreal forest to the south and west. Red foxes lack adaptations to the tundra and marine ecosystems: they usually occur in low density or even discontinuously, may resort to drastic behavioral adjustments to cope with environmental harshness, and seem unable to exploit the sea ice like Arctic foxes do to compensate for food shortage (Roth 2003; Gallant et al. 2020; Lai et al. 2022; Chapter 2). The sea ice may thus offer an opportunity for resource partitioning between the two species. We define the start of the sea ice at the low tide line (Ponomarenko et al. 2014), i.e., beyond the intertidal flats (see Fig. 3.1). The proximity of the boreal forest may favor a continuous source of red foxes, which are likely to increase on the tundra as winters become milder. The presence of transitional habitat, with patches of trees increasing in density and size near the boreal forest and along the river corridors (Ponomarenko et al. 2014), may offer further opportunities for the red fox to spatially segregate from the Arctic fox.

Capture and satellite telemetry. – Between 2017 and 2019 we captured 10 red foxes and 13 Arctic foxes using padded leghold traps (Softcatch # 1.5, Oneida Victor Ltd, USA) and Tomahawk live traps (Model CB12DD-36, Tomahawk Live Trap Co., WI). Traps were deployed each year between March and May opportunistically on tundra dens and spruce islets, wherever we identified fox signs (see Chapter 1 for additional details on trapping procedures). We fitted all captured foxes with an Iridium satellite collar (#4170 or 4270, Telonics, Mesa, Arizona, USA; ~100g, or 2-4% of body mass) before releasing the animals. Median handling time was 25 min. [11-50] from our arrival at the trap station to fox release. All handling procedures were approved by the University of Manitoba Animal Care Committee (Protocol F17-012). Our research was carried under Parks Canada permits WAP-2017-25781 and WAP-2018-27938, and Manitoba Wildlife Scientific Permits WB20226 and WB21856.

Movement analyses. – Our satellite collars collected fixes at different schedules throughout the year (see Table 2.S1 in Chapter 2). Our focal period here (March 15 to June 15) corresponded to the highest location frequency, with one location per 1.5 to 2 hours (12-16 daily locations). We first plotted all fox tracks in ArcGIS 10.3 (ESRI 2017, Redland, CA, USA) to remove major erroneous locations (i.e., fixes with a pre-deployment timestamp or fixes that would require impossible speed to be obtained), and identify movement strategies: residency and long-range movements (Chapter 2). Foxes that were not obvious residents were excluded from subsequent analyses.

Using package ctmm 0.6.0 (Fleming and Calabrese 2021), we next produced empirical variograms (i.e., plots of the semi-variance of the relocations which measures variability in the distance between pairs of locations against time lags between relocations) (Fleming et al. 2014) of the foxes deemed residents in ArcGIS (see Fig. 3.B.1). This tool provides further details on the track structure, including the convergence toward an asymptote — suggesting range residency if present — or the autocorrelation structure. One case was ambiguous, but we tested it for range shift using package marcher v0.0.2 (Gurarie et al. 2017). Evidence suggested that he simply changed his center of activity, and so we included him as a resident and excluded the period during which he relocated elsewhere outside the estimated home range. Based on the confirmation of range residency by the empirical variograms, we created a second dataset of resident foxes with their extra-territorial excursions removed to produce home ranges. To identify excursions, we first produced the distribution of distances between locations and the track centroid (using ArcGIS 10.3), and excluded outliers using a one-sided Hampel filter with R packages fitdistrplus 1.1.1 (Delignette-Muller and Dutang 2015) and rcompanion 2.3.25 (Mangiafico 2020), where:

(1) upper bound = median (Tukey-transformed distance) + 3 median absolute deviations.

We based all range analyses on Time Local Convex Hulls (T-LoCoH; Lyons et al. 2013), a family of non-parametric methods to build Utilization Distributions (UD) that extends the classic LoCoH non-parametric methods (Getz et al. 2007) by integrating both time and space in the construction of the local hulls associated with each location. The Time Scaled Distance metric (TSD) transforms the time interval between locations into a distance representing a third axis in Euclidian space, by scaling the individual's maximum theoretical velocity (i.e., the maximum observed velocity between two consecutive points: $v_{\max}$) with a dimensionless scaling factor (s). So, if $s = 0$, the third axis is ignored (i.e., time is ignored) and thus hulls are only space selected. As s increases, points that are far away in time get pushed apart regardless of their proximity in space: hulls become time selected as well as space selected (see Lyons et al. 2013 for a detailed explanation). Given the median of the position autocorrelation of our tracks of 9.4 hours, our 12 to 16 locations per day, and the general context of our study, we defined a 12-hour period of interest for all foxes. We selected individual-specific values of s based on the recommendations and tools provided in the package T-LoCoH v.1.40.07 (Lyons et al. 2013). Specifically, we selected s values for each individual such as

$$(s{*}v_{\max}\,\Delta t_{ij})^2 = \Delta x_{ij}^2 + \Delta y_{ij}^2 \qquad (2)$$

holds for all points i and j with coordinates x and y, that are located $\Delta x_{ij} = x_i - x_j$ on the longitude axis, $\Delta y_{ij} = y_i - y_j$ on the latitude axis, and $\Delta t_{ij} = 12$h apart. Our s values thus ranged between $s = 0.01$ and $s = 0.1$. To create the hullsets, we defined the number of nearest neighbors (nnn) using the adaptive method (i.e., nearest neighbors are all points whose cumulative distance to the focal point is $\leq a$), which is less sensitive to outlying locations and better suited when location densities are heterogeneous (Getz et al. 2007). We selected an a-value for each animal following the recommendations and using the graph tools provided in the T-LoCoH package to minimize the risks of type I (excluding used areas) and type II (including unused areas) errors.

We first produced home range estimates by aggregating and sorting the hulls based on the number of enclosed nearest neighbors. The resulting isopleths thus represent the likelihood of occurrence, and those home range estimates can be used to assess the intensity of use. We used the 95% (home range) and 50% (core area) isopleths to compare space requirements between red and Arctic foxes (P1) and assess the potential for exploitation competition (P2).

A key property of the T-LoCoH is that hulls include points spatially close but temporally distant (Lyons et al. 2013). These points indicate recurring visits to the hull, based on a specified temporal threshold (the inter-visit gap) that defines the time to pass before another observation counts as a new visit. They thus contain time-use information from which we can derive time-use metrics. We used this property to produced behavioral maps to assess the potential for spatio-temporal and resource segregation between the two fox species (P4). We sorted the hulls for each fox based on the number of separate visits (nsv)—a measure of revisitation rate—and the mean number of locations per visit (mnlv)—a proxy for duration of use — based on our 12-hour period of interest as the inter-visit gap. To be conservative in estimating the key resources for our foxes without excluding important resources that may represent a potential for segregation, we selected the 50% isopleths to minimize both type I and type II errors.

We measured the extent of nnn home-range overlap between heterospecific (i.e., of or belonging to different species) and homospecific (i.e., of or belonging to the same species) neighbors (P2 and P3). Foxes were considered neighbors when the distance between their home range boundaries (based on the 95% isopleths nnn estimate) was less than the radius of a red fox's home range (i.e., <3.2 km) (see Results). We calculated home-range overlap of a dyad as:

(3) $$HR_{overlap} = [(area_{AB}/home\ range_{A})*(area_{AB}/home\ range_{B})]^{0.5}$$

where $area_{AB}$ is the area delimited by the overlap of the two home ranges and $home\ range_{A}$ and $home\ range_{B}$ are the individual home range areas of individuals A and B.

We then quantified the spatial and temporal use of the shared areas with package wildlifeDI v. 0.4.1 (Long et al. 2014) using Minta's (1992) set of coefficients ($L_{A:\bar{A}}$, $L_{B:\bar{B}}$, and L_{ixn}) and compared them for each type of dyad (heterospecific, homospecific red foxes and homospecific Arctic foxes). The $L_{A:\bar{A}}$ and $L_{B:\bar{B}}$ coefficients are purely spatial, testing the observed number of occurrence of the animals in $home\ range_{A}$, $home\ range_{B}$, and $area_{AB}$ against the expected number of occurrences—i.e., the probability of finding A and B in a specific zone given the proportion of areal overlap (Minta 1992). The spatial behavior towards the shared area can thus be characterized as random ($L_{A:\bar{A}}$ or $L_{B:\bar{B}} \sim 0$), attraction ($L_{A:\bar{A}}$ or $L_{B:\bar{B}} > 0$), or avoidance ($L_{A:\bar{A}}$ or $L_{B:\bar{B}} < 0$). Based on the response of each animal, a dyad's spatial response to the shared area can be symmetric (same response), asymmetric (opposite response), or singular (only one individual shows a significant response). The L_{ixn} coefficient is calculated from the ratio of simultaneous presence and simultaneous absence to solitary presence in the shared area (Minta 1992; Long et al. 2014) as follows:

(4) $$L_{ixn} = Ln[(n_{AB}/p_{AB}+n_{00}/p_{00})/(n_{A0}/p_{A0}+n_{0B}/p_{0B})]$$

Where n is the observed and p the expected simultaneous use (AB) and non-use (00), and solitary use (A0 and B0), by animals A and B, of their shared area. When $L_{ixn} \sim 0$, each individual's temporal use is random, whereas if $L_{ixn}>0$, they show a pattern of simultaneous use of the shared area, and when $L_{ixn}<0$, they use the shared area solitarily (Minta 1992; Long et al. 2014). We defined simultaneous locations using a 15-min. buffer related to variation in location calculation by the collars. We used these indices to further indicate the possibility of interference competition between the fox species (P3) and used the L_{ixn} in the context of symmetric attraction for the shared area as evidence of time segregation (P4).

We exported the nsv and mnlv hulls created in T-LoCoH as shapefiles in ArcGIS Pro 2.4 (ESRI, 2020) to compare key habitats for red *versus* Arctic foxes. We extracted the proportion of habitats of all home ranges by clipping the Canadian Landcover 2015 vegetation map (Natural Resources Canada 2019, Latifovic et al. 2017; see description in Table 3.B1) and the intertidal zone (a key habitat that was missing from the Canadian Landcover map) of the Wapusk National Map Ecotype map (Ponomarenko et al. 2014) with the clip raster function. We then converted the obtained raster layers to polygons, which we intersected with the desired home range isopleth and obtained the total area of each habitat within the 50% isopleths of nsv and mnlv home ranges using the summarize function. We, finally, calculated the mean proportion of each habitat type, excluding 2 Parks Canada compounds and water (ponds, lakes, and streams).

Statistical analyses. – We conducted all analyses in R version 4.0.5 (R Core Team 2021) using R Studio version 1.4.1717 (RStudio Team, 2021). We checked all our models for: residual normality and applied transformations when necessary, heteroscedasticity and adapted our tests accordingly, and presence of outliers that we reviewed individually to keep or discard (Zuur et al. 2010). Two dyads of red foxes had a home range overlap of at least 85%, whereas the median of all overlaps was 6%: one dyad was a mated pair, and the other was two females who may have been mother-daughter, based on the age difference suggested by tooth wear. Despite the relative independence of their movements (DI: DI = 0.05, DI.θ = 0.10, DI.d = 0.38, P_{pos} = 0.002, P_{neg} = 1; Long and Nelson (2013)), we also considered them as a pair to avoid pseudoreplication.

We compared species' requirements for space (P1) using a GLMM (family gaussian, link identity) from package lme4 v.1.1-25 (Bates et al. 2015) and lmerTest v.3.1.3 (Kuznetsova et al. 2017), controlling for fox-pair ID as a random effect. When comparing home-range overlap within and between species (P2), excluding overlaps between foxes that belonged to a pair, we used two-sided permutation tests based on the t statistics (n_{perm} = 999) to first compare overlap between red-fox and Arctic-fox homospecific neighbors, and between heterospecific neighbors. We repeated the analysis for the overlap between core areas, using Wilcoxon signed-rank tests. We assessed the possibility that interference (P3) and time segregation (P4) occurred: we tested if the behavioral response (random, attraction, or avoidance) and the symmetry of that response differed between the type of fox neighbors (heterospecific, Arctic- and red-homospecific pairs) with a Fisher exact test. We tested if a fox was more likely to avoid a heterospecific neighbor than a homospecific one using a GLMM, using the odds of solitary use as response variable and the type of neighbor as explanatory variables (family Gaussian and identity link), controlling for fox ID as a random effect, and allowing the variance to differ between neighbor types (Zuur et al. 2009; Harrison et al. 2018) using the varIdent function of package nlme v.3.1.152. We assessed space-time segregation by measuring the overlap between the 50% UD nsv and mnlv range areas of neighboring foxes and testing with a series of Fisher's randomization tests if the overlap significantly differed from 0 for each type of dyad. Because the overlap can only be greater than 0, we considered a one-tailed P-value at the α = 0.05 level. We had one outlier with Cook's distance = 0.57: one pair of male Arctic foxes with a large overlap. We had no ecological reason to exclude this observation, however, so ran the tests with and without the outlier to assess its leverage. We report the results of the test ran on the full set only. Finally, to assess the potential for resource segregation, we first compared the habitat composition of the nsv- and mnlv-range areas of the two species using a MANOVA (e.g., Schweiger et al. 2015) with package MANOVA.RM v.0.5.2 (Friedrich et al. 2021). We grouped all forested habitats into one category and used species as a predictor. Our habitat variable had multivariate normal distribution. We dealt with heteroscedasticity using a parametric bootstrap resampling method (n_{iter} = 10,000), and report the modified ANOVA-type statistic (MATS) instead of a Wald-type statistic because it can also deal with singularity (Friedrich and Pauly 2018). To control for pseudo-replication, we kept one value for the foxes that were present multiple years and dropped one fox of each of our two pairs at random. We thus included 9 Arctic- and 6 red-fox home ranges in that analysis.

Results

Between March 15 and June 15 of 2017 to 2020, we tracked 17 foxes that exhibited range residency, and four that did not. The resident foxes — eight red and nine Arctic foxes — yielded a total of 12,840 locations after removing their excursions. Because two red foxes were present for two seasons and one red fox for four seasons, we obtained 22 home ranges over the four years (13 red fox and 9 Arctic fox). Although our observations are indirect in this study, we opportunistically recorded direct observations, from trail cameras, the people of Churchill, other researchers, and from tourists. We thus obtained direct evidence of a range of interactions between the two fox species, including indifference (Fig. 3.B.2-A), and agonistic interactions where the pursuer was not always the red fox (Fig. 3.B.2-C). Agonistic interactions occasionally escalated to intraguild killing events (Fig. 3.B.2-B); these extreme events were always observed in November, with invariably the red fox killing the Arctic fox (B. Debets, pers. obs., November 2014; J. Waterman, pers. obs., November 2017; D. Alcorn, pers. obs., November 2020). November in Churchill marks the beginning of food-scarcity, and of harsher climate (Chapter 2).

Space requirements and potential for exploitation competition. – Arctic and red foxes had home ranges and core areas of similar size over the period of interest (GLMM; home range: $t = 0.24$, $DF = 13.15$, $P = 0.82$, $n_{red} = 13$, $n_{Arctic} = 9$; core area: $t = -0.57$, $P = 0.58$, $n_{red} = 13$, $n_{Arctic} = 9$; Fig. 3.2). The overlap of nnn-home ranges between neighboring foxes was generally low (Table 3.1), and the overlap of core areas virtually nonexistent (except in one case where two male Arctic fox neighbors overlapped highly with an index of 0.28, representing 0.25 and 0.31

of their core areas). The amount of home-range or core area overlap was similar between heterospecific and homospecific neighbors (permutation test: t = 0.814, P = 0.352; Wilcoxon signed-rank test: Z = -0.93, P = 0.56; n_{hetero} = 3, n_{homo} = 12), and within each type of homospecific neighbors (t = -0.156, P = 0.95; Z = -0.51, P = 0.68; $n_{\text{red-red}}$ = 8, $n_{\text{Arctic-Arctic}}$ = 4). Furthermore, the amount of overlap of the nsv (number of separate visits) and mnlv (mean number of location per visit) 50% UD did not differ from 0 for both heterospecific (Fisher's randomization one-tailed; nsv: Sum = 0.009, P = 0.5; mnlv: Sum = 0.05, P = 0.5), homospecific red fox neighbors (nsv: Sum = 0.058, P = 0.25; mnlv: Sum = 0.006, P = 0.125) and homospecific Arctic fox neighbors (nsv: Sum = 0.102, P = 0.5; mnlv: Sum = 0.267, P = 0.25).

Interference and segregation. – Twelve of the 15 dyads shared some area of their home range, including all three heterospecific dyads (Table 3.2; Fig. 3.3). The three heterospecific dyads showed different spatial and temporal responses. In one dyad, both foxes were using their shared area randomly. In one case, the Arctic fox was attracted to the shared area, and the odds of the two foxes using the area together were nearly 6 times higher than expected despite the spatial indifference of the female red fox to the shared area. In the last heterospecific dyad, the Arctic fox showed spatial avoidance. Two dyads of Arctic foxes showed singular attraction to their shared area, and a solitary use trend (Table 3.2); their odds of solitary use ranged from 2 to 5 times higher than expected. The last dyad of Arctic foxes that involved two males, in addition to having a particularly large shared area (of both their 95% and 50% UD), showed a strong symmetric attraction to that shared area and the L_{ixn} = 1.49 with p <0.001 indicated strong temporal attraction. Their odds of simultaneous use were 33 times higher than expected, and both males used the share solitarily in a similar way (pair Gi-Gh, table 3.2). These results suggest simultaneous temporal and symmetrical-spatial attraction. The spatio-temporal relationships between red fox dyads suggested dominance relationships in half cases, with asymmetric attraction to the shared area, and one fox having much higher odds of solitary use than expected while the other had much lower odds of solitary use than expected. The remaining red fox dyads showed singular attraction to the shared area or symmetric attraction but solitary use. The spatial response to a shared area did not differ between dyad types (Table 3.2; P = 0.15). On a temporal axis, however, the odds of solitary use of a shared area were higher for homospecific than heterospecific neighbors (GLMM: t = 3.78, DF = 9, P = 0.004, $n_{hetero} = 6$, $n_{homo} = 18$).

We found moderate evidence that habitat composition of both the mnlv (MANOVA: MATS = 3.5, P = 0.09) and nsv (MANOVA: MATS = 2.8, P = 0.12) ranges differed between species (Fig. 3.4). Red foxes never used the sea ice and only one individual used a relatively large area of intertidal flats in his nsv and mnlv ranges (accounting for 23% and 3% respectively), whereas no Arctic fox used denser forested habitats (i.e., sub-polar broadleaf, needleleaf and mixed forests; see Tables B3.1 and B3.2). Sea ice was never part of the Arctic foxes' nsv home ranges but composed 3 to 39% of the mnlv home ranges of 3 out of 9 Arctic foxes. Only one red fox used mixed forest habitat, but this type of forest is scarce in our study area. Two red foxes had established their home ranges on the coast, in pure tundra habitat and thus did not include any patch of denser forest; one did not even have access to the sparse-canopy forest (i.e., subpolar taiga needleleaf forest). Conversely, the 4 other red foxes' mnlv home ranges were composed of 1 to 12% of denser forest patches and 5 to 22% of the sparse-canopy forest type (see Tables B3.1 and B3.2).

Discussion

Overall, we did not find evidence of conspicuous interference, nor a strong asymmetry in interactions in favor of the red fox. Yet, Arctic and red foxes belong to the same genus, with an intermediate difference in mass (Appendix 3.A), spine length and skull length (ratios of red to Arctic fox metrics were 1.4, 1.2 and 1.2, respectively; see Table 3.A1), which is usually associated with unbalanced co-existence and strong interference (Donadio and Buskirk 2006). Evidence of partitioning between the two fox species was scarce. Our results thus suggest potential for strong exploitation competition between red and Arctic foxes over the niche axes we tested (as expected) should resources become limited, but the patchy landscape of our study area also holds the potential to facilitate the coexistence of the two species.

Red and Arctic foxes ranged similarly, contradicting P1. Based on body-size differences and red foxes' lack the adaptation to food scarcity and extreme tundra conditions (Fuglesteg et al. 2006; Careau et al. 2007b), we expected that red foxes would have maintained a home range at least 40% larger than Arctic foxes (Harestad and Bunnell 1979). Over this specific period, red foxes maintained similar home ranges to those they maintain over the whole winter (November 1- May 15; chapter 1), despite the arrival of geese in May, but Arctic foxes seemed to range more than they did over winter (Chapter 1) or in the high Arctic (Lai et al. 2022). Arctic foxes have evolved physiological adaptations to prey scarcity and extremely low temperatures (Fuglesteg et al. 2006; Careau et al. 2007b), but the increase in energetic costs associated with reproduction may be larger in Arctic than red foxes. Reproductive energetic costs are high in mammals, and increase with litter size (Thompson and Nicoll 1986); Arctic foxes have the largest litters among carnivores, with a mean of 10 pups in Canada (Macpherson 1969), whereas red foxes usually have a maximum of 5 to 7 pups (Allen 1984; Lindström1988; Kauhala 1996). Furthermore, Arctic foxes have the highest litter weight (controlled for gestation time) compared to female weight of all canids, including red foxes (Geffen et al. 1996). We previously estimated space use over winter using one daily location (Chapter 2), and LoCoH methods performance increases with number of locations per day (Stark et al. 2017); however, red fox home range estimates are comparable to over-winter home ranges as we expected and in both studies fox-ranging behavior had reached an asymptote, suggesting a methodological artefact is not the sole reason for the discrepancy. Both explanations are not mutually exclusive.

The virtual absence of overlap between neighbors indicates that our two fox populations behaved territorially as evidenced elsewhere, thus supporting P2 (Strand et al. 2000; Goszczyński 2002). High territoriality is consistent with the hypothesis of scarce, scattered, and unpredictable resources (Eide et al. 2004), which suggests that geese do not become an important resource until later (i.e., after foxes start to reproduce) and that conditions at the beginning of the reproductive period are challenging regarding resource acquisition. Furthermore, spatiotemporal segregation was similar within and between species: most individuals had exclusive (or nearly exclusive) use of their patches with highest revisitation rates and highest visit length (despite some minor overlap between some neighbors, notably those showing a dominant-subordinate relationship). That observation strengthens the idea of territoriality, and thus strong exploitation competition, but does not suggest any spatial-behavior asymmetry between red and Arctic foxes.

No overlapping fox dyad showed strong symmetric spatial avoidance of the shared area despite resource scarcity, which was surprising given the general sense of territoriality we infer from their spatial behavior. When neighbors shared space, the overlap and level of spatial attraction for the shared area were similar for homospecific and heterospecific dyads, contradicting P3. The competitive exclusion principle states that for two species to coexist, intraspecific competition should be stronger than interspecific competition (Amarasekare 2003; Vandermeer and Goldberg 2013). Therefore, the similarity of within- and between-species space use and spatial avoidance and generally strong territoriality suggest that exploitation competition for space between Arctic and red foxes could be substantial if their densities were to increase. Thus, the spatial axis would offer little possibility for the two species to coexist if fox densities increased or resources became even scarcer, since it did not favor intraspecific over interspecific competition (Amarasekare 2003).

On a temporal scale, however, intraspecific avoidance was greater than interspecific avoidance; foxes more likely used a shared area solitarily in homospecific neighbor pairs. Particularly, we only found evidence of dominant-subordinate interactions between red fox neighbors (i.e., asymmetric spatial attraction and temporal pattern of use with Minta's index), suggesting that intraspecific interference competition might be strong in red foxes. The harsh conditions on the tundra in winter and spring make it a poor habitat for that species (Lai et al. 2022, Chapter 2): red foxes' lack of adaptation to resource scarcity likely intensifies intraspecific competition, making it possibly stronger than both interspecific competition and intraspecific competition between Arctic foxes. Stronger intraspecific competition in red foxes could induce self-limitation, which may benefit Arctic foxes, especially if red fox expansion was to increase (e.g., as a consequence of Arctic warming) because it would locally maintain a certain threshold of red fox density, at which both species could persist (Case and Gilpin 1974; Vance 1984; Amarasekare 2002). Thus, contrary to P3 and in partial contradiction with P4, red and Arctic foxes did not strongly avoid each other temporally in their shared areas. Like in the Canadian High Arctic, red foxes around Wapusk do not seem to exclude Arctic foxes from the vicinity of their home range by interference (Lai et al. 2022). This observation differs markedly from those made in Eurasia, where interference is strong—red foxes exclude Arctic foxes from breeding dens, and Arctic foxes spatially avoid red foxes (Tannerfeldt et al. 2002; Rodnikova et al. 2011). A finer temporal resolution (and larger sample size), however, could reveal fine-scale temporal avoidance between heterospecific neighbors, and further shed light on complex coexistence mechanisms (McCann et al. 2017).

We found moderate evidence of habitat segregation based on the habitat composition of Arctic and red foxes' nsv- and mnlv-50%-UD ranges, thus partially supporting P4. Increased habitat complexity may reduce competition and promote coexistence of similar predators (Janssen et al. 2007; Davies et al. 2021). The unusual situation of our study area—which lies at the convergence of three biomes—entails that the landscape changes drastically in both north-south and east-west directions (Ponomarenko et al. 2014). Interestingly, the usage patterns of sea ice, intertidal flats, and denser-canopy forests differed markedly between the two species in terms of intensity (i.e., as designated by the mnlv ranges) and frequency (i.e., nsv range). Some Arctic foxes used the intertidal flats relatively often and travelled many kilometers away from their dens to remain on the sea ice for long periods. These observations suggested that these individuals foraged there, potentially detecting marine mammal carcasses from their terrestrial range (Lai et al. 2015). In contrast, red foxes seemed to have little use of intertidal zone and never used the sea ice (despite the coastal home ranges of 5 out of 8 individuals). Thus, the marine environment may help the two species to coexist, providing exclusive (or nearly exclusive) resources to the Arctic fox. Furthermore, only red foxes used the most heavily forested areas (sub-polar needleleaf, mixed and sub-polar broadleaf forests), both intensively and frequently, suggesting they are important habitats and are used as hunting grounds (Castañeda et al. 2021). Red foxes may thus favor those forested patches because they offer alternative prey to tundra rodents, such as snowshoe hares (*Lepus americanus*), red squirrels (*Tamiasciurus hudsonicus*) and red-backed voles (*Myodes gapperi*). These treed areas are mostly situated south and west of the coast and increase in density along a south-western gradient; they also occur along the river corridors, specifically towards the southern parts of Wapusk and on slightly warmer sites (Ponomarenko et al. 2014); red foxes could also favor these forested patches because they offer shelter from the wind, thereby lessening the abiotic challenges imposed by tundra conditions. Alternatively, the different habitat composition may simply reflect a southeast-northwest gradient of red fox density that reflects the directionality of their range expansion.

Species interactions can range from facilitation to predation, and within the same context they are not necessarily mutually exclusive (Périquet et al. 2015). Sympatry of two predators can be both positive and negative; individuals can engage in agonistic interactions resulting in intraguild predation (Donadio and Buskirk 2006) but also forage on each other's kills (scavenging or kleptoparasitism). Coexistence is thus contingent on complex mechanisms, and interactions between two species vary depending on context (e.g., spatially, seasonally, along a gradient of abiotic conditions, prey abundance) (Chamberlain et al. 2014; Périquet et al. 2015). Notably, prey abundance can be key in determining coexistence between predators that substantially overlap spatially, temporally and in their diet (Périquet et al. 2015). For example, interactions between red and Arctic foxes in Churchill included indifference and agonistic interactions where the pursuer was the smaller species. In the first case, the heterospecific individuals were around in town where they likely benefited from anthropogenic subsidies. In the second case, the Arctic fox was likely defending its breeding den: in early June, resources become more abundant because geese reproduce but pups are still vulnerable.

Intraguild killing events are infrequently but regularly observed in our study area in fall, with invariably the red fox killing the Arctic fox (B. Debets, pers. obs., November 2014; J. Waterman, pers. obs., November 2017; D. Alcorn, pers. obs., November 2020). Red and Arctic foxes are closely related, and all differences in body size between the combinations of interspecific sex cohorts were “intermediate” (see Appendix 3.A) as per categories described in Donadio and Buskirk (2006), indicating that the likelihood of red foxes initiating aggression in interference encounter and ending killing Arctic foxes could be high (Donadio and Buskirk 2006). Some level of interference that we did not detect under the conditions of our study may occur during fall, and red foxes dominated these encounters as expected given their larger body size (Appendix 3.A). During that period, juveniles are dispersing, temperatures drop (likely increasing red fox energetic requirements), and resources become scarce, thus providing red foxes with a size advantage and strong motivation to escalate the aggression (Donadio and Buskirk 2006; Monterroso et al. 2020). However, high risk linked to interference may not always translate into spatial exclusion (Monterroso et al. 2020). Dietary and behavioral flexibility are often particularly high in medium-size carnivores (Roemer et al. 2009), and thus fine-scale spatiotemporal partitioning may be key in favoring larger-scale spatial coexistence, despite high risks of interference encounters (including interspecific killing; Soto and Palomares 2015; Monterroso et al. 2020).

In our area, interference seemed to be low, which could be due to a low fox density and the fact that shared resources are spread throughout the landscape. In contrast, when red foxes reproduced in the Canadian High Arctic, they excluded Arctic foxes from their preferred dens, which were located in the food-rich valleys of Herschel Island (Gallant et al. 2014). If density of either or both fox species were to increase in our area, we may observe more interference encounters during reproduction. Interference during the reproductive period may be costly for both species, but those costs may not be symmetrical. Theory predicts that interference must benefit (i.e., increase offspring production) the lesser exploiter to allow coexistence under the condition of an interference-exploitation trade-off (Amarasekare 2002). Such a trade-off may apply to our fox populations: although interference is likely low under the current conditions in our area (low den occupancy of red foxes relative to Arctic foxes; Moizan et al. *submitted*), red foxes have the potential to benefit from interference. Arctic foxes, in contrast, are likely better exploiters. With their adaptations to resource scarcity, their population would be able to withstand and persist at a lower resource threshold than the red fox population (Fuglesteg et al. 2006; Careau et al. 2007b; Polechová and Storch 2008). Furthermore, red foxes living on the tundra are situated at the margin of their tolerance to abiotic factors and are more vulnerable than Arctic foxes to resource scarcity. We thus suggest that red foxes' lower tolerance to abiotic conditions of the tundra could allow both species to coexist despite their large overlap along other important niche axes: the red fox may benefit from interference and monopolize crucial resources, but the Arctic fox may survive and reproduce under a larger range of resource conditions.

The establishment of this red fox population on the tundra is recent, and competitive exclusion may be an ongoing process; coexistence is measured as a function of population trends in the long term (Chesson 2000). When species are highly similar, competitive exclusion may even depend on stochastic processes (Polechová and Storch 2008), but we believe that the potential exists for local coexistence of those two species under the current condition in our area. However, Arctic warming may alter the probability of long-term coexistence of boreal-forest species with their tundra competitors by advantaging the former and compressing the realized niche of the tundra dwellers. Increased winter temperatures will likely lower the costs associated with thermoregulation for both tundra-native and boreal-forest species that currently occur as edge populations (Pálsson et al. 2016; Nater et al. 2021). However, tundra species that rely on their ability to exploit alternative resources that will be negatively affected as the Arctic warms may lose the potential to do so. Tundra species may thus experience a range shift towards areas where the conditions still allow them some exploitative advantages over the poorly adapted boreal-forest species.

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Tables

Table 3.1. Overlap index of the nnn-home range (Utilization Distribution 95%;UD95) and nnn-core area (UD50) of red foxes (RF) and Arctic foxes (AF) fitted with a satellite collar in the Churchill area (Manitoba, Canada) between 2017 and 2020. Overlap summary statistics are displayed for homospecific (AF-AF and RF-RF) and heterospecific (AF-RF) neighbors (nnn: number of nearest neighbors).

UD	Species pair	mean	SE	min	max	median	n
95	**AF-AF**	0.05	0.04	0.00	0.16	0.01	4
	RF-AF	0.08	0.04	0.02	0.16	0.06	3
	RF-RF	0.05	0.02	0.00	0.15	0.05	8
50	**AF-AF**	0.07	0.07	0.00	0.28	0.00	4
	RF-AF	0.00	0.00	0.00	0.00	0.00	3
	RF-RF	0.00	0.00	0.00	0.00	0.00	8

Table 3.2. Minta's indices and odds (i.e., ratio of frequency of observed (n) to expected (p) simultaneous use (AB), solitary use (A0 and B0), and non-use (00) of the area of overlap shared by individuals A and B; Minta 1992) for each overlapping fox dyad with their p-value, reflecting the probability of attraction to or avoidance of the area of overlap. $L_{A:\bar{A}}$ and $L_{B:\bar{B}}$: probability of finding A and B in home range$_A$, home range$_B$, and area$_{AB}$ given the proportion of areal overlap. L_{ixn}: ratio of simultaneous presence and absence to solitary presence in the shared area.

Dyad type*	Fox ID		LA:Ā	PA:Ā	$L_{B:\bar{B}}$	$P_{B:\bar{B}}$	L_{ixn}	P_{ixn}	Dyad's response		Odds			
	A	B							Spatial	Temporal	$\frac{n_{AB}}{p_{AB}n}$	$\frac{n_{A0}}{p_{A0}n}$	$\frac{n_{0B}}{p_{0B}n}$	$\frac{n_{00}}{p_{00}n}$
RF-AF	AB	MM	-0.09	0.52	0.45	0.15	-0.10	0.86	random	random	1.15	1.42	0.82	0.90
	FJ	MM	0.45	0.54	-1.83	0.02	-0.55	0.88	singular avoidance	solitary trend	0	0.14	1.34	0.85
	W	Gh	0.17	0.92	0.76	0.00	1.21	0.00	singular attraction	simultaneous	5.62	1.21	0.70	0.80
AF-AF	Gi	Gh	2.35	0.00	2.29	0.00	1.49	0.00	symmetric attraction	simultaneous	33	3.66	3.83	0.34
	Gi	GK	0.79	0.15	1.78	0.00	-2.11	0.53	singular attraction	solitary trend	0	4.99	1.88	0.83
	DL	T	1.17	0.16	1.60	0.01	-2.11	0.85	singular attraction	solitary trend	0	4.00	2.61	0.80
RF-RF	A	S	0.88	0.00	-0.50	0.00	-0.45	0.30	asymmetric	solitary trend	0.84	0.55	2.17	0.89
	A	Br	2.13	0.00	-0.42	0.00	-0.70	0.00	asymmetric	solitary	2.7	0.53	6.42	0.74
	S	LR	1.68	0.00	0.07	0.84	0.66	0.01	singular attraction	simultaneous	7.91	0.61	3.85	0.73
	S	I	1.33	0.00	-0.47	0.12	-1.51	0.18	singular attraction	solitary trend	0	0.55	3.16	0.82
	LR	Br	1.15	0.00	1.75	0.00	-2.32	0.01	symmetric attraction	solitary	0	4.40	2.84	0.71
	I	Br	-1.01	0.10	0.72	0.03	-0.90	0.67	asymmetric	solitary trend	0	1.90	0.34	0.92

* AF: Arctic fox, RF: Red fox.

