



# Arctic and red fox population responses to climate and cryosphere changes at the Arctic's edge

Jacqueline S. Verstege<sup>1</sup> · Sean M. Johnson-Bice<sup>1</sup> · James D. Roth<sup>1</sup>

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## Abstract

Responses of one species to climate change may influence the population dynamics of others, particularly in the Arctic where food webs are strongly linked. Specifically, changes to the cryosphere may limit prey availability for predators. We examined Arctic (*Vulpes lagopus*) and red fox (*V. vulpes*) population dynamics near the southern edge of the Arctic fox distribution using fur harvest records from Churchill, Manitoba, Canada between 1955 and 2012. Arctic foxes showed a declining population trend over time (inferred from harvest records corrected for trapping effort), whereas the red fox population trend was relatively stable. The positive relationship between the annual Arctic and red fox harvests suggested interspecific competition did not promote the Arctic fox decline. To investigate alternative mechanisms, we evaluated the relative influence of sea-ice phenology, snow depth, snow duration, winter thaws, and summer temperature on the harvest dynamics of both species in the most recent 32 years (1980–2012;  $n = 29$ ) of our data. Arctic fox harvests were negatively related to the length of time Hudson Bay was free of sea ice. Shorter sea ice duration may reduce access to seal carrion as an alternative winter food source when lemming densities decline. Contrary to our prediction, red fox harvest was not related to summer temperature but was positively related to snow depth, suggesting winter prey availability may limit red fox population growth. Predators have an important ecological role, so understanding the influence of changes in the cryosphere on predator–prey interactions may better illuminate the broader influence of climate change on food-web dynamics.

**Keywords** Harvest · Predator population dynamics · Sea ice · Snow · *Vulpes lagopus*

## Introduction

Climate warming is disproportionately intense in polar and mid-latitudes, with even more extreme warming recently (Post et al. 2009; Tang et al. 2014; Huang et al. 2017). This warming may allow the range expansion of species previously limited by historical climate conditions (Parmesan and Yohe 2003). Further, a warming climate has instigated changes to the cryosphere, including reduced snow and sea ice cover and extent across the Northern Hemisphere (Brown et al. 2010; Comiso 2012; Lunn et al. 2016). These alterations to the climate and cryosphere can impact northern species that rely on snow and sea ice as an important winter

habitat (Kausrud et al. 2008; Lunn et al. 2016). As such, climate can significantly impact trophic interactions, and rapid changes in climate can produce predicted or unanticipated effects on the organization and function of an ecosystem (Sala et al. 2000; Tylianakis et al. 2007).

Arctic foxes (*Vulpes lagopus*), an ecologically important predator in the Arctic, may be impacted by changes in climate within the southern extent of their range. Warming temperatures and a longer growing season are mechanisms that predict further range expansion of southern species into the Arctic (Post et al. 2009). The southern edge of the Arctic fox and the northern extent of red fox (*V. vulpes*) ranges overlap, but a warming climate may support a growing red fox population, generating greater resource competition between the two species (Frafjord et al. 1989; Tannerfeldt et al. 2002; Rodnikova et al. 2011). Red foxes are larger than Arctic foxes and can both overtake their dens and kill Arctic foxes (Elmhagen et al. 2017). An increase in red fox abundance may promote population declines of Arctic foxes.

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✉ James D. Roth  
jim.roth@umanitoba.ca

<sup>1</sup> Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

Another important driving force of predator population dynamics is food availability. The reproductive success of Arctic foxes over much of their range is positively related to lemming density (Angerbjörn et al. 1999, MacDonald et al. 2017), with high juvenile mortality in low lemming years (Tannerfeldt and Angerbjörn 1998; MacDonald et al. 2017; Samelius and Alisauskas 2017). Although the red fox diet may be more generalized, a large portion of their diet consists of rodents, similar to the Arctic fox, which may cause high dietary overlap between sympatric Arctic and red foxes (Elmhagen et al. 2002; Warret Rodrigues 2022).

Climate change may also influence predator population dynamics through altered prey habitats and consequently the availability of prey. Recently, rodents in northern Manitoba and other low Arctic areas have experienced dampened population fluctuations (Ehrich et al. 2020). Northern rodents, such as lemmings, may benefit from greater snow duration, increased snow depth, fewer winter thaws, and warmer summers (Shelford 1943; Pruitt 1970; Kausrud et al. 2008; Bilodeau et al. 2013a,b). Since tundra rodents primarily live and breed in the subnivean layer, persistent and high-quality snow that provides insulation, access to food or other resources may benefit lemmings by providing habitat conditions that promote population growth (Pruitt 1970; Fauteux et al. 2015). Snow quality characteristics are strongly influenced by weather conditions (wind, precipitation, and temperature); therefore, annual weather patterns may also provide insight into the conditions of subnivean space for rodents (Pruitt 1970; Callaghan et al. 2011). Changes in weather and reduction in snow quality may further limit suitable rodent winter habitats and reduce population growth through lower winter survival and reproduction (Kausrud et al. 2008; Callaghan et al. 2011; Dushesne et al. 2011; Fauteux et al. 2015).

