

Feast to famine: sympatric predators respond differently to seasonal prey scarcity on the low-Arctic tundra

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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 strategies of both species are primarily driven by temporal variability of resources. We also predicted that the harsh tundra conditions in winter affect red foxes more than Arctic

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Key-words: climate change, movement ecology, seasonality, resource fluctuation, range expansion, telemetry

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 strategies 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 emigrate or become nomadic if the cost of staying 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 (*sensu* 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 or 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).

Resources influence not only movement strategy 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 et al. 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 et al. 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 strategy 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 crossed (Korpimäki and Hongell 1986; Roth 2003; Powell and Mitchell 2012). Therefore, terrestrial predators typically favor residency over nomadism (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), or 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). Both fox species 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 (Hersteinsson and Macdonald 1992), and are less adapted than Arctic foxes to prey scarcity during the harsh Arctic winters (Fuglestad et al. 2006; Careau et al. 2007b).

We examined movement strategies and space use of red and Arctic foxes on the low Arctic tundra in northern Manitoba, where red foxes recently expanded from the adjacent boreal forest and now reproduce in sympatry with Arctic foxes (Moizan 2019, Zhao et al. submitted). We hypothesized that seasonal variability of resources primarily drives movement strategies in both red and Arctic foxes, but winter conditions are more limiting to red foxes. Specifically, red foxes lack adaptations to exploit the sea ice, and their increased energetic requirements during winter 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 (P2), red foxes always maintain larger home ranges than Arctic foxes (P3), and extra-territorial excursions are more frequent for resident red foxes than Arctic foxes, and more frequent in winter in both species (P4).

Methods

Study area and species. – Our study area near Churchill, Manitoba (Fig. 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 consider that the sea ice starts at the low tideline (Ponomarenko et al. 2014).

Lemmings are available year-round, but their abundance has dramatically damped throughout the Arctic (e.g., Bilodeau et al. 2013), particularly low Arctic populations 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. 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 recovery 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 covers the ground and facilitates travel over large distances, except two adult foxes caught near our field camps in June 2018. 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 from the start of a given season until the end of that season or until its death (i.e., we did not include the season of capture in movement strategy and home range comparisons). All foxes that underwent long-range movements (hereafter dispersals) were considered dispersers, since none of the foxes returned to its departure area, but these dispersal events were not natal dispersal because we only captured adults.

For each dispersal 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 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 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). Due to heterogeneous location densities, we used the adaptive method (a-LoCoH). However, we still excluded locations (or clusters of consecutive locations) > 20 km from the mean center of all locations, because including them distorted some home ranges.

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). 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.

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 away from the current home range followed by a return to the home range. Because we estimated home ranges as a 95% utilization distribution, we differentiated excursions from movements near the home range border, based on the distribution of the distances between a location and the centroid of the estimated home range. Locations that appeared to be outliers using a one-sided Hampel filter (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” 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 proportion of dispersal events (P1, P2) and home-range size (P3) between species and between seasons, we ran generalized linear mixed-effect models (GLMM) 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 ($n_{\text{perm}} = 9999$) 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 used Fisher’s exact test to test if commuting trips were more frequent in Arctic foxes (P2). We then tested if land excursions by resident foxes were more likely in winter and in red foxes (P4) 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. All summary statistics are presented as mean \pm 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 S2 for capture details), which yielded a total of 6159 locations after thinning their tracks to one daily location, but 10 Arctic and 7 red foxes yielded enough data to perform home-range analyses and assess the seasonal shift 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 S4). 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 30. Foxes settled in a new area (at least temporarily) after 10 of the dispersal events, but 7 died 11 days to 4 months after dispersing (at least one was caught by a fur trapper). Of the four foxes that died while dispersing, at least two were caught by fur trappers, but we have no information on the cause of death for the other two.

All red foxes dispersed towards 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). 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 exclusively used land. No red foxes dispersed using the 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 (perm. test, $n_{\text{Arctic}} = 9$, $n_{\text{red}} = 5$, $t = 1.44$, $P = 0.002$), 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: $z = -1.99$, $P = 0.046$; $n_{\text{disperse}} = 14$, $n_{\text{resident}} = 7$) 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 that winter ($z = 1.29$, $P = 0.20$; $n_{\text{red}} = 10$, $n_{\text{Arctic}} = 11$) or the following year ($z = 0.42$, $P = 0.67$).