Table 3.3. Overlap of the 50% Utilization Distribution of ranging areas for homospecific and heterospecific neighbors, using both number of separate visits (nsv, reflecting revisitation rate) and mean number of locations per visit (mnlv, reflecting duration of use). AF: Arctic fox, RF: Red fox.

home range metric	**Species pair**	**median**	**mean**	**SE**	**min**	**max**	**n**
NSV	**AF-AF**	0.00	0.03	0.03	0.00	0.10	4
	RF-AF	0.00	0.00	0.00	0.00	0.01	3
	RF-RF	0.00	0.01	0.01	0.00	0.05	8
MNLV	**AF-AF**	0.00	0.07	0.07	0.00	0.27	4
	RF-AF	0.00	0.02	0.02	0.00	0.05	3
	RF-RF	0.00	0.00	0.00	0.00	0.01	8

Figures

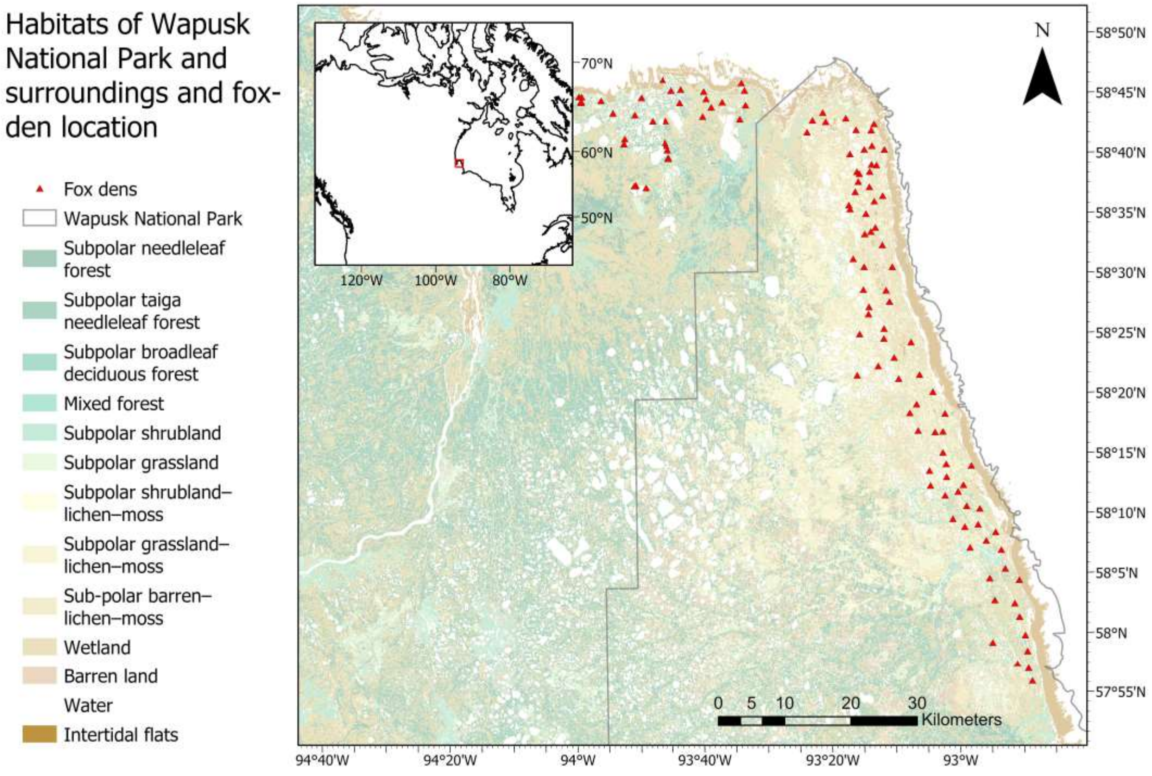


Fig. 3.1. Habitat map of study area in and around Wapusk National Park, Canada (Canada Land cover 2015; Latifovic et al. 2017).

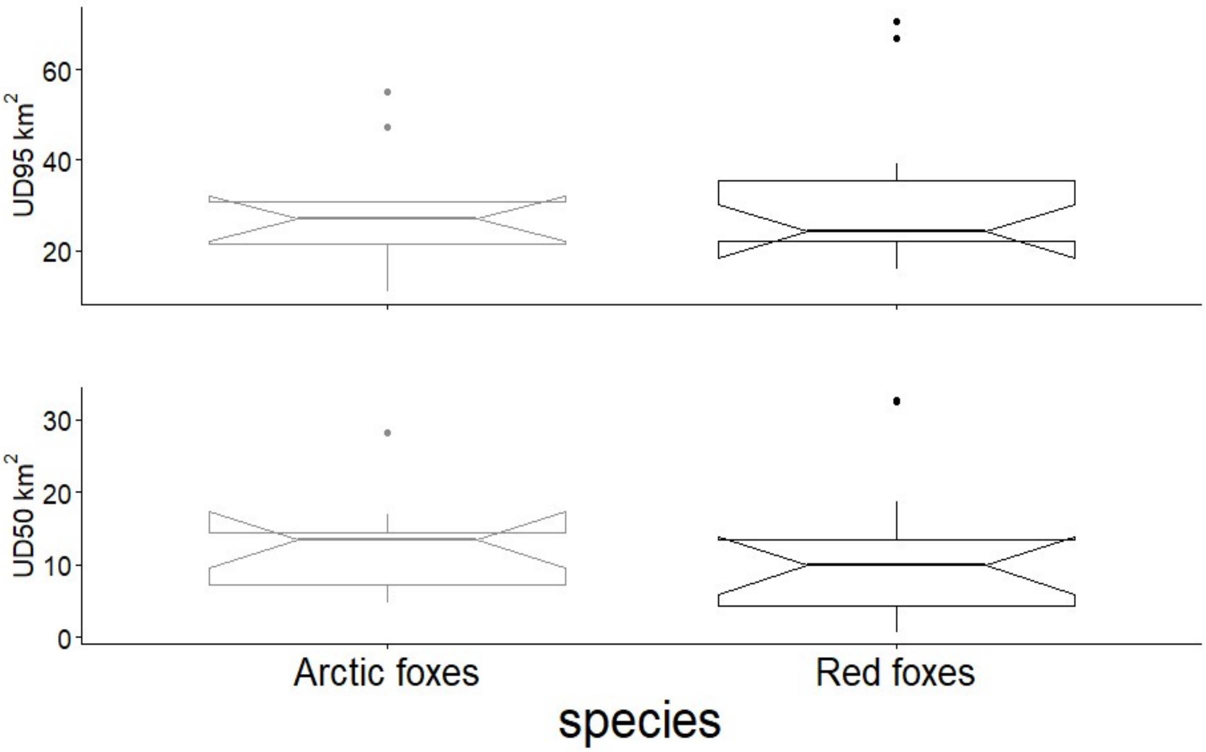


Fig. 3.2. Home range area of Arctic and red foxes (March – June) in northeastern Manitoba. Home ranges were estimated using Time Local Convex Hulls (*a*-method; Lyons et al. 2013).

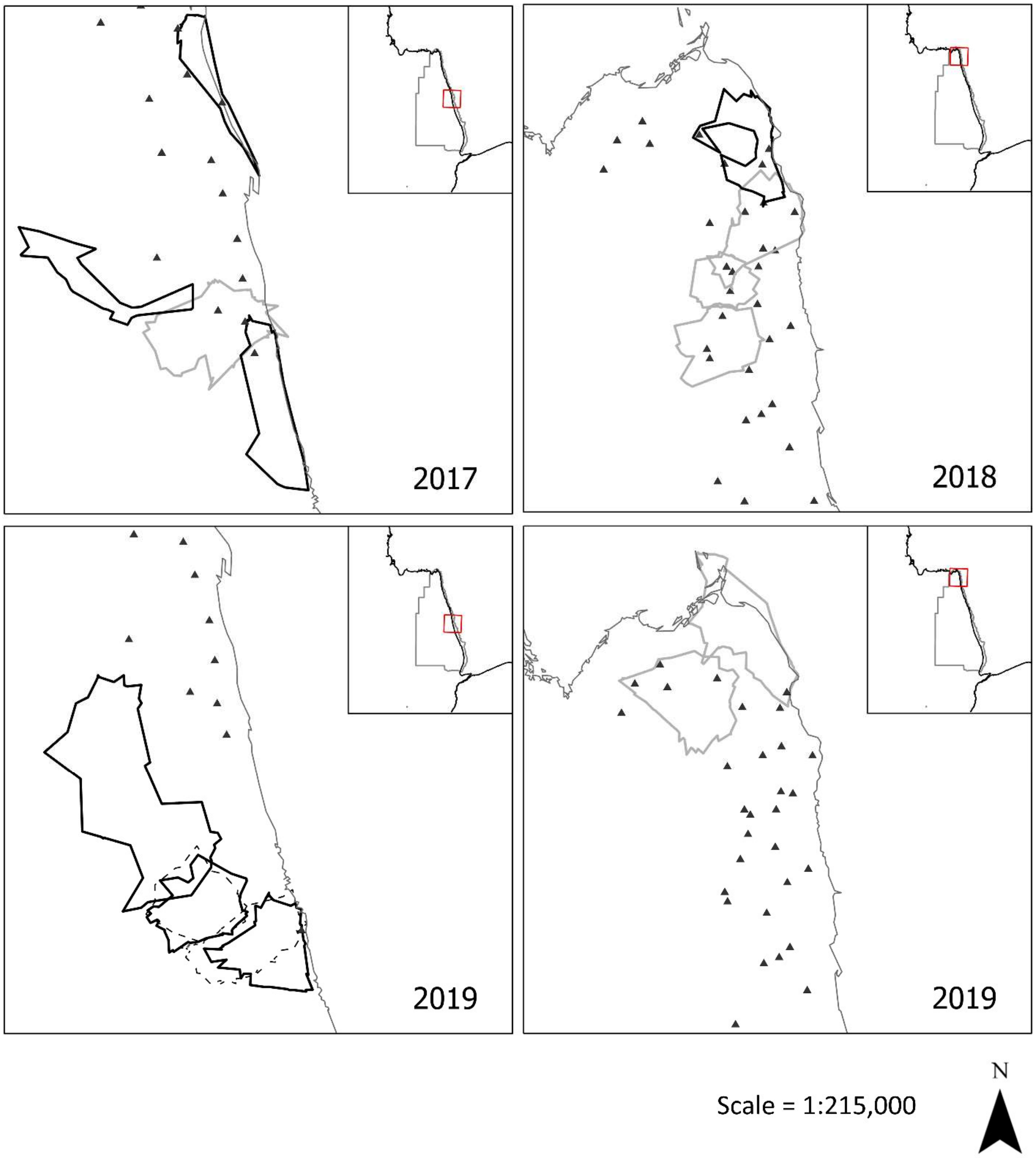
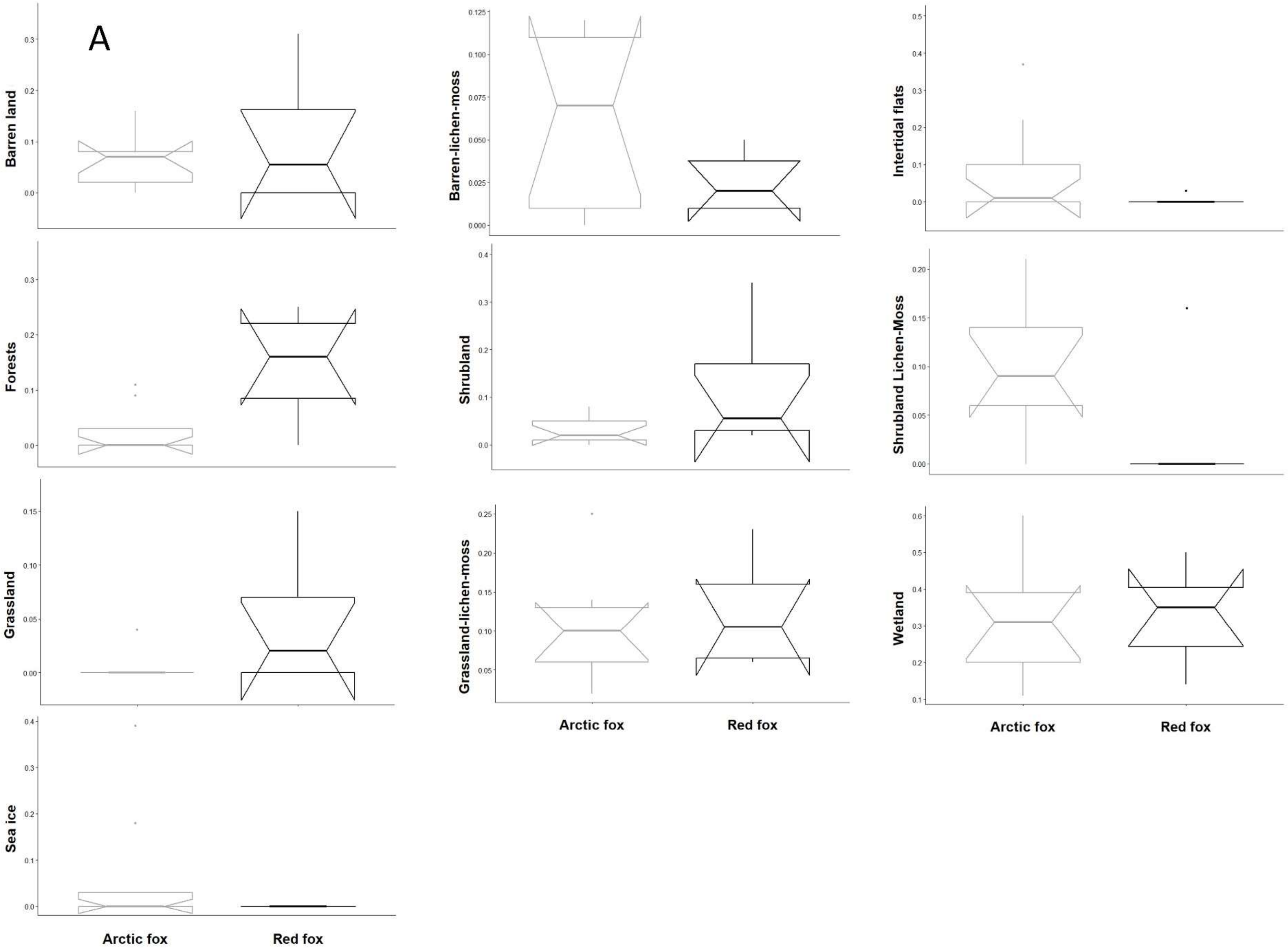


Fig. 3.3. Overlapping fox dyads over the study period. Arctic foxes are in grey, red foxes in black (for clarity we used dashed lines when foxes were living together, and their home ranges overlapped substantially). Dens are shown as black triangles.


A
Barren land
Barren-lichen-moss
Intertidal flats
Forests
Shrubland
Shrubland Lichen-Moss
Grassland
Grassland-lichen-moss
Wetland
Sea ice
Arctic fox
Red fox
Arctic fox
Red fox
Arctic fox
Red fox

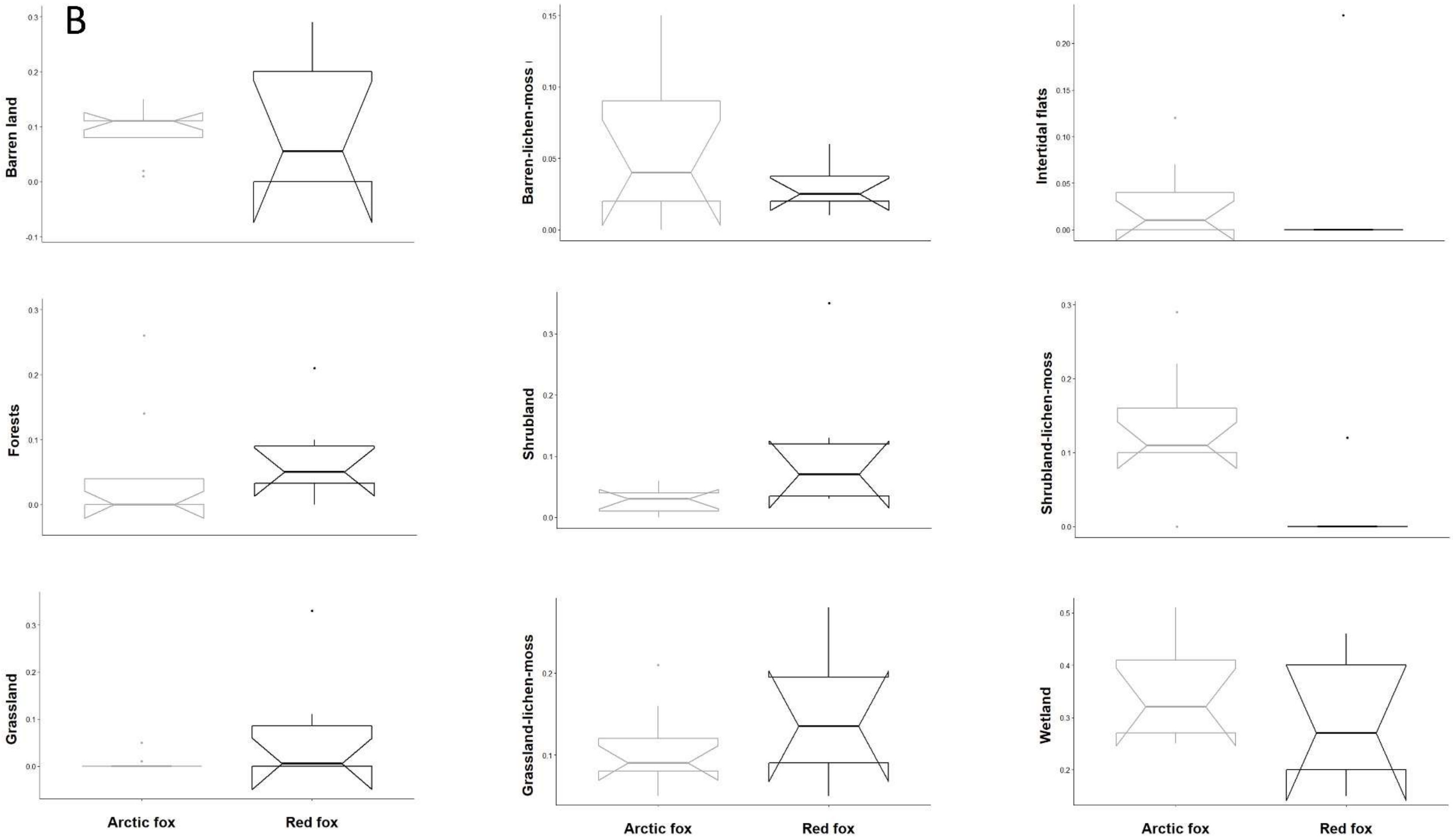


Fig. 3.4. Comparison of each habitat proportion constituting the 50% Utilization Distribution mnlv (A) and nsv (B) ranging areas for red and Arctic foxes in northeastern Manitoba. The notches represent the 95% confidence interval of the median, while the box itself represent the interquartile (IQR), i.e, 50% of the data from 1st to 3rd quartile. The whiskers extend from the greater of 25th percentile - 1.5IQR to the smaller 75th percentile + 1.5IQR.

Appendix 3.A. Morphometric comparison of Arctic foxes and red foxes near Churchill, MB, Canada

Background

Red and Arctic foxes have similar requirements and use the same resources (food or dens). As stated in the main text, when ecologically similar species have similar body sizes, and overlap widely in their use of resources, the likelihood of interference encounter increases (Palomares and Caro 1999). The likelihood of interference resulting in interspecific killing, however, depends non-linearly on the magnitude of body size difference, being maximal at intermediate size differences (Donadio and Buskirk 2006). We assessed fox size differences to predict the likely magnitude of exploitation competition and interference risk for the Arctic fox and, thus, to what extent Arctic foxes should avoid red foxes.

Methods

Fox morphometrics. – Foxes in Manitoba can be legally harvested during the trapping season (November – March). To verify the magnitude of size difference between the two fox species in our study area (which is related to the expected level of interference; Donadio and Buskirk 2006), we collected fox carcasses from local fur trappers in Churchill after pelts were removed in 2017 and 2018, and kept them frozen until processing. We measured body mass (minus pelt mass) using Pesola scales (5 kg and 10 kg), skull length from the rhinion to the occipital protuberance using an electronic caliper, and spine length using a tape measure applied flat on the fox spine starting at the cervical C1 to the end of the sacrum. We extracted canines for aging. We first X-rayed the canines using standard radiography techniques and measured pulp cavity and tooth width at its widest point in ImageJ (Schneider et al. 2012). We then sent all teeth with a pulp cavity-tooth width ratio <41% to Matson's lab (Manhattan, Montana, USA) for aging using cementum annuli count; we assumed teeth with larger pulp cavities were from subadults born the previous April/May (Grue and Jensen 1976).

Statistical analysis. – We tested the difference between species in body length with linear models using sex and species as predictors. The residuals of these linear models did not show outliers or signs of heteroscedasticity. To test the difference between species in body mass we used a generalized linear mixed model (GLMM), controlling for age range (i.e, 0-1, 1-3, 3-5, 5-7, 7-9, 9+) as a random effect and using the varIdent function to account for heteroscedasticity for the species variable (Zuur et al. 2009). We included age as a random effect to account for the fact that age may affect foraging performance, and the propensity to engage in nomadism (Lai et al. 2017). Lastly, we compared skull length (log-transformed) using a generalized least square model (GLS) with the varIdent function to allow the variance in each species to differ. We compared models with age category (as a fixed effect in the skull-length models only), sex, and species and their interaction terms because canids are sexually dimorphic (males are usually larger) and age can be strong driver of intraspecific variations in skull morphometry (Forbes-Harper et al. 2017). We selected the model with the lowest Akaike information criterion (Burnham and Anderson 2002), and selected the most parsimonious one if models were less than 2 AIC apart; we only report the results from the best model, which did not include interaction terms, nor age category. Both the GLMM and GLS were functions of the package nlme v.3.1.152 (Pinheiro et al. 2007). We then tested intraspecific sexual dimorphism with a series of linear models including only sex as a predictor. We tested these model residuals for outliers, deviation from normality, and homoscedasticity (Zuur et al. 2010), and report no issue.

Donadio and Buskirk (2006) computed the body size difference (BSD) as a proportion (so, unitless) between carnivores, with an arcsin square root transformation, as follow:

$$\text{BSD} = \arcsin(\text{SQRT}((BM_L - BM_S)/BM_L)) \quad (5)$$

where BM_L is the body mass of the larger species and BM_S is the body mass of the smaller species. To assess how much the Arctic fox should avoid red foxes (because of interference-related risk of injury and mortality), we used their index to classify the body-size difference between species (i.e., small = [0%-41.3%], intermediate = [41.4%-88.3%], large = [88.4%-100%]), overall and for each sex combination.

Results

We obtained 193 Arctic and 43 red fox carcasses from Churchill trappers that were intact (not scavenged), with pelts removed. Red foxes had larger linear dimensions (Fig. 3.A1, Table 3.A1), both in spine length (LM: $t_{233} = 21.57$, $P < 0.001$) and skull length (GLS: $t_{228} = 13.00$, $P < 0.001$, $n_{AF} = 190$, $n_{RF} = 41$). They were also heavier than Arctic foxes (GLMM: $t_{227} = 10.49$, $P < 0.001$). Male red foxes were heavier than females ($t_{41} = 2.95$, $P = 0.005$), but had similar linear dimensions (spine length: $t_{41} = 0.99$, $P = 0.329$; skull length: $t_{39} = 1.49$, P =

0.15). In Arctic foxes, males were heavier ($t_{191} = 2.79$, $P = 0.006$) and longer than females (spine length: $t_{191} = 2.47$, $P = 0.014$; skull length: $t_{188} = 1.96$, $P = 0.052$), although the evidence of sexual dimorphism in skull length was weaker.

The overall proportional BSD between red and Arctic foxes was 0.60, and between males and females of each species the proportional BSD was also intermediate (*sensu* Donadio and Buskirk 2006): BSD between male red foxes and male Arctic foxes was 0.62, between male red foxes and female Arctic foxes was 0.70, between female red foxes and male Arctic foxes was 0.45, and between female red foxes and female Arctic foxes was 0.50.

Conclusion

Red foxes are larger and heavier than Arctic foxes with intermediate size difference, whether we compare both populations as a whole, or between species within each sex cohort.

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Table 3.A1. Morphometric data for red and Arctic foxes captured by fur trappers near Churchill, MB, Canada. Body mass was measured without the pelt.

		Red fox				**Arctic fox**			
		mean	SE	(range)	n	mean	SE	(range)	n
Body mass		**3.50**	**0.10**	**(1.80-5.00)**	**45**	**2.40**	**0.03**	**(1.30-3.60)**	**193**
(kg)	F	2.98	0.22	(1.80-4.30)	11	2.15	0.11	(1.30-2.90)	18
	M	3.67	0.10	(2.70-5.00)	34	2.42	0.03	(1.35-3.60)	175
Spine length		**48.72**	**0.36**	**(43.60-55.20)**	**45**	**40.56**	**0.16**	**(35.20-47.00)**	**193**
(cm)	F	48.11	0.57	(45.50-51.00)	11	39.31	0.43	(36.50-43.00)	18
	M	48.92	0.44	(43.60-55.20)	34	40.69	0.17	(35.20-47.00)	175
Skull length		**136.30**	**1.68**	**(119.20-163.00)**	**43**	**116.40**	**0.45**	**(102.20-138.90)**	**190**
(mm)	F	131.00	2.58	(119.20-144.40)	10	113.70	0.98	(106.70-122.80)	18
	M	137.90	1.98	(121.10-163.00)	33	116.70	0.48	(102.20-138.90)	172

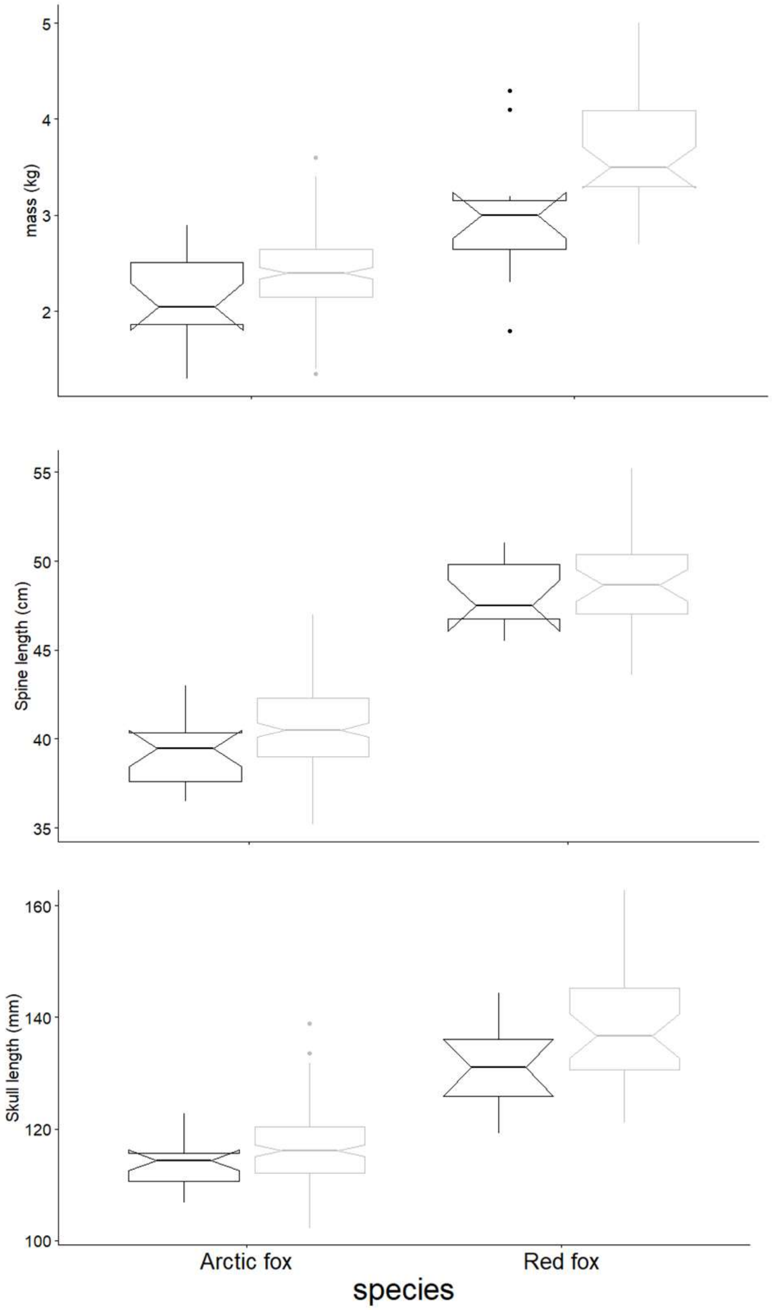

Fig. 3.A1. Body measurements of Arctic and red fox carcasses (females in black, males in grey) collected by local fur trappers near Churchill, Manitoba. A) mass, B) spine length, and C) skull length. The notches represent the 95% confidence interval of the median, while the box itself represent the interquartile (IQR), i.e, 50% of the data from 1st to 3rd quartile. The whiskers extend from the greater of 25th percentile - 1.5IQR to the smaller 75th percentile + 1.5IQR.

Appendix 3.B. Additional supplementary information on resident Arctic fox and red fox space use during the reproductive period near Churchill, MB, Canada

Table 3.B1. Description of habitats at the tundra-taiga transition near Churchill, MB, Canada selected to test for differences between fox species in home range composition (adapted from Latifovic 2019)

Habitat	ID	description
Barren land	1	Bare mineral material, vegetation accounts for <10% of total cover
Sub-polar barren-lichen-moss	2	Mixture of bare area with lichen-moss accounting for at least 20% of total vegetation cover
Intertidal zone	3	Marine-terrestrial ecotone between high and low tides
Sea ice	4	Marine ecosystem of Hudson Bay, covered by ice during the study period
Mixed forest	5	Forest >3m accounting for >20% of total vegetation cover, broadleaf and needleleaf tree species co-dominate, neither reaching 75% of total tree cover
Sub-polar broadleaf deciduous forest	6	Forest >3m accounting for >20% of total vegetation cover, broadleaf deciduous species account for >75% of canopy coverage
Sub-polar needleleaf forest	7	Forest >3m accounting for >20% of total vegetation cover, needleleaf-tree species account for >75% of canopy coverage
Sub-polar taiga needleleaf forest	8	Woodlands, treed wetland with needleleaf-tree species >3m accounting for >5% of total vegetation cover, shrub-lichen understory often present, canopy variable and sparse
Sub-polar shrubland	9	Woody perrenial plants <3m accounting for >20% of total vegetation cover
Sub-polar shrubland-lichen-moss	10	Dwarf shrubs with lichen and moss accounting for at least 20% of vegetation cover
Sub-polar grassland	11	Herbaceous vegetation accounting for at least 80% of total vegetation cover
Sub-polar grassland-lichen-moss	12	Grassland with lichen and moss accounting for at least 20% of total vegetation cover
Wetland	13	Herbaceous or woody vegetation influenced by water table at or near surface and present for a substantial part of the year

Table 3.B2. Proportion of each habitat type in each individual fox's mnlv- and nsv-core area (UD50) (habitat IDs described in Table 3.B.1).

