



Different selection criteria may relax competition for denning sites between expanding red foxes (*Vulpes vulpes*) and endemic Arctic foxes (*Vulpes lagopus*) on the low-Arctic tundra

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Abstract

Climate warming is favoring the expansion of non-native species onto the Arctic tundra, where they may compete over resources with native species. In the harsh tundra conditions, sympatric red foxes (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) may compete over denning sites, which are important for their reproduction and survival. We studied den selection by red and Arctic foxes in spring and summer and their possible competition over this resource in an ecotone near Churchill, Manitoba, on the west coast of Hudson Bay, by examining patterns of den occupancy related to den characteristics and spacing patterns between neighbors. Based on 11 years of occupancy data for 42 tundra dens, we determined that red and Arctic foxes favored dens based on shelter quality in both spring and summer, rather than proximity of specific habitats (and thus specific prey). Mechanisms of den selection differed between species, which may promote coexistence, and areas of high den density were avoided by red foxes and preferred by Arctic foxes. We did not find evidence of exclusion of Arctic foxes by red foxes: spacing patterns showed that foxes spaced themselves based on their need for space, territoriality and food availability but not interference. In the current abiotic Arctic conditions, taiga species settling on the tundra could coexist with tundra endemics, at given density thresholds of both competitors. As Arctic conditions may become milder, an increase in newcomer abundance could disrupt the current balance that favors species coexistence.

Keywords Interspecific competition · Climate warming · Arctic · Habitat selection · Resource fluctuation

Introduction

Climate change is modifying northern ecosystems rapidly (Callaghan et al. 2004). The taiga is progressing onto the tundra (Brodie et al. 2019) and taiga species are expanding their range in other Arctic habitats where they were previously unable to cope with the harshness of the abiotic conditions and the lack of food resources (Hersteinsson and Macdonald 1992; Tannerfeldt et al. 2002; Bartoń and Zalewski 2007).

The presence of non-native species on the tundra may alter existing communities through diverse mechanisms,

including competition. Competition typically occurs through interference or exploitation mechanisms (Case and Gilpin 1974). In the former, individuals directly alter their competitors' ability to exploit a common resource, and in the latter, individuals reduce the abundance of a shared resource, thus indirectly impairing other consumers. Competition intensity usually increases with the magnitude of overlap between competitors' niches (Donadio and Buskirk 2006). The relative importance of exploitative competition depends on resource availability for each individual, whereas interference competition usually increases with consumer density (Holdridge et al. 2016). The abundance of resources plays a minor role as interference competition increases (Park 1954; Smallegange et al. 2006; Holdridge et al. 2016). Interference competition is often asymmetrical, a larger body size leading one competitor to be dominant over the other(s) (Donadio and Buskirk 2006). As such, interference competition is often a major structuring driver of carnivore communities and warrants coexistence mechanisms such as spatial segregation. It may lead to decreased abundance of the weaker

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competitor or even its exclusion from shared resources (e.g., Palomares and Caro 1999; Elmhagen et al. 2002; Berger and Gese 2007).

Red foxes (*Vulpes vulpes*) have expanded their range throughout the Canadian Arctic during the twentieth century (Gallant et al. 2020) and are now sympatric with Arctic foxes (*Vulpes lagopus*) across much of their range in both North America and Eurasia. Red and Arctic foxes are ecologically and morphologically similar, which may lead them to compete over limiting resources, such as shelter, food, or habitat (Tannerfeldt et al. 2002; Gallant et al. 2014). Red foxes can be twice as heavy as Arctic foxes; they are thus expected to dominate interference competition (Pamperin et al. 2006). Red foxes' larger size and their lower adaptation to the harsh cold climate of the tundra entail higher energetic needs (Hestéinsson and Macdonald 1992), which may impose stricter habitat requirements and less behavioral flexibility than the Arctic fox.

Numerous studies in Scandinavia have examined the interactions and mechanisms of competition between Arctic and red foxes in a context of sympatry (e.g., Linnell et al. 1999; Tannerfeldt et al. 2002; Frafjord 2003; Rød-Eriksen et al. 2023). In Norway, red foxes are considered a significant threat to the critically endangered Arctic fox (Frafjord 2003), while in Sweden, red foxes excluded Arctic foxes from their denning area; Arctic foxes were forced to breed at least 8 km away from the nearest red fox to prevent pup killing (Tannerfeldt et al. 2002). In the Canadian high Arctic, there is no evidence of interference competition despite the high potential for exploitation competition, but at the northernmost edge of their distribution red foxes occur in low abundance (Lai et al. 2022). Theory predicts that low densities of a dominant competitor may facilitate coexistence (Amarasekare 2002). In the Canadian low Arctic near treeline, the higher density of red foxes may thus induce stronger interference competition than in the high Arctic.

The tundra is an open habitat where foxes choose their dens to maximize their chances of survival and reproduction (Doligez and Boulinier 2008). Although the proximity of food resources is an important consideration (Jepsen et al. 2002; Szor et al. 2008), foxes may also choose their dens for their quality as shelter to rest and escape pests and predators. The role of dens as shelters is also crucial for mating and rearing the pups (Uraguchi and Takahashi 1998; Tannerfeldt et al. 2003; Gallant et al. 2014). When foxes settle in dens in spring to reproduce, the ground is still frozen and they can't excavate new dens (Eberhardt et al. 1983; Gallant et al. 2014). The selection of reproductive dens is therefore restricted to preexisting ones, and some dens are preferred over others (Frafjord 2003). For example, in the Canadian high Arctic, Arctic foxes favored the shelter aspect of dens, while red foxes favored habitats highly productive during the springtime (Gallant et al.

2014). Furthermore, den selection by Arctic foxes was contingent on red fox reproduction (Gallant et al. 2014); Arctic foxes selected dens for their easy access when red foxes were present, and for shelter quality when red foxes were absent. In contrast to the high Arctic, taiga–tundra transition areas are close to the source population of red foxes, and therefore experience a constant presence and higher density of red foxes than the northernmost edges of their distribution (Elmhagen et al. 2017) when an anthropogenic disturbance is low. This population of red foxes near the treeline could constrain Arctic foxes to choose suboptimal dens.