Seasonal home range. – 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: $t_{\text{season}} = 0.72$, $P = 0.48$, $n_{\text{summer}} = 24$, $n_{\text{winter}} = 12$; $t_{\text{species}} = 0.14$, $P = 0.89$, $n_{\text{red}} = 19$, $n_{\text{Arctic}} = 17$; $t_{\text{species*season}} = 3.06$, $P = 0.006$, $n_{\text{total}} = 36$). 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. Table S3 provides all parameters from all GLMMs.

Individuals' summer and winter home ranges overlapped moderately in both species, although the seasonal change was small for some (red foxes: $55.8 \pm 11.9\%$ [33.2-70.7%], $n = 7$; Arctic foxes: $62.3 \pm 12.3\%$ [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 ± 0.4 km [0.3-1.1 km], $n = 4$). Core areas, however, generally overlapped only slightly to moderately between seasons (red foxes: $21.4 \pm 20.2\%$ [0-55.7%], $n = 7$; Arctic foxes: $29.9 \pm 29.3\%$ [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 (Fisher's exact test: $P = 0.001$, $n_{\text{Arctic}} = 5$, $n_{\text{red}} = 7$). We found no overall difference in land excursion frequency between seasons or species (GLMM: $t_{\text{species}} = -0.859$, $P = 0.397$; $t_{\text{season}} = -0.539$, $P = 0.593$; $t_{\text{season*species}} = 1.650$, $P = 0.109$, $n = 36$). 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: $t_{\text{season}} = 3.113$, $P = 0.004$, $n = 36$) but occurred at a similar frequency in both species ($t_{\text{species}} = -1.547$, $P = 0.131$).

Discussion

Both red and Arctic foxes showed mixed movement strategies 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 and likely reflected their 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. 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 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), which could further indicate that Churchill foxes were less likely than other populations (such as Bylot Arctic foxes living near the large snow goose colony) to capitalize on summer-abundant resources, caching items to survive winters as residents (Rioux et al. 2017).

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. 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 residents (11 of 12) survived long enough to raise pups successfully. However, remaining resident during prey scarcity may compromise reproduction too, as resources may be allocated to overwinter survival at the cost of next-season reproduction (Löfgren et al. 1986). Although each strategy may have a cost, our results suggest that dispersing is risky for both red and Arctic foxes, and may be a desperate strategy 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). When rodent abundance is low, they 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). Two-thirds of our Arctic foxes indeed dispersed using the sea ice as a platform, whereas red foxes never did, likely denoting their lack of adaptation to exploit marine resources. 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, in Sweden and the Canadian high Arctic (Walton et al. 2018; Lai et al. 2022), but unlike in Sweden, they dispersed towards the boreal forest. The low cumulative to straight-line dispersal distance ratio of these red foxes suggests straight relocation until finding suitable habitat, unlike Arctic foxes, which 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.

Red foxes' difficulty overwintering on the tundra is further reflected in the seasonal change in home-range size of residents. 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 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 $\sim 35 \text{ km}^2$ (up to 56 km^2), among the largest reported for this species (Goszczyński 2002; Walton et al. 2017; Lai et al. 2022). Large home ranges suggest a low fox density in our area (Trehella 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 was much higher quality 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 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 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).

In partial agreement with P3, all Arctic foxes commuted to the sea ice (one Arctic fox even had 76.7% of her winter home range on the sea ice, yet still took five exploratory trips farther onto the sea ice; Fig. S1), whereas our red foxes did not. Red foxes are opportunistic feeders (e.g., Kidawa and Kowalczyk 2011) and may occasionally feed on beached marine carrion (Andriashek et al. 1985; Killengreen et al. 2011). Although 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 environment. 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 to obtain enough prey. This winter expansion 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; Fuglestad 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 at the same time increases their energetic requirements (Fuglestad et al. 2006).

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. The high proportion of adult red and Arctic foxes that disperse in winter may indicate that winter food is even scarcer in our area than elsewhere (e.g., Lai et al. 2017; Walton et al. 2018), or sea ice may be more productive for Arctic foxes than elsewhere. 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 treeline, where they may be able to use sparse forest patches to buffer the low food availability on the tundra.