					Proportion of habitat (ID)												
species	**year**	**Ind***	**type**	**area**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
AF	**2017**	MM	MNLV	9.35	0.02	0.11	0.00	0.00	0.00	0.00	0.00	0.11	0.07	0.00	0.04	0.14	0.43
			NSV	12.67	0.02	0.09	0.00	0.00	0.00	0.00	0.00	0.14	0.06	0.00	0.05	0.09	0.47
AF	**2017**	U	MNLV	16.90	0.08	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.12	0.00	0.25	0.33
			NSV	9.39	0.08	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.05	0.16	0.00	0.21	0.40
AF	**2018**	Gh	MNLV	4.90	0.05	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.14	0.00	0.10	0.24
			NSV	8.83	0.13	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.10	0.00	0.16	0.31
AF	**2018**	Gi	MNLV	8.51	0.09	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.18	0.00	0.11	0.31
			NSV	5.98	0.11	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.22	0.00	0.12	0.26
AF	**2018**	GK	MNLV	4.60	0.08	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.13	0.39
			NSV	7.97	0.09	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.12	0.32
AF	**2019**	B	MNLV	23.28	0.07	0.01	0.10	0.39	0.00	0.00	0.00	0.03	0.02	0.06	0.00	0.06	0.20
			NSV	18.09	0.11	0.02	0.07	0.00	0.00	0.00	0.00	0.04	0.03	0.12	0.00	0.09	0.32
AF	**2019**	DL	MNLV	11.92	0.16	0.00	0.22	0.03	0.00	0.00	0.00	0.00	0.04	0.09	0.00	0.06	0.15
			NSV	17.58	0.15	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.04	0.10	0.00	0.07	0.25
AF	**2019**	M	MNLV	4.73	0.00	0.00	0.37	0.18	0.00	0.00	0.00	0.09	0.08	0.00	0.00	0.03	0.11
			NSV	30.41	0.01	0.01	0.04	0.00	0.00	0.00	0.00	0.25	0.04	0.00	0.00	0.08	0.27
AF	**2019**	T	MNLV	13.76	0.02	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.02	0.60
			NSV	9.88	0.11	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.01	0.05	0.51
RF	**2017**	AB	MNLV	3.83	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.13	0.08	0.00	0.00	0.23	0.50
			NSV	6.10	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.10	0.09	0.00	0.01	0.28	0.44
RF	**2017**	FJ	MNLV	9.34	0.11	0.03	0.03	0.00	0.00	0.00	0.01	0.22	0.03	0.00	0.00	0.06	0.39
			NSV	9.74	0.29	0.03	0.23	0.00	0.00	0.00	0.00	0.04	0.05	0.00	0.00	0.13	0.14
RF	**2018**	W	MNLV	2.40	0.31	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.16	0.00	0.18	0.14
			NSV	3.01	0.23	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.12	0.00	0.22	0.18
RF	**2017**	LR	MNLV	18.74	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.05	0.34	0.00	0.04	0.13	0.31
			NSV	10.58	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.06	0.35	0.00	0.00	0.15	0.28
RF	**2019**	S	MNLV	4.26	0.00	0.01	0.00	0.00	0.00	0.00	0.04	0.15	0.20	0.00	0.08	0.08	0.41

			NSV	6.09	0.00	0.01	0.00	0.00	0.01	0.00	0.09	0.12	0.13	0.00	0.11	0.05	0.46
RF	**2020**	A	MNLV	16.67	0.18	0.04	0.00	0.00	0.00	0.00	0.12	0.13	0.03	0.00	0.15	0.06	0.22
			NSV	30.87	0.11	0.02	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.33	0.08	0.26

*Ind: individual identification code

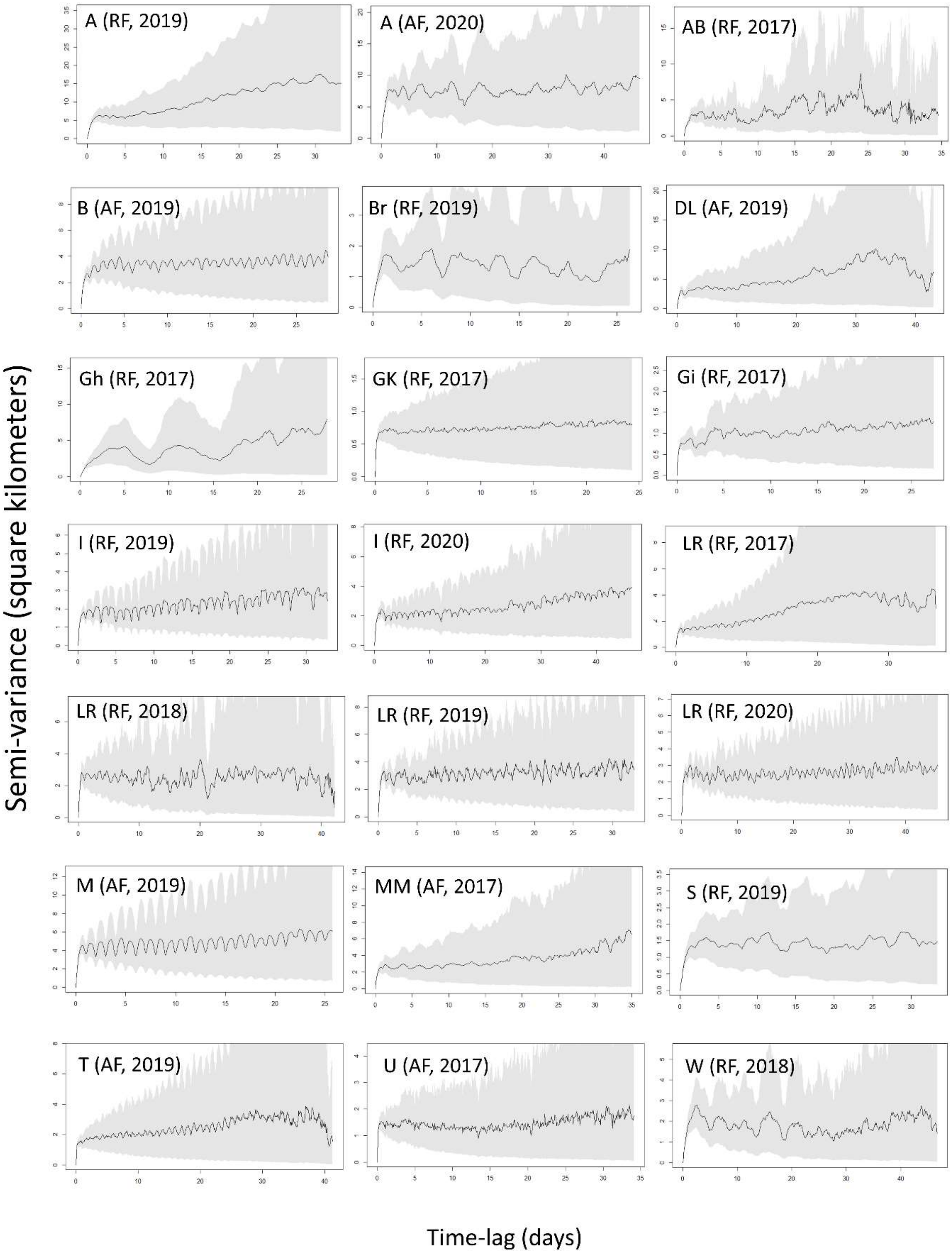

Fig. 3.B1. Variograms of red foxes (RF) and Arctic foxes (AF) tracked near Churchill (Manitoba, Canada) and identified as resident after inspection of their raw tracks at large time lags (25-40 days).

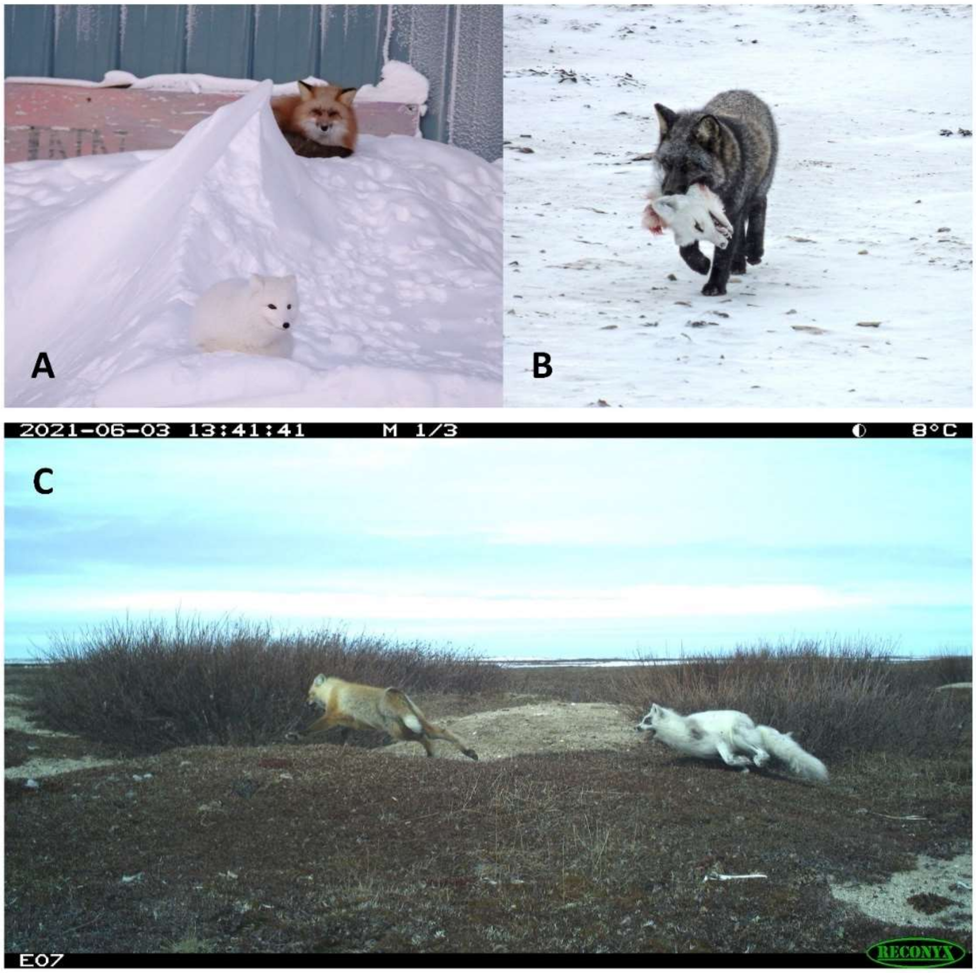

Fig. 3.B2. Examples of interactions between Arctic and red foxes in the Churchill and Wapusk area (Manitoba, Canada). A) The two species can be observed tolerating each other, notably where they may access anthropogenic food subsidies (in town). B) Rarely but regularly, interference interactions can be lethal for the Arctic foxes. C) Arctic fox chasing a red fox from its den (interference interaction) in June, when geese have started reproduction and resources are becoming more abundant, but pups are likely born and highly vulnerable (both foxes remained alive at least until the camera stopped working the following week). Photos courtesy of Churchill resident Dave Allcorn (A; March 2022) and Dr. J. Waterman (B; November 2017). Photo from our Reconyx trail camera retrieved by Sean Johnson-Bice (C; June 2021).

Prelude to Chapter 4

Feeding ecology determines ecosystem functioning through diverse pathways, like animal movements (and thus interactions), population dynamics, and exposure to pathogens and contaminants (Paine 1980; McKinney et al. 2011; Colborn et al. 2020). In Chapter 4, I examined the diet of red and Arctic foxes from the Churchill region. This area has several characteristics that are advantageous to further understand how northern wildlife communities will respond to ongoing climate-related changes. First, the Churchill landscape is transitional due to the merging of three habitats: boreal forest, coastal tundra, and marine ecosystem of Hudson Bay. Second, only one lemming species occurs south of the Seal River, and collared lemming cycles have become damped, with continuously low abundance. Finally, both red and Arctic foxes occur as edge populations.

Theory predicts that under such conditions, competition should be particularly intense (Hersteinsson and Macdonald 1992; Elmhagen et al. 2017), but in Chapters 2 and 3, I found that resident red and Arctic foxes used space differently; both species used tundra patches, but red foxes also relied on forested patches, while Arctic foxes used the sea ice. In the following chapter, I am addressing again the second part of the overarching hypothesis (i.e., although the potential for exploitation is high in winter, due to prey scarcity, the heterogeneity of the Churchill-area landscape allows the two fox species to relax competition), but along a different ecological-niche axis, the foxes' diet, which relates to their exposure to mercury. Specifically, I hypothesized that the presence of forested habitats and of the marine ecosystem offer an opportunity for resource segregation, especially because resources are particularly low, driving red foxes to switch between forest and tundra. Furthermore, the sea ice should provide Arctic foxes with a near-exclusive resource. The generally high levels of mercury in the marine environment might disadvantage Arctic foxes by predisposing them to higher mercury exposure than red foxes, due to alternative consumption of marine resources.

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Chapter 4: Diet and mercury exposure of sympatric red and Arctic foxes in a transition ecosystem with fluctuating resources

Abstract

Northern ecosystems are characterized by interannual resource fluctuation, which can strongly impact individual survival and reproduction. Boreal-forest species expanding onto the tundra face stressful abiotic conditions, likely aggravated by recurring resource scarcity. Periods of resource scarcity may generate competition between the expanding species and endemic tundra species, which could disrupt trophic interactions on the tundra and drive populations to forage differently, potentially increasing exposure to contaminants and their detrimental effects. We determined the diet of sympatric red (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) and their exposure to mercury to assess the potential for resource segregation and how mercury exposure changes as resources fluctuate, in a transitional ecosystem where boreal forest, coastal tundra, and marine habitats merge. We used stable isotope analysis to reconstruct fox diet in winter (when the potential for competition is highest) between 2011 and 2018 and quantified mercury concentration in fox muscle to relate level of exposure to individual traits and diet. Both species strongly relied on tundra-arvicoline rodents, but red foxes relied as much on snowshoe hares, implying some level of resource segregation, which was not specific to low-rodent years and may relax exploitation competition. In addition to snowshoe hares and rodents, red foxes relied on migratory birds, suggesting they were challenged by the low hare and rodent densities. Although few foxes foraged on marine resources, marine diet increased mercury exposure. We found further evidence of bioaccumulation with age and different age-specific response in mercury accumulation to main-prey density fluctuations in each species. Overall, diet in each species tracked main-prey densities closely, but they opportunistically used alternative resources, and because their diets were mostly terrestrial, muscle mercury concentrations were below thresholds associated with harmful effects. Boreal-forest species may depend on habitat diversity at treeline to acquire enough resources to support their expansion, which may lessen their possible negative impact

on tundra species. Relaxing competition for prey may also reduce pressure to forage on marine resources, reducing exposure of tundra species to mercury.

Introduction

The Arctic is warming at a rate two to four times faster than the rest of the world (You et al. 2021), prompting substantial changes in northern ecosystems (Post et al. 2009). Arctic-ecosystem changes notably include a prolonged growing season, shrub encroachment onto the tundra, and shorter warmer winters, which should favor temperature-limited and shrub-dependent species. Consequently, many species of the boreal forest have expanded their range, with leading-edge populations encroaching onto the tundra (Henden et al. 2011; Elmhagen et al. 2015; Tape et al. 2016), and possibly disrupting local species interactions, especially trophic interactions (Schweiger et al. 2015; Dudenhoeffer et al. 2021).

Treeline ecotones are thus characterized by the convergence of populations from species native to each transitioning ecosystem (Rehm et al. 2015). These peripheral populations may face challenges related to the severity of the environmental conditions, low habitat quality, or expansion of competitors and pathogens (Sexton et al. 2009). Peripheral populations face harsher climates and more frequent extreme climatic events at the edge compared to the core of their distribution (Rehm et al. 2015). In the case of leading-edge populations, the main limiting factor is related to abiotic stress, while rear-edge populations would be mostly limited by the presence of competitors (Louthan et al. 2015).

Foraging ecology (including trophic interactions) is central to ecosystem functioning: food habits determine individual movements and interactions, population dynamics, and community structures (McNab 1980; Paine 1980; Gravel et al. 2016). Optimizing diet is a crucial aspect of achieving energetic balance, which in turn is critical to the persistence of populations through individual survival and reproductive success (McNab 1980; Marquet et al. 2004; Martin et al. 2020). An optimal diet maximizes net energy intake after the animal integrates into its foraging behavior biotic and abiotic factors (such as intra- and interspecific competition, patch depletion, or fluctuating abundance of prey), their internal state (like specific nutrient requirements or satiation state; Pyke 1984), and adaptations to stochastic events.

Diet also determines contaminant intake, which can have severe repercussions on individual health and thus population persistence. For example, contaminants compromise bone mineralization, reproduction, and immune function; they also increase oxidative stress, cause histological damage in diverse tissues, have neurotoxic effects, and interfere with the endocrine system (Dietz et al. 2019). Mercury is a widespread contaminant with an established negative impact on wildlife health (including Arctic biota; e.g., Dietz et al. 2019). Different mercury exposure between species could thus play a role in the long-term interactions, notably by disadvantaging species with a higher burden by compromising their reproduction, immune or neurological functions (e.g., Bocharova et al. 2013; Peterson et al. 2015). Mercury bioaccumulates and biomagnifies throughout both terrestrial and aquatic food webs (Lavoie et al. 2013; Luo et al. 2020; Li et al. 2021), and thus deleterious impacts are mostly seen in top predators (Dietz et al. 2019).

Animals foraging in aquatic habitats usually have higher mercury concentrations than species that are restricted to terrestrial habitats (Kalisinska et al. 2009; Jackson et al. 2015; Ackerman et al. 2016). Mercury can therefore be used as a tracer to quantify the contribution of aquatic (including marine) resources in animal diets, especially for species with mixed foraging strategies or feeding across a gradient of habitats (Peterson et al. 2017; Hallanger et al. 2019; Clatterbuck et al. 2021). In addition, contaminants (including mercury) can complement other diet determination techniques, by providing information about population health, and can help predict climate-related changes in food-web dynamics including potential deleterious effects on ecosystem health (Ramos and González-Solís 2012; Hallanger et al. 2019).

The red fox (*Vulpes vulpes*) is a widespread medium-sized carnivore, occupying a diversity of habitats (Bartoń and Zalewski 2007; Fairfax 2019), including the Arctic and alpine tundra where it overlaps with the Arctic fox (*Vulpes lagopus*) (Hersteinsson and Macdonald 1992). The Arctic fox has a circumpolar distribution and is a tundra-adapted species of North America and Eurasia (Macpherson 1969). Both fox species usually behave as opportunistic specialists: most populations prioritize arvicoline rodents even at low abundances, exhibit functional responses to other prey, and broaden their diet when preferred prey is scarce (Englund 1980; Angerbjörn et al. 1999; Elmhagen et al. 2011). Although lemming cycles have become damped throughout the Arctic, lemming consumption by Arctic foxes still varies with lemming abundance (Dudenhoeffer et al. 2021). Arctic foxes usually forage on alternative prey, notably marine species in low rodent years (Roth 2002; Dudenhoeffer et al. 2021), thus likely increasing mercury intake when their preferred prey is scarce. Across their range, red foxes prioritize either arvicoline rodents or lagomorphs, although they often exhibit functional responses to local prey items (Jędrzejewski and Jędrzejewska 1992; Dell'Arte et al. 2007), and like Arctic foxes use alternative prey if preferred prey is less available (Kidawa and Kowalczyk 2011; Killengreen et al. 2011). Thus, in the North, red foxes use resources from both the boreal forest and the tundra, while Arctic foxes likewise use resources from two biomes, the tundra and the marine environment.

Lemmings and snowshoe hares (*Lepus americanus*) play a central role in northern ecosystem dynamics, being key prey in tundra and boreal forest food webs, respectively (Krebs 2011). Furthermore, in the low Arctic, lemmings are often sympatric with voles (*Microtus spp.*), and, at a given site, often show synchronous fluctuations in abundance (Krebs et al. 2002; Ehrich et al. 2020). We thus hypothesized that population cycles of arvicoline rodents (i.e., lemmings and voles) generate annual variation in diet and mercury exposure of both foxes, while snowshoe hares also affect diet and mercury exposure in red fox. As a corollary we posit that treeline, a transitional habitat with patches of forest and tundra, offers potential for resource segregation (especially in low rodent years). We thus predicted that 1) red fox diet will be co-dominated by snowshoe hares and tundra-arvicoline rodents, whereas Arctic foxes' diet will be dominated by tundra-arvicoline rodents only, 2) dietary proportions of tundra rodents will be more similar between fox species in low hare years than in high hare years, 3) foxes use different alternative resources in low rodent years: red foxes consume more forest prey, while Arctic foxes consume more marine prey, 4) both foxes should rely more on cached resources (i.e., migratory birds) during low main-prey years, 5) mercury concentration increases with the consumption of marine items and decreases with the consumption of terrestrial resources, and finally, 6) Arctic foxes should have a higher concentration of mercury in their tissues than red foxes, particularly in low-rodent years, due to a higher reliance on the marine food web.

Methods

Study area. – We examined the diet and mercury exposure of red and Arctic foxes in the Hudson Bay Lowlands (58°N, 94°W) (Fig. 4.1). This uniformly flat and low-elevation (<200m) transitional ecosystem is made of the tundra-marine ecotone to the north and east, and the tundra-boreal forest ecotone to the south and west (Brook and Kenkel 2002). At the broadest scale, the landscape of our study area comprises three bioclimatic zones (high boreal woodland, low hypoarctic tundra, and subarctic), resulting in drastic changes in the landscape along both north-south and east-west gradients (Ponomarenko et al. 2014). On land, diverse factors interact to determine the mosaic of vegetation communities: the cooling effect of Hudson Bay, the warming effect of major rivers, the presence of saline sediments, and the amount or distribution of solar energy (Ponomarenko et al. 2014). The Hudson Bay Lowlands lie on continuous permafrost (Gough and Leung 2002) and are thus mostly wetlands. The patchiness of the landscape may thus offer opportunities for the red and Arctic foxes to partition resources.

A red fox population has recently successfully colonized the coastal tundra of western Hudson Bay and reproduces there every year in sympatry with Arctic foxes (Chapters 2 and 3). Red foxes in this area are thus continuously present and in higher density than in the Canadian High Arctic (Gallant et al. 2013; Lai et al. 2022), but the sympatric Arctic fox population is more abundant than in Fennoscandia and not at risk (Elmhagen et al. 2017). However, demographic models suggested that even at low densities, red foxes could greatly impact Arctic foxes (Shirley et al. 2009). Although evidence for interference competition between these two species in the Canadian Arctic is scarce, the potential for exploitation competition is high (Lai et al. 2022, Chapter 3).

Few prey species remain in our study area over winter (McDonald et al. 2017). On the tundra, collared lemmings (*Dicrostonyx richardsoni*) and meadow voles (*Microtus pennsylvanicus*) dominate the fox-prey community (Dudenhoeffer et al. 2021). Like elsewhere in the Arctic, lemming cycles are damped, peaking at 2 lemmings per hectare (2010-2021; Ehrich et al. 2020), whereas in the 1990s they peaked at 12 per hectare (Roth 2003), and reached peaks of 40 per hectare in the 1930s (Shelford 1943). When rodent abundance decreases, Arctic foxes consume alternative resources, notably marine species by scavenging carrion left by polar bears on the sea ice, or hunting seal pups (Smith 1976; Roth 2002). In addition, the numerous patches of forest in the Churchill area shelter snowshoe hares and forest rodents, mainly American red squirrels (*Tamiasciurus hudsonicus*) and red-backed voles (*Myodes gapperi*).

Estimation of resource abundance – From 2011 to 2018 we measured lemming abundance in June, shortly after snowmelt, using mark-recapture methods. For each mark-recapture session, we deployed Sherman live-traps in 2 8x8 grids (2 traps per stake, with 15-m spacing) and 2 300-m transects (3 traps per stake, with 15-m spacing) in preferred lemming habitat (lichen-heath tundra) for a total of 72h (MacDonald et al. 2017). We estimated variation in snowshoe hare abundance between 2013 and 2018 using fecal pellet counts (Ewacha et al. 2014; Freeth et al. 2016). Briefly, 8 transects with 10 1-m^2 circular plots 30 m apart were established in forested areas east of the town of Churchill. Each year we counted and removed all hare pellets in each plot. Numbers of pellets were then averaged (x) for each transect and hare density (y) calculated using the formula:

(6) $y = 0.398 + 0.06x$ (McCann et al. 2008).

We estimated nesting goose abundance each year in June using line-transect distance sampling methods in sedge meadow/beach ridge habitat west of the Hudson Bay coastline where substantial inter-annual variation in goose nest success has been documented (Reiter and Andersen 2011). Teams of at least three persons (one navigator and two observers with binoculars) walked along 15 parallel 2-km transects south of Cape Churchill in Wapusk National Park. Transects ran east-west, generally perpendicular to beach ridges, and were numbered sequentially (1-15, north to south). Transect 1 started on easting 489000 and ran east along a northing that was randomly generated each year between 6505000 and 6506000 (projection: UTM, datum: NAD83, zone: 15N). Subsequent transects started every 500m south, on the same easting, with even-numbered transects heading west and odd-numbered transects heading east. Coordinates of goose nests detected from transects were determined with a GPS, and nest densities were then estimated in the DISTANCE software (Thomas et al. 2010) using a half-normal detection function (key part; because detection near transect is not guaranteed to be near perfect) and cosine series expansion with 250-m truncation.

Sample collection. – We obtained carcasses of red foxes (n=135) and Arctic foxes (n=276) legally harvested in the Churchill area during the trapping season (November 1 - March 15) from 2010-11 to 2017-18 (excluding the 2012-2013 and 2015-2016 trapping seasons because no Arctic foxes and only a few red foxes were collected). Skinned carcasses were kept frozen until sampling each year. We collected muscle samples from the biceps femoris or the semimembranosus (more rarely, we sampled the vastus lateralis part of the quadriceps if the carcass was damaged). We also extracted a canine tooth for aging. Canines were X-rayed using standard radiography techniques and we measured the ratio of the pulp cavity to tooth width at its widest point using ImageJ (Schneider et al. 2012). When the ratio was >41% foxes were considered <1 year old (approx. twice the average ratio of a 2-year-old fox, to ensure we would not wrongly assign the age 0; Cavallini and Santini 1995). All foxes for which the pulp cavity-tooth width ratio was <41% were aged using cementum annuli counts by Matson's lab (135 Wooden Shoe Ln, Manhattan, Montana 59741, USA).

Stable isotope analysis. – We used stable isotope analysis to estimate diet. The isotopic signature of consumer tissues closely reflects the integrated isotopic composition of their diet, after accounting for the metabolism-related discrimination between consumer and prey tissues (Ben-David and Flaherty 2012). Unlike visual or DNA methods of diet identification, stable isotope and fatty acid analyses quantify assimilated diet instead of just assessing ingested diet. However, stable isotope analysis, like fatty acid analysis, has a lower resolution than the less quantitative methods (DNA and visual assessment), and thus, is not designed to evidence rare diet items. We used carbon (C) and nitrogen (N) stable isotope ratios ($\delta^{13}C \sim {}^{13}C/{}^{12}C$ and $\delta^{15}N \sim {}^{15}N/{}^{14}N$) in muscle to estimate the foxes' diet. Stable-isotope ratios in muscle provide an estimate of diet integrated over approximately two months prior to trap date (Vander Zanden et al. 2015) and thus, in our foxes, reflected a late-fall and winter diet.

Prey C and N stable isotope ratios were obtained from prey tissues collected opportunistically during our annual field surveys or, in the case of snowshoe hare fur, obtained from elsewhere in northern Manitoba (Szumski et al. *submitted*; Roth 2002, 2003; McDonald et al. 2017). Tissues from both foxes and prey were freeze-dried and lipid extracted with petroleum ether using a Soxhlet apparatus (Elliott et al. 2017). We then sent between 0.4 and 0.6 mg of those prepared samples to the Fisk Lab (Great Lakes Institute For Environmental Research, University of Windsor, Canada); they measured the C:N and the $\delta^{13}C$ and $\delta^{15}N$ values. When hair (in snowshoe hares) was used instead of muscle, we subtracted 1.5‰ from $\delta^{13}C$ to approximate muscle values (Codron et al. 2007; Hocking et al. 2007). For marine resources, we calculated the weighted mean and SD from the different seal species and cohorts from Young et al. (2010). Finally, we obtained values of migratory-shorebird egg values from Churchill by averaging the yolk and albumen values in Hobson and Jehl (2010) and then calculated the weighted mean and SD of all species.

Anthropogenic fossil fuel burning has massively released CO_2 with low ^{13}C content into the atmosphere, leading to declined atmospheric $\delta^{13}C$ in both terrestrial and aquatic ecosystems—a process called the Suess effect (Keeling 1979). We, therefore, corrected all $\delta^{13}C$ values for sample year, using the following equation for terrestrial species:

(7) $\delta^{13}C_{corrected} = \delta^{13}C_{raw} + 5.5656 - e^{(6.0932\times10^{-5})t^2}$ (Long et al. 2005)

where t reflects years since 1879. To correct for the Suess effect in seals, we subtracted 0.024‰ per year (Allison and Francey 2007), as previously used for Arctic marine wildlife (e.g., Mckinney et al. 2009).

Diet estimation. – We visually assessed the assumption of bivariate normal distribution of fox stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) using the packages threesj v.0.3.3 (Lewis 2020) and rgl v.0.108.3 (Murdoch and Adler 2021) in R 4.0.2 (R Core Team 2020), because MANOVA assumes multivariate normal distribution of the response variable within each group of the explanatory variable. We verified that isotopic signature of foxes varied among years with a MANOVA using MANOVA.RM v.0.5.2 (Friedrich et al. 2021). We allowed the variance to differ between years using a parametric bootstrap resampling method (n_{iter} = 10,000), and report the modified ANOVA-type statistic (MATS) (Friedrich and Pauly 2018).

We then implemented two Bayesian mixing models using package MixSIAR v.3.1.12 (Stock et al. 2018) in R 4.0.2 and JAGS 4.3.0 modules to estimate the probability of the contribution of tundra, forest, and marine sources (i.e., prey and prey groups characterized by their combination of $\delta^{13}C$ and $\delta^{15}N$) to the diet of Arctic and red foxes (i.e., the $\delta^{13}C$ and $\delta^{15}N$ mixture). The main advantages of the Bayesian approach lie in the opportunity to incorporate prior information, uncertainty in the parameters estimates, covariates (as both fixed and random effects), and variability in the consumer population (e.g., Stock and Semmens 2016; Stock et al. 2018). To test predictions 1 to 4, we defined "species" (2 levels) as a fixed effect and "Year" (6 levels) as a random effect. To test predictions 5 and 6, we ran a second mixing model that estimated the diet for each fox using "fox ID" as a fixed effect. We initially considered 18 possible prey (see Table 4.S1), but results with >6 prey will likely be uninterpretable in a two-tracer system (Stock et al. 2018). Therefore, we combined prey into source categories based on ecological relevance or discarded them based on the results of preliminary mixing models (i.e., if a prey consistently appeared to be unimportant in results of all preliminary models) until we had 5 and 6 prey groups for the two models, respectively (Table 4.1; Fig. 4.2). When prey were combined into a new source, the mean $\delta^{13}C$ and $\delta^{15}N$ from individual prey were weighted based on *a priori* importance using results from Dudenhoeffer et al. (2021), or if no knowledge was available, they participated equally (weighted by the number of available samples) to the new source mean. We added caribou as a source for our second mixing model to improve model convergence.

We calculated mean and variance of trophic discrimination factors (TDF) for each fox species using SIDER v.1.0.0.0 (Healy et al. 2018). SIDER uses a Bayesian phylogenetic regression based on a dataset compiling published TDFs ($\Delta^{13}C$ and $\Delta^{15}N$) obtained following the criteria by Caut et al. (2009). Notably, the compiled dataset includes the TDF calculated for red fox tissues (Roth and Hobson 2000), obtained by feeding the red foxes with pellets; we, therefore, used SIDER to adjust this TDF for red and Arctic fox muscle samples with a carnivorous diet (Healy et al. 2018; Morgenthaler et al. 2021). We averaged the two TDFs and their variance, weighted by the number of each fox species present in our dataset.

For our first model, we built our priors by defining the hyperparameter α of the Dirichlet distribution using the frequency of occurrence of prey DNA in fox feces collected during winter on the tundra dens of our study area (Dudenhoeffer et al. 2021). No prior information was available for forest habitats, so we arbitrarily attributed the median frequency of occurrence of the main six sources from Dudenhoeffer et al. (2021) to the forest prey. Feces represent the diet of a fox during the 24h before defecation, thus weakly representing the two-month diet integrated into muscle samples. To obtain weakly informative priors, we scaled the frequencies of occurrence so that the total weight of the priors equals the number of prey (here 5 and 6). We ensured that the posterior distribution was driven by the data and not our priors by running the same model with uninformative priors (i.e., probability of contribution to the diet is equal for all prey). In our second model, we did not inform the priors and thus considered an equal probability of prey contribution to the diet of each individual. The parameters of our three MCMC (Markov Chain Monte Carlo) chains in model 1 were: iterations = 7,000,000; burn-in = 4,000,000; thinning = 500. In model 2, the parameters were: iterations = 6,500,000; burn-in = 5,000,000; thinning = 300.

We assessed MCMC convergence using visual inspection of trace, autocorrelation, and running mean plots, and we ensured the Gelman-Rubin diagnostic for each variable was < 1.01. Convergence was particularly slow, and we thus considered the Geweke diagnostic acceptable when no more than 10% of the variables were > |1.96| and no variable was > |2.58|.

Total mercury analysis. – We analyzed 20-140 mg of muscle tissue per sample using a direct mercury analyzer (Hydra IIc, Teledyne Leeman Laboratories, Hudson, NH). We calibrated the instrument using low-detection linear calibration curves calculated with blank sample boats for blank correction and the certified reference materials and 95% confidence interval MESS-3 (91 ± 9 ng/g) and MESS-4 (90 ± 40 ng/g), and high-detection linear calibration curves calculated with the certified reference material PACS-3 (2980 ± 360 ng/g). Curves included at least 5 determination points and were validated when $R^2>0.995$. The instrument detection limit is <0.001 ng. We tested quality assurance and quality control by testing the certified reference materials (including MESS-3, MESS-4, TORT-3 (292 ± 12 ng/g), DORM-4 (412 ± 36 ng/g), DOLT-5 (440±180 ng/g ng/g), NIST2709a (900 ± 200 ng/g), NCP III-9 S2 (933 ± 55.5 ng/g), and PACS-3) two to three times every 14 samples (recovery: 8.1%±0.3). Most samples were analyzed in wet weight, but over time samples stored in a freezer become dryer (Chapter 6). Comparing samples spanning over 8 years may thus introduce bias, with older samples being more concentrated due to a lower proportion of water (Chapter 6). To account for water evaporation in older samples and include samples that were analyzed in dry form, we converted all values into dry weight using year-specific conversion factors based on year-specific average moisture content. All values in this study are thus reported in dry weight (see Table 4.S2 for muscle composition and year-adjusted conversion factors). In 2016, 2017 and 2019 we analyzed some prey muscle opportunistically found fresh (e.g., prey freshly caught at fox den) or collected from Churchill residents, to verify mercury burden was as expected (see results in Table 4.S3).

Linking diet, mercury, and resource fluctuation. – We verified if the fluctuations of prey items in fox diet reflected resource-abundance fluctuations using a series of one- or two-sided permutation Spearman correlation tests ($n_{replication} = 10{,}000$) with the package wPerm v.1.0.1 (Weiss 2015). We tested the co-variation between rodent density and winter mean dietary proportions of 1) tundra rodents and 2) migratory birds in both fox species, plus 3) seal in Arctic fox, and 4) snowshoe hares in red fox. For these analyses we used rodent densities the previous June, as lemming population declines typically occur between late summer and winter (Fauteux et al. 2015) and these estimates more likely reflect the densities experienced by our trapped foxes than densities the subsequent June. We also tested the co-variation between winter snowshoe hare density and dietary proportion of 1) snowshoe hare, 2) tundra rodents and 3) migratory birds in red foxes.

