



Evaluating the use of marine subsidies by Arctic foxes without direct coastal access; insights from stable isotopes

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Abstract

The trophic structures of tundra ecosystems are often viewed as a result of local terrestrial primary productivity. However, other resources can be brought in through long-distant migrants or be directly accessible in coastal areas. Hence, trophic structures may deviate from predictions based on local terrestrial resources. The Arctic fox (*Vulpes lagopus*) is a small canid that may use marine resources when available. We used stable isotope values in Arctic fox fur and literature data on potential prey to evaluate Arctic fox summer resource use in a mountain tundra without coastal access. The dietary contribution of local prey, presumably mostly rodents, declined with declining rodent abundance, with a subsequent increased contribution of migratory prey relying on marine resources. Stable isotope values did not differ between this terrestrial area and an area with direct coastal access during years of high rodent abundance, but isotope values during low rodent abundances suggested less marine input than in a coastal population feeding primarily on marine prey. Our study shows that marine resources may be used by animals in areas without any coastal access, and we highlight that such partial coupling of ecosystems must be included in the modeling and assessments of tundra environments.

Keywords Delta ¹³C · Delta ¹⁵N · Allochthonous resources · Predator–prey relations · Fennoscandia · Ecological subsidies

Introduction

Tundra ecosystems are often regarded as closed systems that are influenced only by the terrestrial species communities. For instance, Oksanen et al. (1981) and Oksanen and

Oksanen (2000) suggested a model where the primary productivity of an area would dictate both the number of trophic levels occurring and also the regulation of biomass across trophic levels. Top down regulation of herbivore biomass would not occur until some critical threshold in primary productivity has been reached. However, empirical observations of biomass distributions within tundra ecosystems, which include observations across extended areas (Krebs et al. 2003) and time frames (Legagneux et al. 2012), suggest that terrestrial ecosystems can be regulated by predator–prey interactions even in areas of relatively limited primary productivity. One potential reason for this mis-match between theory and empirical observations may be that the observed ecosystems were influenced by resources from other biomes or geographic areas, i.e., ecological subsidies (Polis et al. 1997; Montagano et al. 2018).

One particularly important class of subsidies for terrestrial ecosystems are those from the marine biome, marine subsidies (Nater et al. 2021). Marine subsidies can either be accessed by predators directly, e.g., at marine shore lines (Hersteinsson and Macdonald 1996), or indirectly through migratory species such as anadromous fish (Wilson and Halupka 1995) or migrating birds (Gauthier et al. 2004).

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In coastal areas, marine subsidies are directly accessible to predators, for instance as marine mammal carcasses, seabirds or marine organisms such as fish (Hersteinsson and Macdonald 1996; Roth 2003), although the area of which these marine resources are available may be restricted to relatively narrow areas along the coast line (Killengreen et al. 2011; Dalerum et al. 2012). Marine subsidies can also be available in areas without coastal access through migratory birds, such as geese and waders (Gauthier et al. 2004, 2011). In contrast to directly accessible subsidies, which are generally available throughout the year, the availability of these indirect subsidies is highly seasonal.

Many tundra ecosystems are also heavily influenced by strong temporal fluctuations in small rodent populations (Ims and Fuglei 2005). In these ecosystems, lemmings (*Lemmus* sp. and *Dicrostonyx* sp.) and other small rodents go through considerable fluctuations in population size with a 4-year cycle as the most re-occurring pattern (Krebs 2013). This cyclic hyper abundance is used by a number of mammal and avian predators (Krebs 2013). Hence, many tundra ecosystems, most notably in areas without direct coastal access, are influenced by fluctuating resources at multiple temporal scales, with local terrestrial prey generally fluctuating on an inter-annual scale whereas ecological subsidies fluctuate on a seasonal scale. Since many Arctic areas are without direct coastal access, it is important to quantify the relative influences of these two temporally fluctuating resources for terrestrial Arctic predators.

One species that may be particularly useful for investigations into such relative importance of resources that fluctuate on contrasting time scales is the Arctic fox (*Vulpes lagopus*), a small canid with a circumpolar distribution. Arctic foxes feed primarily on small rodents in tundra areas, but may rely on marine resources in areas without small rodents (Hersteinsson and Macdonald 1996; Dalerum et al. 2012; Berthelot et al. 2023), or during periods with limited rodent availability (Roth 2002, 2003; Tarroux et al. 2012; Ehrich et al. 2015). However, most areas where arctic foxes have been shown to rely on ecological subsidies have direct coastal access, or access to large colonies of breeding geese (Gauthier et al. 2004; Giroux et al. 2012; McDonald et al. 2017). In northern Sweden, in contrast, Arctic foxes forage in mountain areas without coastal access year round, and hence do not have direct access to marine environments such as coastlines or sea-ice. Furthermore, there are no large colonies of geese such as those occurring in other parts of the Arctic. However, we currently have a limited understanding of the importance of local resources versus ecological subsidies for the Arctic fox, especially during periods of limited availability of small rodents, their main prey.

