



**UiT** The Arctic University of Norway

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**Long-term fluctuations in an arctic fox (*Vulpes lagopus*)  
population: a matter of diet?**

Fanny Berthelot

Master's thesis in Biology: "Northern Populations and Ecosystems" BIO-3950 June 2021



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**Under the supervision of :**

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Cover photograph : © Clément Brun - Arctic fox from the western fjords of Iceland.



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## Abstract

The long-term dynamics of predator populations may be driven by fluctuations in resource availability and reflect ecosystem changes in response to climate change. The Icelandic arctic fox population has known major fluctuations in size since the 1950s, starting with a decreasing period until late 1970s, followed by a six-fold increase until 2008 when the population dropped to half its size within five years until it recently bounced back again.

Using stable isotope analysis of bone collagen over a long-time series (1979-2018), I aimed at identifying the main resources used by Icelandic arctic foxes during periods of growth and decline to assess if the recent variations in their population size are linked to fluctuations in the availability of resources. Building on the results of Carbonell Ellgutter & al. (2020), I hypothesized that the decline in seabirds abundance was responsible for the decrease in the fox population. Additionally, I expected that the preceding growth period led to increased competition among foxes, causing a rise in inter-individual variations in their diet, ultimately leading to variations in their isotopic niches at the population scale. The isotopic signatures of arctic foxes differed drastically between their habitats, as well as trends in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios over time. Inland foxes showed an overall shift towards more terrestrial preys, whereas coastal foxes displayed a relatively stable use of marine resources over the years. Stable isotopes mixing models suggested that marine resources and rock ptarmigans were the most important food sources, and highlighted a rather stable diet in coastal habitats compared to inland habitats where more fluctuations in dietary composition were observed. Isotopic niche breadths showed broader niches for coastal foxes than inland foxes, and also highlighted more variations in inland habitats where foxes seemed to diversify their diet during periods of growth, when their preferred prey became scarce and when the number of conspecifics increased. On the other hand coastal foxes had a constant niche breadth throughout the study period, and seemed to adopt a more generalist behavior.

Fluctuations in the Icelandic arctic foxes population occurred without major changes in their dietary composition despite the variations in the abundance of their main resources.

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**Key words:** Arctic fox, population fluctuations, stable isotopes, diet, Iceland, isotopic niche

# 1. Introduction

Changes in population size and structure over time can arise from both biotic and abiotic factors. Biotic factors include predation, changes in resource availability, which influences consumer resource interactions, density-dependence as well as inter- and intra-specific competition. Abiotic factors, such as climate change, may represent the ultimate drivers of the observed ecosystem changes as they directly or indirectly influence biotic factors (Leach & al. 2016, Lewis & al. 2016).

Knowledge about population dynamics and the processes affecting them is fundamental to understand the structure of ecological communities and inform ecosystem-based management of populations (Butchart & al. 2010, Stephens & al. 2016). Resources fluctuations, often driven by climate change or other human impacts, represent a major cause of changes in predator populations (Voigt & al. 2003, Springer & al. 2007).

The magnitude of the response of a consumer population to temporal variations in the abundance and quality of their prey can also be modified by the degree of individual variation in the diet, which can result in differences in niche breadth (Newsome & al. 2009). The optimal foraging theory would predict for increased niche breadth at the population level when preferred resources decline, as such conditions of scarcity usually lead consumers to supplement their diet with additional prey items (Estes & al. 2003, Darimont & al. 2009). Such a decline in resource availability could also lead to niche partitioning, meaning that individuals would specialize on some prey items and reduce their dietary overlap (Svanbäck & Bolnick 2007), which might lead to an even greater increase in niche breadth than the variant where each individual uses different resources among the same alternative preys. As a result, at the population scale, both strategies would indirectly mitigate the effects of intra-specific competition, and could possibly attenuate a population decline caused by a lesser availability of the preferred resource.

High latitude ecosystems are usually considered as rather simple, with very strong species interactions making them relatively convenient to study. They usually display little functional redundancy among species, which leads to strong ecological interconnections (Post & al. 2009). In these systems where species highly rely on one another, the distribution and

abundance of preys - or nutrient flow - have substantial impacts on the feeding ecology of generalist predators, ultimately leading to fluctuations in the abundance and dynamics of consumer populations (Roth 2003, Eide & al. 2005).