We tested if mercury concentration (natural log-transformed) differed between years using an ANOVA and between species using a Student's t-test. For each species, we then used linear models to assess the effects of age category (adult vs juvenile), sex, diet (as estimated by our 2nd mixing model at the individual level), and densities of rodents (for both fox species) and hares (for red foxes only) on mercury concentration in fox tissues. We explored possible interactions between age and prey densities. For these analyses, we used the percent change of rodent density between two consecutive years (change in June density divided by the initial density) as a proxy for variation in rodent availability as foxes would experience this change over a given fall and winter. Hare density estimates were based on pellet accumulation over winter, so were unmodified. Diet types were proportions, and therefore highly correlated. To avoid multicollinearity issues, we defined three prey groups representing three food-related hypotheses (see Tables 4.2 and 4.3) that could affect mercury concentration in fox tissues —

seals, terrestrial prey (i.e., tundra and forest rodents, caribou and snowshoe hares combined) and migratory birds — and repeated each model for each prey group. For each model designed, we thus obtained three versions that only differed by the prey group representing diet. Specifically, we tested if mercury concentration increased with seal consumption or decreased with increased terrestrial prey or migratory bird consumption. We ranked the models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). If two models were < 2 ΔAIC, we selected the most parsimonious one; if the level of parsimony was the same, we selected the best model based on the confidence intervals of the β coefficients of the differing variables. Residuals for all models were checked for normality, homoscedasticity, and outliers with high leverage (Zuur et al. 2010; Zuur and Ieno 2016). One data point corresponding to a fox with particularly low THg given the high seal consumption seemed to be an outlier, with a studentized residual value of -3.4, hat value (reflecting the leverage of a point) of 0.4, and Cook's distance of 1.6 in one competing model. However, the coefficients of that model were robust to the presence of this outlier, and we had no methodological or biological reason to discard this data point. We thus decided to keep it, as we think the point is still representative of the fox population of Churchill (some seals show low mercury concentration compared to published estimates, see Table 4.S3). We otherwise report no issue with model diagnostics. We performed this statistical analysis in R 4.1.2 (R Core Team 2021) with the packages AICcmodavg v.2.3.1 (Mazerolle 2020), car v. 3.0.12 (Fox and Weisberg 2019), and MASS v. 7.3.54 (Venables and Ripley 2002) and base R; data exploration and handling, and plots were done with packages dplyr v. 1.0.7 (Wickham et al. 2021), tidyr v. 1.1.4 (Wickham 2021), ggplot2 v. 3.3.5 (Wickham 2016) and ggpubr v.0.4.0 (Kassambara 2020). We also ran power analyses using package pwr v.1.3.0 (Champely 2020) to obtain an idea of the extent to which sample size should be increased to strengthen weak to moderate evidence of a relationship.

Results

Resource fluctuation. – Prey densities in the Churchill area were generally low (Fig. 4.3). Over our entire study period, rodent densities continued to exhibit low-amplitude cycles as previously reported (McDonald et al. 2017; Ehrich et al. 2020). Peak rodent densities (2013 and

2017) were around 2 per ha, but cycle period was still 4 to 5 years. Hare densities were similarly low, with even lower amplitude, ranging between 0.52 and 1.02 hares per ha, but whether they exhibit extremely damped 10-year cycles or continuously low stable densities is still unclear. Nesting goose densities ranged from 0.05 to 0.11 nest per ha, and goose nest density estimates in the three years we also had stable isotope data were all 0.08 nest per ha, precluding use of this variable in our analyses.

Diet estimate of red and Arctic foxes. – Based on the criteria described above, our models converged properly. The population-level model gave very similar results whether we used informed or uninformed priors. None of the posterior distributions for any of the models was clearly bimodal, despite some correlated sources ($r > |0.50|$, see Fig. 4.S1A-C), which indicates they achieved a consensus on the proportional contribution of prey items to fox diets. In this section, we will only report diet estimates at the population level (i.e., from our first model).

Isotopic signature of foxes differed between years (MANOVA: MATS = 88.31, $p < 0.001$), despite low annual variability (Fig. 4.4). Red foxes usually had higher $\delta^{15}N$ values than Arctic foxes, except in 2017 and 2018. In 2011, Arctic foxes showed particularly low $\delta^{13}C$ and $\delta^{15}N$, but our sample size for Arctic foxes in 2011 was only three. Both species had similarly low $\delta^{13}C$ across all years, suggesting a terrestrial diet. Isotopic signatures of red and Arctic foxes differed most years, except in 2018. Red foxes in 2014 showed considerable individual variation, particularly on the $\delta^{13}C$ axis, corresponding to a decline in both lemming and hare densities that year.

The result from our stable isotope analysis indicated that tundra rodents largely dominated the winter diet of Arctic foxes, representing at least half of the prey consumed every year (up to 83%). Arctic fox consumption of tundra rodents was substantially higher than that of red foxes every year, with little overlap of their credible intervals (0-3.9%). Red foxes, in contrast, relied on three main items that constituted the bulk of their diet every year: snowshoe hares, tundra rodents, and migratory birds. The relative importance of those three dietary items varied between years and the credible intervals of two dietary proportions of those three prey had no to moderate overlap with the third prey in each year (Table 4.2); the only exception was the 2014-2015 winter, corresponding to a year of similar abundance of rodents and snowshoe hares, when red foxes consumed all three prey in similar proportions as indicated by the substantial overlap of the associated credible intervals. Dietary proportions of seals and forest rodents (red-backed voles and squirrels) were marginal for both species, and although the average varied slightly between years, the credible intervals overlapped and included 0% every year. Contrary to red fox diets, snowshoe hares were marginal prey for Arctic foxes and their dietary proportion varied little between years (large overlap in credible intervals), but they were still occasionally consumed, especially when their abundance was the highest (i.e., an average of 14.8% CI [6.0%-25.0%] and 12.3% CI [3.9%-23.9%] the two years of higher hare density). Consumption of migratory birds by Arctic foxes varied slightly between years (large overlap in credible intervals, which extended approximately from 6% to 40% or 2% to 18% most years), but never represented more than 20% of the diet on average, unlike red foxes.

Overall, the dietary proportions of tundra rodents for both fox species reflected the abundance of this prey group, except in winter 2010-2011. We found evidence of a strong co-variation (permutation Spearman correlation: $r_{Arctic} = 0.87$, one-tailed $p_{Arctic} = 0.048$; $r_{red} = 0.80$, one-tailed $p_{red} = 0.061$; n = 5) when excluding the first trapping season (2010-2011) but not when that particular year was included ($r_{Arctic} = 0.44$, one-tailed $p_{Arctic} = 0.203$; $r_{red} = 0.41$, $p_{red} = 0.207$; n = 6). It is worth remembering here that 2010-2011 diet data for Arctic foxes are based on only three individuals, and may thus be an outlier value. There was no relationship between migratory birds in Arctic fox diet and rodent abundance, regardless of whether we excluded the 2010-2011 trapping season (r = -0.4, one-tailed p-value = 0.256, n = 5) or not (r = -0.06, one-tailed p = 0.461, n = 6). Rodent density was not a major driver of dietary proportion of migratory birds in red fox diet, regardless of whether that first year was excluded (r = -0.10, one-tailed p = 0.46, n = 5) or not (r = -0.06, one-tailed p = 0.48, n = 6). We found moderate evidence of a strong negative co-variation between seal consumption by Arctic foxes and rodent density when 2010-2011 was excluded (r = -0.9, one-tailed p = 0.040, n = 5), which was weak when 2010-2011 was included (r = -0.64, one-tailed p = 0.097, n = 6). The dietary proportion of snowshoe hare in red fox diet did not depend on the variation in rodent density, regardless of if we included 2010-2011 trapping season in the calculation ($r = -0.30$, one-tailed $p = 0.34$, $n = 5$) or not ($r = -0.09$, one-tailed $p = 0.44$, $n = 6$). We failed to statistically support the apparent negative co-variation between consumption of tundra rodents and hares in red foxes ($r = -0.60$, one-tailed $p = 0.12$, $n = 6$) and found no evidence of covariation between rodent and hare densities ($r = -0.20$, $p = 0.92$, $n = 4$). A power analysis revealed that a minimum of 15 years of data (<2 snowshoe hare cycles) is necessary to detect a $r = -0.60$ between consumption of rodents and snowshoe hares at $p = 0.05$ with a power of 0.80 at $\alpha = 0.10$ when performing a permutation Spearman correlation test. We also failed to statistically support the strong apparent positive association between hare consumption by red foxes and fluctuations in hare abundance ($r = 0.80$, one-tailed $p = 0.164$, $n = 4$). However, a power analysis suggested that $n = 8$ is the minimum sample size to detect a strong effect ($r = 0.80$) of hare density fluctuations on red foxes' consumption of hare, with a statistical power of 0.8 at $\alpha = 0.10$ when performing a permutation Spearman correlation test. In contrast, fluctuations of snowshoe hare abundance did not influence the consumption of tundra rodents by red foxes ($r = -0.4$, one-tailed $p = 0.38$, $n = 4$), nor did it affect their consumption of migratory birds ($r = -0.60$, one-tailed $p = 0.21$, $n = 4$). A power analysis suggested that $n = 15$ is the minimum sample size to achieve a medium effect ($r = -0.6$) of fluctuations of snowshoe hare abundance on red foxes' consumption of migratory birds with a power of 0.80 at $\alpha = 0.10$ when performing a permutation Spearman correlation test.

Total mercury in fox muscle. – We found substantial interindividual variation in muscle THg concentrations, ranging from 0.031 to 8.696 mg/kg, and moderate and strong differences between years in both red foxes ($F_{5,129} = 2.551$, $p = 0.031$) and Arctic foxes ($F_{5,270} = 6.294$, $p<0.001$), respectively. Specifically, THg levels in red foxes in 2012, 2017, and 2018 were substantially lower than in 2015, and that THg levels in Arctic foxes were lower in 2011 (although $n_{Arctic} = 3$ in 2011) and 2012 compared to other years (Table 4.2). Mercury concentration was similar in both species ($t_{409} = -1.68$, $p = 0.094$, Cohen's D = -0.177, $n_{Arctic} = 276$, $n_{red} = 135$).

In red foxes, our best model to explain muscle THg concentration did not depend on diet type, but on the inclusion of hare density as a predictor. Diet did not influence mercury concentration, and there was no difference between adults and juveniles, but hare density and to a lesser extent sex affected mercury concentration, with males more contaminated than females (Table 4.3). Models that did not include snowshoe hare density performed poorly, with R^2 = [0.06-0.07], while other models performed similarly to each other's (R^2 = [0.15-0.17]; best model parameters are displayed in Table 4.4). In Arctic foxes, our best model to explain muscle THg concentration included sex, age interacting with lemming density, and terrestrial diet (Table 4.3). We found strong evidence of interaction between Arctic fox age and changes in rodent density — i.e., mercury concentration in juveniles increased during rodent population increases, while adults' exposure to mercury increased in years when rodent density decreased. Both age and, to a lesser extent, sex influenced mercury concentration in muscle, with juveniles less contaminated than adults, and males less contaminated than females. Contrary to red foxes, diet was the most important predictor of mercury concentration in Arctic fox muscle in all models (Table 4.4). Notably, a terrestrial diet was associated with markedly lower mercury exposure than a diet including seals. Unexpectedly, migratory bird consumption was positively associated with exposure to mercury in Arctic foxes.

Some sources were highly negatively correlated (Fig. 4.S1A). Notably, consumption of seals and migratory birds were negatively correlated (see Fig. 4.S1A-B), suggesting the mixing model may have sometimes assigned “migratory bird” instead of “seal”, especially in Arctic foxes. Wrongly assigning seal instead of migratory bird (and vice-versa) could be misleading when interpreting fox mercury exposure, because these two prey usually have very different mercury contents. We thus ran an extra model to test for an interaction between migratory bird consumption and fox species, which would likely indicate that the effect of consuming migratory birds on Arctic fox mercury exposure is artificial, because migratory bird consumption should affect both species similarly. This extra model indeed indicated a strong interaction between dietary proportion of migratory birds and species (Arctic foxes had a substantially higher intake of mercury by eating migratory birds; $t_{3,407} = -2.69$, $p = 0.007$). We thus have good reasons to think that the mixing model underestimated seal and overestimated migratory bird consumption to some extent.

Discussion

Dietary habits differed between red and Arctic foxes, supporting the idea that habitat heterogeneity in our study area may allow these two species to partition resources (Chapter 3). Our results also suggested that both species were opportunistic predators influenced by preferred prey fluctuations, showing dietary flexibility and adapting to scarcity of preferred prey by consuming alternative resources. We found that feeding on the terrestrial food web was indeed clearly associated with decreased mercury exposure compared to feeding in the marine food web, but age was an important factor only in Arctic foxes, and mercury concentrations in juvenile Arctic foxes increased with rodent densities and with a higher dietary proportion of migratory birds (the latter may be a model artifact; see below). Furthermore, mercury concentration in red fox muscle varied with hare densities, likely indicating that red fox exposure to mercury may increase when they must find alternative resources to compensate for the lack of that key prey; determining the source of mercury exposure in this red fox population requires further investigation.

Red foxes relied on three prey groups in similar proportions: tundra rodents, snowshoe hares and migratory birds. Dietary proportions of the first two prey were overall similar; red fox consumption of tundra rodents tracked the density fluctuations in lemmings, and their consumption of snowshoe hare may still be tracking hare-density fluctuations despite the low amplitude, suggesting that both items are main prey to this population of red foxes. It was unclear if the consumption of these two prey groups by red foxes was negatively related, but abundances of tundra rodents and snowshoe hares were unrelated. Either microtine rodents or hares typically dominate red fox diet over most of their range (e.g., Jędrzejewski and Jędrzejewska 1992; Cypher 1993; Kidawa and Kowalczyk 2011), but predation of hares likely is energetically more efficient (Malo et al. 2004). Optimal foraging theory states that animals' feeding habits should maximize their net energy intake (e.g., Pyke 1984); red foxes likely favor feeding on snowshoe hares over rodents whenever hares are abundant enough — the most likely reason for the weak negative relationship between hare and rodents in their diet despite no relation between abundance of these prey — and switch between the two prey as rodents reach peak densities and hares decrease. Snowshoe hares at tree line are living in marginal habitats and this low-density peripheral population does not exhibit the high-amplitude population cycles typical at the core of their range (Krebs et al. 1992; Freeth et al. 2016). The continuously low abundance and very low-amplitude variations in abundance of snowshoe hares may lead our red fox population to depend in equal parts on hares and rodents. A consequence may be that red foxes with insufficient access to forested patches in their home range might be more likely to leave the area in search of food during winter, thus lowering their chances of survival (Lai et al. 2017, Chapter 2).

Important subsidies become the most important dietary item when preferred prey is scarce (Killengreen et al. 2011). Ungulate carrion is often reported as an important subsidy to red foxes during scarcity of preferred prey, both in forest and tundra habitats (Kidawa and Kowalczyk 2011; Killengreen et al. 2011; Sokolov et al. 2016; Ims et al. 2017). In constrast, all our preliminary models indicated that caribou was unimportant at the population level. Migratory birds as cached items could instead fulfill that role, since they seem to be as important to our red fox population as snowshoe hares and rodents. Our data did not allow us to detect a relationship, or test a combined effect of low rodents and low hares on the consumption of migratory birds, but it would be reasonable to think that red foxes increase their consumption of migratory birds, specifically when both rodents and hare are scarcer than usual.

Both red and Arctic foxes are known to cache food (Macdonald 1976; Sklepkovych and Montevecchi 1996; Careau et al. 2007); this adaptive behavior allows species that rely on highly fluctuating resources to compensate for food scarcity and thus increase chances of survival (Vander Wall 1990; Sklepkovych and Montevecchi 1996). The challenging conditions at the tree line and the low occurrence of ungulates in this area in winter may force red foxes to heavily rely on caching. In that case, migratory birds could experience a higher predation pressure when snowshoe hares decrease, as red foxes may have to switch from forest to tundra habitats; thus, these two prey would link the forest and the tundra food webs through a common predator that switches between two habitats. However, we were unable to test the changes in proportion of migratory birds in red fox diet from fall to the end of winter: the time frame represented by our muscle samples may include weeks during which geese and shorebirds are still around. More research is needed to quantify the reliance on cached items of this edge population of red foxes when preferred prey is scarce.

Arctic foxes consumed tundra rodents in substantially higher quantities than any other prey: winter dietary proportions of rodents represented at least half of their diet, even at lowest rodent densities, but they still varied between years with rodent-density fluctuations. We found further support that when rodents are scarce, Arctic foxes used marine prey as alternative resources as indicated by increased consumption of seals in lowest rodent years. However, like Dudenhoeffer et al. (2021), our samples contained generally low evidence of seal consumption compared to previous research from the same area (Roth 2002, 2003), which could be related to either lower availability of marine resources, due to decreasing sea ice leading to a decreasing bear population in the Western Hudson Bay (Regehr et al. 2007; McCall et al. 2015), or the sampling strategy. Our samples were from foxes trapped on land, sometimes far from the coast, and thus represented inland-resident foxes or on-land dispersers. Since distance to coast may positively influence the propensity to use marine resources (Killengreen et al. 2011; Dudenhoeffer et al. 2021), and most dispersing Artic foxes use the sea ice (Chapter 2) so are less likely to be captured by fur trappers on land, our sampled foxes may be less likely than the general population to use marine resources.

Churchill Arctic foxes fed mainly on rodents, depended on sea ice during rodent scarcity, but also opportunistically consumed other resources. We found no evidence that consumption of alternative terrestrial prey or migratory birds fluctuated with rodent abundance. On Bylot Island in the Canadian High Arctic, Arctic foxes' hoarding behavior varied with the lemming cycle. During high and moderate phases, Arctic foxes cached most of the eggs they took from nests, which suggests that as lemmings declined, foxes could further propagate the seasonal pulse of resources throughout winter. During the low lemming phase, Arctic foxes eat most of the captured eggs, likely to achieve energetic requirements they cannot achieve with lemmings alone (Careau et al. 2008). In Churchill, in contrast, there was no relationship between rodent abundance and dietary proportion of migratory birds, likely because most of our foxes were juveniles who would not have been able to cache geese during the previous reproductive season, when they were still pups. Migratory bird consumption, thus, likely mostly reflected a late fall opportunistic diet and not cached items, because eggs and flightless goslings are accessible in June and early July; juvenile foxes thus have less opportunity to cache geese than adults.

Although both foxes used the same prey to a certain extent, red and Arctic foxes of Churchill had different feeding strategies that likely allow resource partitioning during rodent scarcity, but also during high rodent abundance. That resource partitioning likely participates in relaxing exploitation competition (e.g., Leal and Fleishman 2002; Ramesh et al. 2012), and maybe could even drive a differential tundra-distribution pattern at the landscape scale, with the ratio of red to Arctic foxes increasing south- and westward where tree density increases (anecdotally, we were more likely to catch red foxes farther south along the coast (Chapters 2 and 3)).

The main source of mercury contamination in organisms is through diet (e.g., Lavoie et al. 2010; Bocharova et al. 2013; Jackson et al. 2015). In Arctic foxes, a terrestrial diet was associated with lower tissue concentration in total mercury, whereas increased consumption of seals induced greater exposure. Our results are thus consistent with previous research that found higher mercury contamination in marine compared to terrestrial wildlife (Bocharova et al. 2013; Hallanger et al. 2019). Preliminary mercury analyses on some prey items from the Churchill area further confirmed that terrestrial prey had extremely low mercury burdens (see Table 4.S2). In red foxes, however, we did not find an effect of diet, but mercury exposure increased with decreased snowshoe hare density. Our results thus suggest that red foxes may acquire mercury through switching diet, although red foxes do not forage in the marine environment, and all the terrestrial prey we included in our diet models have generally low mercury. A more detailed assessment of red fox diet may be necessary to understand how diet affects their mercury intake. Overall, muscle THg concentration in both Churchill fox species was below levels associated with harmful effects in terrestrial wildlife, i.e., ~30 mg/kg w.w. liver (or ~ 11 mg/kg w.w. muscle; see Chapter 4); their substantial use of the terrestrial food web likely prevented a too high exposure.

Interestingly, migratory bird consumption was also somewhat associated with increased exposure to mercury, but in Arctic foxes only. Shorebird consumption may expose foxes to mercury, since some shorebird species may have relatively high tissue concentrations of mercury (Braune and Noble 2009; Hargreaves et al. 2011), but in our population, their consumption is likely opportunistic and thus likely too marginal to have obvious effects on mercury concentration. In our study area, Canada and snow geese substantially dominate the bird community in Arctic fox fall diet (McDonald et al. 2017; Dudenhoeffer et al. 2021). As herbivores, geese usually have low mercury concentrations in their tissues (including in Manitoba) (Braune and Malone 2006; Tsipoura et al. 2011). The posterior dietary proportions of migratory birds and seals showed a strong negative correlation, thereby indicating a trade-off in the contributions of these two sources and the difficulties the model had in differentiating between the relative contribution of these two sources to the diet (Parnell et al. 2010; Ryan et al. 2014).This positive effect of migratory bird consumption on mercury levels was, thus, likely due to the relatively high negative correlation (see Fig. 4.S1C) between seals and migratory birds in our mixing model: part of the dietary proportion assigned to migratory birds might have been from seals, in fact, and thus some mercury exposure might be wrongly associated to migratory bird instead of seals (especially because an additional model we ran found that the positive association only concerned Arctic and not red foxes).

Mercury levels were weakly influenced by sex in red foxes, unlike other red fox studies (e.g., Kalisinska et al. 2012; Dainowski et al. 2015). Sex differences in tissue mercury concentration in mammals could be due to differences in physiology or mercury intake, or excretion. Other studies have found higher mercury excretion in females related to reproduction — i.e., through placental and milk transfer — (Wagemann et al. 1988; Habran et al. 2011, 2012), but that is unlikely the main explanation for our population of red foxes, since at the time of trapping, females are not yet pregnant. Previous studies have found sex differences in red fox diets (e.g., Cavallini and Volpi 1996; Kidawa and Kowalczyk 2011; Viranta and Kauhala 2011; Forbes-Harper et al. 2017). Female red foxes usually eat higher proportion of small mammals than males (Cavallini and Volpi 1996; Kidawa and Kowalczyk 2011; Forbes-Harper et al. 2017), and have a smaller diet breadth (Cavallini and Volpi 1996; Kidawa and Kowalczyk 2011); such an effect could induce slightly lower exposure to mercury in females. In contrast, male Arctic foxes had lower muscle mercury concentration than females, but the effect was relatively weak. A previous study from the Churchill area suggested that males may rely more on small mammals than females (Friesen et al. 2015), which could induce a lower exposure to mercury than consuming alternative marine resources. Further study of sex difference in diet and ranging behavior of foxes is required to fully understand these sex differences in mercury concentration.

We found considerable interindividual variation in mercury exposure (up to ~281 fold), which is consistent with fox opportunistic feeding behavior (Elmhagen et al. 2000; Kidawa and Kowalczyk 2011; Clatterbuck et al. 2021) and commonly reported (e.g., Duffy et al. 2005; Kalisinska et al. 2012; Bocharova et al. 2013; Lurz et al. 2017). Stable isotope analysis does not have the high taxonomic resolution of other diet-tracking tools such as molecular methods (Bonin et al. 2020; Dudenhoeffer et al. 2021). Indeed, stable isotope analysis ideally needs prior knowledge of the species or populations studied, as this method is best used to quantify the relative importance of the main dietary items (over time or over a specific timeframe); this method is not the best suited to detect atypical dietary items consumed exceptionally by a few individuals and in marginal quantities. However, some dietary items even consumed exceptionally could induce detectable higher mercury contamination: contingent to the opportunistic feeding behavior of foxes, some individual red foxes could have been more likely than usual to feed on human subsidies (e.g., refuse), which can be associated with higher contaminant exposure than a natural terrestrial diet (Newsome et al. 2010). Some Churchill residents also feed their sled dogs with seal meat (pers. obs.): red foxes could scavenge the remains of seal hunts, without going on the sea ice. Complementary diet estimation methods might help verify sources that would expose red foxes to higher levels of mercury when both rodents and hares are at low densities. The lack of age effect in our red fox models may have been due to a combination of the low number of adults in our data set and the generally low red fox intake of mercury associated with the high interindividual variation.

Older age in Arctic foxes was unsurprisingly associated with increased levels of mercury in muscle. Mercury is widely known to bioaccumulate in organisms, and age is often an important factor in predicting levels of mercury in tissues (e.g., Sánchez-Chardi et al. 2007; Jackson et al. 2015; Heiker et al. 2018). Age also interacted with rodent density, indicating behavioral differences between Arctic fox age cohorts. Juvenile Arctic foxes were more likely exposed as rodent populations were increasing, whereas adults of both species showed higher mercury concentrations in declining rodent phases. Arctic foxes heavily rely on rodents, including for reproduction (Roth 2003; McDonald et al. 2017), and the lemming decline makes them a limiting resource, likely eliciting competition (both intra- and interspecific) and thus high dispersal rates (Waser 1985). Adult dispersers may then forage on alternative resources opportunistically maybe switching to the marine habitat, which would, in turn, induce higher mercury exposure. The pattern observed in juvenile Arctic foxes was less intuitive but could be driven by longer-distance natal dispersal. Lemming populations build up throughout winter, influenced by reproduction during winter and the demography in the previous late summer (Fauteux et al. 2015); when carnivores live in habitats with high resource fluctuations, their propensity to tolerate other individuals (including their offspring) in their home range increases when resources are abundant (e.g., MacDonald 1983). Juvenile Arctic foxes may thus be more likely to disperse far away from their natal home range, and for example, use the sea ice when rodents were at their lowest the previous summer. Our research covers two rodent cycles, and the observed pattern may be driven by one particular year: in 2015 and 2016 rodents were particularly low and increased during the 2016-2017 winter. The juveniles harvested that winter may have been more likely to use the sea ice during natal dispersal due to the extreme scarcity of prey on land (a third of the juveniles captured during this season had among the highest mercury concentrations, ranging from 0.913 to 8.695 mg/kg d.w. muscle). Alternatively, the higher mercury concentration detected in juveniles as lemming populations increased could result from bioaccumulation at an early age. The previous year, low lemming densities may have favored sea-ice foraging in female foxes, which could then have transferred mercury to the pups through the placenta and milk (Habran et al. 2011), although shedding to their adult fur would provide an important route for excreting the mercury accumulated as pups (Wiener et al. 2002). More replicates (both in space and time) are needed to elucidate the cohort-specific patterns in mercury exposure with rodent population dynamics.

Our study thus suggests that contaminants, such as mercury, can be a good complementary tracer to stable isotopes to understand diet. For example, although the Arctic foxes we sampled ate relatively low proportions of seals, some individuals had high mercury levels (> 1mg/kg; including juveniles), likely indicating that they foraged on the sea ice. A few red foxes also had high mercury concentration, and because red foxes usually do not forage on the sea ice (Chapter 2) their high load could be indicative of scavenging on occasional items, like human subsidies, or some cached prey with higher contamination (like some shorebirds). The combined use of stable isotopes and contaminants as feeding ecology tracers can thus provide an effective way to gain a finer understanding of interindividual or temporal variation in foraging strategy while gaining insights into the health of a population.

As the Arctic warms, Arctic communities may undergo substantial changes (Post et al. 2009), further complicated by the interconnectedness of multiple food webs (here marine, tundra, and boreal forest). The future effects of these changes may be particularly challenging to predict. Exploitation competition likely occurs in our area because both foxes rely heavily on arvicoline rodents (Holdridge et al. 2016), but some resource partitioning occurs, facilitated by the transitional character of the western Hudson Bay ecosystem. Red foxes may preferentially feed on snowshoe hares, but the low density of this prey and spatial patchiness of forested habitats in this area entails suboptimal conditions for the red fox, which likely forced that species to also rely on tundra rodents (Malo et al. 2004). As snow conditions deteriorate, lemmings may further decline (Berteaux et al. 2017), while voles may expand onto the tundra following a change in the plant composition (Morris et al. 2011; Ehrich et al. 2020). Although some studies suggested that voles could provide alternative resources to foxes, they likely provide a lower energetic reward than lemmings due to their lower mass (nearly half) and much lower fat content (Zuercher et al. 1999; Powell et al. 2002). Therefore, despite an improvement of abiotic conditions in winter, red foxes may suffer as much as Arctic foxes if lemmings decline further, especially those individuals that could not secure access to richer forest patches that would allow them to eat snowshoe hares. Both fox species are opportunists and therefore may be more resilient to future changes related to Arctic warming than specialist Arctic predators such as the stoat (*Mustela erminea*), snowy owl (*Bubo scandiacus*), or long-tailed skuas (*Stercorarius longicaudus*) (Schmidt et al. 2012; Barraquand et al. 2014).

Arctic foxes forage on the sea ice to cope with rodent scarcity (Roth 2002, 2003; Dudenhoeffer et al. 2021). This strategy may heighten their risk of exposure to mercury, which may impair reproduction or have other harmful effects (Dietz et al. 2013; Hallanger et al. 2019). In the future, Arctic foxes in our area may be particularly impacted during rodent low phases due to sea-ice decline in Hudson Bay (Florko et al. 2018), because they would lose access to important subsidies (Roth 2003), but those shifting to an increased terrestrial diet could be less exposed to mercury. Finally, many processes (such as forest fire frequency or changes in sea-ice dynamics and characteristics) will be impacted by climate change, which will contribute to altering THg levels in wildlife through a diversity of pathways (e.g., flux of carbon and nutrients between habitats, food-web changes, increased primary productivity), some decreasing while others increase mercury exposure of Arctic biota (Stern et al. 2012). The contribution of these diverse drivers may change spatially, thus challenging our forecasting abilities. Continued long-term monitoring of Arctic food webs is needed to understand the broader effects of climate change on Arctic food webs and improve our forecasting capacities.

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Tables

Table 4.1. Isotopic signatures (mean ± SD, ‰) of the final 6 prey groups used in our two mixing models for diet estimation of the red and Arctic foxes trapped in northern Manitoba, Canada, between 2010 and 2018. Caribou were added to the individual mixing model only. n = sample size.

Prey	**$\delta^{13}C$**	**$\delta^{15}N$**	**n**
Caribou	-22.23 ± 0.58	4.62 ± 0.23	2
Forest rodents	-23.73 ± 1.09	2.24 ± 2.06	15
Migratory birds	-23.09 ± 1.17	7.37 ± 0.74	33
Seals	-19.13 ± 0.35	15.05 ± 0.38	44
Snowshoe hare	-28.53 ± 0.59	2.93 ± 1.35	29
Tundra rodents	-25.91 ± 0.75	1.37 ± 3.39	18

Table 4.2. Prey density estimates, estimated consumption of prey group (%, mean and 95% CI), and total mercury concentration (THg) in fox muscle (mg/kg dry weight) for each fox species and each trapping season (November – March). Rodent densities (#/ha) are listed chronologically (year_t – year_{t+1}). Hare densities (#/ha) estimated the subsequent June correspond to the winter trapping season (Freeth et al. 2016). Goose nest densities (#/100 ha) were estimated the previous June. N = fox sample size each trapping season.

Species	**Year**	**N**	**Prey density**			**Prey consumption**					**THg**
			lemmings	hares	Canada goose nests	**Forest rodents**	**Snowshoe hares**	**Tundra rodents**	**Migratory birds**	**Seals**	mean ± SE
Arctic Fox	2010-2011	3	0.35-0.35	Not estimated	Not estimated	1.8 (0.0-7.4)	3.6 (0.4-10.2)	82.7 (69.8-92.4)	8.2 (2.0-17.9)	3.6 (0.1-9.8)	0.11 ± 0.02
	2011-2012	52	0.35-1.74	Not estimated	Not estimated	4.2 (0.1-13.8)	11.0 (3.5-20.3)	55.0 (42.8-67.0)	20.0 (5.9-39.8)	9.8 (0.2-17.4)	0.53 ± 0.09
	2013-2014	99	1.92-0.60	0.73	Not estimated	2.4 (0.1-10.3)	5.9 (0.8-13.9)	71.0 (58.1-84.2)	17.5 (5.9-28.5)	3.2 (0.1-8.5)	0.33 ± 0.06
	2014-2015	48	0.60-0.00	0.63	8.34	4.1 (0.1-13.8)	11.4 (2.9-22.3)	60.6 (46.9-74.0)	17.6 (5.5-32.0)	6.4 (0.2-13.3)	0.59 ± 0.08
	2016-2017	31	0.23-1.99	1.02	8.11	4.3 (0.1-15.6)	14.8 (6.0-25.0)	56.0 (42.2-69.4)	14.1 (3.0-35.6)	10.9 (0.2-18.3)	1.03 ± 0.32
	2017-2018	43	1.99-1.44	0.95	7.97	3.0 (0.1-10.4)	12.3 (3.6-23.9)	71.0 (56.1-84.1)	8.4 (2.3-18.4)	5.3 (0.2-10.9)	0.52 ± 0.10
Red Fox	2010-2011	19	0.35-0.35	Not estimated	Not estimated	2.4 (0.0-9.3)	14.0 (3.9-25.8)	55.5 (38.6-73.7)	25.9 (9.6-38.5)	2.3 (0.1-8.4)	0.56 ± 0.17
	2011-2012	17	0.35-1.74	Not estimated	Not estimated	3.9 (0.1-14.2)	29.4 (18.7-39.9)	23.4 (13.5-35.7)	39.4 (21.1-51.4)	3.9 (0.2-11.1)	0.40 ± 0.10
	2013-2014	14	1.92-0.60	0.73	Not estimated	2.3 (0.0-8.5)	17.3 (5.5-29.6)	36.1 (20.7-60.6)	42.7 (18.6-56.4)	1.6 (0.1-6.4)	0.51 ± 0.08
	2014-2015	22	0.60-0.00	0.63	8.34	4.1 (0.0-15.6)	30.5 (19.3-41.1)	26.7 (15.0-41.1)	36.1 (21.9-45.7)	2.6 (0.1-7.9)	0.66 ± 0.11
	2016-2017	22	0.23-1.99	1.02	8.11	3.7 (0.1-13.1)	40.8 (29.8-51.5)	24.3 (12.9-37.1)	26.8 (10.6-39.3)	4.3 (0.2-11.0)	0.37 ± 0.08
	2017-2018	41	1.99-1.44	0.95	7.97	3.5 (0.0-13.5)	38.4 (28.7-48.4)	35.9 (22.8-49.2)	19.8 (9.5-28.1)	2.4 (0.1-6.6)	0.46 ± 0.08

Table 4.3. Relative performance (using Akaike Information Criterion, AIC) of each model explaining the total mercury concentration (natural logarithm transformation) in muscle from foxes captured by fur trappers near Churchill, MB Canada. Sex: male, female; age_cat: juvenile <1 year old, and adult ≥ 1 year old; hare: density of snowshoe hares; lem: % change in tundra rodent densities over winter; TerrDiet: sum of dietary proportions of tundra and forest rodents, snowshoe hares and caribou; MigBirds: dietary proportion of migratory birds; Seals: dietary proportion of seals.