We examined the factors affecting den selection by populations of red and Arctic foxes near Churchill, Manitoba, using 11 years of data on den occupancy. A breeding red fox population has recently settled in this area, using coastal tundra dens historically occupied by Arctic foxes only (Roth 2003). Although red foxes are more abundant at treeline than in the high Arctic, conditions in the Churchill area are still limiting to this species (Warret Rodrigues and Roth 2022). Red foxes settling at the edge of their distribution may not have reached an ecologically effective density, maintaining low interactivity with conspecifics (Soulé et al. 2003). It is unclear if those red foxes are excluding Arctic foxes from coastal tundra dens, or if they are merely using vacant ones. We hypothesized that (1) drivers of den selection switch during the reproductive period with changes in resource abundance for red foxes but not for Arctic foxes, and that (2) interference competition and energetic requirements drive spacing patterns of the sympatric red and Arctic foxes. We, therefore, evaluated the performance of three food access hypotheses and a shelter quality hypothesis to explain den selection by each species. Competing hypotheses were tested both in April (hereafter spring), when foxes settle in dens to reproduce but resources are still scarce and snow covers the ground, and in August (hereafter summer), after pups have emerged, when resources are plentiful throughout the landscape (e.g., McDonald et al. 2017) and the snow is completely gone. We tested our hypothesis through the following predictions:

- P1. In spring, red foxes should monopolize dens with better access to arvicoline rodents and forested areas, while we expect Arctic foxes to favor shelter quality because they can cope with food scarcity but are the weaker competitor.
- P2. In August, den selection for both species should be driven by the quality of dens as a shelter against competitors, pests, and predators.
- P3. Distances between fox neighbors are inversely related to food availability so should be shorter in August than in April, and shorter in years when lemming density is higher.

- P4. Due to possible interspecific interference, distances between neighbors should be greatest for heterospecific neighbors, shortest for homospecific Arctic fox neighbors, and intermediate between homospecific red fox neighbors.
- P5. Red fox occupancy has increased over the past 11 years, while Arctic fox occupancy has decreased.

Methods

Study area

This study was carried out in and around Wapusk National Park, on the western edge of Hudson Bay near Churchill, Manitoba, Canada ($58^{\circ}45' N$; $94^{\circ}10' W$), where red foxes have settled in tundra dens to reproduce (Zhao et al. 2022), exhibiting a continuous presence since 2010. In this transition zone, three biomes merge: tundra, taiga, and the marine ecosystem (Fig. 1) (Roth 2003). This area, part of the Hudson Bay Lowlands, is a uniformly flat wetland underlain by continuous permafrost with elevated beach ridges resulting

from the isostatic rebound (Rouse 1991; Roth 2003). The vegetation is dominated by graminoid and medium-height shrub communities with scarce tree islets and thin forest patches. Considering that most of the area is constituted by fen underlain by permafrost, good denning sites are limited, and foxes are highly dependent on preexisting dens mostly found on beach ridges, offering slightly elevated dry space suitable for fox den construction (Roth 2003).

Both fox species are central-place foragers (Elmhagen et al. 2007). On the tundra, arvicoline rodents such as collared lemmings (*Dicrostonyx* spp.) and voles (*Microtus* spp.) are the most important part of their diet year-round (Angerbjörn et al. 1999; Roth 2002; Dudenhoeffer et al. 2021). Lemming populations cycle every 3 or 4 years (Scott 1993), and lemming density strongly affects the reproductive success of Arctic foxes (Roth 2003; McDonald et al. 2017). Lemming densities have dramatically declined in many parts of the Arctic (Ims et al. 2008; Ehrlich et al. 2020), sometimes constraining foxes to find other sources of food (e.g., Angerbjörn et al. 1999; Roth 2002; Dudenhoeffer et al. 2021). In winter, foxes can stay on land and use caches (Stickney 1991) or access the sea ice to scavenge carcasses of seals

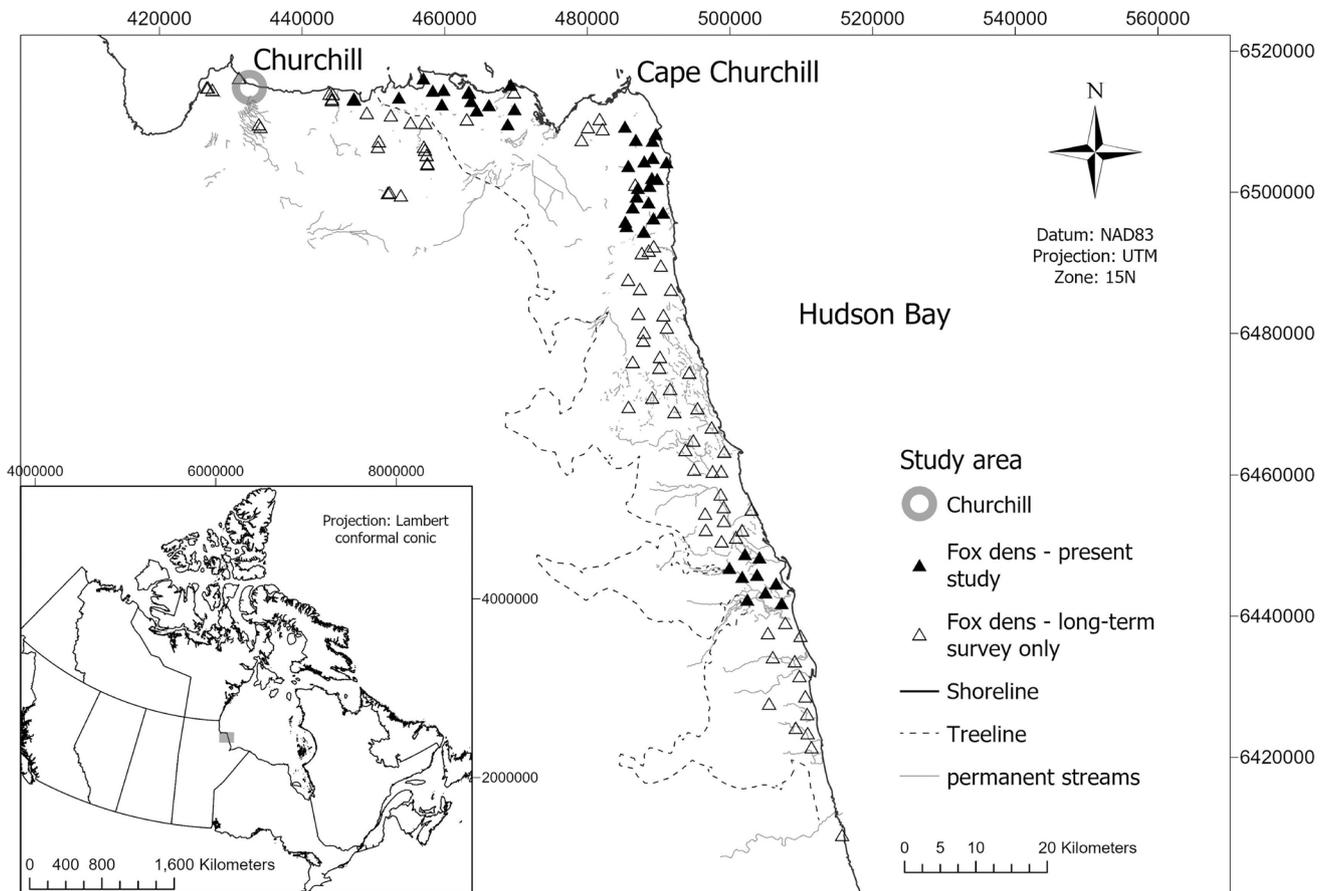


Fig. 1 Study area in and around Wapusk National Park ($58^{\circ}45' N$; $94^{\circ}10' W$) in Manitoba, Canada

(*Phoca hispida*) left by polar bears (*Ursus maritimus*) (Roth 2002). In summer, foxes benefit from the presence of migratory birds, eating juveniles and eggs. In particular, thousands of Canada geese (*Branta canadensis*) and snow geese (*Anser caerulescens*) breed in the region (McDonald et al. 2017), most nests being initiated at the end of May (Raveling 1977; Sammler et al. 2008).