The Arctic fox (*Vulpes lagopus*) is a terrestrial mammalian predator endemic to the Arctic tundra. They have a circumpolar distribution and are abundant across most of their range, including most arctic islands. Different threats such as increasing competition with the red fox (*Vulpes vulpes*), habitat loss arising from climate change and decline in the abundance of key prey make them increasingly vulnerable in part of their range (Killengreen & al. 2007, Ims & al. 2017). Therefore, arctic foxes have been chosen as a climate change flagship species by the International Union of Conservation of Nature (IUCN 2009). They are also target of monitoring as their reliance on tundra ecosystem make them likely to highlight the impacts of climate change through species interactions (Ehrich & al. 2015, Berteaux & al. 2017).

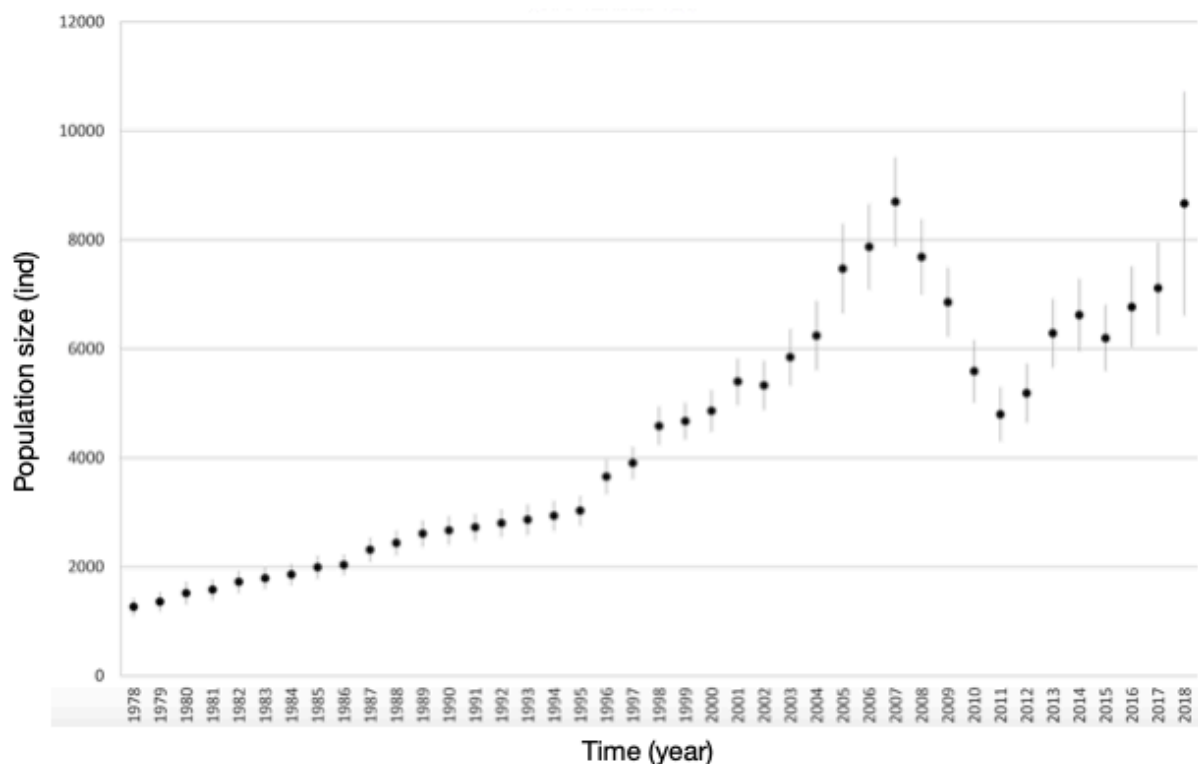
Arctic foxes can be classified into two different ecotypes based on their resource use strategies and reproductive patterns: lemming foxes and coastal foxes (Braestrup 1941, Hersteinsson & MacDonald 1996, Elmhagen & al. 2000). The first ecotype behaves as an opportunistic lemming (*Lemmus and Dicrostonyx spp.*) specialist, highly dependent on lemming population peaks, with the ability to switch to other terrestrial or marine resources in case of low lemming abundance (Elmhagen & al. 2000, Bêty & al. 2002, Roth 2003, Ehrich & al. 2015). To cope with the fluctuations of their preferred prey, these foxes tend to have larger litter size in peak years and larger annual variation in breeding effort. They have also shown the ability for extensive movements to forage for additional food resources in lemming low years (Dalén & al. 2005, Tarroux & al. 2010). The second ecotype is more generalist, and lives on Arctic islands deprived of lemmings such as Iceland, or Svalbard. These foxes feed on both marine and terrestrial resources (Hersteinsson 1984, Hersteinsson & MacDonald 1996, Ehrich & al. 2015) and dispose of a more stable food supply, thus producing fewer cubs per year, but breeding more regularly (Elmhagen & al. 2000). Since they are facing different challenges, the population dynamics of lemming foxes and coastal foxes differ and are respectively driven by their prey cycles or by both terrestrial and oceanic events (Elmhagen & al. 2000, Pálsson & al. 2016).