The changes occurring on the tundra associated with Arctic warming will likely lower the constraints on boreal-forest species' persistence in this environment (Callaghan et al. 2004). For example, increased winter temperatures will lower the costs associated with thermoregulation (Pálsson et al. 2016; Nater et al. 2021), and changing tundra-biotic communities will provide expanding species with increased foraging opportunities (Post et al. 2009; Tape et al. 2016). Meanwhile, Arctic foxes seemed to rely quite heavily on the sea ice instead of expanding their home ranges, but this habitat will be negatively affected as the Arctic warms, and tundra species that rely on their ability to exploit those alternative resources may thus lose opportunities to cope with terrestrial food scarcity.

The species interaction-abiotic stress hypothesis 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). However, in areas particularly vulnerable to the effects of climate change, edge populations may also become

directly limited by climate-induced declines in resource availability. Declines in some crucial prey may trigger important dispersal in highly mobile predators, or prevent newcomers from becoming established, which could lead to local extirpation of predator species.

Conflict of Interest

We have no conflicts of interest to disclose.

Author Contributions

C.W.R and J.D.R. conceived the ideas and designed the methodology; C.W.R. led data collection with support from J.D.R; J.D.R. obtained the funding; C.W.R. analyzed the data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication

Data Availability Statement

Data will be archived in movebank at time of publication.

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References

- Altman, D.G., and Bland, J.M. 1995. Statistics notes: Absence of evidence is not evidence of absence. *BMJ* **311** (7003): 485.
- Andersen, D.E., Bergh, S., Baldwin, F., Nelson, F., Cole, J., Ratson, M., Vasek, C., Endrizzi, D., Walker, D., Roth, J.D., and McDonald, R.S. 2010. Production of EPP Canada geese near Cape Churchill in 2010. Unpublished Parks Canada report.
- Andriashek, D., Kiliaan, H.P.L., and Taylor, M.K. 1985. Observations on foxes, *Alopex lagopus* and *Vulpes vulpes*, and wolves, *Canus lupus*, on the off-shore sea ice of Northern Labrador. *Can. Field-Naturalist* **99** (1): 86–89.
- Avgar, T., Street, G., and Fryxell, J.M. 2014. On the adaptive benefits of mammal migration. *Can. J. Zool.* **92** : 481–490.
- Barraquand, F., and Benhamou, S. 2008. Animal movements in heterogenous landscapes: Identifying profitable places and homogenous movememtn bouts. *Ecology* **89** (12): 3336–3348.
- Bartoń, K.A., and Zalewski, A. 2007. Winter severity limits red fox populations in Eurasia. *Glob. Ecol. Biogeogr.* **16** (3): 281–289.
- Bates, D., Mächler, M., Bolker, B.M., and Walker, S.C. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67** (1): 1–48.
- Bilodeau, F., Gauthier, G., and Berteaux, D. 2013. The effect of snow cover on lemming population cycles in the Canadian High Arctic. *Oecologia* **172** : 1007–1016.
- Brook, R.K., and Kenkel, N.C. 2002. A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *Int. J. Remote Sens.* **23** (21): 4761–4776.