Data collection

From 2011 to 2021, we monitored fox dens located on the tundra in and around Wapusk National Park (Roth 2003; McDonald et al. 2017) twice a year, to assess the occupancy of both red and Arctic foxes. We first visited dens in March–April by snowmobile, when foxes have paired up at den sites to start breeding, and again in late July–August by foot, all-terrain vehicle and/or helicopter, near the end of the breeding season shortly before pups disperse. The species occupying a den cannot always be assessed accurately from the air, so we used 42 of the 120 natal dens of our study area that were visited from the ground both in spring and summer. We determined if a den was occupied in spring based on the presence of tunnels through the snow (Online Resource 1) and assessed the species based on shed fur. In summer, we assessed occupancy based on recently excavated burrows (Online Resource 1), tracks, fresh scats, urine odor, or direct sighting of foxes visually or from trail cameras (since 2015, 21 dens were equipped with cameras). When the species using a den could not be verified (e.g., no shed fur or sightings), we recorded the species as “unidentified” and excluded the den from subsequent analyses.

To characterize the dens, we measured 16 variables (Table 1). We recorded 4 of those variables in the field from March to June 2019 (8 dens still covered in snow in June were revisited in August) and used habitat characteristics as proxies for food availability, based on published habitat preferences of prey from our study area (Smith and Foster 1957; Scott and Hansell 1989; Reiter and Andersen 2008; Dobroski 2022). We extracted these 12 remaining habitat variables using ArcGIS 10.6 (Esri 2018) and ArcGis Pro 2.4 (Esri 2019). Five environmental variables were extracted from Canada’s land cover map (version 2015) (Latifovic 2019). Hydrographic data (length of stream and length of pond bank) were extracted from Natural Resources Canada (2017). We extracted intertidal flats from a 5-m resolution microhabitat map of Wapusk National Park (Ponomarenko et al. 2014) and merged it with the other variables in one raster. Coastline and treeline were drawn as a vector file based on this same microhabitat map. We defined coastline using the western edge of the intertidal flats and defined treeline as the limit between tundra and forested habitats (spruce larch forests and woodland) using the eastern and northern

Table 1 Environmental variables used to model den selection by red foxes (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) in northern Manitoba, Canada

Variable	Model
Number of burrows facing south or southeast ^a	Shelter quality
Surface area (m ²) of the den ^b	Shelter quality
Presence of willow on the den ^c	Shelter quality
Snow depth on the den ^d	Shelter quality
Number of dens within 5000 m ^e	Shelter quality
Distance (m) to the nearest den ^e	Shelter quality
Area (m ²) of barren habitat within 1500 m ^{e,f}	Shelter quality
Area (m ²) of shrubland–lichen–moss within 1500 m ^{e,f}	Tundra food
Area (m ²) of grassland–lichen–moss within 1500 m ^{e,f}	Tundra food
Area (m ²) of wetland within 1500 m ^{e,f}	Tundra food
Length (m) of stream within 1500 m ^{e,f}	Tundra food
Length (m) of pond bank within 1500 m ^{e,g}	Tundra food
Area (m ²) of intertidal flats within 1500 m ^{e,h}	Coastal food
Distance (m) to the shoreline ^{e,h}	Coastal food
Distance (m) to treeline ^{e,h}	Forest food
Area (m ²) of needleleaf forest within 1500 m ^{e,f}	Forest food

^aExposure measured in June and August 2019 with a compass on every burrow present, used only in shelter quality model to characterize dens in spring

^bMeasured in June and August 2019 with a GPS (Garmin GPSMAP 78) using vegetation and most external burrows to determine the edge of the den (average of 2 measurements)

^cBinary: presence or absence of willows on the den

^dMeasured in March and April 2019 with a stick graduated in decimeters at the center of the den and on the four cardinal points at the edge of the den, based on vegetation, or 10 m away from the center of the den if the vegetation was not visible. We averaged these 5 measurements for each den

^eMeasured using ArcGIS version 10.6.1

^fMeasured at a resolution of 30×30 m (Latifovic 2019)

^gPermanent streams and ponds were identified with a map from Natural Resources Canada (2017), scale 1:30 000

^hMeasured using the microhabitat map of Wapusk National Park (Ponomarenko et al. 2014)

edges of the woodland and forest-type microhabitats (Ponomarenko et al. 2014).

We estimated lemming densities using mark–recapture methods each June, after the snow melted, from 2011 to 2021. We captured small mammals using Longworth and Sherman live traps on 2 grids (8×8, with 15-m spacing and 2 traps per station) and 2 transects (1×20 with 15-m spacing and 3 traps per station) on hummocky lichen–heath tundra, the habitat most commonly inhabited by collared lemmings (*Dicrostonyx richardsoni*) (Scott and Hansell 1989). Traps were baited with peanut butter and oats and left open for 72 h, and captured animals marked by hair-clipping (see McDonald et al. 2017 for detailed methods).

Data analysis

Food availability and shelter quality are often invoked to explain den selection by foxes (Jepsen et al. 2002; Szor et al. 2008; Gallant et al. 2014). Based on the specificities of our study area, we built 4 competing models to explain den selection: 3 food access models and 1 shelter quality model.

Model 1—tundra food accessibility

Considering the low productivity of the Arctic tundra when snow covers the ground, food availability in spring may be a crucial driver of den choice when foxes settle for reproduction. We thus tested if foxes chose dens with easier access to preferred lemming habitat and landscape features. Selected habitats included fen where most winter lemming nests are found (Dobroski 2022), stream and pond banks where deeper snow may be favorable spring habitat to lemmings and voles (Duchesne et al. 2011) and vegetation complexes of the beach ridges that lemmings select, attracted by fox dens (Gharajehdaghpour and Roth 2018). In summer, rodents are found on elevated features in the fen and dryer habitats supporting small shrub, lichen, and moss communities such as hummocks and beach ridges (Batzli et al. 1983; Lewis and Rodgers 1986; Predavec and Krebs 2000; Dobroski 2022). Eggs and juvenile geese are also an important part of fox diet to which they respond functionally (McDonald et al. 2017). We thus tested if foxes are choosing dens surrounded by favored lemming habitats and by a higher proportion of fen where lesser snow and Canada geese nest (Rockwell et al. 1993; Nack and Andersen 2006; Reiter and Andersen 2011).

Model 2—coastal food accessibility

Foxes settling on a coastal tundra may prefer dens close to the marine habitat to access marine resources. In the low Arctic, sea ice is accessible until late June, depending on temperatures (Hochheim et al. 2010), and when lemming abundance is low, Arctic foxes wander on the sea ice to eat ringed seal pups and carcasses left by polar bears, despite the risks associated with foraging on the sea ice (Roth 2003). Foxes are also opportunists so beached carrion could be an attractive resource (Roth 2003; Killengreen et al. 2011). We thus tested if Arctic and red fox den occupancies are determined by the accessibility to the coastal habitat.