Species	Rank	Model	AIC	ΔAIC	weight
Red fox	1	logHg ~ sex + age_cat + hare + TerrDiet	232.08	0	0.26
	2	logHg ~ sex + age_cat + hare + MigBirds	232.08	0	0.26
	3	logHg ~ sex + age_cat*hare + TerrDiet	233.88	1.80	0.11
	4	logHg ~ sex + age_cat*hare + MigBirds	233.88	1.80	0.11
	5	logHg ~ sex + age_cat + hare + lem + TerrDiet	233.91	1.83	0.10
	6	logHg ~ sex + age_cat + hare + lem + MigBirds	233.91	1.83	0.10
	7	logHg ~ sex + age_cat*hare + age_cat*lem + TerrDiet	236.17	4.09	0.03
	8	logHg ~ sex + age_cat*hare + age_cat*lem + MigBirds	236.17	4.09	0.03
	9	logHg ~ sex + age_cat + lem + TerrDiet	330.06	97.98	0
	10	logHg ~ sex + age_cat*lem + TerrDiet	329.99	97.91	0
	11	logHg ~ sex + age_cat + lem + MigBirds	330.19	98.11	0
	12	logHg ~ sex + age_cat*lem + MigBirds	330.12	98.04	0
Arctic fox	1	logHg ~ sex + age_cat*lem + TerrDiet	728.02	0	0.76
	2	logHg ~ sex + age_cat*lem + MigBirds	731.52	3.50	0.13
	3	logHg ~ sex + age_cat*lem + Seals	732.02	4.00	0.10
	4	logHg ~ sex + age_cat + lem + TerrDiet	737.51	9.49	0.01
	5	logHg ~ sex + age_cat + lem + MigBirds	741.79	13.78	0
	6	logHg ~ sex + age_cat + lem + Seals	742.16	14.14	0

Table 4.4. β parameters with confidence intervals (CI) and t and p values for each variable of the best performing model (Table 4.3) proposed to explain variation in mercury concentration (log transformed) in muscle of foxes captured by fur trappers near Churchill, MB Canada. Sex: male, female; age_cat: juvenile <1 year old, and adult ≥ 1 year old; hare: density of snowshoe hares; lem: % change in tundra rodent densities between two consecutive years; TerrDiet: sum of mean dietary proportions of tundra and forest rodents, snowshoe hares and caribou.

Model	**Variable**	**β**	**CI**		**t**	**p**
			2.50%	97.50%		
Red foxes	Intercept	5.88	3.35	8.41	4.61	<0.001
	Sex^1	0.34	-0.03	0.71	1.81	0.073
	hare density*	-0.35	-0.54	-0.15	-3.52	0.001
	age_cat^2	-0.17	-0.51	0.18	-0.97	0.334
	TerrDiet	-0.13	-3.13	2.87	-0.08	0.934
Arctic foxes	Intercept	8.47	7.45	9.49	16.39	<0.001
	Sex^1	-0.23	-0.46	0.00	-1.99	0.048
	rodent density*	-0.19	-0.41	0.02	-1.78	0.077
	age_cat^2	-0.42	-0.66	-0.17	-3.31	0.001
	TerrDiet	-2.88	-4.15	-1.61	-4.48	<0.001
	lem*age_cat^2	0.43	0.18	0.68	3.39	0.001

Reference level:
[1]Males
[2]Juveniles
*scaled densities

Figures

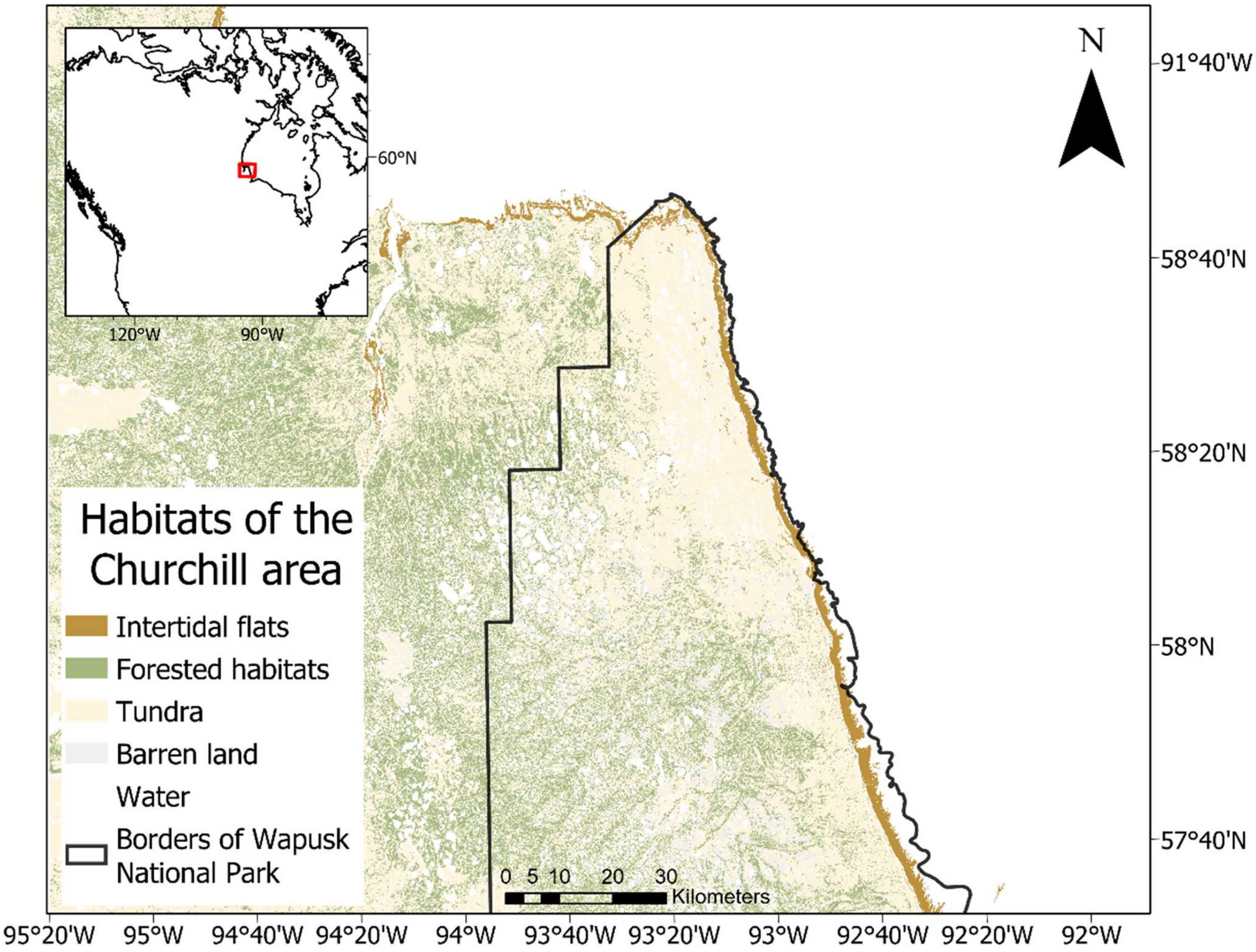


Fig. 4.1. Habitat map of the study area near Churchill, MB, Canada (modified from Canada Land cover 2015; Latifovic et al. 2017).

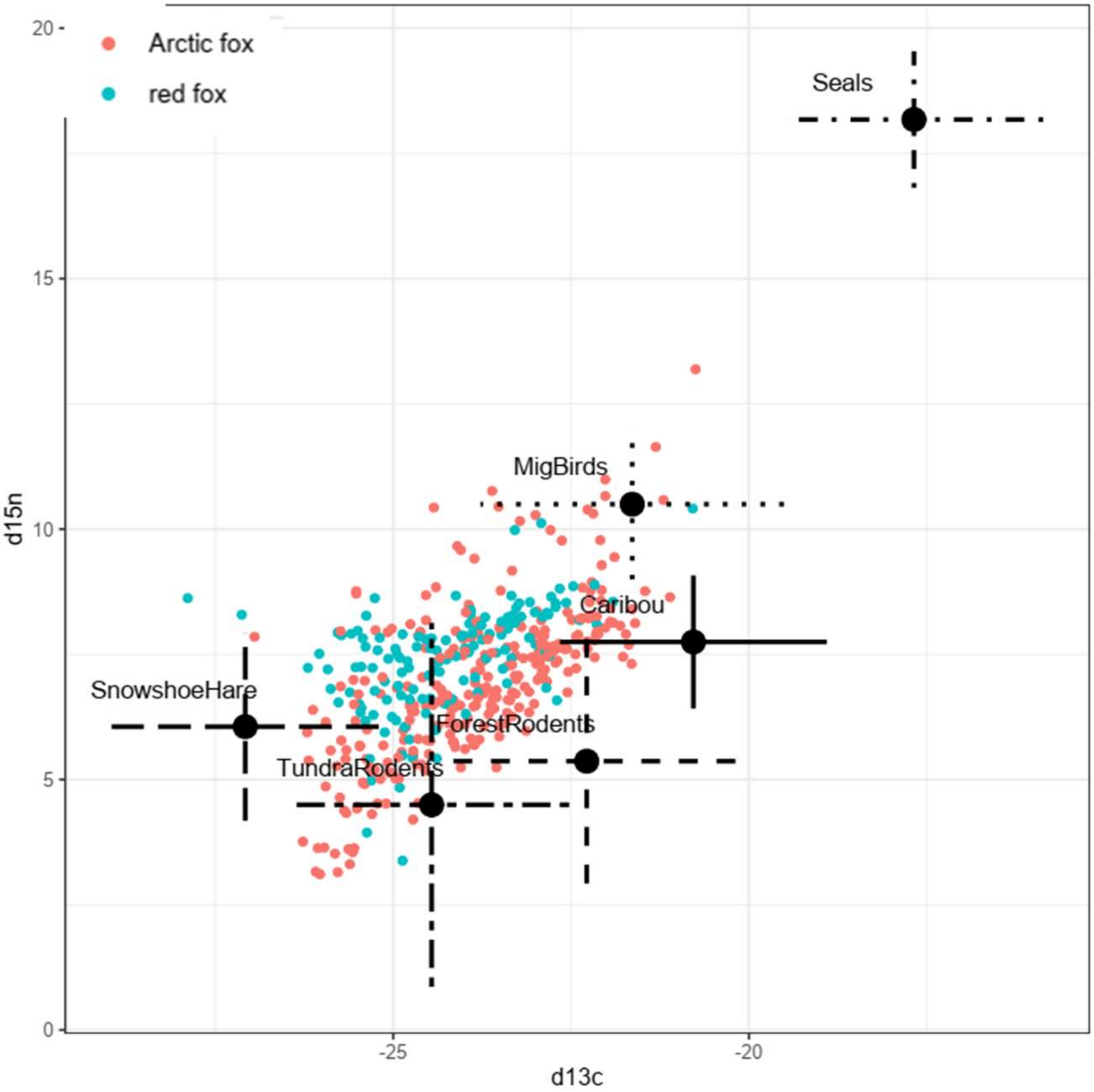


Fig. 4.2. Isospace built with the isotopic signatures (δ^{13}C, δ^{15}N) of 6 possible prey groups (mean ± SD), along with isotopic signatures of all analyzed red and Arctic foxes trapped in northern Manitoba, Canada, between 2010 and 2018. Caribou were only included in the Individual mixing model. Prey values were adjusted for trophic discrimination.

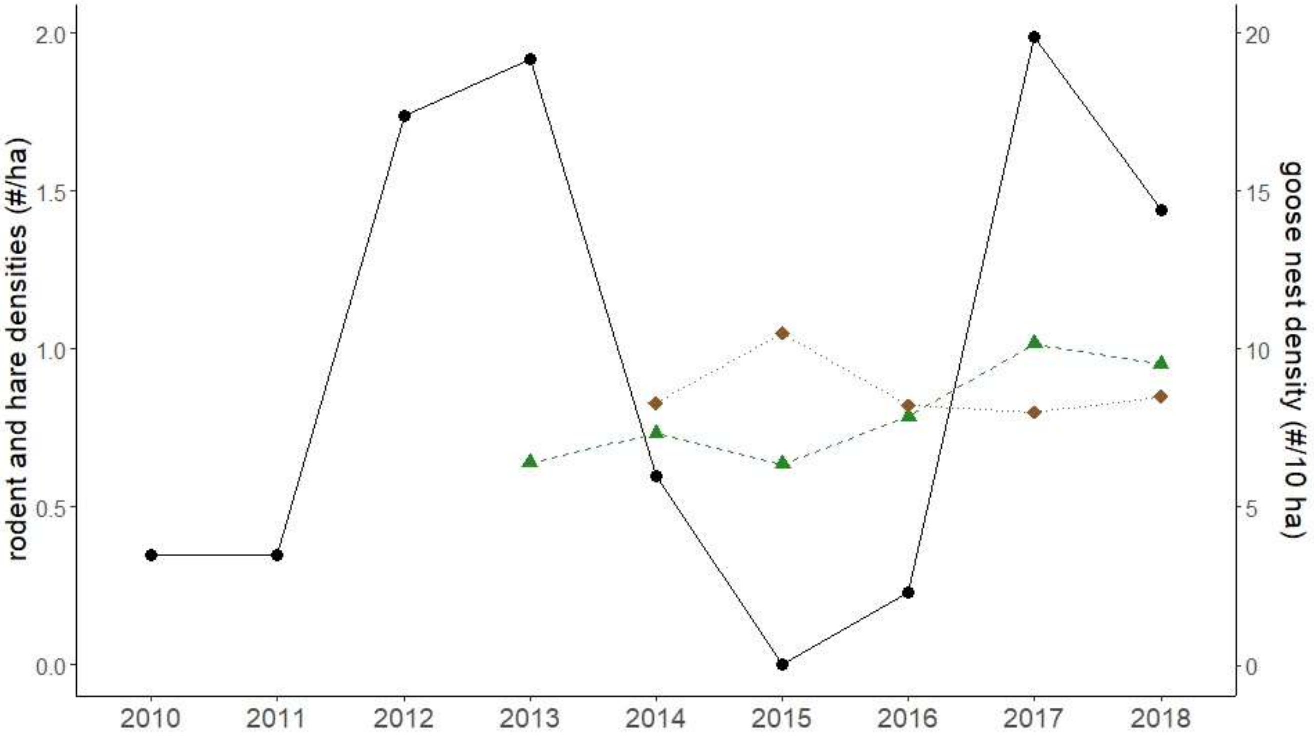


Fig. 4.3. Density variations for the period 2010-2018 of tundra rodents (black dots and solid line) estimated with a mark-recapture protocol, snowshoe hares (green triangles and dashed line) estimated with fecal pellet counts , and Canada goose nests (brown diamonds and dotted line) estimated with a distance sampling protocol from the Churchill area (Manitoba, Canada).

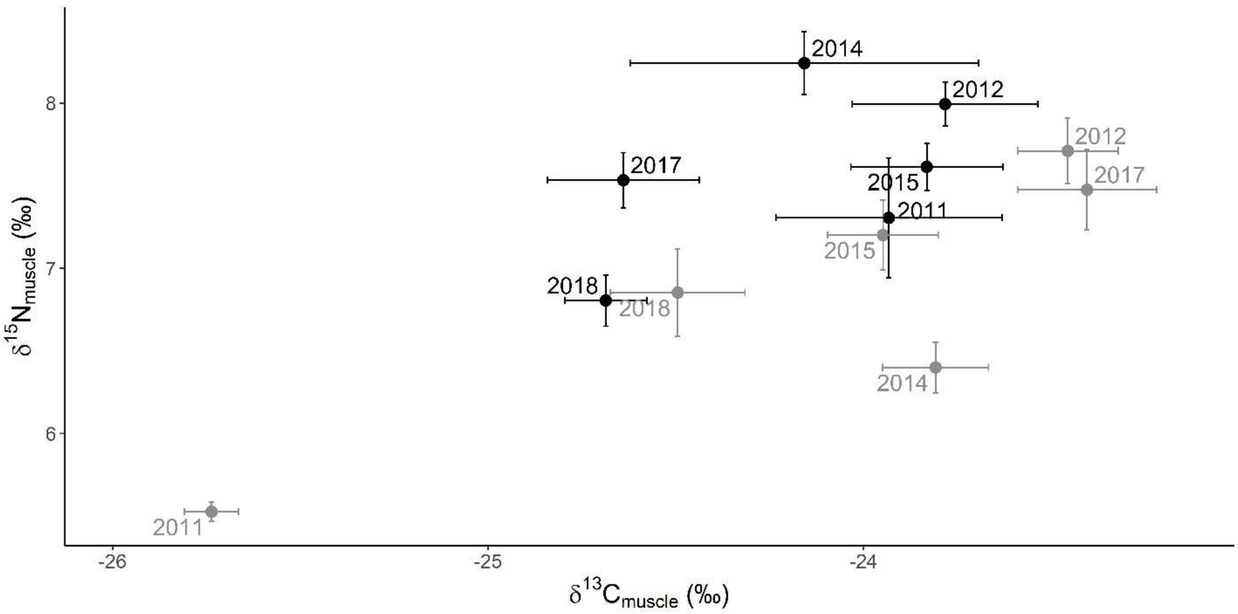


Fig. 4.4. Isotopic signatures (mean ± standard error) of red (black; n_{2011} = 19, n_{2012} = 17, n_{2014} = 14, n_{2015} = 22, n_{2017} = 22, n_{2018} = 41) and Arctic (grey; n_{2011} = 3, n_{2012} = 52, n_{2014} = 99, n_{2015} = 48, n_{2017} = 31, n_{2018} = 43) foxes captured near Churchill, MB Canada each year.

Supplementary material

Table 4.S1. Initial prey considered for building the mixing models. Prey were grouped, discarded, or kept until no more than 6 prey or prey groups remained.

Prey	**Mean δ^{13}C (‰)**	**SD δ^{13}C (‰)**	**Mean δ^{15}N (‰)**	**SD δ^{15}N (‰)**	**n**
Bearded seal (*Erignathus barbatus*)[1]	-18.12	0.54	15.44	0.53	12
Harbour seal (*Phoca vitulina*) [1]	-19.06	0.27	16.37	0.35	16
Ringed seal (*Pusa hispida*) [1]	-19.95	0.21	13.43	0.28	16
Canada goose (*Branta canadensis*) egg[2]	-20.71	0.68	8.7	0.32	10
Canada goose juvenile[2]	-24.87	0.1	5.11	0.23	4
Snow goose (*Anser caerulescens*) egg[2]	-23.78	0.11	7.51	0.15	11
Snow goose juvenile[2]	-24.80	0.24	6.3	1.39	3
Snow goose adult	-19.45	0.83	6.96	0.40	5
Ptarmigan (*Lagopus lagopus*) [2]	-23.51	0.50	0.73	0.92	2
Caribou (*Rangifer tarandus*) [2]	-22.23	0.58	4.62	0.23	2
Shorebird eggs[3]	-23.97	3.23	6.77	1.75	34
Collared lemming (*Dicrostonyx richardsoni)*	-25.41	0.64	-1.04	1.63	10
Meadow vole (*Microtus pennsylvanicus*)	-26.53	0.33	4.39	2.72	8
Red-backed vole (*Myodes gapperi*)	-24.31	0.88	2.24	2.54	8
Shrew species (*Sorex spp.*)	-23.33	1.00	9.8	1.00	1
Snowshoe hare (*Lepus americanus*)	-25.93	1.91	3.38	4.14	2
Red squirrel (*Tamiasciurus hudsonicus*)	-23.07	1.06	2.25	1.75	2
Stickleback (*Pungitius pungitius*)	-25.00	1.14	10.2	1.76	9

[1] (Young et al. 2010)
[2] (McDonald et al. 2017)
[3] (Hobson and Jehl 2010)

Table 4.S2. Year-specific moisture content (%) in fox muscle and associated wet:dry weight conversion factors (CF) of fox muscle mercury content.

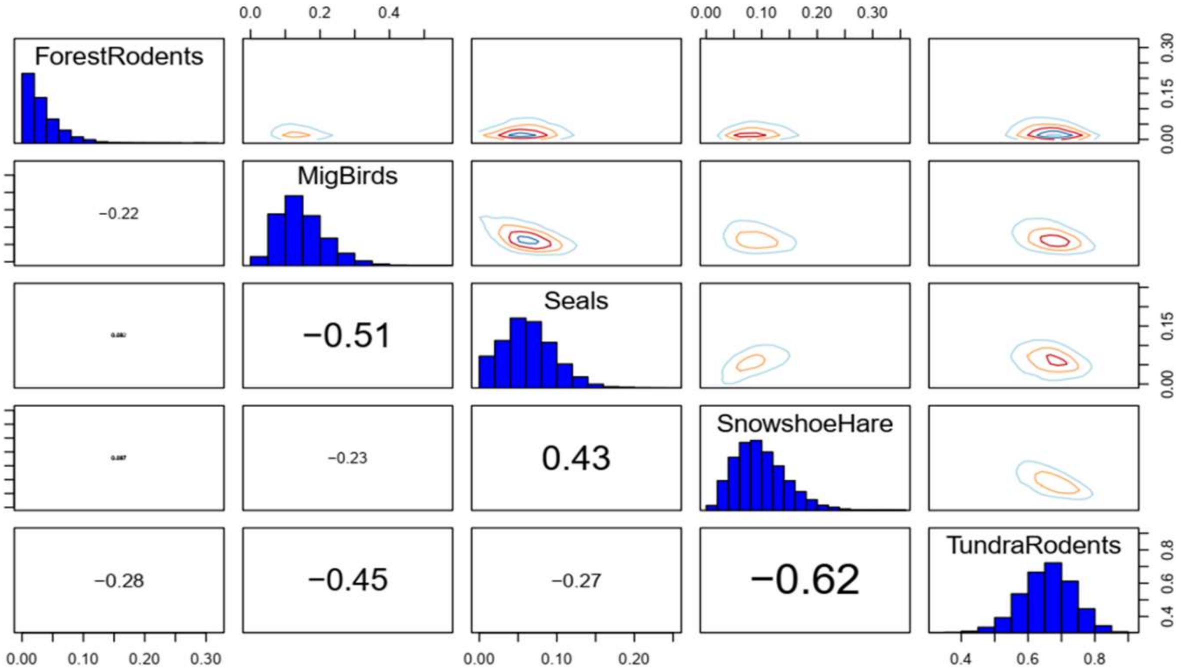
year	**Mean**	**se**	**n**	**CF wet:dry**
2011	69.26	1.77	5	3.25
2012	71.91	0.85	10	3.56
2014	73.72	0.79	10	3.81
2015	71.82	0.55	19	3.55
2017	73.72	0.51	21	3.81
2018	74.16	0.48	17	3.87

Table 4.S3. Total mercury concentration in muscle (wet weight) from fox prey opportunistically collected fresh near Churchill, MB Canada.

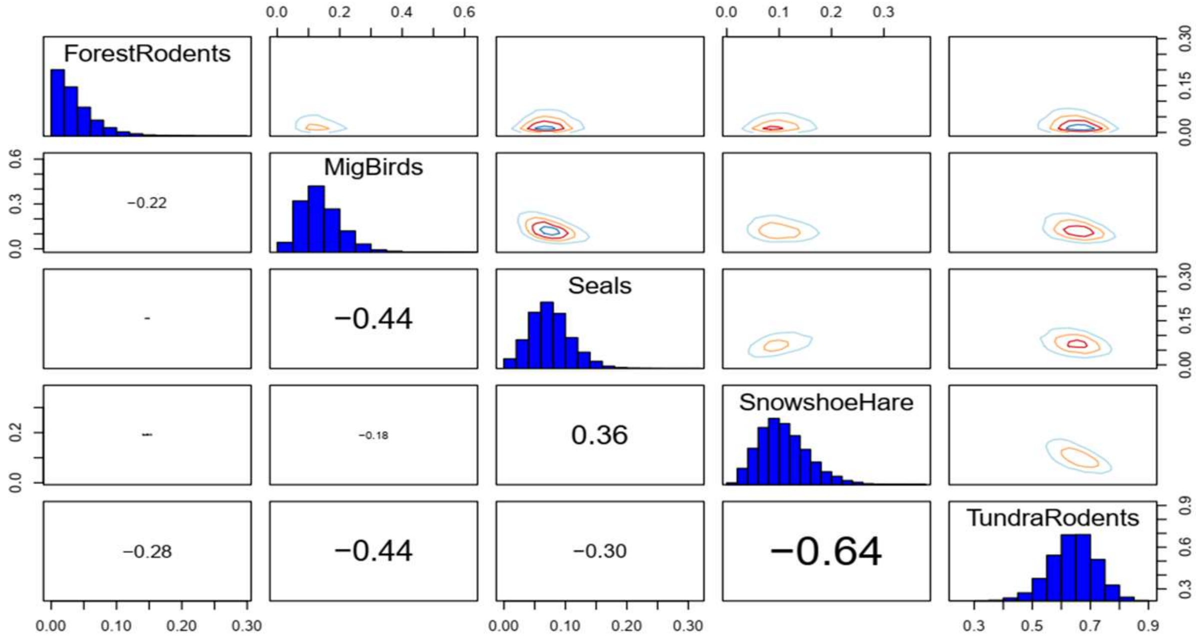
Sample ID	**species**	**age class**	**THg concentration w.w. (ng/g)**	**Weight [g]**	**µ Abs.**	**THg [ng/g]**
C-19-CH-01	Caribou	juvenile	9.22	0.04	7969.50	0.37
C-19-CH-02	Caribou	juvenile	3.08	0.05	5095.00	0.14
LEM-19-01	Lemming	adult	2.26	0.04	4380.00	0.08
SEA-16-01	Seal*	juvenile	161.03	0.04	75461.50	5.67
SQRL-12-01	Red Squirrel	adult	72.30	0.04	41603.00	3.01
VOL-17-01	Meadow vole	adult	9.63	0.04	8238.00	0.39
VOL-17-02	Meadow vole	adult	6.11	0.03	5738.00	0.19
VOL-17-03	Meadow vole	adult	5.18	0.02	4680.00	0.11
VOL-17-04	Meadow vole	adult	-7.01	0.02	1965.00	-0.11
VOL-17-05	Meadow vole	adult	-2.89	0.03	1858.50	-0.07
VOL-17-06	Meadow vole	adult	1.59	0.02	3162.50	0.03

*unknown species, most likely *Pusa hispida* or *Phoca vitulina*

A


ForestRodents
MigBirds
Seals
SnowshoeHare
TundraRodents
−0.22
−0.51
−0.23
0.43
−0.28
−0.45
−0.27
−0.62
0.0
0.2
0.4
0.00
0.10
0.20
0.30
0.00
0.15
0.30
0.4
0.6
0.8

B


ForestRodents
MigBirds
Seals
SnowshoeHare
TundraRodents
−0.22
−0.44
−0.18
0.36
−0.28
−0.44
−0.30
−0.64
0.0
0.2
0.4
0.6
0.1
0.3
0.00
0.10
0.20
0.30
0.15
0.5
0.7
0.9

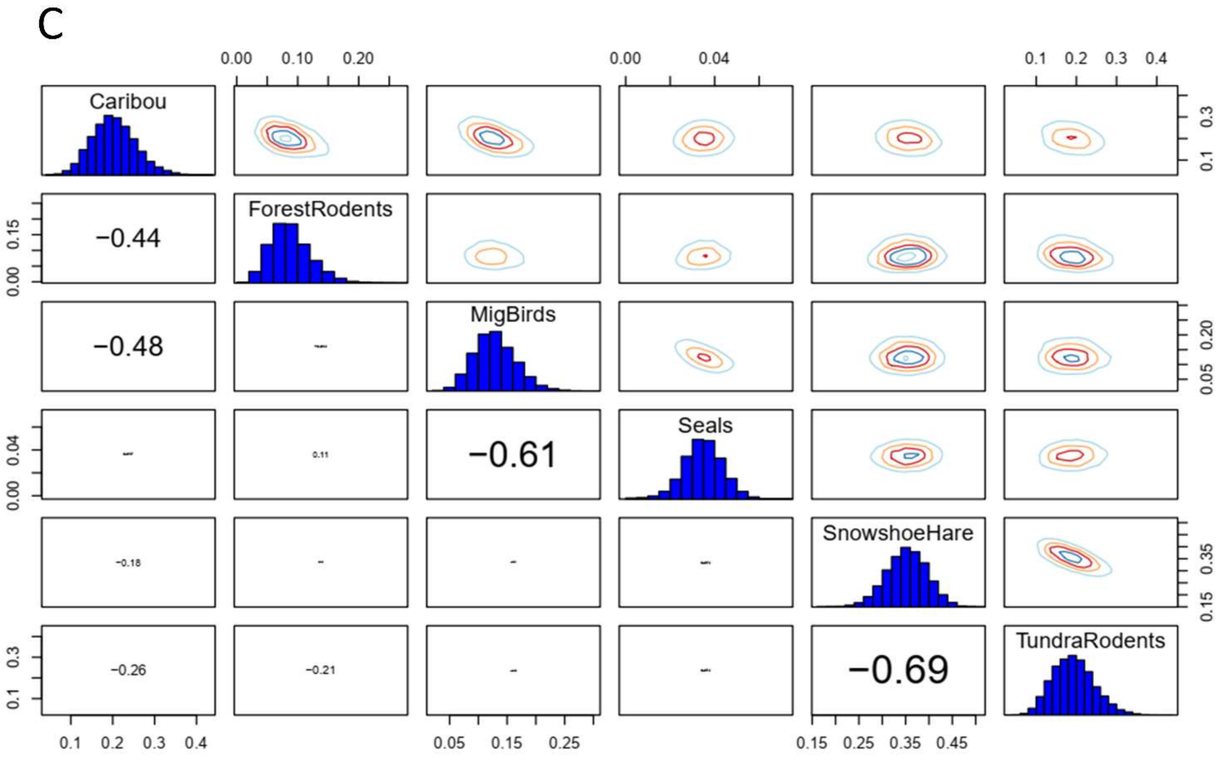


Fig. 4.S1. Source correlation plot of fox diet estimates from the population mixing models (A: with specified priors, B: uniform priors) and the individual mixing model (C), using samples of foxes and prey collected in northeastern Manitoba, Canada. In each panel, diagonal cells show the posterior distribution of each food source, the above-diagonal cells show the contour plots of the joint posterior probability distribution of each source pair (i.e., how and if two sources are correlated), the below-diagonal cells show the correlation coefficient of each source pair.

Prelude to Chapter 5

During the preliminary phases of Chapter 4, we reviewed the pertinence of different tissues to estimate diet and contaminant exposure over the course of winter. We narrowed our selection to muscle and hair from the fox carcasses, but selected muscle because winter hair in juveniles from both species and in adult Arctic foxes grows during late summer and fall and therefore would not represent the desired timeframe.

The work done in this thesis is part of a larger project; although we ended up selecting muscle in the previous chapter, keratinous tissues would allow use of long-term data sets to examine the body burden of diverse substances. Hair is a widely used keratinous tissue, notably because it is noninvasive and easy to collect. However, tracer levels in hair may be hard to interpret because hair-growth rates and molt patterns are seldom characterized. Claws, however, grow continuously and their growth rate would be easier to determine than for hair. I thus decided to establish the potential of claw to assess mercury body burden over a given time frame and compare it to the performance of hair. I also established the relationship between mercury levels in internal organs including the brain, which is seldom collected due to the difficulties sampling it. I chose to focus this chapter on red foxes because they have an almost exclusively terrestrial diet, which would thus provide information about the less-studied contamination of Arctic terrestrial environment. The following chapter is thus part of the overarching Arctic food web framework within which my thesis lies.

Chapter 5: Does claw predict mercury concentration in other tissues of red foxes?

Abstract

Mercury is a ubiquitous trace element that organisms mainly take up through ingestion. Mercury bioaccumulates in organisms, and biomagnifies through aquatic food webs from lower to top trophic levels, causing adverse biological effects above certain concentration thresholds. Environmental monitoring of mercury has primarily focused on aquatic organisms (e.g., fish, marine mammals, and waterfowl). Here we report mercury concentrations in the red fox (*Vulpes vulpes*), which could be a good sentinel species for monitoring mercury in the less-studied terrestrial food webs due to its high trophic position and higher population densities than larger terrestrial carnivores. We quantified total mercury concentration (THg) in tissues of red foxes near Arctic tree line in Canada collected from fur trappers in winter. Hair offers a non-invasive way to assess mercury exposure in diverse species, but variable and poorly understood molt patterns in wildlife often hamper the interpretation of tracer levels in hair. We assessed if THg in red fox claws could be used instead of hair to predict THg in several internal organs because claws grow continuously, and growth rate may be easier to monitor than molt patterns. Like other studies, we found strong relationships between the THg of diverse internal organs, but both THg in claws and hair were poor predictors of THg in internal organs. Because foxes are often nomadic in winter, their mercury exposure likely varies over the course of winters, which translates into a weak match of THg concentrations between active and inactive tissues. During reproduction and young-rearing periods, foxes are constrained to foraging near dens, which would likely result in a more constant exposure to mercury, and therefore THg in claws may better predict THg internal organs within the breeding season. Our results suggest further investigation of the co-variation between THg in internal organs and inactive keratinaceous tissues is warranted.