- Callaghan, T. V, Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R. a, Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E., and Zockler, C. 2004. Climate change and UV-B Impacts on Arctic tundra and polar desert ecosystems: Biodiversity, distributions and adaptations of arctic species in the context of environmental change. *Ambio* **33** (7): 404–414.
- Careau, V., Giroux, J.F., and Berteaux, D. 2007a. Cache and carry: hoarding behavior of arctic fox. *Behav. Ecol. Sociobiol.* **62** (1): 87–96.
- Careau, V., Morand-Ferron, J., and Thomas, D.D. 2007b. Basal metabolic rate of canidae from hot deserts to cold Arctic climates. *J. Mammal.* **88** (2): 394–400.
- Cargill, S.M., and Jefferies, R.L. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-Arctic salt marsh. *J. Appl. Ecol.* **21** (2): 669–686.
- Celis-Murillo A, M Malorodova, E Nakash. 2020. North American Bird Banding Dataset 2017-2019 retrieved 2020-08-12. U.S. Geological Survey, Eastern Ecological Science Center at the Patuxent Research Refuge.
- Ehrich, D., Schmidt, N.M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N.E., Framstad, E., Frandsen, J., Franke, A., Gilg, O., Giroux, M.A., Henttonen, H., Hörnfeldt, B., Ims, R.A., Kataev, G.D., Kharitonov, S.P., Killengreen, S.T., Krebs, C.J., et al. 2020. Documenting lemming population change in the Arctic: Can we detect trends? *Ambio* **49** : 786–800.
- Eide, N.E., Jepsen, J.U., and Prestrud, P. 2004. Spatial organization of reproductive Arctic foxes *Alopex lagopus* : Responses to changes in spatial and temporal availability of prey. *J. Anim. Ecol.* **73** (6): 1056–1068.
- Fauteux, D., Gauthier, G., and Berteaux, D. 2015. Seasonal demography of a cyclic lemming population in the Canadian Arctic. *J. Anim. Ecol.* **84** : 1412–1422.
- Ferreras, P., Delibes, M., Palomares, F., Fedriani, J.M., Calzada, J., and Revilla, E. 2004. Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus* . *Behav. Ecol.* **15** (1): 31–40.
- Fuglei, E., and Øritsland, N.A. 1999. Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (*Alopex lagopus*) at Svalbard. *J. Comp. Physiol. - B Biochem. Syst. Environ. Physiol.* **169** (6): 361–369.
- Fuglei, E., and Tarroux, A. 2019. Arctic fox dispersal from Svalbard to Canada: One female’s long run across sea ice. *Polar Res.* **38** : 3512. Norwegian Polar Institute.
- Fuglesteg, B.N., Haga, Ø.E., Folkow, L.P., Fuglei, E., and Blix, A.S. 2006. Seasonal variations in basal metabolic rate, lower critical temperature and responses to temporary starvation in the arctic fox (*Alopex lagopus*) from Svalbard. *Polar Biol.* **29** (4): 308–319.
- Gallant, D., Lecomte, N., and Berteaux, D. 2020. Disentangling the relative influences of global drivers of change in biodiversity: A study of the twentieth-century red fox expansion into the Canadian Arctic. *J. Anim. Ecol.* **89** : 565–576.
- Gallant, D., Slough, B.G., Reid, D.G., and Berteaux, D. 2012. Arctic fox versus red fox in the warming Arctic: Four decades of den surveys in north Yukon. *Polar Biol.* **35** (9): 1421–1431.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. 2007. LoCoH: Nonparametric Kernel methods for constructing home ranges and utilization distributions. *PLoS One* **2** (2): e207.
- Goszczyński, J. 2002. Home ranges in red fox: Territoriality diminishes with increasing area. *Acta Theriol. (Warsz)*. **47** (SUPPL. 1): 103–114.
- Hersteinsson, P., and Macdonald, D.W. 1992. Interspecific competition and the geographical distribution of red and Arctic foxes *Vulpes vulpes* and *Alopex lagopus* . *Oikos* **64** (3): 505–515.