In the context of a warming Arctic, islands are likely to become a refuge for terrestrial fauna, as the decreasing extent of sea ice will protect these areas from invasions of southern species like the red fox (Fuglei & Ims 2008). Iceland makes up for a particularly interesting system when it comes to understand arctic foxes population dynamics for several reasons. First, this specific coastal population is neither threatened by interspecific competition with the red fox, nor by the collapse of rodent cycles as arctic foxes are the only canid species living in Iceland where lemmings are absent (Hersteinsson 1984). Earlier studies taking place in Iceland also showed a marked difference in diet and population trends between coastal population in Western Iceland and more terrestrial populations in the East (Angerbjörn et al. 1994, Hersteinsson & MacDonald 1996, Dalerum et al. 2012, Pálsson et al. 2016, Unnsteinsdóttir & al. 2016, Carbonell Ellgutter & al. 2020). Second, the species being considered as a pest, hunting is known to be the main cause of mortality (Hersteinsson 1992). However, the hunting pressure is thought to be stable since 1950, and is regulated by Icelandic laws, which makes it an unlikely driver of the population dynamic (Pálsson & al. 2016, Unnsteinsdóttir & al. 2016). The island is also free of infectious diseases that could potentially be fatal to foxes, such as rabies or distemper (Gunnarsson et al. 1993, Fooks et al. 2004). However, despite the stable hunting effort and the apparent absence of these common ecological pressures, striking long-term fluctuations in arctic foxes numbers have been documented and attributed to variations in carrying capacity, likely driven by the distribution and fluctuations in abundance of prey species available to them (Pálsson & al. 2016, Unnsteinsdóttir & al. 2016). In addition, Hersteinsson & al. 2009 found evidence for indirect climatic impacts through food availability. An approximation of arctic foxes population size based on hunting statistics showed a decrease from 1950 to 1970, which has been partly explained by a reduction in the ptarmigan (*Lagopus muta*) population (Hersteinsson et al. 1989; Angerbjörn et al. 2004b; Pálsson et al. 2016). Hersteinsson (1984) even showed that the number of occupied fox dens was positively correlated to ptarmigan abundance, highlighting the importance of this prey item. This period of decline has been followed by a steady six-fold increase until 2008 which has been explained by a global rise in food abundance. Hersteinsson & al. (2009) suggested that climatic variables such as the Sub-Polar Gyre (SPG), the North Atlantic Oscillation (NAO) and summer temperature acted indirectly to increase the food abundance and the presence of the main preys. Based on prey remains at dens, Pálsson & al. (2016) documented

an increased availability and use in waders and geese species during this growth period. They also found support for an important use of fulmars although these birds, like several seabird species in Iceland, are on the decline (Skarphéðinsson 2018, Icelandic Institute of Natural History unpublished data). Using stable isotopes analysis, Carbonell Ellgutter & al. (2020) highlighted the importance of marine resources and suggested that they might have supported the increase in foxes' population. Their results did however not support an increased use in geese species.

Recent population estimates have shown important fluctuations in foxes' numbers, starting with a drastic drop reducing the population to half its size within 5 years (Fig. 1). Since 2011, however, the population seems to recover and foxes' numbers are on the rise again. I hypothesized that the latest decline and growth periods have been driven by variations in the resources available to foxes.



**Figure 1** Minimal population size estimates in autumn (based on age cohort analysis and hunting statistics) with standard error bars of the arctic fox in Iceland from 1978 to 2018 (from Unnsteinsdóttir 2021, in press).