Introduction

Mercury is a naturally occurring trace element that is released in the surface environment from natural and anthropogenic processes (AMAP 2011; UNEP 2013). Mercury is of environmental concern due to its capacity to bioaccumulate in organisms, biomagnify throughout aquatic food webs, and its well-documented negative impact on wildlife and human health, such as reproductive and neurological disorders and reduced survival (Clarkson 1997; Wolfe and Norman 1998; Wiener et al. 2002; Bocharova et al. 2013; Dornbos et al. 2013; Peterson et al. 2015; van den Brink et al. 2018; Eccles et al. 2020). Mercury also has the potential to biomagnify in terrestrial food webs, notably due to links between some terrestrial species with aquatic food webs in terrestrial-aquatic ecotones (Jackson et al. 2015).

Mercury is present in the environment as inorganic mercury and organic mercury, the latter being mainly composed of methylmercury (Wiener et al. in Hoffman et al. 2003). Methylmercury, a form of mercury particularly toxic, is often positively correlated to the amount of total mercury (THg) in organisms (Wagemann et al. 1998; Raimundo et al. 2014), which is mainly influenced by their feeding ecology, but also age and sex (Lavoie et al. 2010; Bocharova et al. 2013; Peterson et al. 2015); in such cases, total mercury can thus act as a proxy for methylmercury (Ackerman et al. 2013). After intestinal absorption, mercury (including methylmercury) enters blood circulation and is distributed to the diverse organs, including the brain (March et al. 1983; Aschner and Aschner 1990; Syversen and Kaur 2014; van den Brink et al. 2018). Mammals and birds mostly eliminate mercury in metabolically inactive tissues and feces (Wiener et al. 2002). Each form of mercury has unique toxic characteristics to target organs (e.g. Aschner and Aschner 1990). If mercury concentration in keratinous tissues, that are typically less invasive to collect than internal ones, correlate to internal concentration, they can be used to infer the implications of mercury exposure in populations or communities.

THg concentration strongly correlates between organs in diverse taxa, including reptiles (e.g., Hopkins et al. 2013; Eggins et al. 2015), fish (e.g., Suzuki et al. 1973; Cizdziel et al. 2003), birds (e.g., Grajewska et al. 2019; Low et al. 2019) and mammals (e.g., Wolfe and Norman 1998; Dainowski et al. 2015; Treu et al. 2018), and researchers have successfully predicted internal mercury concentration using non-invasive keratinaceous tissues (Yates et al. 2014; Dainowski et al. 2015; Treu et al. 2018). However, the performance of mercury concentration in hair to predict internal mercury concentration varies across species, life stages, and timing of sampling (Peterson et al. 2016; Chételat et al. 2020; Eccles et al. 2020). Molt is sequential and several months may be necessary to achieve complete replacement in furbearers (Maurel et al. 1986; Fraser et al. 2013). Knowledge of species-specific molt patterns and regional differences in molt patterns is lacking for many species (Voigt and Lehnert 2019), rendering interpretation of tracer levels in hair difficult (Fraser et al. 2013; Chételat et al. 2020; Eccles et al. 2020).

Mercury levels in claws have shown stronger correlations with mercury levels in internal tissues than other keratinaceous tissues in birds and reptiles (Hopkins et al. 2013; Eggins et al. 2015; Grajewska et al. 2019; Low et al. 2019). Similar studies in mammals are rare, but e.g., Wolfe and Norman (1998) reported a strong correlation between total mercury in claw and liver in raccoons (*Procyon lotor*). Claws grow continuously and the rate of claw growth may be easier to monitor than fur or feather molting patterns, especially in wild populations (Bearhop et al. 2003; Ethier et al. 2010). Patterns of claw growth are well documented in many taxa, including mammals (carnivores and hoofed mammals), reptiles, birds, and amphibians (March et al. 1983; Ethier et al. 2010). Interpretation of tracer levels in claw may, therefore, be easier than in hair.

We quantified total mercury in tissues of wild red foxes (*Vulpes vulpes*) of northern Manitoba, Canada, including the brain for which data are lacking in Arctic populations. Our objectives were to 1) determine if total mercury in claws can predict total mercury burden of internal organs in red foxes and compare the performance of claws and hair as predictors, 2) assess the relationships between multiple internal organs in total mercury concentration, and 3) produce directional predictive equations to characterize these relationships between different tissues and organs. Because anatomical and physiological left-right asymmetry is well documented in many vertebrate taxa (e.g., Mercola and Levin 2001; Hamada et al. 2002; McGrath and Brueckner 2003; Levin 2005), we also tested if total mercury accumulated differently in left and right kidney tissues (renal cortex and medulla).

Material and methods

Study area and sample collection

Our study area is located near Churchill, Manitoba, on western Hudson Bay (58°N, 94°W), where three biomes merge: tundra, taiga, and the marine ecosystem. Red foxes are legally harvested by local fur trappers between November and March, when young may be dispersing and adults are not raising pups.

Trappers from the Churchill area provided us with carcasses from 64 red foxes legally harvested during the trapping season (November – March) in 2017 and 2018. Carcasses were kept frozen until sampling. We harvested the whole left and right kidneys, liver, and brain, 3 to 5 pieces of muscle from the quadriceps, hair from the front paws or around the anus, and claws from digits 2 and 4 of the left front leg when those tissues were in good condition (i.e., neither dried nor damaged). We also collected the jaws to extract a canine tooth for aging. Canines were first X-rayed using standard techniques and we measured pulp cavity-tooth width ratio after tracing a perpendicular axis to the main tooth axis at its widest point on the X-rays in ImageJ (Schneider et al. 2012). When the ratio was >41% foxes were considered <1 year old (approx. twice the average ratio of a 2-year-old fox to ensure we would not wrongly assign the age 0; Cavallini and Santini 1995). All foxes for which the pulp cavity-tooth width ratio was <41% were aged using cementum annuli count by Matson's lab (Manhattan, Montana, USA). Given the low number of foxes older than 1 year, we separated the foxes into two age categories: yearlings, which never had an opportunity to reproduce (<1-year-old), and adults, which may have reproduced at least once (1-year-old and above). We later separated renal cortices and medullas and systematically sub-sampled all parts of each organ (to avoid bias due to intra-organ heterogeneity) at the University of Manitoba. Guard hair and underfur were separated, and we analyzed guard hair only. Claws were cut 2mm away from the vascularized dermis edge, to represent an amount of claw tip that could be safely collected from a living animal. The size of claw tips analyzed ranged from 0.77 to 1.33 cm (straight line along the main axis of the sample), as measured with electronic calipers.

Total mercury (THg) concentration analysis

We analyzed between 4 and 96 mg of tissue (wet weight; see Appendix 5.A for tissue composition) from brain, liver, renal cortex, renal medulla, muscle, hair, and claw using a direct mercury analyzer (Hydra IIc, Teledyne Leeman Laboratories, Hudson, NH). We calibrated the instrument using low-detection linear calibration curves calculated with blank sample boats (blank correction) and the certified reference materials MESS-3 (91 ± 9 ng/g) and MESS-4 (90±40 ng/g), and high-detection linear calibration curves calculated with the certified reference material PACS-3 (2980 ±360 ng/g). Curves included at least 5 determination points and were validated when $R^2>0.995$. The instrument detection limit is <0.001 ng. Quality assurance and control were done by running the certified reference materials (including MESS-3, MESS-4, TORT-3 (292 ± 12 ng/g), DORM-4 (412 ± 36 ng/g), DOLT-5 (440±180 ng/g ng/g), NIST2709a (900 ± 200 ng/g), NCP III-9 S2 (933 ± 55.5 ng/g), and PACS-3) two to three times every 14 samples (recovery: 8.1%±0.3).

Statistical analyses

We performed all statistical analyses using R software (R Core Team 2019). We checked our model residuals for outliers, deviation from normality, and homoscedasticity (Zuur et al. 2010). Due to deviation from normality, we applied a natural log transformation to all mercury concentrations for all analyses. We found no outliers – Cook's distance > 0.7 (Mcdonald 2002). Manuscript and diagnostic plots were produced using the ggpubr v.0.3.0 and ggplot2 v.3.3.0 package. Data exploration and statistical tests were run using the packages car v.3.0.7 (Fox and Weisberg 2019), nlme v.3.1.147 (Pinheiro et al. 2020), lme4 v.1.1.23 (Bates et al. 2015), lmerTest v.3.1.2 (Kuznetsova et al. 2017), fitdistrplus v.1.1.1 (Delignette-Muller and Dutang 2015), rstatix v.0.5.0 (Kassambara 2020), and base R.

We used paired t-tests to assess left-right asymmetry between kidney tissues and difference between renal cortices and medullas. We then used R^2 from linear regressions to characterize the strength of claws and hair as predictors of the internal organs, as well as the strength of the prediction between THg in the diverse internal organs. The linear regressions also produced predictive equations that characterize the relationships between all tissues. For internal organs only we produced each equation in both directions. Sex differences in anatomy, physiology, biochemistry, and behavior affect exposure, bioaccumulation and kinetics of several substances, including contaminants, confirming that sex is important to consider in toxicology studies (Gochfeld 2007; Robinson et al. 2012; Lyytikäinen et al. 2015). We thus designed a minimal model (only the compared organ as a predictor), and a full model with sex and its interaction term, separately for each organ comparison model as follows:

(8) organ Y ~ organ X (minimal model)

(9) organ Y ~ organ X + sex + sex*organ X (full model)

We compared minimal to full models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002; see Table 5B.2), and if the two models were < 2 ΔAIC, we selected the minimal model (i.e., the most parsimonious one). When the full model had the smallest AIC, we checked if the sex interaction effect was significant ($p \leq 0.05$); if so, the full model was compared to the minimal model using a partial-F test (i.e., we tested if the decrease in the residual sum of squares of the interaction model compared to the null model was significant) to determine if the differences in regression slopes were important enough to warrant the production of an equation for each sex. We were not able to add age class in our models, since the maximum number of adults we had for pair comparisons was 8, nor did we test for interactions between sex and age due to unbalanced representation (our samples were heavily male-biased, with only one adult female). We report descriptive statistics as mean±SE.

Results

Hair had the highest THg concentration (1.129±0.145 mg/kg), followed by the claw tip (0.715 ±0.108 mg/kg). The renal cortex had the highest mercury load of all internal organs (0.539±0.093 mg/kg), followed by liver (0.262±0.034 mg/kg), renal medulla (0.160±0.028 mg/kg), muscle (0.110±0.018 mg/kg) and finally brain (0.061±0.012 mg/kg) (Table 5.1). We found higher THg in renal cortices than in renal medullas ($t_{19} = 19.209$, $p < 0.001$), but we found weak evidence that the right and left kidneys accumulate mercury differently (cortex: $t_{19} = -1.664$, $p = 0.113$; medulla: $t_{19} = 1.737$, $p = 0.099$). Renal cortex and medulla were highly related ($R^2 = 0.83$), and that relationship was stronger in males (Table 5.2).

THg in both claw and hair was a poor predictor of THg in internal organs (Fig. 5.B1), with R^2 ranging from 0.02 to 0.14 (Table 5.2). The linear regressions between THg in claw and other internal organs only yielded a significant p-value for the renal cortex, while THg in hair was significantly associated with THg in brain only. Claw and hair THg were more strongly related ($R^2 = 0.61$, $t_{25} = 6.336$, $p<0.001$; Fig. 5.1).

The relationships between THg concentrations of internal organs were strong (Table 5.2; Fig. 5.2), with R^2 (sexes pooled) ranging from 0.75 (between liver and renal medulla) to 0.95 (between muscle and brain), and all linear regressions involving only internal organs were significant (Table 5.2). In six comparisons of THg concentrations between tissues, we found a significant interaction with sex (Fig. 5.3; Table 5.3). For all cases but one, adding sex and interaction terms significantly improved the models according to the partial-F test, suggesting that the relationship between THg in the concerned pairs of organs differed between sexes (Table 5.4). For those five specific Y~X pairs of organs, we thus produced sex-specific equations in addition to a general equation for both sexes (Table 5.2). The predictive ability of THg between these internal organs was weak to moderate in female (R^2 ranged from 0.39 between liver and renal cortex to 0.67 between muscle and brain) but strong in males (R^2 ranged from 0.89 between muscle and renal cortex to 0.97 between muscle and brain). The complete output of all models selected by AIC are provided in Table 5B.3.

Discussion

Contrary to expectations, THg in claws and internal organs were unrelated. Because mercury is incorporated into inert tissues as they grow (March et al. 1983; Ethier et al. 2010; Fraser et al. 2013; Chételat et al. 2020; Eccles et al. 2020), these tissues indicate mercury ingested at the time of growth. In foxes, given a claw growth rate of 1 cm/month (Lecomte et al. 2011), 1 cm of claw tip would provide records of 4 weeks of mercury exposure. However, keratin is produced in different places including all along the dorsal edge of the claw. A claw tip is thus a homogeneous mix of newer and older keratin, some of which would have already been inactive for many weeks before our foxes died (Homberger et al. 2009; Ethier et al. 2010). In contrast, internal organs reflected the diet over the 3 to 4 weeks immediately before trapping, and muscle reflected the diet of the 8 to 10 weeks prior trapping (Vander Zanden et al. 2015). This mismatch between the turnover rates of those different tissues can reduce overlap between mercury load in claws versus organs or muscles, i.e., if an individual's exposure to mercury is constant over time, the mercury load of the claw should be strongly related to the mercury in internal organs and muscle, but not if its exposure to mercury varies over time.

Metal accumulation in organisms may vary spatially depending on multiple factors including local contamination (e.g., Braune et al. 1999; Fortin et al. 2001; Gamberg et al. 2005; Fritsch et al. 2012, 2014), From November to March, foxes' movements are not restricted by breeding, and they likely range over large portions of their landscape (from several dozen up to several thousands of km) in search of food (Fuglei et al. 2016; Rioux et al. 2017; Fuglei and Tarroux 2019; Lai et al. 2022). Therefore, if within those few weeks preceding trapping, they feed in areas with different levels of mercury or on prey items with different concentrations of mercury (e.g., marine vs terrestrial prey which may differ greatly in mercury concentrations), their mercury intake likely varies on a temporal scale, explaining the poor performance of mercury in claw tips as a predictor of mercury in internal organs. Fox exposure to mercury is likely more constant during reproduction and young-rearing periods because foxes' movements are constrained to staying near dens. Therefore, THg in claw tips may better predict THg in internal organs during breeding and young-rearing periods compared to non-reproductive periods.

In contrast to Dainowski et al. (2015) and Treu et al. (2018), we did not find that THg in hair was a good predictor of the internal THg burden, performing similarly to THg in claws. Guard hair of adult red foxes grows once a year, starting in April and being mostly completed by the end of June (Maurel et al. 1985). Between December and March, the winter coat fully covers the fox, and no new hair grows, likely explaining the mismatch between THg in hair and internal organs in our adult population that may largely engage in nomadism over winter. The agreement between hair and claw THg could be surprising since claws reflect exposure from fall throughout winter and hair grows in spring, but most foxes in our study were yearlings. Red fox pups start growing their adult guard hair around 8-12 weeks of age, peaking in August, and completing the process by October (Linhart 1968). That molt pattern may have led to a larger overlap between claw and hair growth than expected in adults. The large proportion of yearlings in our samples may thus explain the agreement between THg in claws and hair, and the mismatch between hair and internal organs.

Like previous research, we found a strong relationship between THg levels of different internal tissues (e.g., Dainowski et al. 2015; Peterson et al. 2016; Treu et al. 2018; Grajewska et al. 2019; Low et al. 2019; Chételat et al. 2020). Although age can influence mercury accumulation (e.g., Hoffman et al. 2003; Chételat et al. 2020), we could not test the effect of age due to the unbalanced representation of older ages in our sample. Unlike some other studies in foxes (Dainowski et al. 2015; Treu et al. 2018), sex influenced the slope of the regression between mercury concentration in some tissue pairs. It is not clear why these specific relationships differ between males and females. Sex-specific differences reported in the literature are inconsistent across studies and species (Hopkins et al. 2013; Dainowski et al. 2015; Low et al. 2019; Chételat et al. 2020) but physiological differences could explain why mercury concentrations and relationships between THg in tissues differ by sex (Chételat et al. 2020). Sex hormones induce sexual dimorphism in the morphology and functions of internal organs (Gustafsson and Ingelman Sundberg 1974; Harris et al. 1974; Kobliakov et al. 1991; Tanaka et al. 1991; Rinn et al. 2004; Miyazaki et al. 2006; Sabolić et al. 2007; De Vries and Forger 2015). For example, sex-specific differences in the rate of excretion of diverse compounds by the kidney have been demonstrated in several mammalian species; in rats, kidneys of females accumulate more, clear more rapidly, and are less sensitive to the nephrotoxic effects of mercury than males' kidneys (Thomas et al. 1987; Miyazaki et al. 2006; Sabolić et al. 2007). Although numerous studies have shown important differences between sexes, notably in renal physiology, we recommend caution when interpreting our result because our sample is strongly male-biased and very few females had high mercury concentrations.

Mercury concentrations in the internal organs of Churchill red foxes were higher in the renal cortex, followed by the liver, muscle, renal medulla, and brain. This trend was consistent with reports from other fox populations, and other mammalian species (e.g., Syversen and Kaur 2014; Dainowski et al. 2015; Khabarova et al. 2018). However, some studies on mammals have found higher levels of mercury in livers including fox species (Dietz et al. 2013; Komov et al. 2016; Treu et al. 2018). Whether mercury primarily concentrates in the renal cortex or the liver depends on the major forms of mercury acquired through the diet and on the physiological differences between species regarding detoxification. Most terrestrial species primarily accumulate mercury in the kidneys, whereas most marine species primarily accumulate mercury in the liver (Dietz et al. 2013; Gamberg et al. 2015). Kidneys are highly susceptible to the toxic effects of methylmercury (Bridges and Zalups 2010). Marine species are exposed to higher levels of mercury (including methylmercury), and thus the higher accumulation of mercury in the liver may reflect a protection mechanism against the nephrotoxicity of methylmercury in adult marine mammals (Ewald et al. 2019). It would be reasonable to think that if some population of terrestrial predators rely primarily or exclusively on highly contaminated marine resources (e.g., marine mammals, or sea birds), such as some Arctic fox populations, the fact that the liver is the primary target for mercury accumulation reflects a similar protection mechanism. The renal cortex and the outer layers of the renal medulla are the primary sites of inorganic mercury accumulation (Bridges and Zalups 2010; Syversen and Kaur 2014), which explains the large difference in THg concentration between renal cortices and medullas found in Dainowski et al. (2015) and our study. We, therefore, encourage researchers to separate renal cortices and medulla when looking at metal accumulation.

Mercury concentration in Churchill fox tissues was moderate compared to other values reported in the literature for fox species in the Arctic (Table 5.B1). For example, Treu et al. (2018) reported values 7 to 30 times higher in Icelandic foxes than in our study area, but Arctic foxes may have a stronger link to the marine food web than red foxes. Treu et al. (2018) and Kalisinska et al. (2012) summarized mercury values for Arctic and red fox populations in Canada, Alaska, Commander Island, Iceland, Svalbard, and throughout continental Europe. Our red fox population was in range with the red fox population of the Bethel region in Alaska (Dainowski et al. 2015), and the Arctic fox populations of Svalbard, Holman (Canada) and Barlow (Alaska), and red fox populations from polluted areas of Europe (e.g., Piskoroyá et al. 2003; Binkowski et al. 2016). The generally low level of mercury in our red fox tissues probably reflects a terrestrial diet and the generally low terrestrial contamination in Churchill's terrestrial environment (Bocharova et al. 2013; Gamberg et al. 2015). Despite these many studies on mercury in fox tissues, no toxicity threshold has been established in vulpine species. In other species, however, different THg-toxicity thresholds caused subclinical (5.4 mg/kg in polar bear hair; Dietz et al. 2011), clinical effects (30 mg/kg in hair of terrestrial mammals; Treu et al. 2018), and lethality (20-30 mg/kg in both kidney and liver wet weight; terrestrial carnivores; Shore et al. 2011). None of our foxes ever reached any of these thresholds.

To our knowledge, our study is the first to quantify total mercury in red-fox claws, a tissue that is under-represented in toxicology studies (Grajewska et al. 2019). Despite the poor relationship between THg in claws and THg in internal organs found in the context of our study, we suspect claws would be a better indicator of fox-population exposure during reproduction and young-rearing periods. If this prediction was supported, claws sampled during the young-rearing period would provide an alternative to hair as a sampling matrix to measure the exposure of live animals over a more precise time frame. We mostly restricted our study to the most commonly investigated tissues but included the brain for which prediction equations were lacking. Although potentially a less accessible organ, the particular sensitivity of the brain to the toxic effects of mercury makes it an important target of toxicology assessment. Given the strong relationship between THg in brain and other internal tissues, we believe our equations would prove useful in assessing brain exposure when sampling brain is difficult. Given the discrepancies between mercury accumulation in kidneys and liver, our set of equations involving kidney tissues and liver may be particularly suited to vulpine populations with a terrestrial diet, which complements previous studies on vulpine populations with a higher reliance on marine items.

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Table 5.1. Total mercury concentrations (mg/kg of wet weight; see Appendix 5.A for dry-weight correspondence) in liver, muscle, renal cortex and medulla, brain, claw, and guard hair of red foxes from northern Manitoba, Canada.

		liver	**muscle**	**ren. cortex**	**ren. medulla**	**brain**	**claw**	**hair**
n		**55**	**54**	**42**	**42**	**26**	**29**	**28**
	F	13	13	13	13	9	10	9
	M	42	41	29	29	17	19	19
Mean		**0.262**	**0.110**	**0.539**	**0.160**	**0.715**	**0.061**	**1.129**
	F	0.144	0.060	0.260	0.087	0.597	0.025	1.094
	M	0.298	0.126	0.664	0.193	0.777	0.080	1.146
SE		**0.034**	**0.018**	**0.093**	**0.028**	**0.108**	**0.012**	**0.145**
	F	0.031	0.014	0.032	0.017	0.169	0.003	0.272
	M	0.042	0.022	0.127	0.038	0.140	0.017	0.175
Median		**0.160**	**0.060**	**0.330**	**0.097**	**0.560**	**0.035**	**0.913**
	F	0.117	0.043	0.226	0.062	0.304	0.022	0.613
	M	0.196	0.065	0.406	0.110	0.591	0.046	1.077
Min		**0.049**	**0.017**	**0.107**	**0.028**	**0.107**	**0.012**	**0.412**
	F	0.049	0.026	0.133	0.028	0.107	0.012	0.492
	M	0.068	0.017	0.107	0.038	0.209	0.015	0.412
Max		**1.348**	**0.680**	**3.495**	**1.035**	**2.135**	**0.269**	**3.424**
	F	0.430	0.184	0.495	0.221	1.606	0.040	2.510
	M	1.348	0.680	3.495	1.035	2.135	0.269	3.424

Table 5.2. Predictive equation parameters (95% confidence interval in parentheses) and statistical results of models comparing total mercury concentrations in tissues of red foxes collected near Churchill, MB Canada.

Y	X	sex	Intercept	β	t	p	n	R^2
Muscle	Claw	M & F	2.144 (-1.094– 5.382)	0.348 (-0.164 – 0.86)	1.403	0.173	26	0.08
Liver	Claw	M & F	2.925 (-0.016– 5.867)	0.367 (-0.097 – 0.832)	1.632	0.116	26	0.10
Renal cortex	Claw	M & F	3.313 (0.824 – 5.801)	0.425 (0.032 – 0.818)	2.234	0.035	26	0.17
Renal medulla	Claw	M & F	2.737 (-0.133 – 5.606)	0.313 (-0.141 – 0.766)	1.424	0.167	26	0.08
Brain	Claw	M & F	0.811 (-2.332 – 3.954)	0.445 (-0.048 – 0.938)	1.871	0.075	24	0.14
Guard hair	Claw	M & F	2.909 (1.622 – 4.197)	0.624 (0.421 – 0.827)	6.336	<0.001	26	0.63
Muscle	Guard hair	M & F	1.369 (-3.037 – 5.774)	0.425 (-0.217 – 1.066)	1.361	0.185	28	0.07
Liver	Guard hair	M & F	2.634 (-1.333 – 6.602)	0.376 (-0.201 – 0.954)	1.339	0.192	28	0.06
Renal cortex	Guard hair	M & F	3.023 (-0.517 – 6.563)	0.434 (-0.083 – 0.950)	1.735	0.096	26	0.11
Renal medulla	Guard hair	M & F	2.290 (-1.684 – 6.264)	0.353 (-0.227 – 0.932)	1.257	0.221	26	0.06
Brain	Guard hair	M & F	-0.454 (-4.325 – 3.417)	0.595 (0.033 – 1.157)	2.196	0.039	24	0.18
Claw	Guard hair	M & F	-0.566 (-2.806 – 1.674)	1.003 (0.676 – 1.329)	6.336	<0.001	26	0.63
Liver	Muscle	M & F	1.712 (1.291 – 2.133)	0.821 (0.725 – 0.918)	17.074	<0.001	54	0.85
Renal cortex	Muscle	M & F	2.693 (2.224 – 3.162)	0.747 (0.640 – 0.852)	14.250	<0.001	41	0.84
Renal cortex	Muscle	F	3.696 (2.412 – 4.980)	0.460 (0.132 – 0.788)	3.086	0.010	13	0.46
Renal cortex	Muscle	M	2.675 (2.163 – 3.188)	0.762 (0.651 – 0.872)	14.190	<0.001	28	0.89
Renal medulla	Muscle	M & F	1.228 (0.733 – 1.722)	0.800 (0.688 – 0.911)	14.470	<0.001	41	0.84
Brain	Muscle	M & F	-0.525 (-0.861 – -0.188)	0.996 (0.916 – 1.076)	25.690	<0.001	28	0.95
Renal cortex	Liver	M & F	1.770 (1.055 – 2.485)	0.793 (0.659 – 0.926)	11.968	<0.001	42	0.78
Renal cortex	Liver	F	3.540 (1.907 – 5.174)	0.407 (0.066 – 0.747)	2.63	0.023	13	0.39
Renal cortex	Liver	M	1.443 (0.584 – 2.301)	0.857 (0.703 – 1.012)	11.402	<0.001	29	0.83
Renal medulla	Liver	M & F	0.354 (-0.454 – 1.161)	0.826 (0.675 – 0.977)	11.041	<0.001	42	0.75
Brain	Liver	M & F	-1.270 (-2.097 – -0.444)	0.957 (0.799 – 1.114)	12.487	<0.001	29	0.85
Muscle	Liver	M & F	-1.121 (-1.762 – -0.479)	1.033 (0.912 – 1.154)	17.074	<0.001	54	0.85
Renal medulla	Renal cortex	M & F	-1.050 (-1.886 – -0.215)	0.968 (0.829 – 1.108)	14.040	<0.001	42	0.83
Brain	Renal cortex	M & F	-3.272 (-4.309 – -2.235)	1.176 (1.002 – 1.35)	13.874	<0.001	29	0.88
Muscle	Renal cortex	M & F	-2.328 (-3.280 – -1.376)	1.123 (0.964 – 1.283)	14.251	<0.001	41	0.84
Liver	Renal cortex	M & F	-0.594 (-1.593 – 0.405)	0.986 (0.820 – 1.153)	11.968	<0.001	42	0.78

Brain	Renal medulla	M & F	-1.048 (-1.894 – -0.203)	1.037 (0.854 – 1.219)	11.668	<0.001	29	0.83
Brain	Renal medulla	F	1.122 (-0.601 – 2.845)	0.497 (0.077 – 0.919)	2.725	0.026	10	0.48
Brain	Renal medulla	M	-1.740 (-2.811 – -0.669)	1.181 (0.963 – 1.4)	11.405	<0.001	19	0.88
Muscle	Renal medulla	M & F	-0.615 (-1.316 – 0.086)	1.054 (0.907 – 1.202)	14.470	<0.001	41	0.84
Liver	Renal medulla	M & F	0.980 (0.183 – 1.778)	0.912 (0.745 – 1.078)	11.041	<0.001	42	0.75
Renal cortex	Renal medulla	M & F	1.906 (1.315 – 2.496)	0.859 (0.735 – 0.982)	14.041	<0.001	42	0.83
Renal cortex	Renal medulla	F	3.420 (2.306 – 4.534)	0.483 (0.224 – 0.742)	4.11	0.002	13	0.61
Renal cortex	Renal medulla	M	1.561 (0.867 – 2.255)	0.936 (0.797 – 1.076)	13.770	<0.001	29	0.88
Muscle	Brain	M & F	0.542 (0.210 – 0.874)	1.005 (0.916 – 1.094)	23.273	<0.001	28	0.95
Muscle	Brain	F	1.772 (0.686 – 2.858)	0.605 (0.262 – 0.948)	4.064	0.004	10	0.67
Muscle	Brain	M	0.453 (0.080 – 0.825)	1.031 (0.939 – 1.124)	23.603	<0.001	18	0.97
Liver	Brain	M & F	1.898 (1.343 – 2.454)	0.891 (0.745 – 1.037)	12.490	<0.001	29	0.85
Renal cortex	Brain	M & F	3.169 (2.750 – 3.587)	0.746 (0.635 – 0.856)	13.870	<0.001	29	0.88
Renal medulla	Brain	M & F	1.60 (1.064 – 2.138)	0.805 (0.663 – 0.946)	11.668	<0.001	29	0.83

Table 5.3. Effect of sex on the relationship between mercury concentration in different tissues of red foxes collected near Churchill, MB Canada in 2017-2018. Parameters for interaction effects from the full models (with sex interaction): t and p value, DF = residual degrees of freedom, and sample size (n) for males and females. Results of the partial F-test comparing the simple to the full model (F = F value, DF = residual degrees of freedom, p = p-value).

models compared		**parameters of the sex interaction effect**					**Results of the partial F-test**		
simple	**with sex interaction**	**t**	**DF**	**p**	**n females**	**n males**	**F**	**DF**	**p**
brain~renal medulla	brain~renal medulla*sex	3.181	25	0.004	10	19	5.084	25	0.014
renal cortex~renal medulla	renal cortex~renal medulla*sex	3.293	38	0.002	13	29	6.383	38	0.004
renal cortex~liver	renal cortex~liver*sex	2.665	38	0.011	13	29	3.985	38	0.027
renal cortex~muscle	renal cortex~muscle*sex	2.086	37	0.044	13	28	3.721	37	0.033
muscle~brain	muscle~brain*sex	2.900	24	0.008	10	18	4.453	24	0.023
muscle~renal medulla	muscle~renal medulla*sex	2.098	13	0.043	13	29	2.208	38	0.125

Figures

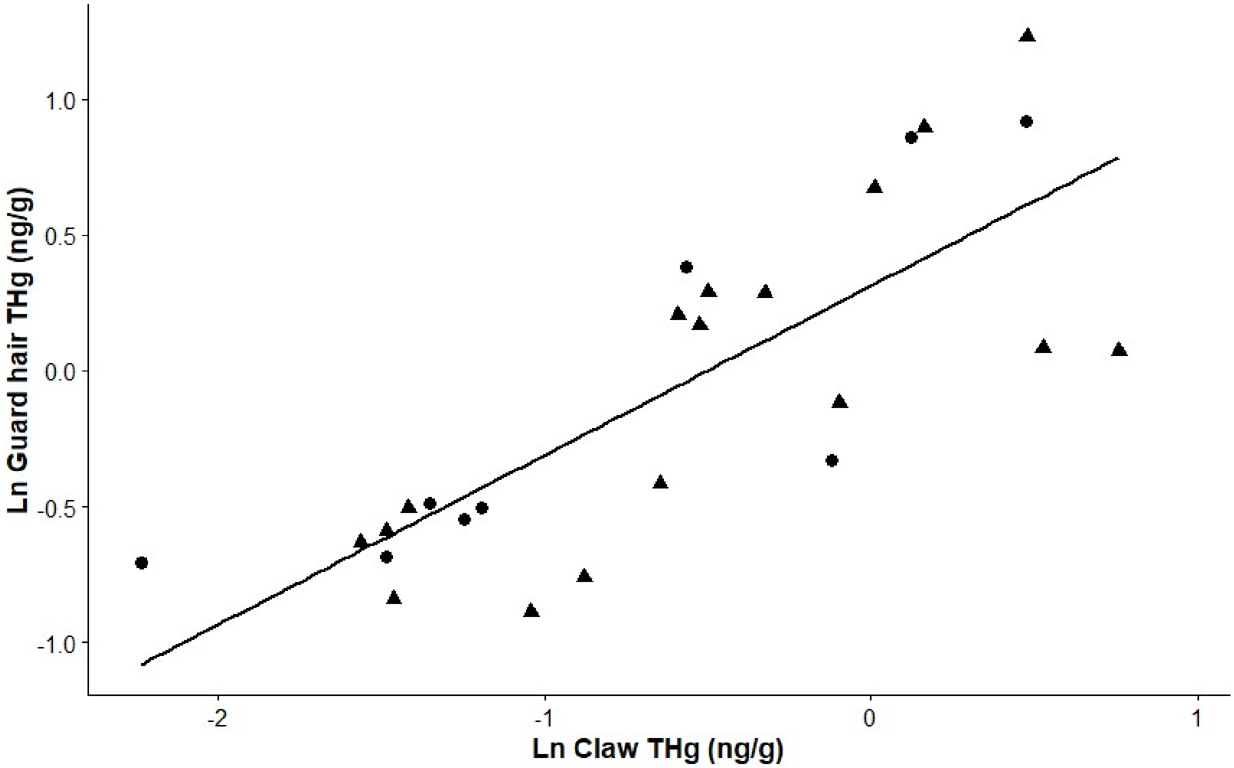


Fig. 5.1. Relationship between mercury concentrations (Ln(THg in ng/g wet-weight)) in red fox claws and hair. Males are displayed as triangles and females as dots, but sex effect was not significant. Foxes were trapped between November 2017 and March 2018, in northern Manitoba, Canada.