Model 3—forest food access

Patches of trees may still be a valuable source of food because they shelter snowshoe hares (*Lepus americanus*), red-back voles (*Clethrionomys* spp.), or red squirrels

(*Tamiasciurus hudsonicus*) (Jędrzejewski and Jędrzejewska 1992). We thus tested if red and Arctic fox den occupancies are influenced by the proximity to forested areas.

Model 4—shelter quality

In spring, foxes use dens as a shelter against harsh environmental conditions and to protect from predators (Eberhardt et al. 1983; Dalerum et al. 2002; Gallant et al. 2014). Dens can be used to rest while foxes disperse over long distances. In summer, foxes also need to protect their pups and avoid insect pests. We tested if foxes are choosing dens based on shelter accessibility, proximity of other dens, and physical characteristics.

First, we tested the performance of these models for each species and season (P1 and P2) separately using hurdle models (Cragg 1971; Zeileis et al. 2008; Hu et al. 2011). The hurdle model is a two-component model combining a zero-hurdle and a zero-truncated count data component. The zero-hurdle model gives information on why some dens are never used (Bayart and Bonnel 2012). The zero-truncated count data model gives information on the variables associated with the frequency of den use. We selected as link functions a binomial distribution in the zero-hurdle model and a zero-truncated Poisson distribution for the count data model, based on a likelihood ratio test and visual examination of rootograms. Models were built with standardized variables, excluding correlated variables from the same set (Spearman $\rho > 0.7$) (Taylor 1987). To choose between two correlated variables, we tested the influence of each variable on the model and retained the variable that had the strongest influence. For both seasons and all four competing models, we used the number of times a den was occupied as a response variable. The response variable was weighted by the number of years a den was assessed.

We selected the best-fit models using three steps. First, we used a backward stepwise regression process for each model to retain only the variables that explained den occupancy at the $p < 0.05$ significance threshold. Second, we compared each model using Akaike's information criterion (AIC) (Akaike 1974). Finally, we assessed the predictive ability of all models by measuring the area under the curve (AUC) of a receiving operating characteristic (ROC) curve on the logistic component (Hanley and McNeil 1982) and a k-fold cross-validation test (Fang et al. 2020) in R environment (R Core Team 2021) on both components. We produced $k = 4-7$ folds with 6-11 observations each to obtain folds with the closest proportion of zeros compared to the full dataset. We considered the predictive ability of our model acceptable if the average root-mean-square error (RMSE) of the k-fold test models was ≤ 2 (Chai and Draxler 2014).

We then used partial Mann-Kendall trend tests (Libiseller and Grimvall 2002) to evaluate if Arctic fox occupancy

decreased while red fox occupancy increased over the past 11 years, which could indicate the displacement of Arctic foxes by red foxes. We partialled out lemming density resulting from our long-term mark–recapture study because our fox population responds numerically to the abundance of arvicoline rodents (McDonald et al. 2017).

We used a generalized linear model using stats v.4.1.2 (R Core Team 2021) to determine whether interspecific competition and food abundance affected fox spacing (P4 and P5). We compared distances between fox neighbors and assessed the effect of fox pair type (Arctic–Arctic, Arctic–red, and red–red), season, and rodent abundance. We tested interactions between the type of fox pair, month, or lemming density, comparing models using likelihood ratio tests, but no interaction term was retained as they did not significantly improve our simplest model (2 interaction terms vs no interaction: $\chi^2 = 5.9$, $p = 0.21$). We considered distances between occupied dens up to 15 km, approximately 3 times the mean home-range diameter of red foxes in our study area (Warret Rodrigues and Roth 2022), and assumed the influence of a fox would be negligible beyond that 15 km threshold. We tested our models for outliers (Cook’s distance > 0.5) and visually assessed homoscedasticity, the correlation structure (due to a possible time-series effect) and the normality of our residuals (Zuur et al. 2010; Zuur and Ieno 2016). We report no issue with these diagnostics.

To determine if red foxes are outcompeting Arctic foxes for den use, we determined what proportion of dens left vacant were dens favored by red foxes. Similar to Tannerfeldt et al. (2002), we considered a den to be favored by red foxes when it was used at least twice by red foxes over the 11 years of the study.

All data handling, model diagnostics, graphs, and hurdle model analyses were performed using R (R Development Core Team 2019) in R Studio v. 2021.9.1.372 (RStudio Team 2021) with packages dplyr v. 1.0.7 (Wickham et al. 2021), ggplot2 v. 3.3.5 (Wickham 2016), ggpubr v.0.4.0 (Kassambara 2020), pscl v.1.5.2 (Jackman et al. 2017), vcd v.1.4.9 (Meyer et al. 2021), Hmisc v.4.4.1 (Harrell 2021), car v3.0.10 (Fox and Weisberg 2019), lme4 v.1.1.25 (Bates et al. 2015), trend v.1.1.4 (Pohlert 2015) and lmerTest v.3.1.3 (Kuznetsova et al. 2017).

Results

Characteristics of dens used in April by red and Arctic foxes

In April of 2011–2021, we observed an average of 4.5 dens (out of 42) occupied by red foxes ($SE = 0.7$), 6.1 by Arctic foxes ($SE = 1.3$), and we could not determine the species occupying 2.8 dens ($SE = 0.6$). The yearly total occupancy

rate (i.e., red, Arctic, and unknown foxes, excluding dens not assessed) averaged 0.37 ($SE = 0.04$). The occupancy rate of red foxes did not change over time ($S = -1.65$, $Z = 0.16$, $p = 0.871$), while the occupancy rate of Arctic foxes declined ($S = -27.93$, $Z = -2.22$, tailed $p = 0.028$) over the past 11 years (Fig. 2). Eight dens were favored by red foxes (used at least twice), and 52% ($SE = 8\%$) of those dens remained vacant each year, while 40% ($SE = 7\%$) were occupied by red foxes and 8% ($SE = 4\%$) were occupied by Arctic foxes (Table 2).

For both species, the best-supported model was shelter quality (Table 3). Red foxes primarily chose dens (logistic component) with more burrows oriented south or southeast, closer to the nearest den, with fewer dens within 5000 m, larger area, willows on top, a shallower snow depth, and less barren habitat within 1500 m than the dens never used (Table 4). Red foxes used dens more frequently (count model) that were closer to the nearest den, had fewer dens within 5000 m and no willow cover (Table 4). Arctic foxes selected (logistic component) dens with more burrows oriented south or southeast, shallower snow, and less barren habitat within 1500 m (Table 4). They used dens more frequently (count model) that had more burrows oriented south or southeast, were farther from the closest den, had more dens within 5000 m, smaller area, and a shallower snow depth on their surface (Table 4). However, although the shelter quality model had the highest support based on AIC, no model strongly predicted den occupation by Arctic foxes (logistic component; Table 3) and the average RMSE of all models was similar and performed adequately.