In this study, we used analyses of stable isotopes to evaluate the relative importance of terrestrial resident prey and marine subsidies for Arctic foxes in northern Sweden during

summer, i.e., the season when ecological subsidies ought to be the highest. We distinguished between marine subsidies, i.e., migratory prey not relying on marine resources, and spatial subsidies provided by migratory prey not relying on marine environments. Stable isotope analysis has become a well-established tool for investigating consumer resource use (Angerbjörn et al. 1994; Dalerum and Angerbjörn 2005; Martínez del Rio et al. 2009), and has been shown to be particularly useful to quantify the relative importance of terrestrial and marine resources in terrestrial predators (e.g., Szepanski et al. 1999; Roth 2002). We here regard migratory prey as species that are not permanent resident to our study region, i.e., species that undertake some form of long-distance seasonal migration away from their breeding areas (Goodenough et al. 1993).

Methods

Study area

The study area is situated within the Vindelfjällen Nature Reserve in north-western Sweden (67°00 N, 17°00 E, hereafter referred to as “Vindelfjällen”, Fig. 1). The reserve covers approximately 5600 km² of terrain, ranging in elevation from 500 to 1700 m above sea level. The area consists of treeless mountain tundra intersected by valleys with birch and coniferous forests. Plant diversity is relatively low, and vegetation is dominated by dry grass heath, meadows and willows (Rune 1981). The climate is continental, with winter temperatures regularly below – 20 °C and short but relatively mild summers. The area lies approximately 100 km



Fig. 1 Location of the Vindelfjällen study area in northern Sweden

from the nearest coastline. Swedish Arctic foxes stay within their home ranges when breeding (Angerbjörn et al. 1997; Herfindal et al. 2010), and in contrast to populations in for instance northern Canada (e.g., Roth 2002, 2003) do not use coastal areas for foraging in winter (Angerbjörn et al. 1991). There is also no pack-ice available, as the Norwegian Sea is ice-free throughout the year. Although Arctic fox in Sweden has been defined as a specialist predator on Norwegian lemmings (*Lemmus lemmus*), they do also feed on a range of other prey items occasionally (Elmhagen et al. 2000). Resident prey for Arctic foxes consists of Norwegian lemmings, bank voles (*Myodes glareolus*), grey-sided voles (*Myodes rufocanus*), field voles (*Microtus agrestis*), mountain hares (*Lepus timidus*), two species of ptarmigan (*Lagopus lagopus* and *L. muta*) and a number of resident small passerines. In summer, there are also relatively high densities of migratory prey. These include migratory waders, waterfowl, and passerines, with the European golden plover (*Pluvialis apricaria*) being the most common species. Of the passerines, the migratory meadow pipit (*Anthus pratensis*), Lapland bunting (*Calcarius lapponicus*) and northern wheatear (*Oenanthe oenanthe*) are the most abundant during the summer (Svensson and Andersson 2013). Only one species of goose occurs above the tree line (the lesser white-fronted goose *Anser erythropus*), but not at high densities. Semi-domestic reindeer (*Rangifer tarandus*) are herded primarily during summer in the area, although foxes have been shown to scavenge off reindeer carcasses even during the winter (Linnell and Strand 2001).

Stable isotope values in Arctic fox fur

We collected fur samples of Arctic foxes in Vindelfjällen as part of a long-term trapping program (Angerbjörn et al. 1995; Elmhagen et al. 2014). In this study, we include fur samples collected from six adult and 33 juvenile (approximate age 1.5 to 2 months) Arctic foxes from 7 independent breeding events. All trapping and handling was carried out according to Swedish legislation, following approval by the Swedish environmental protection agency “Naturvårdsverket” and an ethical board (permits A18-14, A19-14, A10-17). The animals were captured in box traps at breeding dens during July 1995 and 2001 (Table 1), and samples were stored in room temperature until analysed. For juvenile Arctic foxes the hair samples would represent the period from birth in early June to the capture occasion in mid-July. All adult foxes were in summer fur and their hair samples would thus represent the period from moult in early June to mid-July (Zimova et al. 2022). The sampling period would thus be the same for juvenile and adult Arctic foxes. We rinsed hair samples by sonicating them in a chloroform/methanol/water (1:2:1) solution to remove surface attached lipids and contaminants. We conducted analysis of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$