- Hervé, M. 2021. RVAideMemoire: testing and plotting procedures for biostatistics. R package version 0.9-79. Available from <https://cran.r-project.org/package=RVAideMemoire>.
- Hochheim, K., Barber, D.G., and Lukovich, J. V. 2010. Changing sea ice conditions in hudson bay, 1980-2005. *In A Little Less Arctic: Top Predators in the World's Largest Northern Inland Sea, Hudson Bay.* Edited by S.H. Ferguson, L.L. Loseto, and M.L. Mallory. Springer. pp. 39–51.
- Hsiung, A.C., Boyle, W.A., Cooper, R.J., and Chandler, R.B. 2018. Altitudinal migration: ecological drivers, knowledge gaps, and conservation implications. *Biol. Rev.* **93** : 2049–2070.
- Jonzén, N., Knudsen, E., Holt, R.D., and Sæther, B. 2011. Uncertainty and predictability: the niches of migrants and nomads. *In Animal Migration: a synthesis*, Oxford Uni. Edited by E.J. Milner-Gulland, J.M. Fryxell, and A.R. Sinclair. pp. 91–109.
- Kidawa, D., and Kowalczyk, R. 2011. The effects of sex, age, season and habitat on diet of the red fox *Vulpes vulpes* in northeastern Poland. *Acta Theriol. (Warsz)*. **56** : 209–218.
- Killengreen, S.T., Schott, T., Yoccoz, N.G., Lecomte, N., and Ims, R.A. 2011. The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the Arctic tundra. *J. Anim. Ecol.* **80** : 1049–1060.
- Knaub, J.R. 1987. Practical interpretation of hypothesis test. *Am. Stat.***41** (3): 246–247.
- Korpimäki, E., and Hongell, H. 1986. Partial migration as an adaptation to nest site scarcity and vole cycles in Tengmalm's Owl *Aegolius funereus* . *In Vår fågelvärld Suppl.* pp. 85–92.
- Krebs, C.J., Kenney, A.J., Gilbert, S., Danell, K., Angerbjörn, A., Erlinge, S., Bromley, R.G., Shank, C., and Carriere, S. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. *Can. J. Zool.*
- 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.
- Lai, S., Warret Rodrigues, C., Gallant, D., Roth, J.D., and Berteaux, D. 2022. Red foxes at their northern edge: competition with the Arctic fox and winter movements. *J. Mammal.*: gyab164.
- Linnell, J.D.C., Mattisson, J., and Odden, J. 2021. Extreme home range sizes among Eurasian lynx at the northern edge of their biogeographic range. *Ecol. Evol.* **11** (10): 5001–5009.
- Löfgren, O., Hörnfeldt, B., and Carlsson, B.G. 1986. Site tenacity and nomadism in Tengmalm's owl (*Aegolius funereus* (L.)) in relation to cyclic food production. *Oecologia* **69**(3): 321–326.
- López-Bao, J.V., Aronsson, M., Linnell, J.D.C., Odden, J., Persson, J., and Andrén, H. 2019. Eurasian lynx fitness shows little variation across Scandinavian human-dominated landscapes. *Sci. Rep.* **9** (1): 1–10.
- Lyons, A.J., Turner, W.C., and Getz, W.M. 2013. Home range plus: A space-time characterization of movement over real landscapes. *Mov. Ecol.***1** (2): 1–14.
- MacDonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature***301** (5899): 379–384.
- Macdonald, D.W., and Johnson, D.D.P. 2015. Patchwork planet: The resource dispersion hypothesis, society, and the ecology of life. *J. Zool.* **295** : 75–107.
- Maher, C.R., and Lott, D.F. 2000. A review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.***143** (1): 1–29.
- Marneweck, C., Marneweck, D.G., van Schalkwyk, O.L., Beverley, G., Davies-Mostert, H.T., and Parker, D.M. 2019. Spatial partitioning by a subordinate carnivore is mediated by conspecific overlap. *Oecologia***191** : 531–540.
- Maude, G., Reading, R.P., and Harris, S. 2019. Fluctuating food resources and home ranges in brown hyaenas living in a semi-arid environment. *J. Zool.* **307** (1): 53–60.