Instead of the most common methods to study predators' diet, like prey remains at dens, scat dissection and stomach content analysis, I chose stable isotopes analysis to assess the differences in resource use and the temporal changes in dietary composition. In contrast to the

direct methods mentioned above, stable isotopes do not reflect a snapshot information of the dietary intake (last meal), but are indirectly representative of a longer time period, and act as naturally occurring dietary tracers (Angerbjörn et al. 1994, Layman & al. 2012, Healy & al. 2018). Although prey remain at dens are representative of the whole denning period, they are biased towards large dietary items and only represent the reproducing part of the population (Pálsson & al. 2016). Depending on the metabolic activity of the tissue stable isotopes are extracted from, the turnover rate (renewal process of an isotope in a given tissue) varies, being faster for active tissues (e.g liver or pancreas) and slower for less active tissue like bone and can reflect up to a lifetime dietary intake (Tieszen & al. 1983). In addition, stable isotope analyses make it possible to obtain information from museum specimens, allowing to examine variations over long time series (Kelly 2000, Ben-David & Flaherty 2012).

Using isotopic signatures of bone collagen from individuals born between 1979 and 2018, I aimed at identifying the main resources used by Icelandic arctic foxes during periods of growth and decline to assess if the recent variations in their population size are linked to fluctuations in the availability of their food sources. Building on the results of Carbonell Ellgutter & al. (2020), I hypothesized that (1) the declining seabirds populations might have negatively affected the foxes during the last decade, especially in coastal areas. I expected this could either result in a shift towards preys with lower nitrogen signatures, or that no change would be observed in case foxes did not modify their diet. In addition, the decline in one of the foxes' preferred prey combined to the important growth in their population might have also led to an increase in intra-specific competition. Unnsteinsdóttir & al. 2016 showed that density dependence is one of the main driver of Icelandic arctic fox population, pointing out that foxes adapt their territory sizes in response to variations in carrying capacity, which could cause (2) an increase in inter-individual variability in the diet. Subsequently, isotopic signatures from individuals culled in the same habitat could differ over time as their diet diversifies, potentially leading to variations in the niche breadth at the population level. As coastal and inland foxes display different resource use strategies (Angerbjörn et al. 1994, Hersteinsson & MacDonald 1996, Dalerum et al. 2012, Pálsson et al. 2016, Carbonell Ellgutter & al. 2020), we addressed a particular focus to the magnitude of the difference in their responses to potential fluctuations in prey availability. A better understanding of what

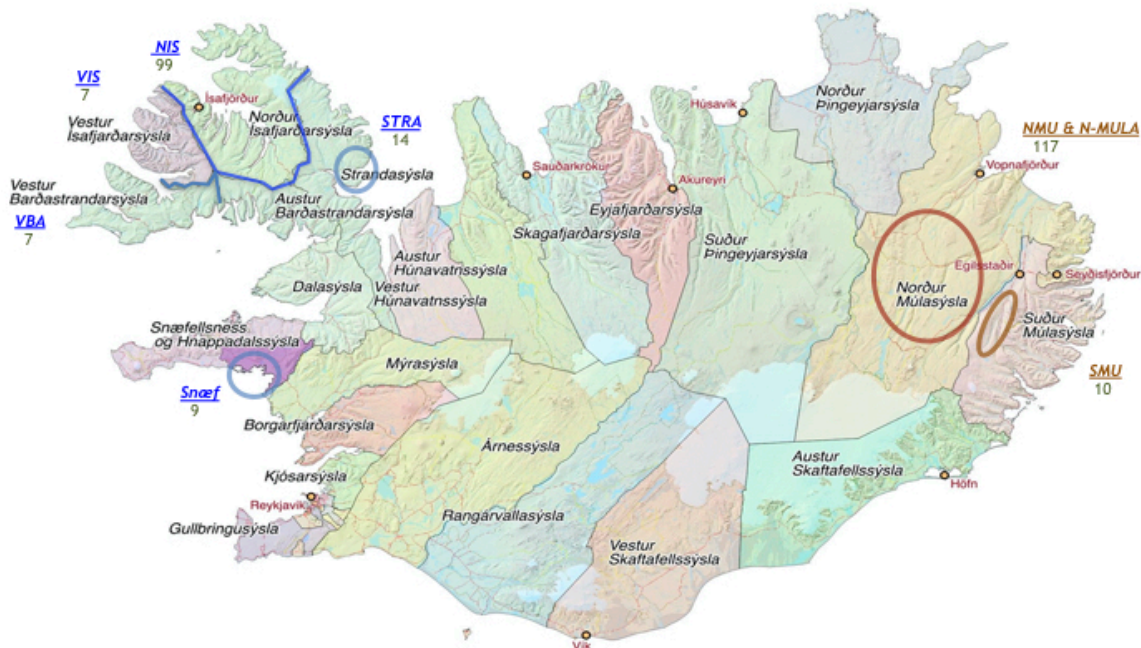
caused the important variations this population experienced in recent years will be important for further management and hunting recommendations.