Table 1 Stable isotope data (mean \pm sd of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for Arctic fox fur from Vindelfjällen, Hudson Bay and Iceland. Numbers in brackets for Vindelfjällen indicates number of adults and juveniles, respectively. Data from Hudson Bay and Iceland all come from adult foxes

Year	Rodent abundance	<i>N</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Vindelfjällen				
1995	High	8 (2:6)	-21.5 ± 0.4	6.2 ± 0.4
1996	Low	9 (1:8)	-22.7 ± 0.1	5.6 ± 0.1
1998	Low	3 (1:2)	-21.4 ± 0.1	7.2 ± 0.5
2000	Low	8 (1:7)	-21.6 ± 0.3	6.3 ± 0.2
2001	High	11 (1:10)	-22.3 ± 0.3	5.7 ± 0.4
Hudson Bay				
1994	High	6	-21.4 ± 1.8	7.2 ± 3.4
1995	Low	16	-19.2 ± 1.2	13.2 ± 3.6
1997	Low	10	-19.8 ± 1.0	10.9 ± 2.6
Iceland				
2002	No rodents available	3	-21.3 ± 2.6	9.8 ± 2.4
2003	No rodents available	19	-20.6 ± 2.0	9.5 ± 2.0

ratios on a Carlo Erba elemental analyzer (E1108 CHNS-O) connected to a Fison Optima isotope ratio mass spectrometer, with an accuracy of ≤ 0.1 ‰ at the stable isotope laboratory at the Department of Geological sciences, Stockholm University. All laboratory preparations and stable isotope analyses took place during 2003. All isotope values are presented as δ values, which represent the proportional deviation in parts per thousand (‰) from a standard (McKinney et al. 1950). The accepted standard for carbon is Pee Dee Belemnite (PDB) and the standard for nitrogen is ambient air. Mean and standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each year in all three areas are given in Supplementary Materials, Table S1.

To be able to compare our isotope values to foxes with direct access to marine resources, we have also included stable isotope values from Arctic fox fur from coastal areas in the southern Hudson Bay (Roth 2002) and Iceland (Dalerum et al. 2012). The Hudson Bay population was sampled in spring and summer 1994–1997 and had access to fluctuating populations of collared lemmings (*Dicrostonyx richardsoni* (Merriam, 1900)) (Roth 2002). One of the four sampling years had high lemming abundance whereas three had low lemming abundance. Icelandic foxes were primarily sampled in June and July, with a few samples collected in April and May, at five coastal sites around Iceland during 2002 and 2003 (Dalerum et al. 2012). These foxes did not have access to any fluctuating small rodents, but potential terrestrial prey may have included rock ptarmigan, small passerines and insects. However, coastal foxes in Iceland feed primarily on

prey of marine origin, such as seal carcasses and seabirds (Angerbjörn et al. 1994; Hersteinsson and Macdonald 1996).

Stable isotope values in potential sources

We assumed that the isotope values of the fur samples from Arctic foxes in Sweden reflected the isotope values in three groups of available prey; terrestrial resident prey, terrestrial migratory prey, and migratory prey relying on marine resources. These three classes cover the majority of the arctic fox diet in the study area, although invertebrates and vegetation may also be ingested in small amounts (Elmhagen et al. 2000). For terrestrial resident prey, we used the mean and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in muscle samples from Norwegian lemming, tundra vole (*Microtus oeconomus* (Pallas, 1776)), grey-sided vole, mountain hare, reindeer, willow ptarmigan and rock ptarmigan from the Varanger Peninsula in northern Norway, taken from Ehrich et al. (2015). All of these species occur in our study area except the tundra vole. However, this species has very similar ecological, physiological and morphological characteristics to the field vole, which does occur in our study area (Björvall and Ullström 1986). We let the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in muscle samples of two common passerines from Varanger, the northern wheatear and the meadow pipit, represent terrestrial migratory prey (Ehrich et al. 2015). Both of these species are very common during the summer in our study area (Svensson and Andersson 2013). They are both insectivores, and although classified as terrestrial prey for our study we recognise that many insects have their earlier life stages aquatic environments. To represent migratory prey relying on marine resources, we compiled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in whole blood from four shorebirds occurring in the study area: dunlin (*Calidris alpina* (Linné, 1758)), redshank (*Tringa totanus* (Linné, 1758)), bar-tailed godwit (*Limosa lapponica* (Linné, 1758)), and Eurasian curlew (*Numenius arquata* (Linné, 1758)). Although both the dunlin and the redshank are common in Vindelfjällen, neither the bar-tailed godwit nor the Eurasian curlew are very common (Svensson and Andersson 2013). However, from an isotope perspective we regard these species to be representative of the shorebird community in our study area, as they all share very similar feeding characteristics during winter (Cramp et al. 1983). The samples were collected during February on intertidal mudflats in the Pertuis Charentais area of western France (Bocher et al. 2014). Hence, they reflect the isotope values of these birds when they have fed on a more or less pure marine diet. Considering a whole-body half-life of approximately 80 days for both carbon and nitrogen for this sized endotherm and ambient temperature (Thomas and Crowther 2015), and that these birds arrive to our study area in late May to early June (Svensson and Andersson 2013;