In years of low lemming density, alternative prey are important resources for foxes (Roth 2002, 2003; MacDonald et al. 2017; Dudenhoefter et al. 2021). In summer, migratory birds such as geese can be an important alternative prey source for Arctic and red foxes (MacDonald et al. 2017; Warret Rodrigues 2022). However, the availability of these prey may also be affected by changes in the cryosphere, as goose reproductive success and the timing of goose nesting have been negatively related to the persistence of snow cover and spring conditions (Reed et al. 2004; Madson et al. 2007). In winter, seals are an important cross-ecosystem resource subsidy for Arctic foxes (Smith 1976; Roth 2002; Tarroux et al. 2012), which may help stabilize their population (Roth 2003; Nater et al. 2021). Smith (1976) estimated that 21–58% of newborn ringed seal (*Pusa hispida*) pups were preyed upon by Arctic foxes, and marine species have also been documented in the red fox diet in the Arctic (Killengreen et al. 2011; Warret Rodrigues 2022). Reduced access to sea ice can also reduce the abundance of seal predators, such as

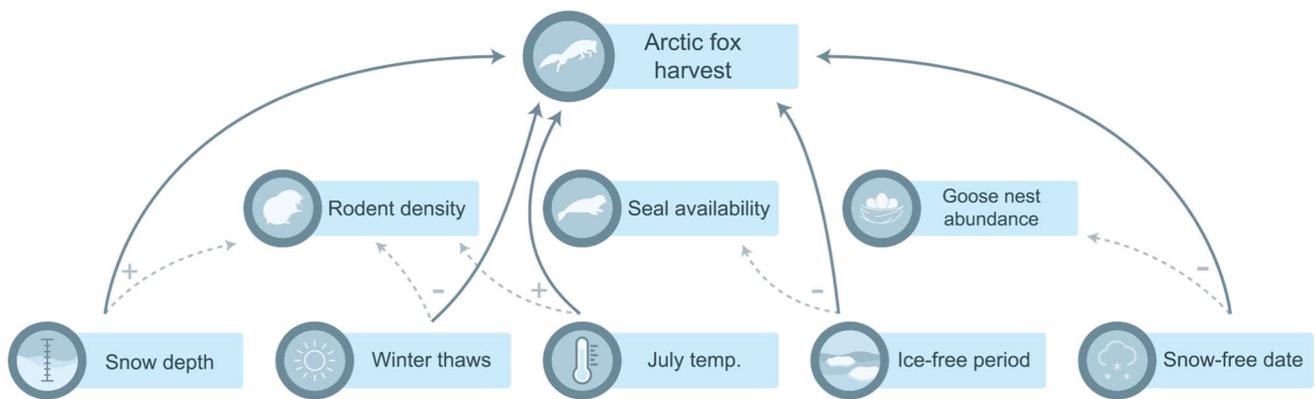
polar bears (*Ursus maritimus*), which are blubber specialists whose diet primarily consists of seals (Stirling and McEwan 1975; Lunn et al. 2016). As polar bears often just consume blubber and leave the remainder of seal carcasses, foxes can scavenge abandoned seal carcasses (Stirling and McEwan 1975).

The objectives of our study were to evaluate population trends of Arctic foxes and red foxes in the southern Arctic—where the effects of climate change may be particularly strong—and investigate how environmental characteristics may affect fox population dynamics. If climate change negatively impacts Arctic foxes at the southern edge of their range, we would expect a decrease in Arctic fox abundance and an increase in red fox abundance over time, and thus we predicted a negative relationship between Arctic and red fox abundance. We also predicted a positive relationship with climate and snow variables associated with higher rodent density, seal carrion availability, and goose nest survival for Arctic foxes (Fig. 1). These variables include increased snow depth, fewer winter thaws, warmer summers, shorter sea ice-free period, and shorter snow persistence in late spring. As red foxes have a more generalized diet, we predicted a weaker relationship with climate variables associated with higher food availability and a stronger relationship with a warming climate, including warmer summers and earlier snow-free dates. Predators have a vital ecological role, so understanding how climate, directly and indirectly, influences fox populations will contribute to a broader understanding of the impact of climate change on Arctic species.

## Methods

### Study area

Our study area near Churchill, Manitoba, Canada (58° N, 94° W), occurs at the intersection of three biomes: the marine biome of Hudson Bay, the Arctic tundra along the western shore of Hudson Bay, and the inland boreal forest. Hudson Bay remains frozen for up to 9 months of the year and has a strong influence on the surrounding habitat (Rouse 1991). However, the annual sea ice duration in Hudson Bay has been shortened recently by a trend of ~0.8 days per year (Gagnon and Gough 2005). Churchill tundra contains relic sand or gravel beach ridges, formed by isostatic rebound, that are often used by Arctic foxes to construct dens (Ritchie 1957; Dredge 1992; Roth 2003; Johnson-Bice et al. 2022). Fox dens are conspicuous on these ridges because of the lush vegetation promoted by nutrient enhancement and small-scale disturbances (Roth 2003; Gharajehdaghipour et al. 2016). Historically, red foxes in this area primarily den inland within the forest (Roth 2003), but their use of tundra dens along the coast has increased since 2010, with