- McCarty, J.P. 2001. Ecological Consequences of Recent Climate Change. *Conserv. Biol.* **15** (2): 320–331.
- McDonald, R., Roth, J., and Baldwin, F.. 2017. Goose persistence in fall strongly influences Arctic fox diet, but not reproductive success, in the southern Arctic. *Polar Res.* **36** (5): 1–9.
- McLoughlin, P.D., Ferguson, S.H., and Messier, F. 2000. Intraspecific variation in home range overlap with habitat quality: A comparison among brown bear populations. *Evol. Ecol.* **14** : 39–60.
- Meia, J.S., and Weber, J.M. 1995. Home ranges and movements of red foxes in central Europe: stability despite environmental changes. *Can. J. Zool.* **73** (10): 1960–1966.
- Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Can. J. Zool.* **63** (2): 239–245.
- Moizan, A. 2019. Factors influencing natal den selection by red foxes on the tundra of western Hudson Bay and impact on Arctic foxes. Masters' Thesis, Université Paris Saclay, Sciences Sorbonne Université, Paris.
- Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? *Oikos* **120** : 1817–1825.
- Nater, C.R., Eide, N.E., Pedersen, Å.Ø., Yoccoz, N.G., and Fuglei, E. 2021. Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate. *Ecosphere* **12** (6): e03546.
- Niedzielski, B., and Bowman, J. 2016. Home range and habitat selection of the female eastern wild Turkey at its northern range edge. *Wildlife Biol.* **22** (2): 55–63.
- Pálsson, S., Hersteinsson, P., Unnsteinsdóttir, E.R., and Nielsen, Ó.K. 2016. Population limitation in a non-cyclic arctic fox population in a changing climate. *Oecologia* **180** (4): 1147–1157.
- Ponomarenko, S., Quirouette, J., Sharma, R., and McLennan, D. 2014. Ecotype mapping report for Wapusk National Park. Monitoring and ecological Information. Natural Resource Conservation. Parks Canada, Gatineau, QC.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T. V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., and Aastrup, P. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* (80-.). **325** (5946): 1355–1358.
- Powell, R.A. 2000. Animal home ranges and territories and home range estimators. *In* Research techniques in animal ecology. *Edited by* L. Boitani and T.K. Fuller. Columbia University Press. pp. 65–110.
- Powell, R.A. 2012. Movements, home ranges, activity, and dispersal. *In* Ecology and conservation of carnivores: A handbook of techniques. *Edited by* L. Boitani and R.A. Powell. Oxford University Press, London, United Kingdom. pp. 188–217.
- Powell, R.A., and Mitchell, M.S. 2012. What is a home range? *J. Mammal.* **93** (4): 948–958.
- Prestrud, P. 1991. Adaptations By the Arctic Fox (*Alopex lagopus*) To the Polar Winter. *Arctic* **44** (2): 132–138.
- Rioux, M.J., Lai, S., Casajus, N., Bêty, J., and Berteaux, D. 2017. Winter home range fidelity and extraterritorial movements of Arctic fox pairs in the Canadian High Arctic. *Polar Res.* **36** (supp1): 11.
- Robillard, A., Therrien, J.F., Gauthier, G., Clark, K.M., and Bêty, J. 2016. Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the snowy owl. *Oecologia* **181** : 423–433.

Rød-Eriksen, L., Skrutvold, J., Herfindal, I., Jensen, H., and Eide, N.E. 2020. Highways associated with expansion of boreal scavengers into the alpine tundra of Fennoscandia. *J. Appl. Ecol.* **57**(9): 1861–1870.

Roshier, D.A., and Reid, J.R.W. 2003. On animal distributions in dynamic landscapes. *Ecography (Cop.)*. **26** (4): 539–544.

Roth, J.D. 2002. Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia***133** (1): 70–77.

Roth, J.D. 2003. Variability in marine resources affects arctic fox population dynamics. *J. Anim. Ecol.* **72** (4): 668–676.

von Schantz, T. 1984. Spacing strategies, kin selection, and population regulation in altricial vertebrates. *Oikos* **42** (1): 48–58.

Sklepkovych, B.O., and Montevecchi, W.A. 1996. Food availability and food hoarding behaviour by red and Arctic foxes. *Arctic* **49** (3): 228–234.

Soulsbury, C.D., Baker, P.J., Iossa, G., and Harris, S. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). *Behav. Ecol. Sociobiol.* **62** (8): 1289–1298.

Stark, D.J., Vaughan, I.P., Saldivar, D.A.R., Nathan, S.K.S.S., and Goossens, B. 2017. Evaluating methods for estimating home ranges using GPS collars: A comparison using proboscis monkeys (*Nasalis larvatus*). *PLoS One* **12** (3): e0174891.

Storm, G.L., Andrews, R. iD, Phillips, R.L., Bishop, R.A., Siniff, D.B., and Tester, J.R. 1976. Morphology, reproduction, dispersal and mortality of midwestern red fox populations. *Wildl. Monogr.* **46** (49): 3–53.

Tannerfeldt, M., Angerbjörn, A., and Angerbjorn, A. 1998. Fluctuating resources and the evolution of litter size in the Arctic fox. *Oikos***83** (3): 545–559.

Tape, K.D., Christie, K., Carroll, G., and O'Donnell, J.A. 2016. Novel wildlife in the Arctic: The influence of changing riparian ecosystems and shrub habitat expansion on snowshoe hares. *Glob. Chang. Biol.***22** (1): 208–219.

Tarroux, A. 2011. Utilisation de l'espace et des ressources chez un carnivore terrestre de l'arctique: le renard polaire. PhD thesis, Rimouski, Québec, Université du Québec à Rimouski.

Therneau, T.M. 2020. *coxme: Mixed Effects Cox Models*. R package version 2.2-16.

Trewhella, W.J., Harris, S., and McAllister, F.E. 1988. Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. *J. Appl. Ecol.***25** (2): 423–434.