Machin et al. 2017), they should still contain a considerable marine signal through the period in which we trapped the foxes. Stable isotope values in potential prey are given in Supplementary Materials, Table S1.

Rodent abundance

To provide a binary quantification of the relative rodent abundances across years in Vindelfjällen and Hudson Bay, we grouped each year with stable isotope data into years with high versus low abundance of rodents based on the relative abundances observed in each study area. We simply assigned the years with the highest abundances as “high” and the years with the lowest abundances as “low”. With this heuristic definition, the average number of lemming nests in Ammarnäs was over 4 times as high during “high” as compared to “low” years. During “high” years, there were a 20 times higher frequency of observations of live animals, and over 5 times more trapped lemmings compared to “low” years. Similarly, for Hudson Bay the only “high” year had an estimated lemming density that was over 9 times as high as the average density for the “low” years (Supplementary Materials, Table S2). For Vindelfjällen the observations came from two sources; the average snap trapping index from spring (May–June) and fall (August–September) sessions made by the Swedish small rodent monitoring program (Ecke and Hörnfeldt 2022) as well our own direct observations of live lemmings and lemming winter nests. For the snap trapping data from Vindelfjällen, we used data on bank, grey-sided and field voles as well as lemmings. These are the species monitored under the program that frequently occur above the tree line, and hence are accessible as prey to Arctic foxes. Our own observations of lemmings and lemming winter nests were made from transects walked on foot during July and August every summer (742–1044 km walked every year). Number of lemming nests have been found to be well correlated to spring densities of lemmings (Krebs et al. 2012). For Hudson Bay we used live trapping data on lemmings presented in Roth (2002) and Roth (2003).

Data analyses

Isotope values from Vindelfjällen did not differ between adults and juveniles, neither for $\delta^{13}\text{C}$ values (Anova: $F_{1,37} = 1.84$, $p = 0.183$) nor for $\delta^{15}\text{N}$ values (Anova: $F_{1,37} = 0.86$, $p = 0.359$). We therefore pooled samples from adult and juvenile foxes for all data analyses. However, because adult and juveniles from the same litter may not have formed independent samples, we grouped all analyses including Swedish data according the litter identity. We used mixed linear models to evaluate differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Arctic fox fur from Sweden during low

and high rodent abundance as well as between each area. We fitted four subset models: one on Swedish data only, one with only data from Sweden and Hudson Bay, one for all areas but only including years of low rodent abundance for Sweden and Hudson Bay and one for all areas but only including years of high rodent abundance for Sweden and Hudson Bay. For all models except the ones including only Swedish data, we fitted the inverse of specific variances estimated for each country as weights, to account for heteroscedasticity (Pinheiro and Bates 2000). Based on these models, we used estimated marginal means (Lenth 2023) to calculate the differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the following specific contrasts: (i) between years of low and high rodent abundance in Vindelfjällen, (ii) between Vindelfjällen and Hudson Bay during low rodent abundance, (iii) between Vindelfjällen and Hudson Bay during high rodent abundance, (iv) between Vindelfjällen and Iceland during low rodent abundance, (v) between Vindelfjällen and Iceland during high rodent abundance, (vi) between Hudson Bay and Iceland during low rodent abundance, and (vii) between Hudson Bay and Iceland during high rodent abundance. The alpha errors for these contrasts were corrected for multiple comparisons using the False Discovery Rate method (Benjamini and Hochberg 1995).