Although the food models had much higher AIC values (Table 3), some associated variables seemed to be important. Notably, the odds of a den being frequently used by Arctic foxes decreased strongly with increasing needleleaf forested habitat within 1500 m. Arctic foxes also seemed to favor the presence of a stream within 1500 m and shrubland–lichen–moss habitat. In contrast, red foxes used more frequently dens with forested habitat nearby, and they seemed to favor dryer habitats as indicated by the high odds ratio of the grassland–lichen–moss habitat and low odds ratio associated with stream length, proportion of wetland, and pond perimeter (Online Resource 2).

Characteristics of dens used in August by red and Arctic foxes

In August of 2011–2021, we observed an average of 3.6 dens (out of 42) occupied by red foxes ($SE = 0.9$) and 4.6 by Arctic foxes ($SE = 0.9$), and we could not determine the species occupying 3.9 dens ($SE = 0.7$). The yearly occupancy rate (i.e., red, Arctic, and unknown foxes, excluding dens not assessed) averaged 0.29 ($SE = 0.03$). The proportion of tundra dens used by red foxes strongly increased over time

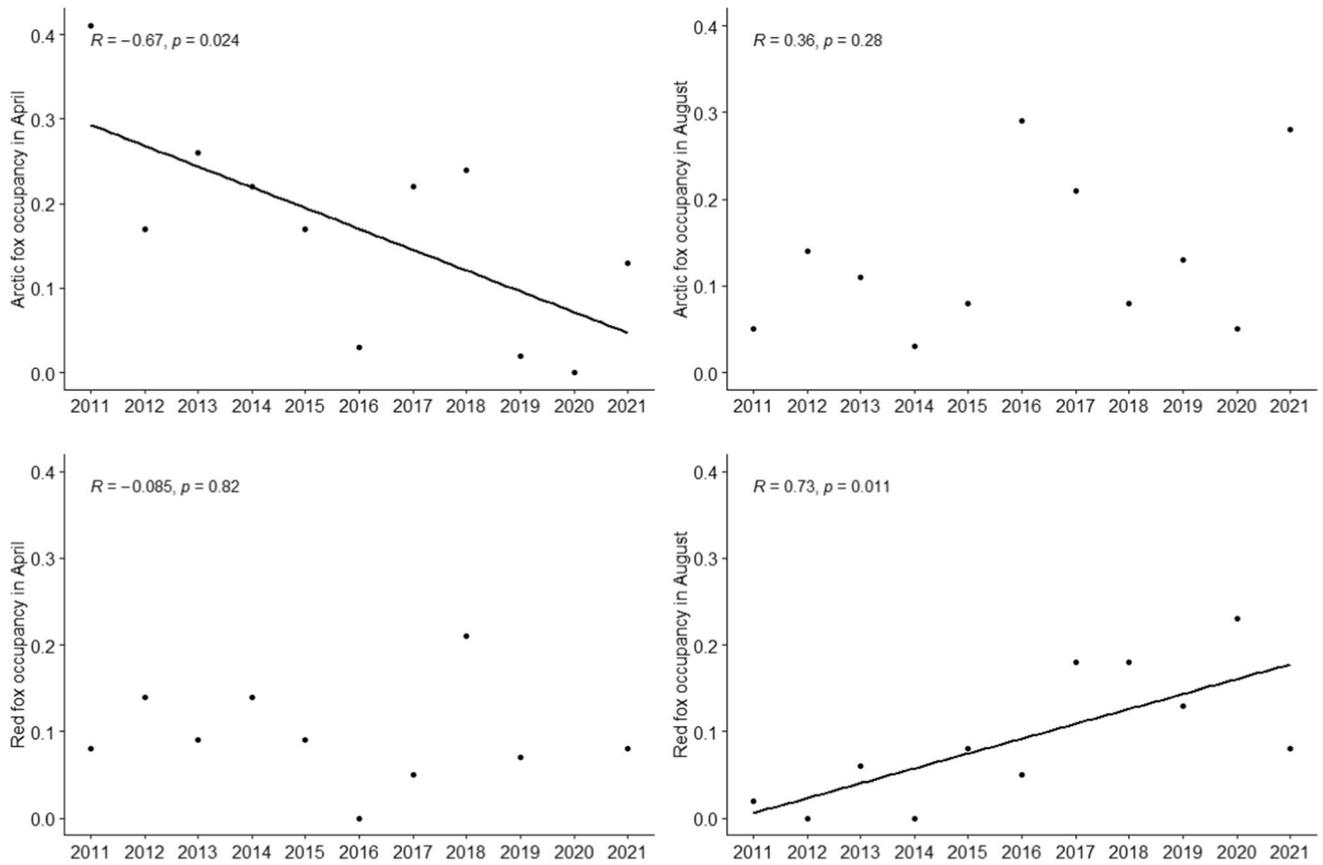


Fig. 2 Den occupancy (proportion of dens) by red foxes (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) in April and August from 2011–2021. Arctic fox occupancy in April decreased over time but

August occupancy was stable, while red fox occupancy in April was stable and increased in August

Table 2 Proportion of dens favored by red foxes (*Vulpes vulpes*) (i.e., occupied at least twice by red foxes between 2011 and 2021) occupied by Arctic foxes (AF) (*Vulpes lagopus*), occupied by red foxes (RF) and left vacant (including used by unknown species) in April and in August each year, plus annual lemming densities (ha^{-1}) estimated from 3 live-trapping grids

Year	April				August				Lemming density
	N	AF	RF	Vacant	N	AF	RF	Vacant	
2011	7	0.43	0.43	0.14	10	0.10	0.10	0.80	0.35 ($SE=0.20$)
2012	7	0.00	0.57	0.43	9	0.11	0.00	0.89	1.74 ($SE=1.00$)
2013	8	0.00	0.38	0.62	10	0.00	0.20	0.80	1.92 ($SE=0.87$)
2014	7	0.00	0.57	0.43	9	0.00	0.00	1.00	0.60 ($SE=0.32$)
2015	7	0.29	0.29	0.43	9	0.00	0.22	0.78	0.00 ($SE=0.00$)
2016	2	0.00	0.00	1.00	8	0.00	0.25	0.75	0.23 ($SE=0.23$)
2017	8	0.13	0.12	0.75	9	0.00	0.78	0.22	1.99 ($SE=0.75$)
2018	7	0.00	0.57	0.43	9	0.00	0.67	0.33	1.44 ($SE=0.44$)
2019	8	0.00	0.25	0.75	10	0.10	0.30	0.60	0.93 ($SE=0.46$)
2020	6	0.00	0.83	0.17	10	0.00	0.60	0.40	0.69 ($SE=0.69$)
2021	8	0.00	0.37	0.63	8	0.13	0.13	0.75	1.62 ($SE=1.01$)

N number of favored dens assessed each year

($S=28.96$, $Z=2.29$, $p=0.022$), while there was no change in the proportion of dens used by Arctic foxes ($S=12.24$, $Z=1.13$, $p=0.258$) over the 11 past years (Fig. 2C and 2D). Among the 10 dens favored by red foxes, 67% ($SE=7\%$) remained available each year, 29% ($SE=8\%$) were occupied

by red foxes and 4% ($SE=2\%$) were occupied by Arctic foxes (Table 2).