**Fig. 1** A conceptual figure illustrating the hypothetical influence of the climate variables on the harvest dynamics of Arctic foxes (solid lines) and their prey (dotted lines). Climate variables included were the average daily snow depth during the month of February ('snow depth') of the previous year, the number of days during winter (November–April) where the maximum temperature recorded

was  $> 0$  °C ('winter thaws'), the number of days where Hudson Bay was considered to be ice-free ('ice-free period'), the average daily mean temperature for the month of July ('mean July temp'), and the last ordinal day of spring when snow was present on the ground ('snow-free date')

up to 22% of these tundra dens now occupied by red foxes in some years (Zhao et al. 2022; Moizan et al. 2022).

Collared lemmings (*Dicrostonyx richardsoni*), the most common species of rodent in our study area, are important prey for Arctic foxes (Roth 2002, 2003; McDonald et al. 2017; Dudenhoefter et al. 2021). Fox and lemming populations in the area historically cycled regularly, but peak lemming densities have declined over time, from 40  $\text{ha}^{-1}$  in the 1930s to 12  $\text{ha}^{-1}$  in the 1990s to 2  $\text{ha}^{-1}$  in the 2010s (Shelford 1943; Roth 2002; Ehrich et al. 2020).

## Data sources

We used the number of Arctic foxes and red foxes commercially harvested in the Churchill Registered Trapline Section during the trapping season (November–March) to reflect annual fox abundance from 1955 to 2012 (harvest and license numbers were available for 56 years during that time span; subsequent changes in reporting methods by auction houses precluded including later years). We also obtained the number of trapper permits issued annually in Churchill (range 12–117 permits) and the mean annual auction value of an Arctic fox pelt sold in Manitoba, adjusted for inflation (range: \$13.10–\$165.55; Statistics Canada 2022), and used these values to correct for annual variation in permitted trappers and financial incentive (Cattadori et al. 2003; Dorendorf et al. 2016). In our study area, Arctic fox harvest in winter strongly reflects the reproductive success of the previous summer (McDonald et al. 2017), as a large proportion of harvested canids are juveniles (Wapenaar et al. 2012; Friesen et al. 2015). Because of their large litters (average litter size in Canada is 10; Macpherson 1969) and low adult survival (average lifespan is 3–4 years; Audet et al. 2002),

reproductive output strongly drives Arctic fox population dynamics (Tannerfeldt and Angerbjörn 1998; Samelius and Alisauskas 2017).

We evaluated the role of five independent climate variables on the population dynamics of the Arctic and red foxes in Churchill: (1) average daily snow depth during the month of February ('snow depth'), (2) the number of days during winter (November–April) where the maximum temperature recorded was  $> 0$  °C ('winter thaws'), (3) the average daily mean temperature for the month of July ('mean July temp'), (4) the number of days where Hudson Bay was considered to be ice-free ('ice-free period'), and (5) the last ordinal day of spring when snow was present on the ground ('snow-free date'). All of the climate variables with the exception of the 'ice-free period' were obtained from Environment Canada's Churchill weather station (Environment Canada 2022). We obtained data on the length of time Hudson Bay was effectively ice-free from Boonstra et al. (2020). Satellite imagery from the National Snow and Ice Data Center (Boulder, Colorado, USA) was used to calculate the percentage of daily ice coverage in Hudson Bay. The 'ice-free period' was calculated as the number of days between break-up (the ordinal date where  $> 50\%$  of all sea ice pixels had been disintegrated for 3 consecutive days) and freeze-up (the ordinal date where  $> 10\%$  of all pixels were identified as sea ice for  $\geq 3$  consecutive days) (Stirling and Parkinson 2006; Cherry et al. 2013; Boonstra et al. 2020). Each of these variables was lagged 1 year prior to the harvest year.

## Rationale for climate variables

Mean snow depth in February and mean temperature in July were selected to represent winter and summer climates as

these months represent the extremes in annual weather (Woo and Ohmura 1997). Further, mean July temperature has been related to vascular plant growth and can represent a large proportion of the growing season for Arctic plants (Scott et al 1988; Jonasson et al. 1999; Buchwal et al. 2013). A similar study conducted by Gallant et al. (2020) used mean February snow depth and mean temperature in July to represent winter and summer climates related to fox harvest records. We estimated winter thaws as the number of days in winter (November–April) that maximum temperature exceeded 0 °C, following methods similar to a study on the effect of climate warming on rodent population dynamics (Gliwicz and Jancewicz 2016). We selected the sea ice-free period because it encapsulates both changes in the break-up and freeze-up date annually, and thus represents the entirety of time foxes would not have access to a marine environment for food. Sea ice duration has shortened (Gagnon and Gough 2005; Boonstra et al. 2020), so the sea ice-free period may be an important factor for fox reproductive success. Lastly, the snow-free date was included to reflect goose reproductive success, as goose nesting is delayed when snow cover persists later (Reed et al. 2004; Madson et al. 2007).