We used a Bayesian implementation to isotope mixing models to estimate the relative contributions from terrestrial resident prey, terrestrial migratory prey and migratory prey relying on marine resources to the isotope values in Arctic fox fur (Parnell et al. 2013). In the model, we used the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Arctic fox fur, grouped by rodent abundance (high or low), as mixtures and the three groups of potential prey, i.e., terrestrial non-migratory, terrestrial migratory and migratory relying on marine resources, as sources. The average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each source was calculated as the unweighted average of the prey species averages within each group. The standard deviation of each source was calculated as from the sum of the variance of the mean values from each species within the source group and the average variance within each species around the species-specific mean:

$$sd = \sqrt{\sigma^2 + \frac{\sum_1^k \sigma_i^2}{k}}$$

Where σ^2 is the sample variance of the mean values from each species within the source group, σ_i^2 the variance of samples within each species, and k the number of species included in the source group. We used the trophic discrimination values for mammalian fur from Caut et al. (2009). For carbon, we used the recommended linear function.

$$\Delta^{13}\text{C} = -9.064 - 0.474 \times \delta^{13}\text{C}$$

and for nitrogen we used the recommended value of 2.59. Standard deviation for the trophic discrimination values of carbon was set to 0.44, based on values in Lecomte et al. (2011), and for nitrogen 0.41 based on Caut et al. (2009). We used four parallel MCMC chains, each consisting of 10,000 posterior draws, from which we excluded a burn-in period of 1000 draws. We thinned the remaining draws by only retaining every fourth value. We did not use any informative priors for any of the isotope contributions. Based on the Brooks-Gelman-Rubin diagnostics (Brooks and Gelman 1998), all posterior distributions showed clear signs of convergence. Each proportional contribution is presented as the mean and standard deviation of the thinned posterior distributions after the initial burn-in period had been removed. We assessed pairwise differences in the proportional contributions of prey classed between years of high and low rodent abundance using 95% credibility intervals of the differences in the posterior draws.

All statistical analyses were done in the statistical environment R (version 4.2.2 compiled for the Linux system, <http://www.r-project.org>). We used the contributed package lme (version 3.1–157, Pinheiro et al. 2022) to fit linear models using generalized least squares, emmeans (version 1.8.5, Lenth 2023), simmr (version 0.4.5, Parnell 2021) to fit the stable isotope mixing model, and functions in the package EnvStats (version 2.7.9, Millard 2013) to do the permutation tests on the posterior draws from the mixing model.

Results

Overall the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Arctic fox fur values from Vindelfjällen were more representative of prey relying on terrestrial than on marine resources (Fig. 2a), but had significantly lower $\delta^{13}\text{C}$ ($b = -0.74$, $SE_b = 0.11$, $p < 0.001$, Fig. 3a) and $\delta^{15}\text{N}$ ($b = -0.65$, $SE_b = 0.13$, $p < 0.001$, Fig. 3b) values in years of high as compared to low rodent abundance (Table 1). Furthermore, there was a higher proportional contribution from terrestrial resident prey during years of high (0.69 ± 0.06) as compared to low (0.62 ± 0.07) rodent abundance (95% credibility interval of difference: -7.10×10^{-2} — 6.84×10^{-2}), and contrarily a higher proportional contribution from migratory prey relying on marine resources during years of low (0.11 ± 0.03) as compared to high rodent abundance (0.04 ± 0.02) (95% credibility interval of difference: 6.68×10^{-2} — 7.30×10^{-2} , Fig. 2b). Finally, there was no difference between years of high and low rodent abundance in the proportional contribution of terrestrial migratory prey (high rodent abundance: 0.3 ± 0.1 ; low rodent abundance: 0.3 ± 0.1 ; 95% credibility interval of difference: -4.24×10^{-3} — 3.79×10^{-3}).