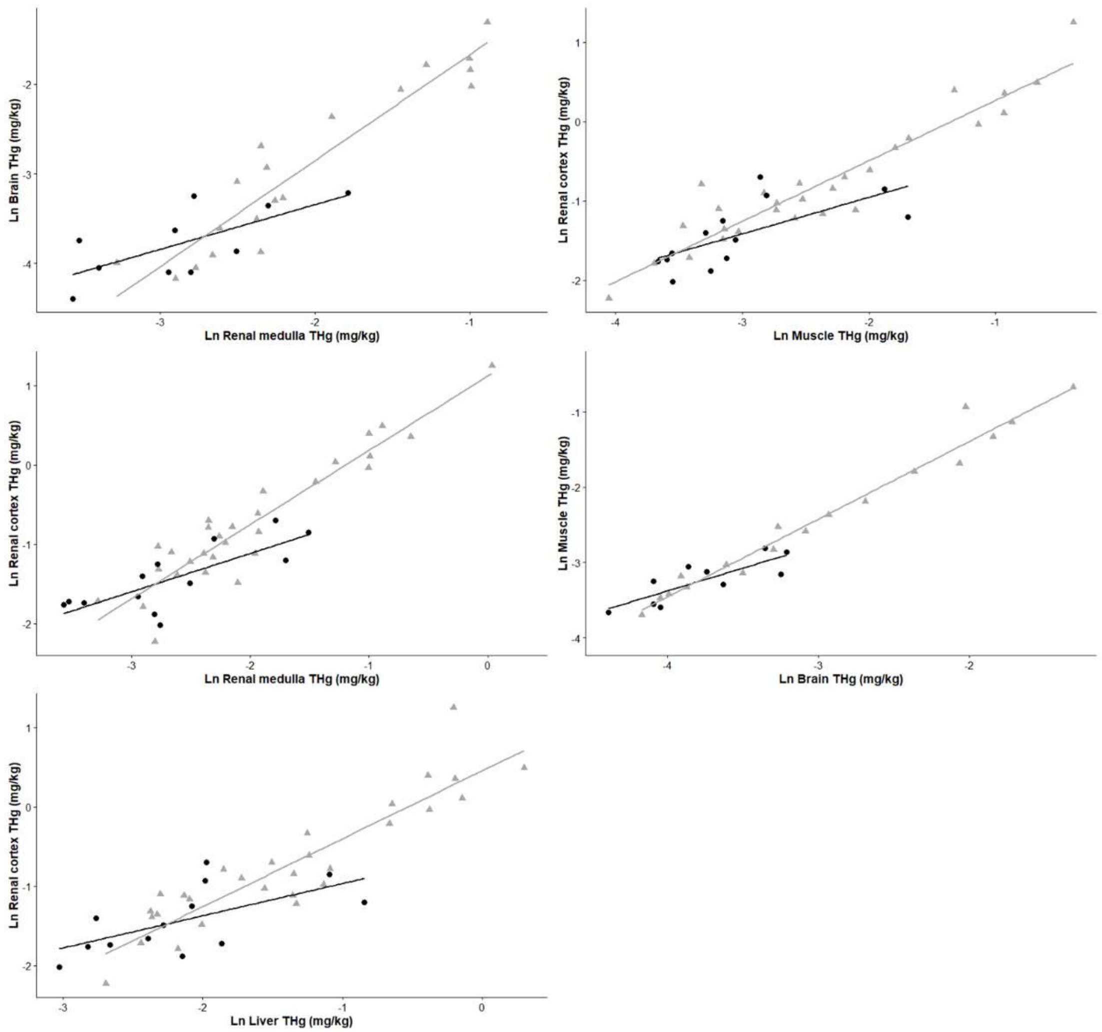


Fig. 5.2. Relationship between mercury concentrations (Ln(THg)) in red fox internal tissues (wet) for males (grey symbols, n= [19-43]) and females (black symbols, n=[10-13]). Foxes were trapped between November 2017 and March 2018, in northern Manitoba, Canada.

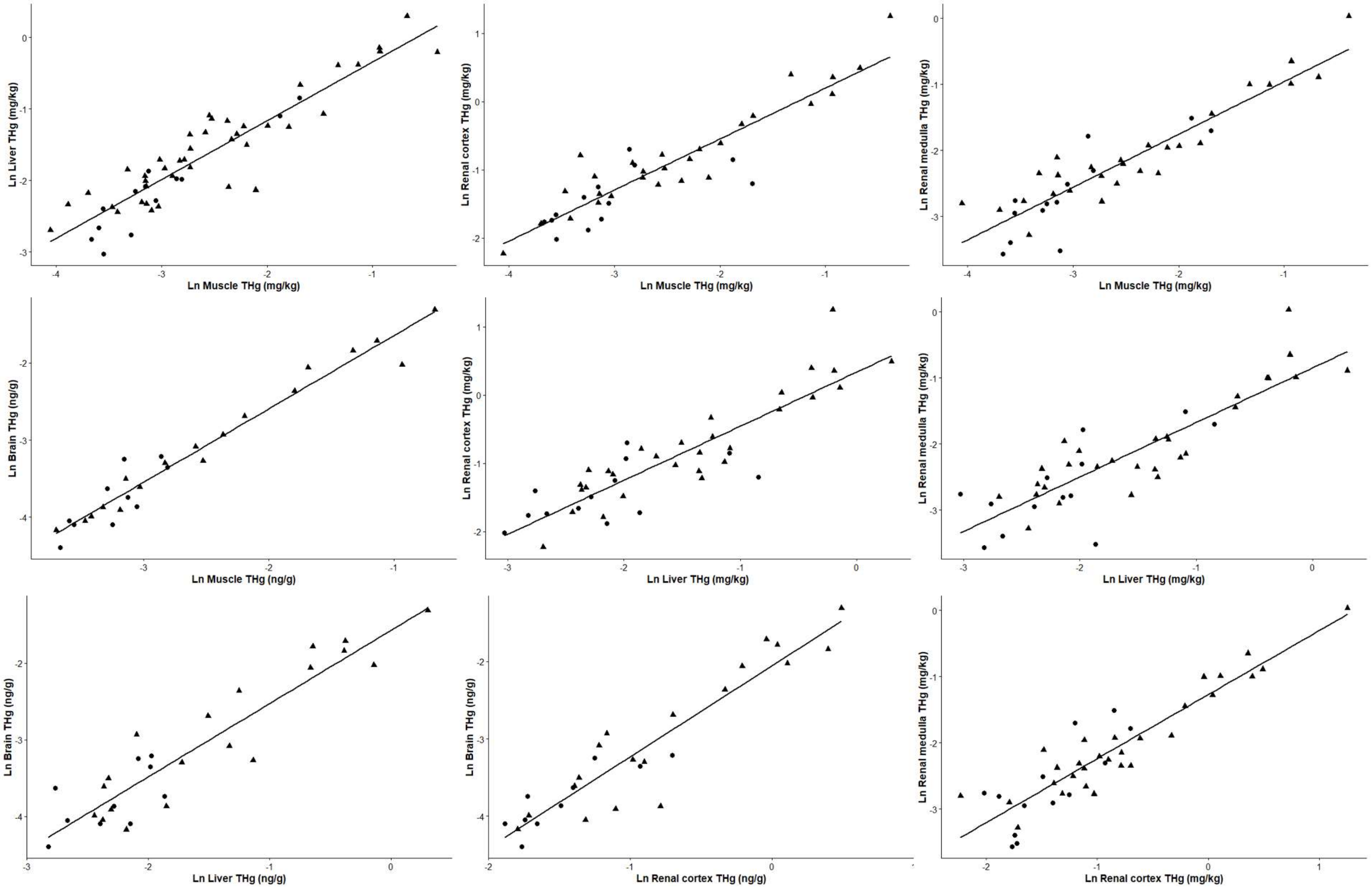


Fig. 5.3. Relationship between mercury concentrations (Ln(THg in ng/g wet-weight)) in red fox internal tissues (wet). Males are displayed as triangles and females as dots, but sex effect was not significant. Foxes were trapped between November 2017 and March 2018, in northern Manitoba, Canada.

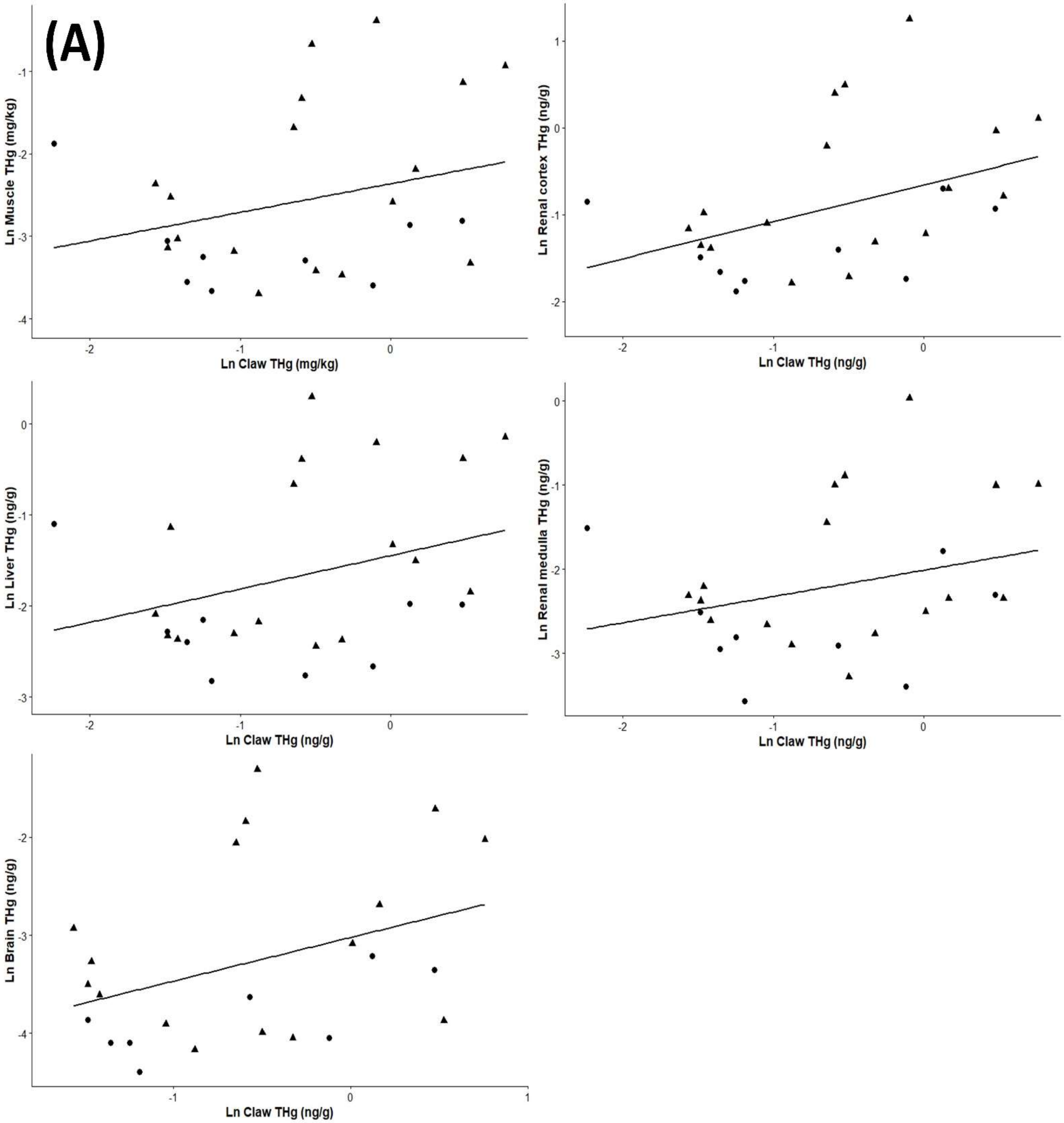
Appendix 5.A. Red fox tissue composition

We estimated moisture by weighing the samples before and after freeze-drying (e.g., Cresson et al. 2017), and lipid content by weighing samples before and after extracting the fat using petroleum ether in a Soxhlet (e.g., Wang et al. 2019).

Table 5.A1. Average moisture and lipid content of red fox tissues (%) from northern Manitoba, Canada.

Tissue	Moisture	n	se	Lipid	n	se
Renal cortex	70.82	32	0.58	2.90	32	0.17
Liver	71.45	28	0.81	2.66	29	0.23
Muscle	73.92	38	0.35	2.92	57	0.18
Brain	76.07	29	0.38	7.97	29	0.49
Renal medulla	78.29	32	0.76	2.18	33	0.40

Appendix 5.B. Additional supplementary information on total mercury concentration and the relationship between concentration in red fox tissues



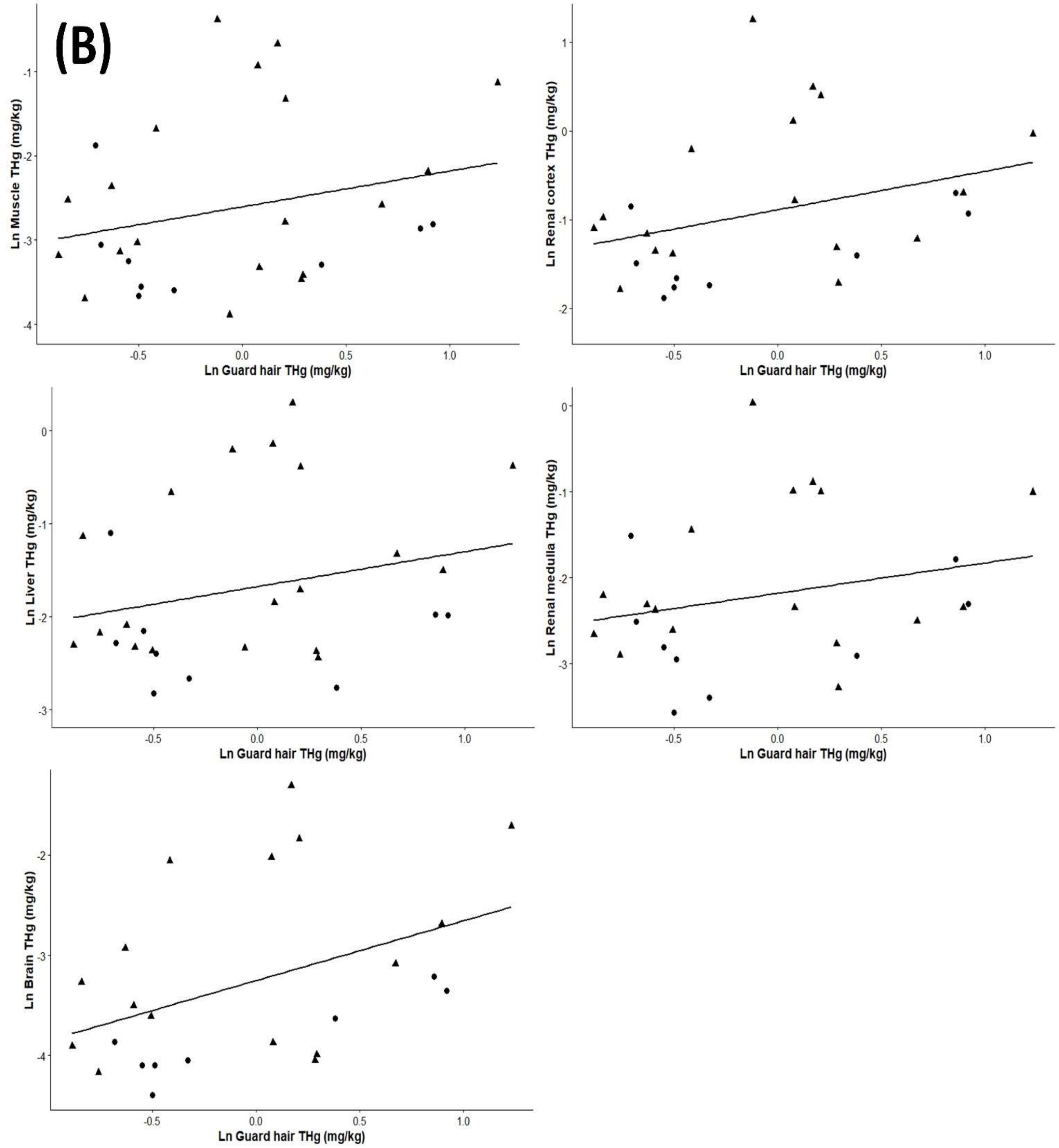


Fig. 5.B1. Relationship between mercury concentrations (Ln(THg in ng/g wet-weight)) in red fox keratinous tissues (A. claw and B. guard hair) and internal tissues. Males are displayed as triangles and females as dots, but sex was not significant. Foxes were trapped between November 2017 and March 2018, in northern Manitoba, Canada.

Table 5.B1. Comparison of total mercury concentration mg/kg wet weight tissues of chosen red fox populations from around the world, 58°N and north.

		mean	SD	min	max	median	n
Dainowski et al.* 2015	Muscle	0.15	0.11	0.03	0.52	0.11	65
	Liver	0.35	0.37	0.03	1.76	0.26	65
	Renal medulla	0.26	0.18	0.05	0.88	0.16	65
	Renal cortex	0.62	0.35	0.13	1.77	0.56	65
	Hair	2.58	1.96	0.43	9.60	2.02	65
Komov et al. 2016	Muscle	0.09	0.07	0.01	0.32	n.a.	6
	Liver	0.31	0.16	0.11	0.64	n.a.	6
	Kidney**	0.28	0.04	0.18	0.42	n.a.	6
	Brain	0.03	0.01	0.01	0.08	n.a.	6
Khabarova et al. 2019	Muscle	0.07	0.07	0.01	0.32	0.05	23
	Liver	0.18	0.16	0.02	0.64	0.13	14
	Kidney**	0.31	0.21	0.07	0.71	0.23	14
	Brain	0.03	0.05	0.00	0.25	0.01	21
This study	Muscle	0.11	0.13	0.02	0.68	0.06	50
	Liver	0.26	0.26	0.05	1.35	0.16	56
	Renal medulla	0.16	0.18	0.03	1.04	0.10	42
	Renal cortex	0.54	0.59	0.11	3.50	0.33	42
	brain	0.06	0.06	0.01	0.27	0.04	29
	Hair	1.13	0.77	0.41	3.42	0.91	28

* Presented values of mean, min, max and median are re-calculated from reported dry weight based on average percent of water in our samples: 73.92, 71.45, 70.82 and 78.29 for muscle, liver renal cortex and medulla respectively (Chapter 5; Appendix 5.A). SD is an approximation based on the formula using min, max, median and n developed by Wan et al. (2014).

**Renal cortices and medulla were not separated in these studies.

Table 5.B2. Akaike Information Criterion (AIC) scores of full (with sex and interaction term) and minimal models relating ln(THg) in each pair of internal fox tissues from northern Manitoba.

Model*	**AIC**	**Δ AIC**
liver~muscle	26.54	0.00
liver~sex*muscle	24.53	2.01
renal cortex~muscle	22.99	0.00
renal cortex~muscle*sex	19.48	3.51
renal medulla~muscle	27.33	0.00
renal medulla~muscle*sex	29.24	1.91
brain~muscle	-11.14	0.00
brain~muscle*sex	-7.85	3.29
brain~liver	24.15	0.00
brain~sex*liver	27.50	3.34
renal cortex~liver	37.00	0.00
renal cortex~liver*sex	33.00	4.00
renal medulla~liver	47.25	0.00
renal medulla~liver*sex	50.97	3.72
brain~renal cortex	18.87	0.00
brain~sex*renal cortex	21.51	2.64
renal medulla~renal cortex	31.22	0.00
renal medulla~renal cortex*sex	33.40	2.18
brain~renal medulla	27.47	0.00
brain~renal medulla*sex	21.57	5.90
muscle ~ liver	38.91	0.00
muscle ~ liver*sex	40.63	1.72
muscle ~ renal cortex	39.73	0.00
muscle ~ renal cortex*sex	43.00	3.27
muscle ~ renal medulla	38.68	0.00
muscle ~ renal medulla*sex	38.07	0.61
muscle ~ brain	-9.56	0.00
muscle ~ brain*sex	-14.40	4.84
liver ~ renal cortex	46.19	0.00
liver ~ renal cortex*sex	49.83	3.64
liver ~ renal medulla	51.39	0.00
liver ~ renal medulla*sex	52.41	1.03
liver ~ brain	22.09	0.00
liver ~ brain*sex	22.97	0.88
renal cortex ~ renal medulla	26.17	0.00
renal cortex ~ renal medulla*sex	18.01	8.16
renal cortex ~ brain	5.65	0.00
renal cortex ~ brain*sex	8.08	2.44
renal medulla ~ brain	20.13	0.00
renal medulla ~ brain*sex	22.29	2.16

Table 5.B3. β coefficient, standard error of the β coefficient (SE), t statistic and associated p value for each variable of the models comparing total mercury concentration in red foxes' internal tissues from northern Manitoba, Canada. Models were selected using Akaike Information Criterion (see Table 5.B2).

model	variable	β coefficient	SE	t	p
liver~ muscle*sex[1]	Intercept	1.015	0.525	1.934	0.059
	muscle	0.967	0.134	7.220	<0.001
	sex	0.970	0.574	1.690	0.097
	muscle*sex	-0.198	0.144	-1.378	0.175
renal cortex~muscle*sex[1]	Intercept	3.696	0.521	7.088	<0.001
	muscle	0.460	0.133	3.454	0.001
	sex	-1.021	0.584	-1.747	0.089
	muscle*sex	0.302	0.145	2.086	0.044
renal medulla~muscle	Intercept	1.228	0.244	5.023	<0.001
	muscle	0.800	0.055	14.470	<0.001
brain~muscle	Intercept	-0.348	0.175	-1.986	0.058
	muscle	0.950	0.041	23.273	<0.001
brain~liver	Intercept	-1.270	0.403	-3.154	0.004
	liver	0.957	0.077	12.487	<0.001
renal cortex~liver*sex[1]	Intercept	3.540	0.725	4.885	<0.001
	liver	0.407	0.151	2.693	0.011
	sex	-2.098	0.839	-2.500	0.017
	liver*sex	0.451	0.169	2.665	0.011
renal medulla~liver	Intercept	0.354	0.400	0.886	0.381
	liver	0.826	0.075	11.041	<0.001
brain~renal cortex	Intercept	-3.272	0.506	-6.472	<0.001
	renal cortex	1.176	0.085	13.874	<0.001
renal medulla~renal cortex	Intercept	-1.050	0.414	-2.540	0.015
	renal cortex	0.968	0.069	14.040	<0.001
brain~renal medulla*sex[1]	Intercept	1.122	0.773	1.451	0.159
	renal medulla	0.498	0.189	2.633	0.014
	sex	-2.863	0.921	-3.109	0.005
	renal medulla*sex	0.683	0.215	3.181	0.004
muscle ~ liver	Intercept	-1.121	0.320	-3.507	0.001
	liver	1.033	0.061	17.074	<0.001
muscle ~ renal cortex	Intercept	-2.328	0.471	-4.945	<0.001
	renal cortex	1.123	0.079	14.251	<0.001
muscle ~ renal medulla	Intercept	-0.615	0.347	-1.774	0.084
	renal medulla	1.054	0.073	14.470	<0.001

muscle ~ brain*sex[1]	Intercept	1.772	0.443	4.000	0.001
	brain	0.605	0.140	4.319	<0.001
	sex	-1.319	0.479	-2.755	0.011
	brain*sex	0.427	0.147	2.900	0.008
liver ~ renal cortex	Intercept	-0.594	0.494	-1.202	0.236
	renal cortex	0.986	0.082	11.968	<0.001
liver ~ renal medulla	Intercept	0.981	0.394	2.486	0.017
	renal medulla	0.912	0.083	11.041	<0.001
liver ~ brain	Intercept	1.898	0.271	7.010	<0.001
	brain	0.891	0.071	12.490	<0.001
renal cortex ~ renal medulla*sex[1]	Intercept	3.420	0.516	6.630	<0.001
	renal medulla	0.483	0.120	4.032	<0.001
	sex	-1.859	0.616	-3.021	0.004
	renal medulla*sex	0.453	0.138	3.293	0.002
renal cortex ~ brain	Intercept	3.169	0.204	15.540	<0.001
	brain	0.746	0.054	13.870	<0.001
renal medulla ~ brain	Intercept	1.601	0.262	6.115	<0.001
	brain	0.805	0.069	11.668	<0.001

Reference level:

[1] Males

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Prelude to Chapter 6

Wildlife studies inconsistently report mercury values in dry or wet weight (Cresson et al. 2017), but seldom report tissue composition to allow meaningful comparison with other studies. Systematically reporting mercury concentration in dry weight would lessen the potential confounding effects associated with moisture loss (during storage, for example), or with differences in tissue composition (e.g., high vs low lipid content). However, it may not always be possible to determine tissue composition upon sampling or to freeze-dry samples before analyses.

The samples we used for Chapter 4 spanned 8 years, during which moisture loss could be a confounding factor increasing estimated mercury concentration during the earlier years. It was necessary to either determine moisture content of our muscle samples, or to work with dry weight to remove the potential bias. We saw an opportunity to contribute to best practices by using our dataset to determine how common practices in biology could bias results or affect comparison across studies, instead of simply report tissue composition for the sole purpose of Chapter 4. Although I only needed muscle samples in Chapter 4, I therefore extend this methodological study to all other available internal organs. Hence, in Chapter 6, I quantified the effect of storage time and tissue composition on the mercury concentration in fox tissues and compared the resulting wet-dry conversion factor to commonly used theoretical conversion factors.

Reference

Cresson, P., Travers-Trolet, M., Rouquette, M., Timmerman, C.A., Giraldo, C., Lefebvre, S., and Ernande, B. 2017. Underestimation of chemical contamination in marine fish muscle tissue can be reduced by considering variable wet:dry weight ratios. Mar. Pollut. Bull. **123**: 279–285. doi:10.1016/j.marpolbul.2017.08.046.

Chapter 6: Effect of tissue composition and storage length on the use of a theoretical wet:dry conversion factor in toxicology studies

Abstract

The potential threat posed by mercury accumulation in the environment and organisms has prompted scores of toxicology studies. Mercury concentrations in wildlife toxicology studies are inconsistently expressed in wet or dry mass units. Tissue composition is rarely reported, and researchers often convert between dry and wet weight using assumed theoretical moisture contents. However, diverse factors (e.g., tissue, storage conditions) may affect tissue composition and render comparisons between studies uncertain. We quantified the effects of diverse variables on moisture and lipid contents and their consequences on mercury concentration when converting between wet and dry forms (lipid extracted or not), using red fox tissue samples. We found that moisture content differed largely between organs and from the 75% theoretical average-moisture content of mammalian soft organs, and decreased rapidly under usual conditions of storage. Although most fox tissues have low lipid concentrations, lipid content affected water content and their extraction affected the wet:dry conversion factor. We thus recommend reporting tissue composition systematically in toxicology studies and using tissue/species specific conversion factors to convert between dry and wet weight concentration.

Introduction

The potential threat posed by mercury accumulation in organisms has prompted scores of toxicology studies (Wiener et al. 2002), in which mercury concentrations may be expressed either per wet or dry mass units. Most studies do not report even moisture concentration in tested tissues, because systematically determining tissue composition adds steps during the analysis process that are resource consuming (e.g., Cresson et al. 2017). Especially, if the main topic of a study does not require accurate knowledge of tested-tissue composition, researchers may understandably see those additional steps as unnecessary. Therefore, researchers have adopted diverse strategies to compare their results to published data. Some convert between mercury concentration per dry and wet mass using species- and/or organ-specific theoretical conversion factors (e.g., Denton et al. 1980; Ma 1989; Siebert et al. 1999; Kalisinska et al. 2012; Eccles et al. 2017), or a theoretical conversion factor. A common assumption is that mammalian soft tissues contain on average 75% moisture (Skelton 1927; Dainowski et al. 2015; Treu et al. 2018), although some other values are sometimes assumed (e.g., 70%) (Eccles et al. 2017; Ziętara et al. 2019). Others measured conversion factors specific to their study but do not provide information on how factors such as tissue composition, lab methods, or sample storage may have influenced those values (e.g., Kucera 1983; Aastrup et al. 2000).

The use of a theoretical factor may generate errors because multiple factors may affect tissue composition and thus mercury concentration. Tissue composition differs between organs, species, or may even vary spatially (Yang and Miyazaki 2003; Kojadinovic et al. 2006). Lipid content, specifically, may be an important source of moisture variation since water and lipid proportions in tissues are usually negatively related (Cresson et al. 2017), but lipids could also affect total mercury concentration *per se* since some mercury forms are not soluble in lipids (Mason et al. 1995). Chilling and freezing (+4°C to -80°C) can affect the chemical composition of animal tissues (e.g., Arannilewa et al. 2006; Gandotra 2012). Yet, biological samples are commonly collected and then stored frozen for multiple years until used. Long-term storage would thus likely affect at least the moisture content, and therefore comparing mercury concentration based on wet mass from samples spanning over multiple years, without knowledge of the dehydration rate, might lead to erroneous conclusions. Understanding how different factors affect tissue composition is thus important to implement best practices for measuring mercury (or other trace-element) concentration, decide when it is necessary to measure and report the tissue composition along with mercury concentrations, or help decide what theoretical conversion factor to use if measuring tissue composition is impossible.

We quantified the effects of variations in moisture and lipid contents on mercury concentration when converting between wet and dry forms (lipid extracted or not) using red fox tissue samples. We also quantified the loss of moisture during long-term storage. Specifically, we quantified 1) composition difference between tissues and 2) deviation from the theoretical 75% moisture content, 3) the relationship between moisture and lipid content, 4) the effect of lipid extraction on mercury concentration, and 5) the effect of storage length on moisture content.

Methods

Sample collection and storage

We used 74 carcasses of legally harvested red foxes acquired from the trappers of Churchill, Manitoba, on Western Hudson Bay (58°N, 94°W) in 2015, 2017, and 2018. The carcasses were collected by the staff of the Churchill Northern Studies Center, where they remained frozen, either stored outside, the temperature being continuously below 0°C or in dedicated -20°C freezers for up to 4 months, until we harvested the tissue samples we needed *in situ*.

Each year we collected 3 to 5 pieces of muscle from the quadriceps, since 2017 we also collected kidneys and livers, and in 2018 we included the brains in the collected organs. At the University of Manitoba, tissue samples were stored in a -20°C freezer until subsampled for analysis or archived in the -80°C freezer. Only the brains, kidneys, and livers harvested in 2018 were used in the present analysis to avoid variation due to storage in addition to factors specific to intrinsic tissue composition. We separated renal cortices and medullas since mercury concentration in the cortex and medulla can differ substantially (Dainowski et al. 2015, Chapter 4). All analyses for this study were done in 2019, thus the 2015 and 2017 archived muscles were stored in a -80°C freezer for 4 and 2 year(s) respectively.

Determination of tissue composition and levels of mercury

We weighed between 0.087g and 2.177g of wet tissue that we freeze-dried for 48 hours at -50°C (collector temperature) using a Labconco FreeZone 2.5 Liter Benchtop Freeze Dry System freeze dryer. We extracted lipids by leaving the ground freeze-dried samples 12 hours in a Soxhlet apparatus and used Petroleum ether as solvent (Elliott et al. 2017). We then dried the samples for 72 hours in a Fisher Scientific Isotemp® drying oven at 60°C. Samples were weighed between each step to determine tissue composition.

We measured total mercury concentration in the samples at each step (wet, freeze-dried, and lipid extracted) using a direct mercury analyzer (Hydra IIc, Teledyne Leeman Laboratories, Hudson, NH) at the Center for Earth Observation Science, University of Manitoba. The instrument was calibrated using low detection linear calibration curves calculated with blank sample boats (blank correction) and the certified reference materials MESS-3 (91 ± 9 ng/g), MESS-4 (90±40 ng/g), and high detection linear calibration curves calculated with the certified reference material PACS-3 (2980 ±360 ng/g). Curves included at least 6 determination points and were validated when $R^2>0.995$. Quality assurance and control were tested by running the certified reference materials MESS-3, MESS-4, TORT-3 (292 ± 12 ng/g), DORM-4 (412 ± 36 ng/g), DOLT-5 (440±180 ng/g ng/g), NIST2709a (900 ± 200 ng/g), NCP III-9 S2 (933 ± 55.5 ng/g), and PACS-3, two to three times every 14 samples (Recovery: 8.1%±0.3). Most samples were replicated 2 to 5 times and we averaged the replicates (Average coefficient of variation: $CV_{wet} = 0.08$, $CV_{dry} = 0.06$, $CV_{dry\text{-}lipid\text{-}extracted} = 0.03$; Standard deviation: $SD_{wet} = 18.07$, $SD_{dry} = 61.93$, $SD_{dry\text{-}lipid\text{-}extracted} = 39.38$; number of samples replicated: $n_{wet} = 165$, $n_{dry} = 126$, $n_{dry\text{-}lipid\text{-}extracted} = 38$).

Statistical analyses

We performed all statistical analyses using the packages car v.3.0.7 (Fox and Weisberg 2019), nlme v.3.1.147 (Pinheiro et al. 2020), lme4 v.1.1.23 (Bates et al. 2015), lmerTest v.3.1.2 (Kuznetsova et al. 2017), fitdistrplus v.1.1.1 (Delignette-Muller and Dutang 2015), rstatix v.0.5.0 (Kassambara 2020), and base R in the R software (R Core Team 2020). Graphs were produced using the ggpubr v.0.3.0 and ggplot2 v.3.3.0 package. We checked data sets for outliers, deviation from normality, and homoscedasticity by inspecting the residual vs fitted values plots and the QQ plot of residuals (Zuur et al. 2009, 2010), and dealt with potential issues as we built and validated models using the guidelines in Zuur et al. (2010) and Zuur and Ieno (2016). Points with a Cook's distance > 0.7 were considered outliers and excluded on the basis that they likely arisen following Hydra II-catalyst impairments, which could affect the calibration and thus produce spurious values (Mcdonald 2002; Zuur and Ieno 2016). All proportion data were percentages. Our in-text results are reported as mean ± SE unless otherwise indicated.