## Data analysis

We split our analysis into two separate components. The first analysis was concerned with evaluating the long-term trend (1955–2012) in the Arctic and red fox populations inferred from the harvest data, while the second analysis evaluated the role of the five climate variables on fox population dynamics from 1980 to 2012. This second time period reflects the maximum time series where data on all five variables were available.

### Long-term population trends

We used a negative binomial generalized additive model with a log link implemented in the *mgcv* R package to evaluate the long-term trends in the Arctic and red fox harvest (Wood 2011). Generalized additive models are particularly useful for evaluating time series data, where the dependent variable often exhibits non-linearity, complex variation, or temporal autocorrelation. For both the Arctic and red fox models, we used the annual number of pelts harvested from each species as the response variable. We adjusted the time series to start at year 0 for 1954 (58 for 2012), fit a smoothing component comprised of thin-plate regression splines to this time series variable (Wood 2003), and allowed the smoother to have a basis size of 20. We used the ‘k.check’ function from the *mgcv* package in R to ensure the basis size was adequate (Wood 2011). We then used the log of the number of trapper licenses sold annually in Churchill as an offset term in each model to account for trapping effort.

We used the previous year’s pelt price as an additional explanatory variable in these long-term population trend models. However, for Arctic foxes, pelt price lagged 1 year was highly correlated with year ( $r = -0.81$ ) and therefore was excluded from the model with year. We instead evaluated the relationship between the previous year’s pelt price and Arctic fox harvest using a generalized linear model with a negative binomial distribution and an offset term for license sales. The weighted red fox pelt price lagged 1 year was not correlated ( $r = -0.15$ ) with year, and was thus included in the red fox long-term population trend model (pelt price not fit to a smoother). The residuals for each model were checked to evaluate model fit and to assess temporal autocorrelation using the ‘acf’ function in R.

### Influence of climate on fox population dynamics

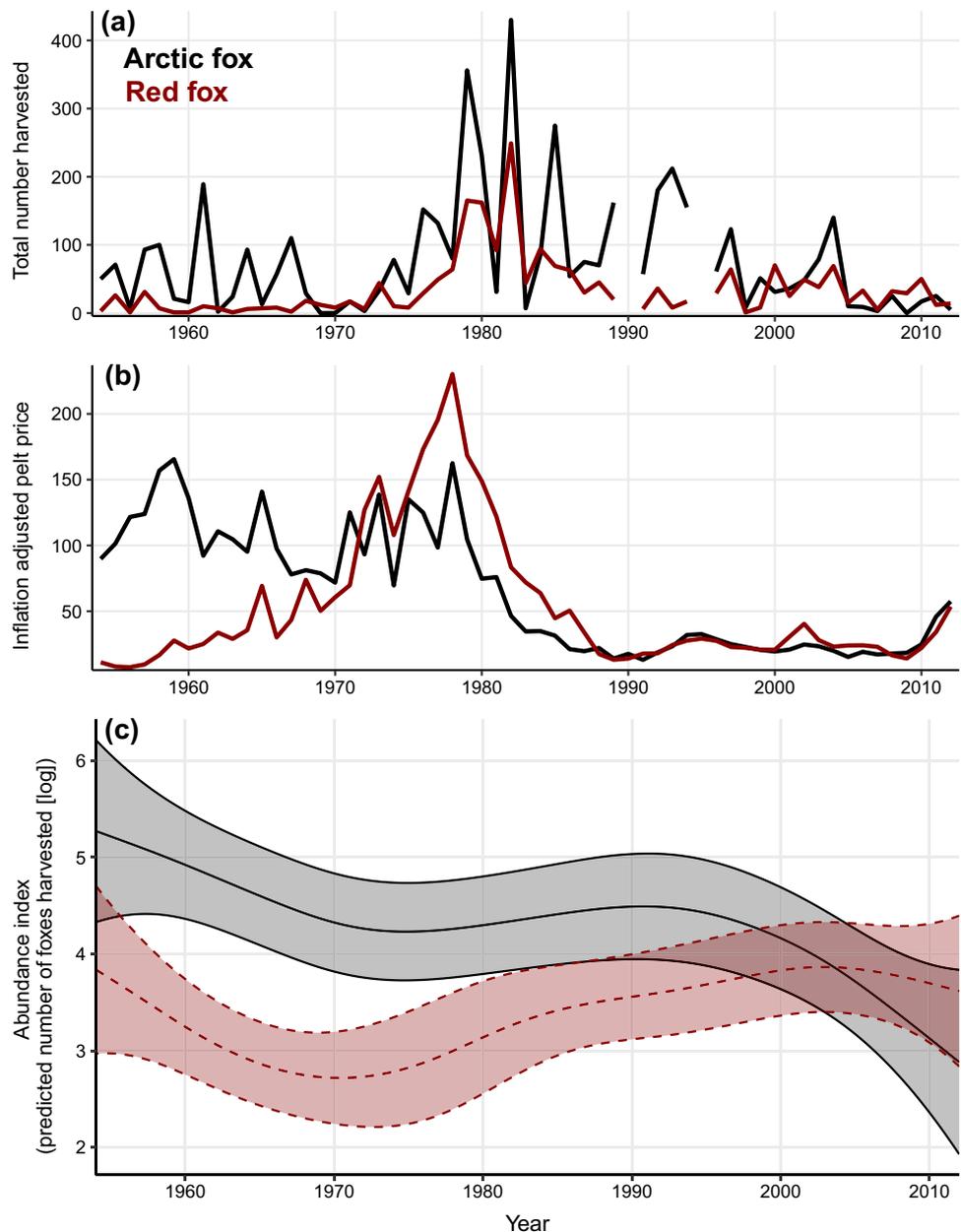
We used a negative binomial generalized linear model with a log link to evaluate the role of the five climate variables on red and Arctic fox population dynamics from 1980 to 2012. Our main objective in this analysis was to gain inference on the effect these variables had on each fox population, and we, therefore, used a single model fit to all climate variables to evaluate their relative influence. We first scaled and centered all climate variables and the previous year’s pelt price to a mean of 0 and SD of 1. We then assessed multicollinearity among the scaled variables. ‘Snow-free date’ and the ‘winter thaws’ were highly correlated ( $r = -0.61$ ), as were ‘ice-free days’ and the year variable ( $r = -0.64$ ). Therefore, we excluded the year and the ‘winter thaws’ from the final model. All other paired correlation values were less than  $\pm 0.5$ . Thus, the final climate model included four climate variables and the price, plus the log of the number of trappers as an offset term to account for trapper influence. We checked the variance inflation factor for all variables fit the model (all values were  $< 2$ , indicating no lingering collinearity; Dormann et al. 2013), checked for temporal autocorrelation in the model’s residuals, and used Nagelkerke’s pseudo- $R^2$  value to assess the amount of variation in Arctic fox harvest that our model explained. We assessed the significance of each individual climate variable using  $\alpha = 0.05$ , and where 95% confidence intervals of parameter estimates did not overlap 0. All analyses were conducted in R version 4.2.0 (R Core Team 2022).