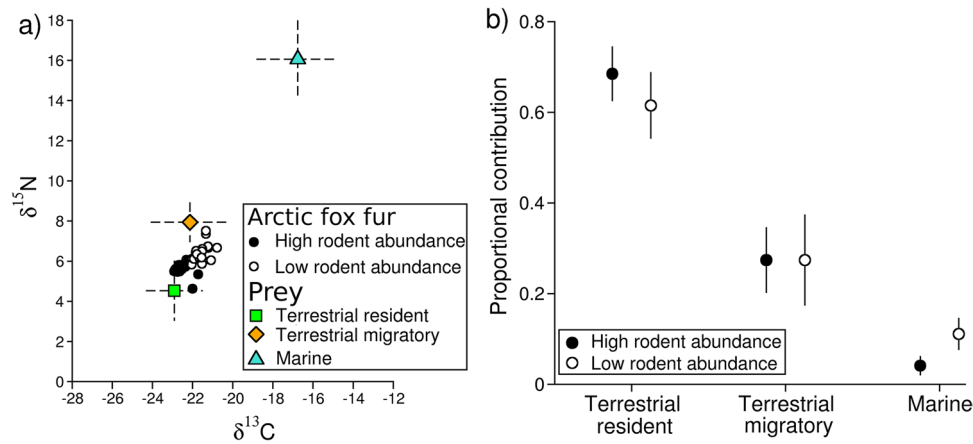


Fig. 2 Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in Arctic fox (*Vulpes lagopus*) fur from Vindelfjällen, northern Sweden, during years of high and low rodent abundance, and the average (\pm sd) stable isotope values corrected for trophic enrichments in three groups of potential prey (terrestrial resident prey [Scandinavian lemming *Lemmus lemmus*, tundra vole *Microtus oeconomus*, grey-sided vole, mountain hare *Lepus timidus*, reindeer *Rangifer tarandus*, willow ptarmigan *Lagopus lagopus* and rock ptarmigan *Lagopus muta*]; terrestrial migratory prey [northern wheatear *Oenanthe oenanthe* and meadow pipit *Anthus*

pratensis]; prey relying on marine resources [dunlin *Calidris alpina*, redshank *Tringa totanus*, bar-tailed godwit *Limosa lapponica*, and Eurasian curlew *Numenius arquata*) (a), as well as posterior draws (mean \pm sd) from a Bayesian implementation of an isotope mixing model describing the proportional contributions of terrestrial non-migratory prey, terrestrial migratory prey and migratory prey relying on marine resources to the isotope values in Arctic fox fur during years with high and low rodent abundance (b)

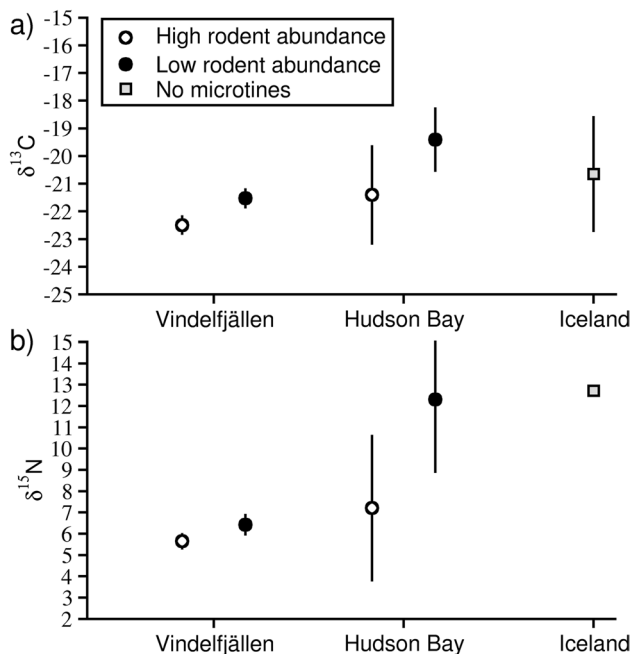


Fig. 3 Mean values (\pm sd) of $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) in Arctic fox fur from an area with fluctuating populations of small rodents without coastal access (Vindelfjällen, northern Sweden), an area with fluctuating populations of small rodents with direct coastal access (Hudson Bay, Canada) and from a coastal area where foxes primarily feed on marine resources (coastal Iceland). Stable isotope values in Vindelfjällen and Hudson Bay are reported for years with high and low abundances of small rodents

Arctic fox fur from Vindelfjällen had significantly lower $\delta^{13}\text{C}$ ($t=6.05$, $df=3$, $p_{adj}=0.027$, Fig. 3a) and $\delta^{15}\text{N}$ values ($t=5.83$, $df=3$, $p_{adj}=0.019$, Fig. 3b) than fur from Hudson Bay during years with low rodent abundance, whereas there were no differences in either $\delta^{13}\text{C}$ ($t=1.10$, $df=1$, $p_{adj}=0.562$, Fig. 3a) or $\delta^{15}\text{N}$ values ($t=1.56$, $df=1$, $p_{adj}=0.462$, Fig. 3b) during years with high rodent abundance (Table 1). Furthermore, Arctic foxes from Vindelfjällen had lower differences than Hudson Bay in both $\delta^{13}\text{C}$ ($b=-1.26$, $SE_b=0.58$, $p=0.032$, Fig. 3a) and $\delta^{15}\text{N}$ ($b=-4.46$, $SE_b=1.55$, $p=0.005$, Fig. 3b) between years of high and low rodent abundances (Table 1).