To determine if moisture content differed among organs, we fitted a generalized Least Square model and allowed the variance to differ between organs using the varIdent function of the nlme package (Zuur et al. 2009) and a posthoc Tukey pairwise comparison. We used a series of one-sample two-sided T-tests with a 99% confidence interval ($\alpha = 0.01$) to assess if the moisture content of each organ deviated from 75%. We reported effect sizes as Cohen's *d*. We calculated the percent error associated when assuming a theoretical value of 75% (and thus a conversion factor of 4) as

$$\%\text{Error} = \frac{|([Hg]dmeasure\quad/4) - [Hg]wmeasured|}{[Hg]wmeasured} \times 100 \tag{10}$$

where $[Hg]d_{measured}$ is the mercury concentration per tissue-mass dry measured and $[Hg]w_{measured}$ the mercury concentration per tissue-mass wet measured.

We determined if the lipid content differed between organs by fitting a generalized linear mixed model controlling for fox ID and a post-hoc Tukey pairwise comparison. We then determined the strength of the correlation between lipid and moisture contents using a Spearman's rank correlation test for each organ. We examined how much of the moisture content was explained by lipid content and assessed the effect of lipid extraction on the dry:wet conversion factor using two GLMMs (family gaussian, link identity). Since we were only interested in the general fixed effect of lipid proportion on the moisture proportion and of lipid extraction on the conversion factor, we ran our GLMM using "organ" and fox ID as crossed random effects (each fox ID appeared in all or multiple organs). We allowed the intercept to vary in the crossed random effects (fox ID and organ), but not the slope.

Finally, we compared moisture content between samples from 19 carcasses from 2015, 21 from 2017, and 17 from 2018 to assess the possible effects of long-term storage on the water content (up to 4 years before analysis in 2019). We used simple linear regression and a post-hoc Tukey pairwise comparison. We calculated effect sizes as Cohen's *d*. We report no issues with our model validation.

Results

The average percent moisture of tissues ranged from 70.8 ± 0.6% to 78.3 ± 0.8%, with renal cortex and medulla showing the most extreme values (Table 6.1). The moisture level of brain and muscle were the closest to the theoretical 75%, yet moisture content in all tissues diverged from that theoretical 75% (Fig. 6.1 and Table 6.2). Moisture content also differed between brain or renal medulla *versus* liver, muscle and renal cortex (Table 6.3), with medium to large effect sizes (Cohen 1988) ranging from $d_{muscle} = -0.48$ to $d_{renal\ cortex} = 1.28$, leading to conversion factors ranging from 2.9 to 4.9 (Table 6.1). The percent errors associated with the use of a 75% theoretical factor for muscle and brain were low (-1.98% and 4.09% respectively) but was >20% for all other tissues (Fig. 6.2).

Most organs had similarly low lipid contents, ranging from 2.18 ± 0.40% to 2.92 ± 0.18%, except the brain for which lipid content was higher 7.97 ± 0.49% (GLMM (brain as reference level): t = [-9.25, -10.04], df = 101, p<0.001, n = 160; Table 6.4). Lipid content significantly affected moisture content after controlling for fox ID and tissue type (GLMM: t = -5.84, df = 157.74, p<0.001, n = 160). The strength of the correlation between moisture and lipid content, however, varied greatly across organs (Table 6.5), from no correlation in the renal cortex ($r_s = -0.03$, n = 32) to moderately correlated in the brain ($r_s = -0.46$, n = 29). Lipid extraction significantly changed the wet:dry conversion factor (GLMM: t = 10.37, df = 260.22, p<0.001, n = 313).

We found a slight but significant decrease in moisture content in our 2015 tissues compared to both 2017 and 2018 tissues ($F_{2,53} = 7.55$, p = 0.001; Table 6.6). The effect size of the loss of moisture between 2017 and 2015, and between 2018 and 2015 were large ($d_{2017\text{-}2015} = -1.12$, $d_{2018\text{-}2015} = -1.07$). We, thus, did not detect differences in moisture content in samples after two years of storage, but moisture loss in samples was detected after 4 years of storage. The lipid content did not vary between years ($F_{2,53} = 0.154$, p = 0.86).

Discussion

Moisture content varied greatly among tissues. Although we only tested measured conversion factors against a theoretical conversion factor of 4 (assuming 75% moisture content), these differences between organs regarding their water composition should preclude the use of a single conversion factor, no matter which one. The level of error generated if using a single conversion factor across all soft internal tissues may cause substantial error (over 20%

in most organs of our study for using a theoretical conversion factor of 4), which may greatly affect comparisons within or between studies.

Although measuring tissue composition may be time-consuming, we strongly support and extend to terrestrial species Yang and Miyazaki's (2003) recommendation that researchers should report moisture content when studying trace element accumulation, at least using a sub-sample of their total sample batch. The difference in moisture between tissues was partly due to a negative relationship between moisture and lipid content. Such a negative relationship between moisture and lipid content was also evidenced in fish and mammals (Cresson et al. 2017; Liwanag et al. 2012). However, in our study, the correlation between moisture and lipid content was weak for most organs and negligible in some (notably renal cortex and muscle). The weak pattern or absence thereof may be due to the generally low lipid content of fox internal tissues and the particularly low variation of lipid content in some specific tissues (renal cortex and muscle; Table 6.1); but lipid content and type can strongly drive the toxicology and toxicokinetics of lipophilic contaminants (e.g., Beckmen et al. 1999; Debier et al. 2003; Peterson et al. 2014). We thus recommend studies provide the percent lipid in tissues, especially when working with lipid-rich tissues and lipophilic contaminants. Using tissues with a larger range of lipid content and accounting for the different types of lipids would provide a better understanding of the relationship between lipid, moisture content and wet:dry conversion factor.

The percent moisture we report differs somewhat from moisture contents reported elsewhere for red fox livers and muscles (Kalisinska et al. 2009, 2012). The differences could be due to sample-storage conditions or laboratory methods (Binkowski 2012). Further research is thus required to understand the relative effects of these variables on tissue composition determination, and how they may affect the relationships we have determined. In addition, we treated renal cortices and medullas separately due to the large anatomical and physiological differences of these kidney tissues and the fact that they accumulate mercury differently (Dainowski et al. 2015, Chapter 5), and found that although lipid content was relatively similar, moisture content differed largely between them.

Finally, we found an important and relatively quick effect of storage time on tissue composition. The moisture level decreased after 3 years in usual conditions of storage of biological samples. The change in moisture content over time is likely to preclude direct comparisons of trace element concentration in tissues between years. Therefore, we believe it a better practice to work on dry tissues when working with multi-year data encompassing more than 2 years, or at least researchers should measure the composition of their tissues and apply a correction factor accounting for water loss.

Conclusion

We provide evidence that diverse factors, including some related to standard laboratory practices, may affect tissue composition, thus generating sources of variation that may greatly affect conclusions regarding trace element accumulation in wildlife tissues. Although some studies may not need a level of precision that warrants detailed knowledge of tissue composition (e.g., low level of contamination, low precision of lab equipment, comparison of tissue with substantial differences in contaminant concentration), tissue composition should ideally be reported regardless, as other studies may require this information for meaningful comparisons.

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Tables

Table 6.1. Water and lipid content in tissues of red fox and associated wet-to-dry conversion factor (w:d CF = wet to dry Conversion Factor, w:LE CF = wet to lipid-extracted conversion factor). Foxes were trapped during winter 2016-2017 (winter 2017 in the main text) and 2017-2018 (winter 2018 in the main text) in northern Manitoba, Canada.

Tissue	% moisture	n	se	% lipids	n	se	w:LE CF	n	se	w:d CF	n	se
Renal cortex	70.82	32	0.58	2.90	32	0.17	3.83	32	0.12	3.15	32	0.11
Liver	71.45	28	0.79	2.65	29	0.23	3.80	28	0.09	2.92	28	0.13
Muscle	73.92	38	0.35	2.92	38	0.18	4.34	38	0.09	3.92	38	0.11
Brain	76.07	29	0.38	7.97	29	0.49	7.73	29	0.21	4.16	29	0.14
Renal medulla	78.34	32	0.76	2.18	33	0.40	5.56	32	0.29	4.77	32	0.25

Table 6.2. Deviation of red fox tissue moisture content from a theoretical 75% moisture content using samples collected from northern Manitoba, Canada. We used this theoretical moisture content sometimes chosen for mammals to illustrate the implications of using values found in the literature or a theoretical value on converting mercury concentrations. Results from one-sample t-tests and confidence interval of the mean.

Tissue	% moisture	t	df	Pr(>|t|)	99% CI low	99% CI high	Cohen's d
Renal cortex	70.82	-7.26	31	< 0.001	69.24	72.40	1.28
Liver	71.45	-4.37	27	< 0.001	69.19	73.70	0.83
Muscle	73.92	-3.08	37	0.003	72.97	74.87	-0.48
Brain	76.07	2.83	28	0.008	75.03	77.12	0.53
Renal medulla	78.29	4.34	32	< 0.001	76.21	80.37	0.75

Table 6.3. Moisture difference between tissue pairs with z statistic and level of significance, using samples of red foxes from northern Manitoba, Canada.

contrasted tissues	Estimate	se	z value	Pr(>|z|)
Renal cortex - Brain	-5.26	0.69	-7.62	< 0.001
Renal medulla - Brain	2.21	0.85	2.61	0.063
Liver - Brain	-4.57	0.87	-5.23	< 0.001
Muscle - Brain	-2.86	0.50	-5.73	< 0.001
Renal medulla - Renal cortex	7.47	0.95	7.85	< 0.001
Liver - Renal cortex	0.69	0.98	0.71	0.952
Muscle - Renal cortex	2.40	0.66	3.64	0.002
Liver - Renal medulla	-6.78	1.09	-6.21	< 0.001
Muscle - Renal medulla	-5.07	0.82	-6.15	< 0.001
Muscle - Liver	1.71	0.85	2.01	0.246

Table 6.4. Difference in lipid content between red fox tissues from northern Manitoba, Canada, with standard error.

contrasted tissues	difference	SE	Z	Pr(>|z|)
Renal cortex - Brain	-5.15	0.52	-10.00	< 0.001
Renal medulla - Brain	-5.87	0.63	-9.25	< 0.001
Liver - Brain	-5.43	0.54	-10.04	< 0.001
Muscle - Brain	-5.15	0.56	-9.27	< 0.001
Renal medulla - Renal cortex	-0.72	0.41	-1.74	0.16
Liver - Renal cortex	-0.27	0.25	-1.11	0.39
Muscle - Renal cortex	0.00	0.28	-1.01	0.99
Liver - Renal medulla	0.45	0.45	1.00	0.40
Muscle - Renal medulla	0.72	0.47	1.54	0.21
Muscle - Liver	0.27	0.33	0.84	0.45

Table 6.5. Spearman correlation coefficients between moisture and lipid content per tissue of red foxes trapped in northern Manitoba, Canada.

organ	r	n	p
Renal cortex	-0.03	32	0.88
Liver	-0.37	28	0.06
Muscle	-0.25	38	0.13
Brain	-0.46	29	0.01
Renal medulla	-0.34	33	0.05

Table 6.6. Effect of storage length on moisture content in red fox muscle from northern Manitoba, Canada. Results of Tukey pairwise comparisons between moisture content in muscle samples fresh, stored 1, 2 and 4 years.

Year	difference	95% CI low	95% CI high	p
2017-2015	2.05	0.45	3.66	0.01
2018-2015	2.26	0.57	3.95	0.01
2018-2017	0.21	-1.45	1.86	0.95

Figures

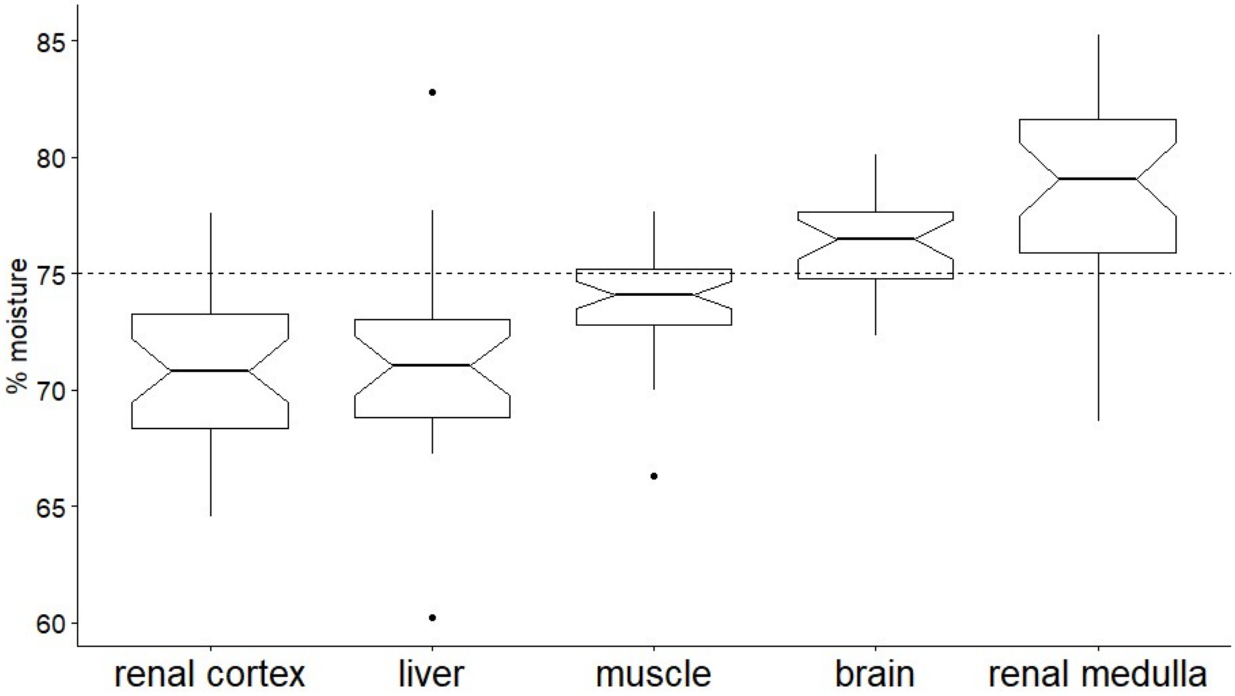

Fig. 6.1. Organ-specific moisture content from tissues from red foxes trapped in the Churchill area (Manitoba, Canada) in 2017 and 2018. Dashed line indicates the most common theoretical average moisture content for mammalian soft organs (75%). The notches represent the 95% confidence interval of the median, while the box itself represent the interquartile range (IQR), i.e, 50% of the data from 1st to 3rd quartile. The whiskers extend from the greater of 25th percentile - 1.5IQR to the smaller 75th percentile + 1.5IQR.

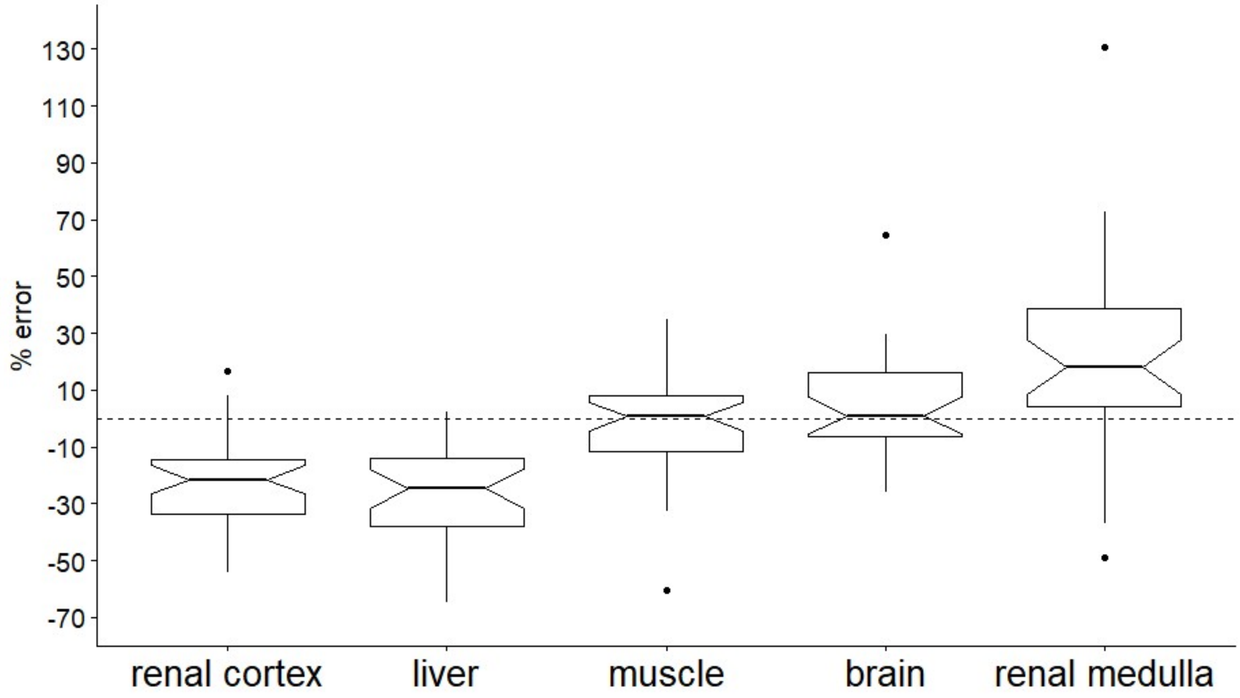

Fig. 6.2. Error in mercury content in different tissues from red foxes trapped in the Churchill area (Manitoba, Canada) in 2017 and 2018 associated with the use of a unique theoretical moisture content (here 75%), when converting from dry to wet weight. Dashed line indicates 0% error. The notches represent the 95% confidence interval of the median, while the box itself represent the interquartile (IQR), i.e, 50% of the data from 1st to 3rd quartile. The whiskers extend from the greater of 25th percentile - 1.5IQR to the smaller 75th percentile + 1.5IQR.

Chapter 7: Conclusion

Overall discussion of the main findings

My thesis has addressed some of the mechanisms by which expanding red foxes survive in tundra habitats, and how they compare to, and interact with Arctic foxes near treeline, in a setting where access to anthropogenic food-subsidies is scarce or lacking. Previous research on the topic has suggested that food scarcity favors coexistence between the two species, and that without anthropogenic subsidies a red fox population cannot reach high enough densities to exclude Arctic foxes by interference (Gallant et al. 2012). However, climate change could favor red foxes because it dampens rodent population cycles (Henden et al. 2010) and favors the expansion of shrubs that can support alternative prey populations, such as the snowshoe hare, thus providing habitat patches favorable to red foxes (Tape et al. 2016; Elmhagen et al. 2017). Furthermore, landscape changes driven by anthropogenic expansion can provide favorable habitats for boreal-forest species (Elmhagen et al. 2015), which could provide refugia on the tundra or neighboring ecosystems for a red fox population during time of scarcity, contributing to stabilize tundra population of red foxes (Henden et al. 2010; Killengreen et al. 2012; Elmhagen et al. 2017). Finally, research has largely emphasized that, for Arctic foxes, the negative effect of competition with red foxes exceeds the benefits of climate-induced food increases (Pálsson et al. 2016; Elmhagen et al. 2017).

My findings support most of these hypotheses, but also suggested that climate-induce negative effect on prey population directly limit the Arctic fox population at its southern distribution edge. We found no conspicuous interspecific interference (Chapter 3), which suggested that, as was observed in the few other sites where both species overlap and anthropogenic presence is scarce or absent (Gallant et al. 2012; Lai et al. 2022), red foxes in the Churchill area have not reached high enough densities to exclude Arctic foxes. Spatially, red foxes responded to winter food scarcity on the tundra in two ways (Chapter 2). While most red foxes dispersed towards the boreal forest, those that remained resident year-round increased the size of their winter home ranges. These findings further suggest that food scarcity could prevent the red fox to reach sufficient densities to exclude the Arctic fox. In the transitional ecosystem of the Churchill region, red foxes relied as much on snowshoe hares (*Lepus* *americanus*) as they did on tundra rodents (*Dicrostonyx richardsoni* and *Microtus pennsylvanicus*), thus highlighting the importance of forest patches to that species (Chapter 4). When anthropogenic infrastructure is absent, the patches of forest and shrubland could also act as natural refugia and provide a pool of red foxes that continuously spill over to tundra habitat, thereby stabilizing the presence of the red fox population over time, although not favoring its building-up. Compared to the high Arctic (Lai et al. 2017), Arctic foxes in our study area were highly likely to disperse during winter (Chapter 2). Food scarcity may thus not only directly limit red foxes, but also Arctic foxes. In the Churchill area, den occupancy of Arctic foxes declined since 2011, while that of red foxes increased (Moizan et al. *submitted*), further suggesting that other factors than the red fox presence negatively impact Arctic foxes at treeline. Furthermore, I addressed the link between prey fluctuation, diet and mercury exposure in the framework of species competing for resources. To my knowledge, although researchers have largely explored red or Arctic fox exposure to mercury in a variety of contexts, none have addressed mercury exposure in wild-overlapping populations of red ad Arctic foxes competing for resources. Both foxes had low levels of mercury because they had a mostly terrestrial diet (Chapter 4). Although this result was expected for red foxes, it suggested that despite the continuously low lemming abundance, the proximity of the coastal habitat, and the presence of a competitor, Arctic foxes could still access enough alternative terrestrial prey, which kept their mercury exposure low.

Movement strategies may stem from individual decision processes and result from compromising between immediate survival (likely linked to resource availability) and chances of reproduction (Dean et al. 2009). All strategies have costs: male Tengmalm's owls (*Aegolius funereus*), for example, remain resident even when their main prey is low, whereas females of the same species disperse when vole populations decline. Although female mortality is high during dispersal, males may trade off their ability to breed against a higher survival when voles are not abundant enough to sustain both thermoregulatory and reproductive costs (Korpimäki and Hongell 1986; Löfgren et al. 1986). Here, fox dispersal was associated with extremely high cost, as none of the 5 dispersing red foxes survived into the following reproductive season, like both red foxes died while dispersing from Herschel island in the high Arctic (Lai et al. 2022), and only half the Arctic fox dispersers survived long enough to reproduce during the next summer.

The large proportion of foxes that dispersed in the low Arctic, compared to the relatively high level of residency on Bylot Island in the high Arctic (Lai et al. 2017), suggested that overwinter survival near treeline was particularly difficult for both fox species. Food availability and the fact that Churchill Arctic and red foxes are both edge populations likely contributed to this substantial difference in individual movement strategy. Bylot has higher densities of tundra rodents than Churchill, which may allow a larger proportion of those foxes to remain resident (Lai et al. 2022). Churchill foxes also may be less able to capitalize on the abundant summer resources as cached items to survive as residents throughout winters than Bylot Arctic foxes living near the large goose colony (Rioux et al. 2017).

Individuals who choose residency despite resource scarcity often must exhibit flexibility to survive (Dean et al. 2009). They may increase the size of their home range during resource scarcity (flexible strategists; von Schantz 1984), but the costs may include fighting neighbors to expand home range borders or repel intruders because a larger home range is harder to defend. They could also maintain a constant home range large enough to meet their needs during resource scarcity, which may be less costly in some cases (obstinate strategists; von Schantz 1984). For example, red foxes in central Sweden behaved as obstinate strategists, responding to resource fluctuation by decreasing group size rather than increasing home range size during resource scarcity (MacDonald 1983). Similarly, red foxes on Bylot maintained a similar home range size year-round (Lai et al. 2022). In contrast, resident red foxes in Churchill behaved as flexible strategists, expanding home range size in winter, could have induced reproductive costs to red foxes, as moving over such large distances may increase the resource proportion allocated to maintenance at the expense of the portion allocated to reproduction (von Schantz 1984). As in male Tengmalm's owls, choosing to remain in a known area might cost the foxes their ability to reproduce the following breeding season. Spatio-temporal differences in both food availability and fox density might have driven that strategy, as enlarging a home range is less costly when congener density is low. However, further information on fox density in these sites is needed to draw conclusions. Red fox inter and intrapopulation differences regarding spatial response to different environmental conditions across the Canadian Arctic collectively indicate behavioral plasticity, which may play an important role in red fox persistence and maybe in red fox expansion in Arctic habitats.

Red foxes compensate for their lack of adaptation to cold winters and food scarcity with a higher basal metabolic rate, which increases their energetic requirements (Fuglesteg et al. 2006). Therefore, snowshoe hares constituted an important resource for red foxes in the low Arctic, as hares are more profitable prey than rodents, especially as their density increases (Malo et al. 2004). Red fox dependence on hares could have important repercussions for their overwinter survival, movement strategy, distribution across the landscape, and population dynamics, which can in turn affect interspecific competition. Yet, snowshoe hares in Churchill occur as a peripheral population and, thus, live in marginal habitats, resulting in low hare density, which in turn could limit the red fox population and explain the large size of their winter home ranges (Koehler 1990; Freeth et al. 2016). Although one Churchill red fox reproduced (we observed 6 pups in June 2018) while foraging exclusively on the tundra (since at least mid-April, when we fitted her with a satellite collar), she did so during one of the highest rodent years and left her home-range area the following winter (inferred from trail camera photos). Another red fox with a home range of exclusively tundra habitat that was lactating upon capture in early May 2017, remained resident over the following winter (still a high lemming year) and summer but dispersed when tundra rodents declined the next winter. In contrast, the only red foxes that remained resident in tundra habitats for 2 to 4 years, including during rodent decline and low rodent years, had access to forested habitat patches within their home ranges. These anecdotal observations suggest that under current conditions, the tundra near treeline can support individual red foxes in the long term only if they have access to patches of forest. Scarcity of treed patches large enough to sustain snowshoe hares could thus emphasize intraspecific competition, which may be more important than interspecific competition, and thus favor red-Arctic fox coexistence (Amarasekare 2002). However, if shrubs continue growing in height and expanding, the snowshoe hare population may also become more abundant (e.g., Tape et al. 2016), which could in turn support a more abundant red fox population. An increasing red fox population could reach a threshold density that negatively impacts the Arctic fox population.

The low level of home range overlap suggested high territoriality in both fox species and was similar within and between species, indicating that intra- and interspecific competition for space were similar, and red foxes did not exclude Arctic foxes by interference. Although red foxes on Herschel Island in the high Arctic monopolized the dens that offered better food access in spring (Gallant et al. 2014), the large interspecific overlap of home ranges suggested that resources were high enough to relax territoriality, and thus red foxes did not completely exclude Arctic foxes from food-rich patches (Lai et al. 2022). In contrast to the Canadian Arctic, red foxes in Fennoscandia and Alaska have excluded Arctic foxes from reproductive dens (Hersteinsson and Macdonald 1992; Savory et al. 2014; Stickney et al. 2014). In those study areas, red foxes are subsidized by anthropogenic resources, like human food waste (Savory et al. 2014), semi-domesticated reindeer or road kill (Selås et al. 2010; Killengreen et al. 2011; Rodnikova et al. 2011; Rød-Eriksen et al. 2020). The absence of anthropogenic food sources in our study site and the two high-Arctic sites likely helped balance the competition between the fox species, because red foxes mostly rely on fluctuating resources (tundra rodents, plus snowshoe hares in Churchill), likely leading these populations to fluctuate in abundance (Henden et al. 2010). The negative impact of red foxes on Arctic foxes increases with red fox abundance and decreases with variability of red fox abundance over time (Henden et al. 2010). The absence of consistent food subsidies stabilizing red fox populations may be a major reason for the dramatically different outcome of red-Arctic fox interactions between these Canadian sites and the Fennoscandian or Alaskan sites.

Red and Arctic foxes' diet was mostly terrestrial in the Churchill region. Foxes' exposure to mercury was, therefore, generally low. Foraging on the Arctic marine food web induces higher exposure to mercury than foraging on terrestrial food webs (Bocharova et al. 2013; Hallanger et al. 2019; Clatterbuck et al. 2021). As expected, we found that consuming seal was associated with a higher level of mercury in muscle; only 5% of the foxes showed high mercury levels in muscle (>0.5 mg/kg), but only four of these foxes (i.e., 20%) were >1 year old, suggesting that the propensity to forage in the marine environment did not vary between age classes and that the observed difference between age categories might likely be mostly driven by bioaccumulation rather than dietary differences.

Arctic foxes' consumption of seals was much lower than previously found in the same population (Roth 2002). Although sea ice duration has declined over this period (Regehr et al. 2007; Florko et al. 2018), differences in study design may also explain this difference. Here, I used muscle samples from animals that were trapped in March at the latest, while winter diet from 1994 to 1997 was either estimated based on summer hair (which grows during late winter) or muscle from adult foxes captured on coastal dens from April - June, both of which would represent late-winter diet (Roth 2002, 2003). Arctic foxes can commute to the sea ice for a short length of time, or spend weeks to months engaged in long-range movements that may result in dispersal or loop migration (Lai et al. 2017). Commuters tend to be foxes with an established home range, to which they return after their short excursion on the sea ice (Lai et al. 2017). Most individuals trapped are likely natal dispersers attracted to places where residents have been removed (Kukka et al. 2017, 2022), which have likely been dispersing on land for the most part. Our samples representing early-winter diet are less likely to represent commuters and sea-ice dispersers.

Fundamental ecology research is the first crucial step to developing and implementing conservation measures and applied research (Courchamp et al. 2015). Arctic foxes are of economic and cultural importance for Indigenous people of the Canadian Arctic. The fur of foxes caught during winter is a non-negligible source of income across the Canadian Arctic, including in Churchill; some northern communities also still consume their meat (Hoekstra et al. 2003). Furthermore, Arctic foxes are linked to many other species (including rodents, birds, caribou and seals) through both terrestrial and marine food webs, many of which are also consumed by northern communities (Wein et al. 1996). Despite being classified as a species of Least Concern on the IUCN red list of threatened species (Angerbjörn and Tannerfeldt 2014), several Arctic fox populations are decreasing (including the Churchill population; Verstege and Roth, *submitted*) or occur at low densities (Berteaux et al. 2017), while red foxes are encroaching onto their habitats. Although red foxes in the Canadian Arctic are not yet excluding Arctic foxes, they may do so in the near future. As shrubs and trees are encroaching onto the tundra, the prey composition of the tundra may shift towards boreal-forest species (Elmhagen et al. 2015), which in turn would favor boreal-forest predators. In addition, anthropogenic expansion in the Arctic may provide sufficient food subsidies (Gallant et al. 2020) to buffer the negative effects of food scarcity on the tundra that were likely limiting boreal-forest predators (Killengreen et al. 2011; Gallant et al. 2020). The synergetic consequences of climate change and increasing availability of anthropogenic subsidies will likely favor boreal forest predators over tundra predators (Elmhagen et al. 2017) by altering the relative strength of intra versus interspecific competition (Amarasekare 2002) and lowering the amplitude of fluctuations in these forest predators (Henden et al. 2010). In addition, increased contact between fox species could also favor the spread of zoonotic viruses, many of which are of concern to human communities, directly or economically. Notably, expansion of red foxes may cause a northward range expansion of sylvatic rabies, create a reservoir for Arctic rabies (e.g., Nadin-Davis et al. 2021), and increase the spread of canids' pathogens that may, for example, negatively impact sled dog kennels that are important for tourism. Further understanding of how boreal-forest species respond to changing conditions on tundra ecosystems, and how tundra species respond to changes in tundra communities, will be key in forecasting the trajectory of populations of sensitive tundra species, such as the Arctic fox, and thus re-evaluating the urgency with which conservation measures should be implemented.

Future directions

My work has highlighted the importance of landscape heterogeneity at tree line, yet most quantitative data originated from the tundra. To fully understand the dynamics of the expanding red fox population on the coastal tundra, future research must integrate studies over the different biomes such as quantifying the expansion of the boreal-forest prey community. Furthermore, I mostly focused on factors limiting the red fox population driven by bottom-up effects, but climate change could favor larger carnivores like the wolf (following moose expansion; Vors and Boyce 2009), which could limit red foxes via top-down effects. Further work could, thus, expand on possible top-down effects, notably related to possible wolf increased presence. Understanding the fine spatial-scale drivers of residency and adult dispersal in both species, notably in terms of habitat and prey availability, would provide insight on why the dispersal rate of both species is high, and we would further gain knowledge on the local population dynamics.

I used satellite collars with QFP technology to study Arctic and red foxes' spatial ecology. The high-quality data provided by these collars, notably in terms of spatial accuracy and fix success rate, came at a trade-off with sample size, because of their cost. Continued deployment of satellite collars to increase the sample size will strengthen our conclusions or refine our insight in fox spatial behaviors (notably in relation to resources). Because I needed the collars to last at least one year, I compromised between collars' battery life and data resolution: refined understanding of intra- and interspecific fine-scale spatial interactions will require to focus on one season at the time with a higher fix resolution (to properly use spatial and velocity autocorrelation in modelling foxes' spatial behavior, I recommend a fix frequency of 15 min. at least).

Although I collected 4 years of data for my thesis, this time frame corresponds to only one lemming cycle. Because I had archived samples, I could examine fox diets spanning 8 years, but that still corresponded to only two lemming cycles and approximately one snowshoe hare cycle. Repeating these studies after adding one to a few more prey cycles would allow to disentangle the contribution of these key prey to driving the foxes' spatial behavior and diet.

To assess mercury exposure in winter in foxes, and relate it to diet, I used muscle from animals trapped during the winter trapping season on land, so our samples were likely biased in favor of Arctic foxes using terrestrial resources. Although I have found that hair and claw poorly represented the mercury burden of internal tissue, they still are good indicators of trace elements taken up by the animals. Using summer hair that grows at the very end of winter, or sampling claw in spring would likely reduce the bias against Arctic foxes that use the sea ice. Keratinous tissues would thus be valuable to further understanding the link between prey-abundance fluctuation, diet, and mercury (or other trace element) exposure. Within the framework of a multidisciplinary study, compiling data on these different drivers, and inter- and intraspecific competition, would refine our understanding on how new species interactions resulting from Arctic warming drive changes in exposure to deleterious substances, such as mercury.

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