## Results

### Long-term harvest and population trends

The long-term trends in raw harvest totals showed a peak in the late 1970s to early 1980s for both Arctic and red foxes (Fig. 2a), corresponding with relatively high pelt prices

**Fig. 2** Long-term trends in the total number of foxes harvested annually (A), the average annual pelt price of Arctic and red foxes adjusted for inflation (B), and the abundance index (C) of Arctic and red foxes near Churchill, Manitoba, Canada. Panel A shows the total number of pelts reported to provincial authorities in the Churchill Registered Trapline District. Panel C shows the long-term trend in abundance index (log of the predicted number of foxes harvested) for Arctic and red foxes, as predicted from the generalized additive models fit each species' harvest time series. The Arctic fox trend accounted for just trapping effort, whereas the red fox trend accounted for trapping effort and the previous year's inflation-adjusted pelt price



given at the auction (Fig. 2b). Reported Arctic fox harvest ranged from a low of 0 (3 years) to a high of 430 (in 1982), whereas red fox harvest ranged from 1 (several years) to 249 (1982). There was a positive relationship between the number of Arctic and red foxes harvested annually (log + 1 transformed linear model results:  $r = 0.494$ ,  $p = 0.002$ , 95% confidence interval [CI] 0.194, 0.795).

After accounting for trapping effort, Arctic fox harvest showed a long-term decline throughout the time series ( $n = 56$  years of data) (Fig. 2c). Harvest declined until about 1970, leveled off until 1990, and then showed another steady decline through to the end of the time series in 2012. The generalized additive model results suggested the long-term

trend was non-linear, as the smoothing effect of year was significant ( $p = 0.004$ , effective degrees of freedom [edf] = 3.26). The model explained 19.5% of the deviance in Arctic fox harvest numbers. Inflation-adjusted pelt price lagged 1 yr was significantly positively related to Arctic fox harvest after accounting for trapping effort ( $\beta = 0.006$ ,  $p = 0.035$ , 95% CI 0.001, 0.013).

After accounting for trapping effort and pelt price, red fox harvest showed a generally long-term stable population trend (Fig. 2c). Red fox abundance appeared to have declined until 1970, at which point it then began to increase and eventually stabilize by around 2000. We also found evidence that the red fox population trend showed periods

of non-linearity, as the smoother fit to year was significant ( $p=0.038$ ,  $\text{edf}=3.73$ ). Inflation-adjusted pelt price lagged 1 yr had a positive influence on red fox harvest ( $\beta=0.007$ ,  $p=0.041$ , 95% CI 0.000, 0.013). The model explained 22.8% of the deviance in red fox harvest numbers.