## 2. Material and methods

### 2.1 Study area

Iceland (63°20'-66°30'N; 13°30'-24°30'W) is located in the Atlantic Ocean, close to the Arctic circle. Its climate is influenced by the Gulf Stream and varies between temperate and polar type (Einarsson 1984). The resulting mild temperatures usually prevent the shorelines from freezing throughout the year.

Icelandic arctic foxes can adopt two different resource use strategies, referred to as coastal and inland. Interior habitats are more subject to seasonal variations in temperature influencing the availability of resources. Resident birds like rock ptarmigans (*Lagopus muta*) and migrating birds like waders, geese and passerines make up for most of the inland foxes' diet (Hersteinsson 1984, Angerbjörn & al. 1994; Hersteinsson & Macdonald 1996; Hersteinsson &



**Figure 2** Map of Iceland displaying the different culling locations. Coastal areas are shown in blue, and inland areas in brown. Culling location are circled when hunting does not occur in the whole region. The number of foxes culled per region is specified.

al. 2009). The Western part of Iceland bears the most productive seashores, with a greater productivity than northern, southern and eastern Iceland combined (Ingólfsson 1975). It also supports most of the large seabirds colonies that nest on the cliffs during summer (Hersteinsson & al. 2009). Ice-free shores provide a more stable availability of food supply (Dalerum & al. 2012), enabling coastal foxes to benefit from carrion from marine mammals, fish, marine invertebrates and seabirds in addition to some terrestrial preys (Hersteinsson 1984, Hersteinsson & MacDonald 1996, Elmhagen & al. 2000). Thanks to their more stable food resources, coastal foxes are thought to be more territorial and have shorter movement while inland foxes are more mobile (Hersteinsson 1984). This tendency seems to be recently supported by Norén & al. (2009), who showed a genetical divergence in coastal foxes from the north-western part of Iceland compared to foxes from the rest of the country. Both coastal and inland foxes can occasionally consume sheep and reindeer (*Rangifer tarandus*) carcasses (Hersteinsson & Macdonald 1996). As foxes can be culled legally in all seasons (Dalerum & al. 2012), cattle carcasses can also be part of the diet when used as baits by hunters (Hersteinsson & Macdonald 1996).

## **2.2 Arctic fox samples**

### **2.2.1 Sample selection**

For this study, we used fox mandibles that are part of the collection of the Icelandic Institute of Natural History in Reykjavik, which consists of 11,800 mandibles from arctic foxes culled from 1979 to present. Fox carcasses are donated voluntarily by hunters from all over Iceland. All foxes have been aged by counting annual cementum lines of canine tooth roots (Allen & Melfi 1985). To account for the differences in resources between habitats and to assure a sufficient sample size, we chose jaws of foxes culled in Nordur Isafjardarsýsla (henceforth NIS) and Nordur Múlasýsla (NMU), two counties respectively representing the Western productive seashores and the Eastern inland areas (Fig. 2). Individuals from NIS were culled within 5km from the coast and can thereby be qualified as coastal whereas foxes culled in NMU were located further than 50km from the coast and are thus defined as inland. Additional samples from Carbonell Ellgutter & al. (2020) culled in the same counties were added to the analysis, along with samples coming from 5 other counties whose ecology was either similar to NIS or NMU (Ester Unnsteinsdóttir, personal communication). To ensure that

these additional areas are representative of both habitats, we also used the distance from the coastline as a criterion to define them as coastal or inland (foxes culled within 5km from the coast were considered as coastal, while foxes further than 50km from the coast were considered as inland). Altogether, this added up to a total of 256 samples, 127 of them being from inland areas and 129 being from coastal areas, spreading over almost 40 years, from 1979 to 2018. All the foxes analyzed were between one and two years old, hence we assume that the culling location is a good proxy for the area where the fox grew up, and that it is representative of its resource use strategy. As previous research showed that sex does not seem to infer on dietary rates of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Angerbjörn & al. 1994, Lecomte & al. 2011), male and female individuals have been picked at random among the dataset using a random number selection procedure to choose among the available foxes for each year (supplementary material; A, B). Samples analyzed during the present study covered a timescale slightly overlapping with Carbonell Ellgutter & al. (2020), spanning over 15 years from 2003 to 2018. They have been chosen as evenly as possible over this period to highlight potential trends over time.