Walton, Z., Samelius, G., Odden, M., and Willebrand, T. 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLoS One* **12** (4): e0175291.

Walton, Z., Samelius, G., Odden, M., and Willebrand, T. 2018. Long-distance dispersal in red foxes *Vulpes vulpes* revealed by GPS tracking. *Eur. J. Wildl. Res.* **64** : 64.

Zhao, S-T., Johnson-Bice S.M., and Roth J.D. *Submitted* . Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Glob. Ecol. Conserv.*

Tables

Table 1. Dispersal track parameters for each fox species, indicating different behaviors while dispersing.

species	parameter	mean	se	median	min	max	n
Red fox	Duration ¹	15.40	2.94	15.00	8.00	23.00	5
	Distance ²	200.80	28.81	167.90	144.80	280.60	5
	CSLD ratio ³	1.50	0.16	1.31	1.17	2.03	5

species	parameter	mean	se	median	min	max	n
Arctic fox	Speed ⁴	15.24	3.74	12.38	7.30	28.06	5
	Duration ¹	43.11	12.96	29.00	6.00	135.00	9
	Distance ²	1243.00	529.60	781.70	216.30	5197.27	9
	CSLD ratio ³	4.36	1.95	1.90	1.26	19.62	9
	Speed ⁴	27.96	4.83	28.69	9.63	55.58	9

¹days between start and end points of dispersal

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

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

⁴average daily speed (km/day).

Table 2. Home range (Utilization Distribution 95) and core area (UD 50) sizes (km²) per season and species.

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

Figures

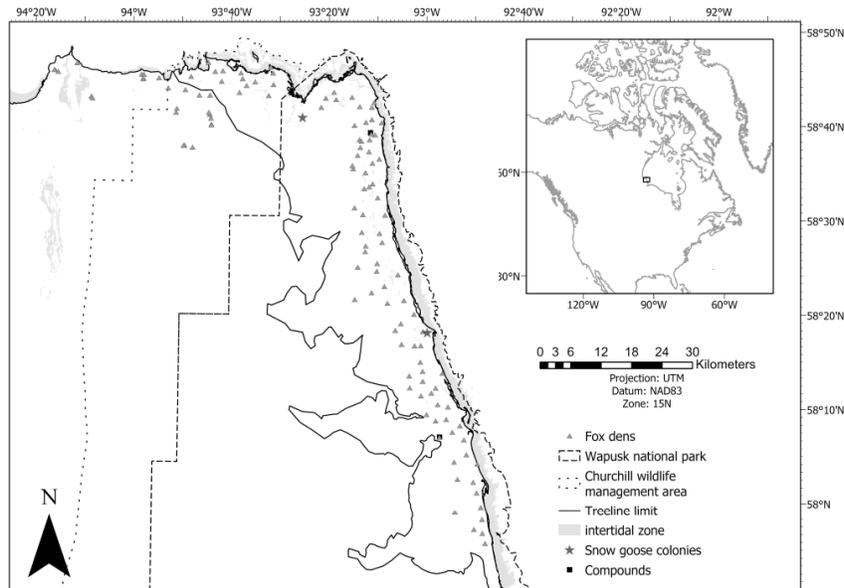


Fig. 1. Map of our study area in northern Manitoba, Canada.