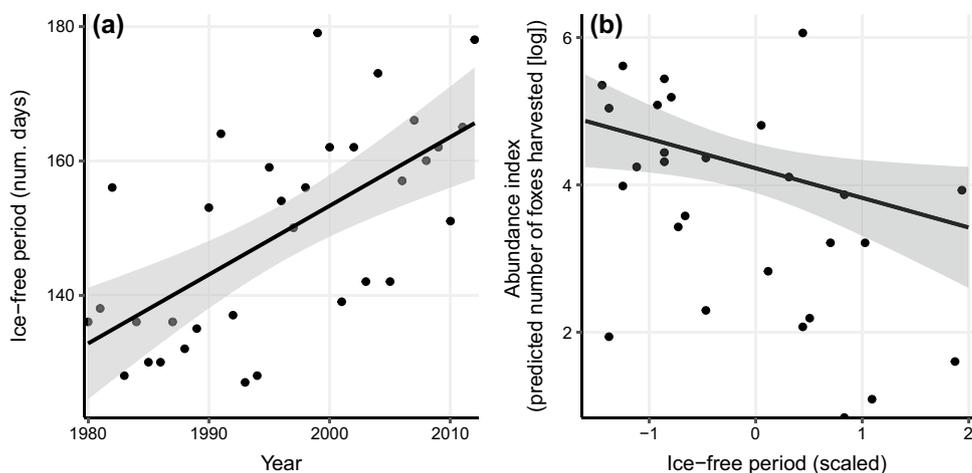
### Influence of climate variables on harvest-inferred fox abundance

For Arctic foxes, results from our generalized linear model analysis suggested that the average daily snow depth during February and the length of time Hudson Bay was ice-free each year had a significant influence on annual harvest patterns near Churchill, Manitoba ( $n=29$  yrs of data). Specifically, we found a negative relationship between ice-free period and Arctic fox harvest ( $\beta=-0.401$ ,  $p=0.028$ , 95% CI  $-0.775$ ,  $-0.032$ ; Fig. 3b, Table 2A), and a positive relationship between average daily snow depth and Arctic fox harvest ( $\beta=0.412$ ,  $p=0.034$ , 95% CI 0.027, 0.865; Fig. 4a, Table 2A). However, the relationship between snow depth and Arctic fox harvest appeared largely driven by one year

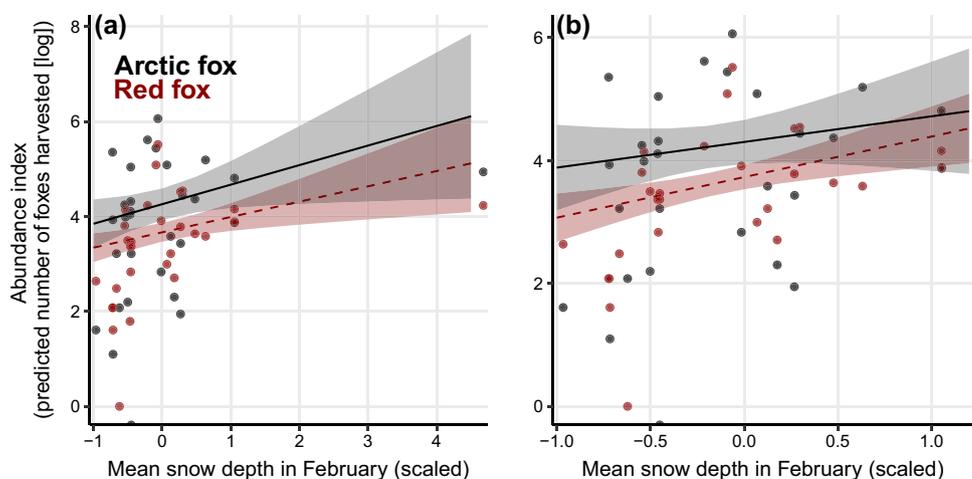
with extreme snow depth (2004). When we excluded this year and re-ran the model, snow depth was no longer significantly influential ( $\beta=0.417$ ,  $p=0.251$ , 95% CI  $-0.247$ , 1.15, Fig. 4b, Table 1). Ice-free period remained influential in the model excluding the 2004 extreme snow depth data ( $p=0.044$ ). The annual ice-free period for Hudson Bay significantly increased during 1980–2012 at a rate of  $\sim 10$  days/decade ( $\beta=1.025$ ,  $p<0.0001$ , 95% CI 0.580, 1.47; Fig. 3a, Table 1), suggesting that warming of the bay had a negative effect on Arctic fox harvest. None of the other variables evaluated in the model appeared to have a significant independent effect on Arctic fox abundance (Table 1). Pseudo- $R^2$  values for the climate models with and without the high snow depth year (2004) were 0.357 and 0.299, respectively.