Bone collagen may reflect individual and regional dietary variations, but has a slow turnover rate and is indeed less subject to punctual variation in the diet (Tieszen & al. 1983). It can reflect a lifetime average dietary intake although it is biased towards the period of greatest growth (Roth & al. 2003), which is until 8-9 months old for arctic foxes (Hersteinsson & al. 2009). Indeed, we will assume that the isotope signatures are representative of the diet of arctic foxes during their first year of life, thereby reflecting their average resource use strategy during this period.

### **2.2.2 Collagen extraction**

Collagen has been extracted from lower jaws following the same protocol as Carbonell Ellgutter & al. (2020), based on a standardized method from Brown et al. (1998) and modified according to Richard and Hedges (1999). Bone samples have been ground to powder and demineralized in 0.25 N HCl, filtered under vacuum and dried. As lipids are depleted in  $\delta^{13}\text{C}$ , their concentration can influence stable isotopes analysis (DeNiro & Epstein 1977, Ehrlich & al. 2011). Consequently, lipids were extracted using an excess of 2:1 chloroform/methanol solution before the samples were freeze-dried. Collagen has then been weighted (1.0 - 1.2mg),

packed in tin foil capsules and analyzed for stable isotopes of carbon and nitrogen at the Stable Isotopes in Nature Laboratory (SINLAB) at the Canadian Rivers Institute, University of New Brunswick.

### 2.3 Prey samples

Greylag goose (*Anser anser*) muscle and egg samples along with northern fulmar (*Fulmarus glacialis*) muscle samples conserved in 70% ethanol have been provided by the Icelandic Institute of National History. Ethanol preservation has a negligible effect on dietary rates of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and is thus a valuable storage method prior to stable isotopes analysis (Javornik & al. 2019). Both muscle and egg samples have been prepared for stable isotope analysis following the method from Ehrich & al. (2011). Because lipid-rich tissues such as muscle and egg content are depleted in  $\delta^{13}\text{C}$ , lipids have been chemically extracted prior to analysis. However, since this process can affect the measurements of  $\delta^{15}\text{N}$  for egg content (Ehrich & al. 2011), the four egg samples were prepared in duplicate, and I kept the  $\delta^{13}\text{C}$  values of samples that went through chemical extraction, and the  $\delta^{15}\text{N}$  values of the samples that did not. All prey samples have been analyzed for stable isotopes in carbon and nitrogen at SINLAB, along with fox collagen samples.

Additional prey signatures of ptarmigan, common eider (*Somateria mollissima*), wood mouse (*Apodemus sylvaticus*), golden plover (*Pluvialis apricaria*), whimbrel (*Numenius phaeopus*), sheep, horse, kittiwake (*Rissa tridactyla*), starfish (*Asteria rubens*), redshank (*Tringa totanus*), common snipe (*Gallinago gallinago*), and black guillemot (*Cepphus grille*) were obtained from Carbonell Ellgutter & al. (2020).

### 2.4 Statistical analysis

All the statistical analysis were performed using R version 4.0.4 (R Core Team 2021). The stable isotopes ratios were expressed using the standard  $\delta$  notation in parts per thousand (‰) (Ben-David & Flaherty 2012). The international standards, i.e the Vienna Peedee Belemnite for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ , were used as reference (Ben-David & Flaherty 2012). The distribution of arctic foxes' isotopic signatures with respect to their different potential preys was assessed graphically by plotting individual values from both habitats. Prey values were corrected for isotopic discrimination, which corresponds to the amount of change