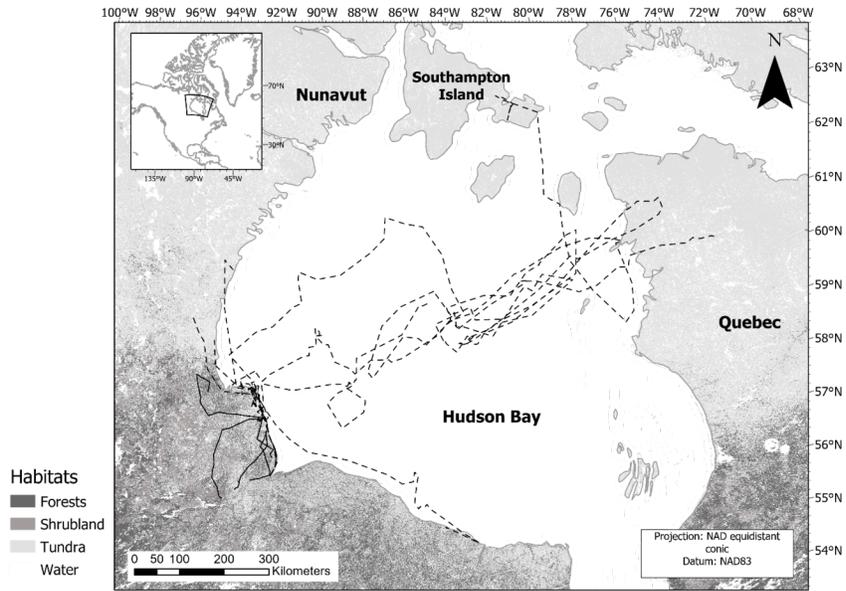


Fig. 2. Dispersal tracks of red (solid lines) and Arctic (dashed lines) foxes captured in Wapusk National Park, Canada, from 2017-2019.

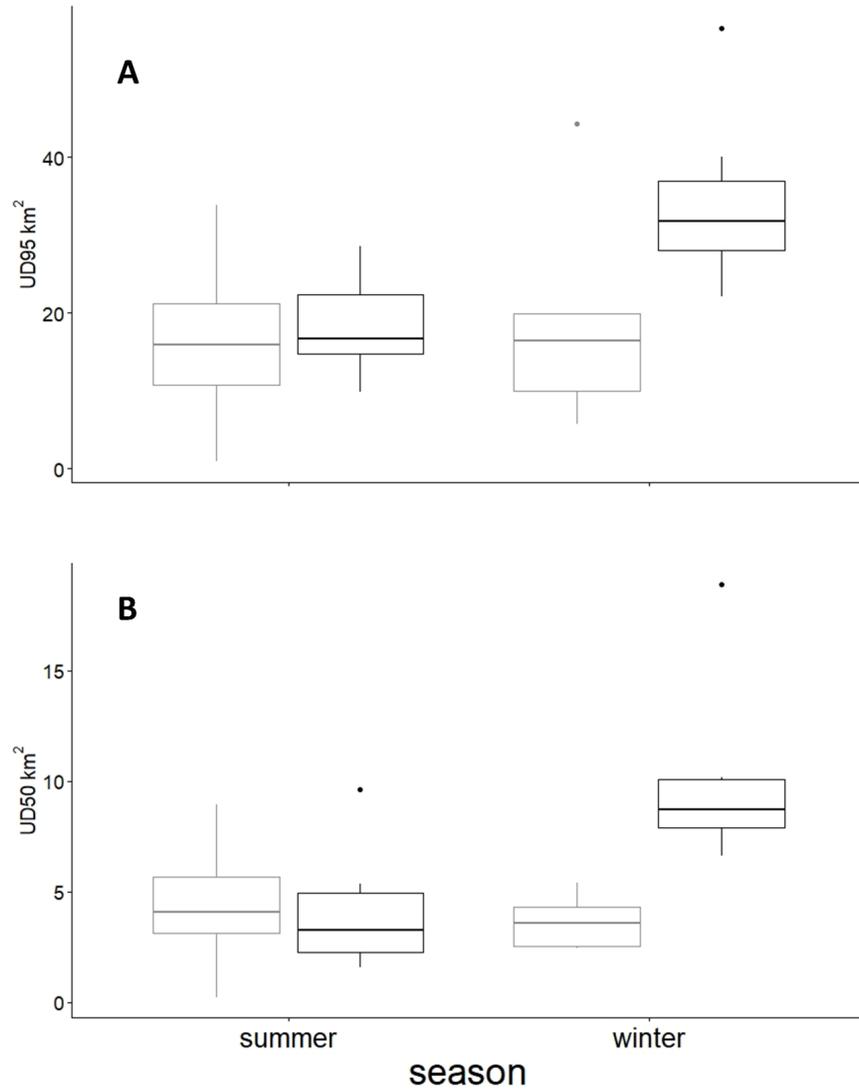


Fig. 3. Size of (A) home ranges and (B) core areas of Arctic (grey) and red (black) foxes in northern Manitoba, Canada, in summer ($n_{\text{red}} = 12$, $n_{\text{Arctic}} = 12$) and winter ($n_{\text{red}} = 7$, $n_{\text{Arctic}} = 5$).