The shelter quality model again performed best in terms of AIC for both species (Table 3). However, based on AUC, the tundra food model performed slightly better to predict

Table 3 Comparison of performance of 4 hurdle models on den selection in April and August for Arctic foxes (*Vulpes lagopus*) and red foxes (*Vulpes vulpes*) in northern Manitoba, Canada, between 2011 and 2021

	Model	AIC	Δ AIC	AUC	Mean RMSE	Folds with RMSE > 2
Arctic fox April	Shelter quality	816	0	0.56	2	Yes
	Tundra food	1165	350	0.60	2	No
	Forest food	1196	381	0.57	2	No
	Coastal food	1224	408	0.55	2	No
Red fox April	Shelter quality	391	0	0.92	2	Yes
	Tundra food	555	164	0.88	2	Yes
	Coastal food	814	423	0.63	2	Yes
	Forest food	966	575	0.51	2	No
Arctic fox August	Shelter quality	684	0	0.85	2	Yes
	Tundra food	918	234	0.94	2	Yes
	Forest food	1096	413	0.83	2	No
	Coastal food	1260	576	0.66	2	No
Red fox August	Shelter quality	536	0	0.89	1	No
	Tundra food	828	292	0.81	2	No
	Forest food	1078	542	0.59	1	No
	Coastal food	1087	551	0.70	1	No

Indices of performance used: Akaike information criterion (AIC), area under the curve (AUC; zero component of the hurdle model), mean root-mean-square error of the k-fold cross-validation (RMSE), and we reported if any of the folds yielded a RMSE > 2

den occupancy by Arctic foxes (logistic component; Table 3) than the shelter quality model. We gave priority to the AIC, because the AUC only applies to the logistic component of the model, and both models (shelter quality and tundra food) had the same RMSE. We thus acknowledge that the probability of a den being occupied by an Arctic fox may also depend on the proximity of some landscape features associated with rodents. The general predictive ability of all models tested was good for red foxes and acceptable for Arctic foxes.

Dens occupied by red foxes in August (logistic component) were closer to the nearest den, had a larger area, willow on top, shallower snow in spring and less barren habitat within 1500 m (Table 4). Red foxes more frequently (count model) occupied dens closer to the nearest den, with fewer dens within 5000 m, a larger area and less barren habitat within 1500 m. (Table 4). A few variables from the food models seemed to strongly affect red foxes' use of dens. Notably, they avoided streams, pond banks, and had higher odds of using dens near forested habitats (Online Resource 3).

Arctic foxes occupied dens (logistic component) closer to the nearest den, with more dens within 5000 m, a larger area, less snow depth in spring and more barren habitat within 1500 m. Arctic foxes more frequently occupied dens (count model) with more dens within 5000 m, a larger

area, without willow cover, and with more barren habitat within 1500 m. Like for red foxes, some variables associated with our food models impacted the odds of Arctic foxes using a den. Notably, the odds of a den being used by Arctic foxes decreased strongly with more intertidal flats within 1500 m. They also favored dens farther from the forested areas, and with shorter length of stream within 1500 m (Online Resource 3).

Spacing patterns to assess interference competition

Over the study period, in August, the shortest distance between a red fox den and an Arctic fox den was 2.3 km, in the northern part of our study area. We recorded similarly short distances multiple years at lemming densities varying from 0 to 1.62 rodents ha⁻¹ (Table 2) and even more frequently at higher lemming densities. In April, the shortest distance between dens occupied by neighboring red and Arctic foxes was 1.3 km at high lemming density (3.2 km for a low-rodent year—i.e., < 1 lemming ha⁻¹), also in the northern part of our study area (dens visited the same day, fresh sign). The average distance between homospecific Arctic fox pairs was 5.4 km and was significantly lower than heterospecific fox pairs (7.5 km; $t_{432} = 7.04$, $p < 0.001$) and homospecific red fox

Table 4 Detailed results of den selection models with the lowest AIC (shelter quality model) for red (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) between 2011 and 2021, in April and August

	Model	Variable	Coefficient	SE	Odds ratio	CI 2.5–97.5	z value	p value
Arctic fox April	Count	(Intercept)	−0.10	0.12	0.90	0.72–1.14	−0.86	0.39
	Count	Burrows oriented S-SE	0.23	0.06	1.26	1.11–1.42	3.64	<0.001
	Count	Distance to the nearest den	0.34	0.08	1.40	1.20–1.63	4.38	<0.001
	Count	Number of dens within 5000 m	0.54	0.08	1.72	1.48–1.99	7.11	<0.001
	Count	Surface area	−0.73	0.12	0.48	0.38–0.61	−6.10	<0.001
	Count	Snow depth	−1.01	0.18	0.36	0.26–0.52	−5.65	<0.001
	Zero	(Intercept)	1.31	0.17	3.70	2.67–5.12	7.90	<0.001
	Zero	Burrows oriented S-SE	0.60	0.16	1.82	1.32–2.51	3.65	<0.001
	Zero	Snow depth	−1.24	0.23	0.29	0.18–0.46	−5.32	<0.001
	Zero	Barren habitat	−1.12	0.21	0.32	0.22–0.49	−5.39	<0.001
Red fox April	Count	(Intercept)	0.07	0.19	1.07	0.73–1.56	0.35	0.73
	Count	Distance to the nearest den	−0.72	0.11	0.48	0.39–0.60	−6.46	<0.001
	Count	Number of dens within 5000 m	−0.70	0.17	0.50	0.35–0.70	−4.01	<0.001
	Count	Willow on top	−0.44	0.09	0.65	0.54–0.77	−4.81	<0.001
	Zero	(Intercept)	0.32	0.62	1.38	0.41–4.66	0.51	0.61
	Zero	Burrows oriented S-SE	3.41	1.19	30.21	2.95–309.50	2.87	<0.001
	Zero	Distance to the nearest den	−3.16	0.85	0.04	0.01–0.23	−3.70	<0.001
	Zero	Number of dens within 5000 m	−3.81	1.03	0.02	0.00–0.17	−3.70	<0.001
	Zero	Surface area	2.90	0.92	18.18	3.01–109.97	3.16	<0.001
	Zero	Willow on top	4.48	1.19	88.61	8.59–914.02	3.77	<0.001
	Zero	Snow depth	−12.38	3.45	0.00	0.00–0.00	−3.59	<0.001
	Zero	Barren habitat	−3.06	0.95	0.05	0.01–0.30	−3.22	<0.001
Arctic fox August	Count	(Intercept)	−0.52	0.17	0.60	0.43–0.84	−3.00	<0.001
	Count	Number of dens within 5000 m	1.02	0.11	2.77	2.23–3.45	9.11	<0.001
	Count	Surface area	0.88	0.12	2.41	1.89–3.07	7.14	<0.001
	Count	Willow on top	−0.46	0.09	0.63	0.53–0.76	−5.03	<0.001
	Count	Barren habitat	0.56	0.14	1.75	1.33–2.30	3.99	<0.001
	Zero	(Intercept)	0.70	0.21	2.01	1.32–3.04	3.28	<0.001
	Zero	Distance to the nearest den	−0.59	0.19	0.55	0.38–0.80	−3.17	<0.001
	Zero	Number of dens within 5000 m	2.65	0.39	14.10	6.58–30.21	6.81	<0.001
	Zero	Surface area	1.40	0.27	4.05	2.39–6.84	5.21	<0.001
	Zero	Snow depth	−1.80	0.31	0.17	0.09–0.31	−5.77	<0.001
	Zero	Barren habitat	0.69	0.18	1.99	1.41–2.82	3.89	<0.001
	Red fox August	Count	(Intercept)	−1.42	0.35	0.24	0.12–0.48	−4.08
Count		Distance to the nearest den	−0.29	0.15	0.75	0.56–1.00	−1.97	0.05
Count		Number of dens within 5000 m	−1.02	0.37	0.36	0.17–0.75	−2.73	0.01
Count		Surface area	1.14	0.20	3.12	2.10–4.63	5.64	<0.001
Count		Barren habitat	−0.47	0.14	0.62	0.47–0.82	−3.40	<0.001
Zero		(Intercept)	−0.06	0.16	0.94	0.68–1.29	−0.39	0.69
Zero		Distance to the nearest den	−0.57	0.16	0.57	0.41–0.78	−3.49	<0.001
Zero		Surface area	1.25	0.21	3.48	2.32–5.23	6.01	<0.001
Zero		Willow on top	1.25	0.19	3.50	2.39–5.12	6.45	<0.001
Zero		Snow depth	−0.90	0.23	0.41	0.26–0.64	−3.91	<0.001
Zero		Barren habitat	−0.63	0.17	0.53	0.38–0.74	−3.73	<0.001