in isotope ratios occurring as a prey is incorporated into the consumer's tissue (Bond & Diamond 2011, Ben-David & Flaherty 2012). Since the discrimination factor for arctic fox bone collagen has not been determined experimentally, we used the experimentally determined values from arctic fox fur (Lecomte & al. 2011), modified according to Crowley & al. (2010), who estimated the fractionation between different tissues within the same species ( $\Delta^{13}\text{C} = 2.58 \pm 0.44$  and  $\Delta^{15}\text{N} = 3.64 \pm 0.69$ ). Both foxes and preys' raw  $\delta^{13}\text{C}$  values have also been corrected for the Suess effect, which consists in a depletion in  $\delta^{13}\text{C}$  in the biosphere driven by the input of  $\text{CO}_2$  from fossil fuel since the Industrial Revolution (Keeling & al. 2017). We followed the same method as Carbonell Ellgutter & al. (2020), i.e using a mean  $\delta^{13}\text{C}$  rate of change of  $-0.026\%$  per year (Olsen et al. 2006) and correcting all the  $\delta^{13}\text{C}$  isotopic ratios to levels, which correspond to the first year of the study (1979).

Temporal changes in arctic foxes isotopic values were determined using generalized additive models (GAM) with the `mgcv` package to allow for non-linearity (Wood 2017). A GAM can fit complex and non-linear relationships with smooths functions that can take a wide variety of shapes because they are made of several smaller functions multiplied by a coefficient, each of which being a parameter in the model. The smoothness of the relationship is reflected in the effective degree of freedom (edf), where a high edf describes a wiggly curve, while an edf close to 1 describes a linear relationship. Changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  have been modelled as a smooth function of the birth year of each individual. An interaction allowed to fit different changes over time for the two habitats, and their different means with respect to the two isotopes ratios were modelled as a fixed effect. I chose the restricted maximum likelihood method and used the default parameters of the program for both smoothing parameter and the number of basic functions. Both `gam.check()` and `concurvity()` functions (Table 2) were used to test for the fit of the model as recommended by Ross & al. (2019).

The proportions of different prey items in arctic foxes' diet over time were estimated using Bayesian stable isotope mixing models as implemented in the `MixSIAR` package (Stock et al. 2018). As mixing models perform best with few potential sources, the different prey items were grouped considering the similarity of their isotopic signatures and their ecological relevance. We created four distinct source groups: seabirds (black guillemot, northern fulmar



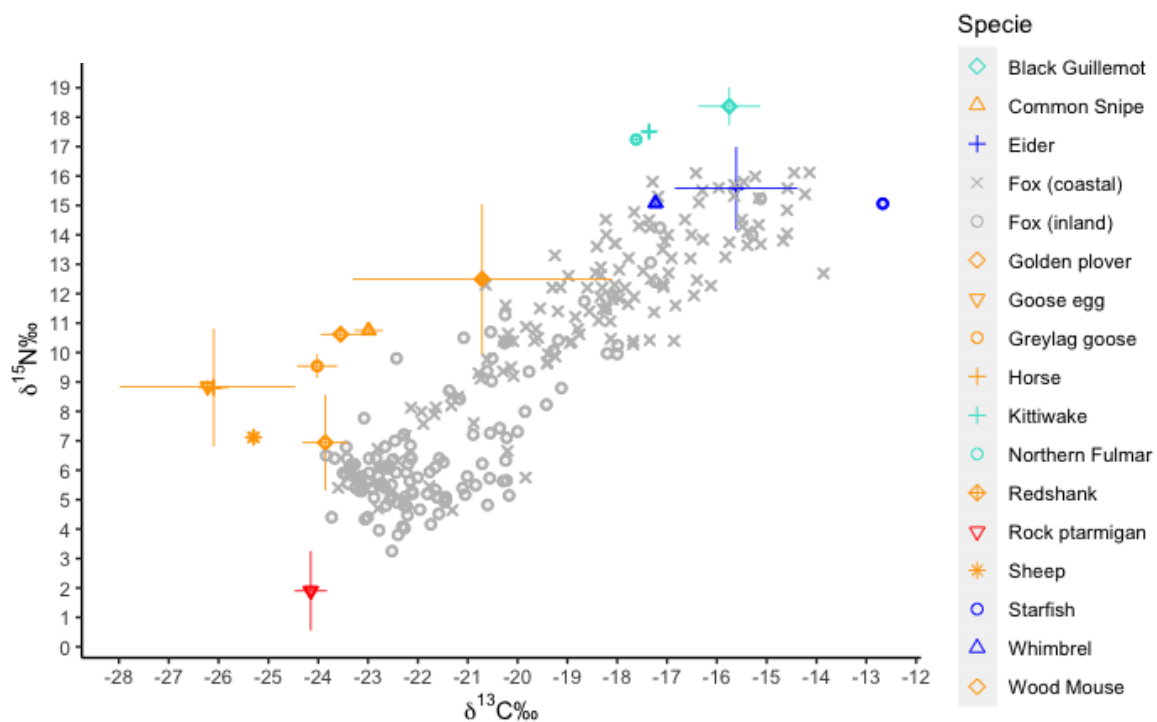
and kittiwakes), alternative marine resources (eider duck, whimbrel, starfish), the rock ptarmigan, that I kept as a focal species, and alternative terrestrial preys (common snipe, greylag goose, goose egg, redshank, golden plover, wood goose, horse, sheep). Because of their more marine signature, whimbrels were placed with the alternative marine resources even though the other waders species were placed in the alternative terrestrial resources. To highlight a potential contrast in dietary composition, the time period has been divided into four parts, considering the pattern of growth or decline in the arctic fox population: period 1 (slight growth from 1979 to 1996), period 2 (sharp growth from 1997 to 2006), period 3 (sharp decrease from 2007 to 2011), period 4 (sharp growth from 2012 to 2018). The mixing models were run separately for coastal and inland foxes. To account for the uncertainty considering the discrimination factor and because the results of mixing models can depend on how correct the discrimination value is (Bond & Diamond 2011), the analysis was repeated with four other discrimination factors, subtracting or adding 2 standard deviations for both carbon and nitrogen ratios, or adding 2 standard deviation to one isotope and subtracting it to the other (supplementary material; C). We ran the analysis following the MixSIAR manual recommendations, and did 300,000 MCMC replicates, (preceded by 200,000 burn-in) and used a residual\*process error, as advised by Stock & Semmens (2016). The convergence of the estimations was assessed based on Gelman-Rubin and Geweke diagnostics, and a particular focus has been drawn to the correlation between different sources. In addition, I checked if the posterior distributions were unimodal. The isospace plots for the converging models have been added in supplementary material; D.