For red foxes, results from our generalized linear model analysis suggested that the only climate variable with a significant influence on annual harvest patterns was average daily snow depth during February ( $n=29$  yrs of data;  $\beta=0.323$ ,  $p=0.005$ , 95% CI 0.084, 0.596; Table 2A). The relationship was still positive after excluding the outlier snow depth year, 2004 ( $\beta=0.660$ ,  $p=0.002$ , 95% CI 0.252,

**Fig. 3** Temporal trend and influence of the length of the ice-free period in Hudson Bay on Arctic fox harvest near Churchill, Manitoba. Panel A shows the increasing trend in the length of the ice-free period. Panel B shows the marginal effect of the ice-free period on Arctic fox harvest (and 95% confidence interval) as predicted from the generalized linear model. Points in both panels are the observed values



**Fig. 4** Relationship between mean snow depth in February (cm) and red and Arctic fox harvest near Churchill, Manitoba, Canada. Panel A shows the relations include an outlier snow depth in 2004. Panel B shows the relationship excluding the snow depth outlier in 2004. The lines and ribbons are the predicted marginal effects and 95% confidence intervals of mean snow depth in February, while the points are the observed values



**Table 1** Results from the generalized linear models evaluating the influence of climate variables and pelt price on Arctic and red fox harvest trends near Churchill, Manitoba, Canada, 1980–2012

Variable	Estimate	Std. error	z value	p value	95% CI
Arctic fox					
(Intercept)	0.079	0.348	0.227	0.82	– 0.562, 0.761
Snow-free date	– 0.045	0.228	– 0.200	0.84	– 0.524, 0.408
Feb. snow depth	0.417	0.363	1.15	0.25	– 0.247, 1.15
Ice-free period	<b>– 0.401</b>	<b>0.199</b>	<b>– 2.02</b>	<b>0.044</b>	<b>– 0.790, – 0.017</b>
Mean July temp	– 0.032	0.187	0.87	0.87	– 0.404, 0.315
Pelt price (lag-1)	0.006	0.009	0.664	0.51	– 0.010, 0.025
Red fox					
(Intercept)	– 0.241	0.104	– 2.33	0.020	– 0.440, – 0.031
Snow-free date	0.030	0.127	0.234	0.82	– 0.228, 0.289
Feb. snow depth	<b>0.660</b>	<b>0.203</b>	<b>3.25</b>	<b>0.002</b>	<b>0.252, 1.09</b>
Ice-free period	0.100	0.114	0.881	0.38	– 0.126, 0.330
Mean July temp	– 0.178	0.011	– 1.68	0.092	– 0.413, 0.051
Pelt price (lag-1)	<b>0.255</b>	<b>0.108</b>	<b>2.36</b>	<b>0.018</b>	<b>0.044, 0.483</b>

Results shown are from the models excluding extreme snow depth year (2004;  $n=28$  yrs)

Bold indicates significance

1.09; Table 1). The previous year's inflation-adjusted pelt price also had a significant influence on red fox harvest ( $\beta=0.287$ ,  $p=0.011$ , 95% CI 0.071, 0.522).

## Discussion

Reproduction strongly drives annual variation in Arctic fox abundance (Tannerfeldt and Angerbjörn 1998; Samelius and Alisauskas 2017), and Arctic fox harvest in winter is positively related to fox reproductive output the previous summer (McDonald et al. 2017). Thus, trends observed in Arctic fox harvest likely reflect changes in Arctic fox population dynamics. Our results suggest Arctic fox harvest in Churchill has declined over time (Fig. 2). However, inflation-adjusted pelt price lagged 1 year was positively related to Arctic fox harvest after accounting for trapping effort. Due to the negative relationship between pelt price and year, and the positive relationship between pelt price and Arctic fox harvest, the decline in Arctic fox harvest found in our analysis was likely influenced in part by declining pelt value in the longer time series (1955–2012). However, in the shorter time series (1980–2012) pelt price was not significantly related to Arctic fox harvest, suggesting that although pelt price influenced Arctic fox harvest when evaluated across the full-time series, its influence on Arctic fox harvest patterns was weaker in the later portion of the time series where the largest declines in Arctic fox harvest were observed.

Contrary to our prediction, red and Arctic fox harvests were positively related. Our hypothesis that interspecific competition between the species may be promoting declines in Arctic fox abundance may not be supported. Moizan et al. (2022) showed resource competition for denning sites was

greater driven by spacing needs than interference competition between the species. Arctic and red foxes have been demonstrated to coexist in our study area (Lai et al. 2022; Moizan et al. 2022); therefore, another driver may be promoting changes in Arctic fox harvest dynamics.

Our analysis of harvest suggests a decline in Arctic fox numbers, whereas red fox harvest has remained stable. The different harvest responses of red and Arctic foxes suggest these species may be responding differently to cryosphere changes near the Arctic treeline. Similarly, interference between Arctic foxes and red foxes in the Canadian High Arctic is low (Lai et al. 2022). Gallant et al. (2012) suggested red fox population growth on Herschel Island, Yukon, may be limited by winter prey availability as reproduction and relative abundance of Arctic and red foxes did not change significantly over four decades, despite increased temperatures and a longer growing season. Similar to Gallant et al. (2012), variables associated with a warmer climate, including warmer summer temperatures and the last day snow was present in late spring, were not significantly related to fox harvest.

Decreased sea ice duration on Hudson Bay may be contributing to the recent decline in Arctic fox abundance (Fig. 3), likely because shorter sea ice duration constrains Arctic foxes' access to important supplementary marine food resources. Considering sea ice is an important habitat for polar bears to hunt seals, a reduction in polar bear hunting success in response to sea ice freezing later in fall and breaking up earlier in spring may consequently reduce the availability of seals for foxes (Stirling and McEwan 1975; Lunn et al. 2016; Descamps et al. 2017). Shorter sea ice duration may further contribute to declines in Arctic fox abundance by causing a trophic mismatch.