pairs (7.7 km $t_{432} = 4.61$, $p < 0.001$). The difference in the average distance between individuals from homospecific red fox pairs and heterospecific pairs was not significant ($t_{432} = -0.96$, $p = 0.337$). Distance between neighboring foxes decreased when lemming abundance increased ($t_{432} = -2.10$, $p = 0.036$), but remained similar between seasons ($t_{432} = -1.14$, $p = 0.25$).

Discussion

Although the high ecological similarity of sympatric red and Arctic foxes could induce strong exploitation competition, the fine-scale mechanisms driving den selection may differ enough to promote coexistence, at least at low densities. Red foxes, contrary to our expectations, did not switch strategies for selecting dens at drastically different prey abundances across seasons. Both species selected dens to occupy based on physical criteria rather than their proximity to landscape features associated with specific prey types, but the physical variables driving den selection differed by species. Furthermore, a large proportion of the dens favored by red foxes remained available each year, suggesting that red foxes did not exclude Arctic foxes from these specific dens. Finally, both species tolerated each other in close proximity, further evidence that interference competition between these species is low in the Canadian Arctic, unlike in Eurasia (Tannerfeldt et al. 2002; Rodnikova et al. 2011; Lai et al. 2022).

Carnivore spatial and social strategies depend on resource availability (MacDonald 1983; Eide et al. 2004). Tundra summers are characterized by a sudden short-term burst of resource availability (Tannerfeldt and Angerbjörn 1998; Eide et al. 2004): over 200 species of migratory birds nest in our study area, and a high density of nests is widely distributed throughout the landscape (Ballantyne and Nol 2011; McDonald et al. 2017). Although foxes mainly feed on arvicoline rodents, they respond functionally to the high abundance of migratory birds (McDonald et al. 2017). In summer, food is homogeneously distributed and abundant in our study area, it is not a limiting resource, and dens have thus the same attractivity regarding food availability. Thus, as expected (P2) food proximity did not drive den selection in August for either species. Instead, foxes favored shelter characteristics, which we also expected given vulnerable pups are present in dens throughout summer (Tannerfeldt et al. 2002), as well as diverse predators (eagles, three bear species, wolves, wolverines) and pests.

However, at the beginning of the fox breeding season, food sources are scarce on the tundra. On Herschel Island, Yukon, red foxes selected dens with better tundra food access in spring, and Arctic foxes always favored physical

shelter characteristics (Gallant et al. 2014). Differences in prey abundance and distribution between Herschel and our study area may explain the difference in red foxes' den selection criteria. On Herschel Island, brown lemmings inhabiting the low-elevation humid habitats can peak at 60 lemmings ha^{-1} , thus creating rodent hot spots for foxes because these habitats represent only 1% of the island (Lai et al. 2022). Such hot spots of spring resources are unlikely to occur in our study area, where rodent density is continuously low (Table 2) and where rodents occupy the most abundant habitats (coastal fen) in spring (Dobroski 2022). The low Arctic is subjected to more melt-freeze cycles, which are highly detrimental to small mammals, rendering winter conditions in our study area even harsher than in the high Arctic. Thus, tundra food access may become secondary to shelter quality if most dens provide similar access to prey.

When primary-prey abundance is low, Arctic foxes may use the sea ice, despite higher mortality rates associated with leaving a home range (Roth 2002; Lai et al. 2017; Warret Rodrigues and Roth 2022). Availability of marine resources is highly unpredictable (Roth 2002), and Arctic foxes can commute up to 40 km to the sea ice in short extraterritorial trips to access marine-mammal carcasses without risking losing their home ranges (Lai et al. 2015). In addition, foxes may share concentrated abundant food resources (Tsukada 1997; Eide et al. 2004; Lai et al. 2015). The low performance of coastal-food models in explaining den selection is thus unsurprising.

Like in Scandinavia, our fox populations are close to tree-line, and red foxes tended to select dens closer to forested habitats more often than Arctic foxes (Linnell et al. 1999; Dalerum et al. 2002; see Table S1). Tree patches should constitute a prized resource for red foxes: they are home to taiga prey such as snowshoe hares and red squirrels and offer milder conditions in this otherwise harsh region (Ponomarenko et al. 2014). However, the proximity of treeline did not drive den selection for red foxes. These red foxes are an edge population and are thus challenged by the scarce availability of preferred habitat, the low availability of food, and their tolerance limits for abiotic conditions (Romeo et al. 2010; Niedzielski and Bowman 2016). Intraspecific competition in red foxes is likely strong, thus red foxes inhabiting tundra dens may be the losers of that intraspecific competition, relegated into suboptimal habitats, forcing them to prioritize the shelter characteristics of the dens, especially in April when winter conditions remain on the tundra. Our treeless study area is dominated by the low hypoarctic tundra and is colder than the other bioclimatic zones in the region because it is strongly influenced by the cooling effect of Hudson Bay (Ponomarenko et al. 2014). The odds of a red fox using a den increased by 30 for each additional burrow oriented to the south or southeast (burrows likely thawing

first when obstructed by ice), supporting the idea that red foxes likely chose dens that can shelter them from the north winds sweeping in from Hudson Bay.