Arctic fox fur from Vindelfjällen had significantly lower $\delta^{15}\text{N}$ values for both high and low rodent abundance compared to fur from coastal Iceland (high rodent abundance: $t=8.98$, $df=1$, $p_{adj}=0.007$; low rodent abundance: $t=4.53$, $df=3$, $p_{adj}=0.020$, Fig. 3b), but no significant differences in $\delta^{13}\text{C}$ values (high rodent abundance: $t=3.43$, $df=1$, $p_{adj}=0.181$, Fig. 3a; low rodent abundance: $t=1.67$, $df=3$, $p_{adj}=0.194$) (Table 1). Arctic fox fur from Hudson Bay had significantly higher $\delta^{13}\text{C}$ ($t=1.24$, $df=31$, $p_{adj}=0.017$, Fig. 3a) and $\delta^{15}\text{N}$ ($t=2.79$, $df=42$, $p_{adj}=0.001$, Fig. 3b) values than fur from coastal Iceland during years with low rodent abundance, whereas there were no differences during years with high rodent abundances ($\delta^{13}\text{C}$: $t=0.92$, $df=9$, $p_{adj}=0.384$; $\delta^{15}\text{N}$: $t=1.61$, $df=6$, $p_{adj}=0.160$) (Table 1).

Discussion

Despite limited sample sizes, our results clearly show that this Swedish population of Arctic foxes relied mainly on local terrestrial resources. Previous studies in this area suggest that over 80% of the diet consist of small rodents (Elmhagen et al. 2000), even during years of relatively low rodent abundance. This feeding behaviour is congruent with other tundra living populations (Macpherson 1969; Angerbjörn et al. 1999; Dalerum and Angerbjörn 2000). We therefore suggest that the terrestrial resident resource group in our study primarily consisted of small rodents. Such reliance on small rodents even during low abundances has resulted in dramatic fluctuations in the Swedish arctic fox populations (Angerbjörn et al. 1995). Our data also suggest that there may have been an increased use of shorebirds during periods of low rodent availability, albeit a relatively limited increase. However, we still believe that our study exemplifies the use of marine subsidies by Arctic foxes even in an area that lies relatively far from the nearest coast and has no major populations of migratory geese or anadromous salmon.

Our results suggest that Arctic foxes in this strictly terrestrial area, as well as Arctic foxes in an area with direct coastal access, were both feeding primarily on small rodents when these were abundant. However, when rodents were scarce, marine resources appear to have been directly used by foxes with direct coastal access in Hudson Bay, and indirectly in Vindelfjällen where foxes had no access to a coastal shore line. In the absence of marine subsidies, Arctic foxes have been shown to rely on migratory geese when present (Gauthier et al. 2004; Giroux et al. 2012; McDonald et al. 2017), but also on invertebrates and alternative local mammalian prey (Dalerum and Angerbjörn, 2000; Ahrham 2024). In Vindelfjällen, however, our stable isotope data suggest that the use of migratory prey relying on terrestrial resources were relatively constant throughout years with different rodent abundances, and therefore did not seem to have been used as alternatives to rodents when these were scarce.

Our study supports previous suggestions that tundra ecosystems may incorporate resources from other biomes and geographic areas (Leroux and Loreau 2008). If these suggestions are to be true, there would be some obvious ramifications for our interpretations of the existing theory regarding predator–prey relationships and trophic ecosystem regulation in the terrestrial Arctic (Krebs et al. 2003; Gauthier et al. 2011; Giroux et al. 2012). Since subsidies may lead to predators occurring at higher abundances than what local primary productivity can sustain (Polis et al. 1997), we suggest that such subsidies may contribute to the considerable biomass transfers from Arctic herbivores to predators that has been observed in these low productivity northern ecosystems (Krebs et al. 2003; Dalerum et al. 2009; Legagneux

et al. 2012). In Vindelfjällen, the most likely marine subsidies are migratory shorebirds, which can be seen as vectors linking seemingly disparate terrestrial systems in northern Scandinavia with coastal habitats in southern Europe and Africa. We recognise that the dietary importance of migratory shorebirds probably was limited for Arctic foxes in our study area. However, subsidies from marine environments elsewhere have allowed this lemming specialist to form thriving populations even in areas completely without small rodents (e.g., Hersteinsson 1984), and the effects of these marine resource have been strong enough to have caused directed evolution in life history traits (Tannerfeldt and Angerbjörn 1998). Such links between disparate biomes or geographic areas highlight the considerable complexities associated with ecological responses to environmental perturbations (Bauer and Hoye 2014), and show that efficient environmental management need to be coordinated across several geographic scales and often varied political landscapes (Gladstone-Gallagher, 2022).