Delayed sea ice freeze-up may create a lag in reliable food resources for foxes between the departure of migratory birds in fall and when seal's carcasses can be scavenged on the sea ice, potentially lowering the survival of juveniles shortly after they become independent and disperse from their natal dens. Furthermore, limited food availability on sea ice may impact Arctic fox reproduction, given litters are produced before migratory birds arrive in spring, and access to marine resources during this critical and energetically-costly period for Arctic foxes (Audet et al. 2002) may increase foxes' body condition during pregnancy and lactation. Tannerfeldt et al. (1994) estimated 21% of juvenile mortality from weaning to 6 weeks of age was attributed to starvation and only 8% of juveniles survived to reproductive age, so food availability at this time, when energetic requirements are high but terrestrial resources are still scarce, may be an important factor for early juvenile survival. The increasing trend of the number of days without sea ice coverage in Hudson Bay is well documented (e.g., Boonstra et al. 2020), and this trend is likely responsible in large part for the negative relationship we found between ice-free days and Arctic fox harvest.

In contrast, red fox abundance appeared unaffected by changes to sea ice duration on Hudson Bay. Previous studies have demonstrated marine resources have been used by red foxes. Killengreen et al. (2011) showed that marine resources were important alternative food sources for coastal red foxes that lived within 20–25 km of the coast, but foxes that lived further from the coast were less reliant on marine resources. In our study area, Warret Rodrigues (2022) detected marine resources in the red fox diet, but other species (including rodents, snowshoe hares, and migratory birds) were relied on much more. Further, red foxes use the marine habitat much less than Arctic foxes (Warret Rodrigues 2022), which may explain the difference in response of fox harvest records between the two species to changes in the ice-free period (i.e., red foxes have an overall reduced reliance on marine subsidies for late-winter food).

Arctic fox harvest was not affected by the length of time snow persisted in late spring, suggesting goose reproductive success had minimal influence on the observed Arctic fox decline. The snow-free date was included as a climate variable as persistent spring snow was shown to influence goose nesting success (Reed et al. 2004; Madson et al. 2007). However, MacDonald et al. (2017) demonstrated that juvenile goose density, although an important alternative food source for Arctic foxes, was not related to their reproductive success, suggesting the seasonal abundance of geese may not be sufficient to minimize declines in Arctic fox abundance. Similarly, in Svalbard, Eide et al. (2012) also did not measure a numerical response of Arctic foxes' reproductive success to goose abundance. Goose abundance is hypothesized to be less impactful on Arctic fox reproductive success

in these regions because geese migrate annually and are therefore not available during late winter, a critical period for Arctic fox reproduction (Roth 2002; Eide et al. 2012; McDonald et al. 2017).

Although our results are based on correlations and indices, these data are the only available sources within the Churchill region to evaluate long-term population changes of these important Arctic predators. Further comparisons of direct relationships may strengthen the support of our results. However, the long-term trends in our indices parallel those of shorter-term research in our study area and thus have further support for their use here. Moizan et al. (2022) demonstrated that Arctic fox den occupancy decreased while red fox den occupancy remained stable in late winter between 2011 and 2021 in the Churchill region. These trends parallel our results using local harvest data: a decline in Arctic foxes continuing from the mid-1990s, while red fox harvest appeared stable during the same time period.

Arctic foxes, similar to other tundra-adapted species, may experience continued stress from changing climate and cryosphere as marine habitat is less reliable with shortened sea ice duration (Gagnon and Gough 2005) and the continued northward encroachment of shrubs and forest reducing tundra habitat (Sturm et al. 2005). As our study area is coastal and along the southern edge of the Arctic fox distribution, these rapid environmental changes appear to be having a detrimental effect on Arctic foxes. Continued alteration to Arctic ecosystems may result in the future exclusion of Arctic foxes within regions of their historical circumpolar distribution (Fuglei and Anker Ims 2008). Conversely, although red fox harvest has remained stable in our study area so far, as the climate continues to change, the area may be able to support higher red fox densities. Arctic and red foxes appear able to coexist in areas of North America (Lai et al. 2022; Moizan et al. 2022), but future climatic trends may lead to greater resource competition and disrupt the balance between the two species. Through greater exploration of the mechanisms that drive population trends, we may better understand the effects of climate change on northern species and predict how these changes may continue to affect wildlife going forward.

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**Author contributions** JV conceived the study and led the writing, SJB led the statistical analysis, and JR provided supervisory input at all stages. All authors contributed to data interpretations and final revisions of the manuscript.

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**Data availability** The data are available from the authors upon reasonable request.

**Code availability** The codes are available from the authors upon reasonable request.

## Declarations

**Conflict of interest** The authors declare they have no conflict of interest.

**Ethical approval** Ethics approval was not required for this study

**Consent to participate** Not applicable

**Consent for publication** Not applicable

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