Tundra food access was always secondary to shelter quality for red foxes and Arctic foxes in both seasons based on AIC, but the AUC values (logistic component) suggested the tundra food model performed slightly better than shelter quality for Arctic foxes in April and August. These results suggest that Arctic foxes may select dens using multiple criteria (for example, their choice may be equally influenced by shelter quality and food availability), or that we did not identify crucial variables that drive den selection in this species. For example, we could not differentiate between settled residents and transient foxes, which could have different needs and priorities for den use. Foxes in our study area disperse from their home ranges in spring in search of better conditions more frequently than in the high Arctic (Warret Rodrigues and Roth 2022; Lai et al. 2017), and Arctic fox occupancy in April, at the beginning of the breeding season, decreased over time, suggesting the low hypoarctic tundra zone is not a favorable zone to settle in spring and Arctic foxes may leave the area to find other sources of food. Red fox den occupancy increased over time only in summer, not at the beginning of the breeding season, suggesting red foxes living at the edge of their distribution may be reluctant to settle in the area in spring.

Willows on the den surface played apparently contradictory roles in the shelter quality model for red foxes in April. When willows were present, the odds of a red fox using a den were 89 times higher than when willows were absent, but among dens used, the presence of willows on top lowered the odds of frequent use by 35%. Although the willows retain snow, which could improve insulation and provide better lemming habitat, the odds of a red fox using a den decreased by nearly 100% per meter increase of snow depth. Foxes are ecosystem engineers: through their activities (digging, excreting, bringing prey carcasses) they concentrate soil nutrients and modify the vegetation composition on dens, notably favoring the growth of shrubs like willows (Gharajehdaghpour et al. 2016; Fafard et al. 2020). The growth of willows in specific dens likely results from their intensive use for decades, possibly over centuries (Macpherson 1969). As a result, this variable in the logistic component of our models may simply reflect the general quality and attraction level of particular dens. As the willows grow, they accumulate more snow during winter, which may make these dens less accessible and therefore less attractive for red foxes over time.

Several studies have suggested that red and Arctic foxes behave with flexibility regarding territoriality (Tsukada 1997; Strand et al. 2000; Goszczyński 2002; Eide et al. 2004). Elsewhere in the Arctic, territoriality was often a key determinant of den selection by Arctic foxes, which preferred

isolated dens (Linnell et al. 1999; Dalerum et al. 2002; Szor et al. 2008; Gallant et al. 2014). Clumped and random-spacing occupancy patterns have also been observed, likely due to topographic features reducing the availability of good denning sites (Fine 1980; Prestrud 1992; Anthony 1996). In our area, Arctic foxes preferred clumped dens, but red foxes disliked dens in aggregations despite favoring a shorter distance to the nearest den. Clumps of dens, although they may attract competitors, allow foxes to split and relocate litters, a practice that may have evolved as an anti-predatory behavior and to lower parasitic loads (Kilgore 1969; Prestrud 1992; Anthony 1996). As mentioned above, larger predators are numerous in our area, likely driving our foxes to prioritize anti-predatory strategies. Red foxes may have adopted an intermediate strategy, avoiding clumped dens to reduce interactions with possible competitors, but still favoring sites that facilitate litter split and relocation to avoid predation and parasitic overload.

Denning distances between heterospecific-fox pairs, both average and minimum, were lower than in Scandinavia (Tanerfeldt et al. 2002) and similar to observations in the Canadian high Arctic, where the minimal distance between breeding red and Arctic foxes was also 2.3 km (Lai et al. 2022). Furthermore, like in the high Arctic (Gallant et al. 2014), previous occupation by a red fox does not deter Arctic foxes, even during the same season (Johnson-Bice et al. 2023). Finally, only a small proportion of dens favored by red foxes are in use each year, suggesting that Arctic foxes are not excluded from high-quality dens. Contrary to our predictions (P3 and P4), season did not affect the average distance between neighbors, and although the distance between homospecific Arctic fox neighbors was shorter than between heterospecific neighbors (as we expected), distance between homospecific red fox neighbors was not. This spacing pattern suggests competition for space and territoriality, but not interference. Red foxes cope with the harsh winter weather by increasing their basal metabolic rate to expand their thermoneutral zone, which also increases their energetic requirements (Fuglesteig et al. 2006; Careau et al. 2007). Over-wintering on the low-Arctic tundra presents challenges for red foxes, as most red foxes had to leave the area altogether in search of milder conditions, while the remaining residents ranged nearly twice as much in winter compared to summer (Warret Rodrigues & Roth 2022). Resident Arctic foxes, in contrast, maintained a similar ranging behavior year-round. The spacing patterns of den occupancy we observed seem to be driven by the red fox's need for space: the average distance between dens occupied by red foxes and neighbors of both species were similar, corresponding approximately to the diameter of a red fox winter home range (~6.7 km; Warret Rodrigues and Roth 2022). Red foxes seem to be more sensitive to the nearest neighbors, regardless of species, than Arctic foxes. The lack of seasonal effect on neighbor

distance could be caused by increased territoriality, and generally lower tolerance for congeners and conspecifics, due to the presence of pups (Tannerfeldt et al. 2002).

Red and Arctic foxes differ in their fine-scale den selection criteria, which likely help relax exploitation competition over denning sites and we did not find evidence of interference competition. In partial agreement with P5, red fox occupancy has increased in August, while Arctic fox occupancy at the end of the breeding season has remained stable, suggesting that currently red foxes are not excluding Arctic foxes. Coexistence mechanisms are widespread and usually involve some sort of segregation, including resource segregation (Ritchie 2002). Our study demonstrates that, under some favorable circumstances, resource segregation can result from fine-scale differences in competitors' realized niches. Taiga species settling on the tundra ("newcomers"), could thus coexist with their tundra competitors, at given densities of both competitors. Under the current Arctic conditions, the abiotic factors and low density of the settling species may still induce stronger intraspecific competition compared to interspecific competition, thus favoring the long-term coexistence of newcomers and native tundra species (Amarasekare 2003; Banks et al. 2006). Milder abiotic conditions resulting from Arctic warming may relax intraspecific competition over key resources for newcomers and thus increase interspecific competition (especially if the abundance of newcomers increases) thus disrupting the current balance that favors species coexistence. In that context, our study provides a starting point to monitor the changes in species relationships that could result from climate change.

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Author contributions AM and CWR conceived and designed the study; all authors collected the data; JDR secured the funding; AM and CWR analyzed the data; AM led the writing, with critical contributions from CWR and JDR. All authors read and approved the final manuscript.

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Data availability Data are available on the Mendeley Data repository. <https://data.mendeley.com/datasets/53kgyy3rth/1>

Declarations

Conflict of Interest We have no conflicts of interest to disclose.

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