We suggest that the partial prey switch during years of low rodent abundances, from resident terrestrial prey to migratory prey relying on marine resources, may have been habitat related. The Norwegian lemming generally prefer patches of high productivity (Le Valliant et al. 2018). Favourable lemming habitats include meadows in winter (Vigués et al. 2022), with a seasonal habitat shift to slightly wetter areas during the summer (Koponen 1970; Henttonen and Kaikusalo 1993). These habitats are generally favourable also for many alpine and sub-Arctic shorebirds (Machin et al. 2017), which are the main vectors of marine resources into this terrestrial ecosystem. The Scandinavian Arctic fox has been described as specialist lemming predator, but one that uses alternative prey when available (Elmhagen et al. 2000). We suggest that further studies evaluate if the Arctic foxes in Sweden keep hunting in lemming habitats also during years of low rodent abundance, especially since such spatially coupled predation patterns can influence ecosystem dynamics (Hastings 2001; Nichols et al. 2005; Zhang et al. 2015). However, we appreciate that a temporal coupling between rodent abundance and the use of shore birds could also be caused by increased movement during years of limited rodent abundance (Beardsell et al. 2022).

We encourage a qualitative rather than quantitative interpretation of the mixing model results, since we recognise several potential short comings with this model. In particular, we highlight that the source values were taken from the literature, and came from samples collected at different times and locations than the analysed Arctic fox samples. Such temporal and spatial mis-matches may confound isotope mixing model solutions (Phillips et al. 2014). However, the method of Long et al. (2005) gives an estimated difference $\delta^{13}\text{C}$ of -0.39‰ between 2000 and 2010 due to the Suess effect (Keeling 1979), which is almost 3.8 times

smaller than the smallest difference between any of our prey classes (1.48 ‰, between terrestrial resident and migratory prey). Similarly, while both anthropogenic and ecological factors similarly may cause temporal variation in $\delta^{15}\text{N}$ values, they also tend to act over longer time scales than the 10–15 years that differed between the samples used for the mixing model (Savard and Siegwolf 2022). We also used shore bird winter values as our isotope source signature for migratory prey relying on marine resources. We justify this choice by the estimated whole-body half-life of carbon and nitrogen, which is approximately 80 days for this sized endotherm and ambient temperature (Thomas and Crowther 2015). This means that the shore birds should still mainly retain winter signatures during the time of fox hair keratin assimilation. Furthermore, we lack spring and early summer isotope data from shore birds in our study area, which means that these winter estimates are likely the most accurate available. Finally, the terrestrial prey were collected from the Varanger Peninsula in northern Norway, approximately 700 km northeast of our study area. Despite this distance, both our study area and Varanger lies firmly in the oroarctic vegetation zone (Virtanen et al. 2016), which should minimise spatial differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values caused by differences in the isotope signatures at the base of the terrestrial food chains.

Apart from the above mentioned issues with the mixing model, we have also interpreted the results as reflecting spring and summer diet. The analysed hair samples were taken in July from juvenile and adult Arctic foxes, and while the isotopes in the hair keratin could reflect winter diet rather than spring and summer diet, we do not regard it likely. Adult foxes moult to their summer fur during June (Zimova et al. 2022) and juvenile foxes grow their summer fur during the same period. We assume that there were no confounding effects of metabolic routing in adults or nursing in juveniles, which is further corroborated by the lack of isotope differences between the age groups. This would mean that the hair keratin would be built up from resources assimilated during spring and summer.

To summarize, our study confirms that the Arctic foxes in the mountain regions of Scandinavia primarily seem to rely on terrestrial resident prey, presumable primarily in the form of small rodents. However, an apparent decline in the use of terrestrial resources seem to have been accompanied by a corresponding increased use of migratory prey relying on marine resources. Our study therefore supports earlier suggestions that marine biomes may supply resources to terrestrial ecosystems. We propose that such subsidies could play important roles in regulating the trophic structures in the terrestrial Arctic, and that current theory of productivity-trophic complexity relationships should be updated to incorporate them. We also suggest that the use of migratory prey relying on marine resources may have been habitat related,

and that a potential spatial coupling of different prey species may be important for ecosystem dynamics on more local scales.

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Data availability Data are included in the supplementary material for this article.

Declarations

Competing interests The authors declare there are no competing interests.

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