The niche breadth have been determined using SIBER package (Jackson & al. 2011). The use of stable isotopes to infer a population's trophic niche width is increasing as isotopic niches are considered to be a good proxy for ecological niches (Layman & al. 2007, Newsome & al. 2007, Newsome & al. 2009, Tarroux & al. 2012, Ehrich & al. 2015).

This analysis was ran separately for coastal and inland foxes, which were grouped considering the same four periods we used for the mixing models analysis to identify potential temporal changes in niche breadth. The ellipses being unbiased for sample size (Jackson & al. 2011), it was possible to compare them even though the periods did not contain an equal amount of individuals.

### 3. Results

The isotopic signatures resulted in a plot (Fig 3) where the fox values were inside the polygon delimited by the prey values. The prey species showed a typical distinction between terrestrial species with low  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values while marine species displayed higher ratios for both isotopes. Highest  $\delta^{15}\text{N}$  values were obtained for seabirds, i.e kittiwakes, black guillemots and northern fulmars, while the lowest value was achieved by the rock ptarmigan.



**Figure 3** Isotopic signatures (‰) of foxes from coastal and inland habitats plotted along with their potential prey species corrected for trophic discrimination (discrimination factor from arctic fox fur; Lecomte & al. 2011, modified following Crowley & al. 2010) and plotted with their respective standard deviation.

Both horses and goose eggs displayed the lowest  $\delta^{13}\text{C}$  values, and had an intermediate ratio of  $\delta^{15}\text{N}$ , like other terrestrial preys. Alternative marine preys were positioned in between, with some of the highest  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  rates, just below seabirds. Waders had heterogeneous isotopic signatures, the common snipe being closer to terrestrial preys while the whimbrel could be assimilated with a marine prey, the redshank signature being in an intermediate position. The isotopic signatures were obtained for a total of 256 foxes, and spread along the gradient of prey signatures. As anticipated, coastal foxes generally had a more marine signature whereas inland foxes had a more terrestrial signature.

Both isotopic ratios showed a significant difference between habitats ( $p < 2e-16$ ), with an average variation of respectively 5‰ and 3‰ in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between coastal and inland areas (Table 1). The GAM identified significant changes in  $\delta^{13}\text{C}$  over the study period.

**Table 1** Parameter estimates from generalized additive models assessing the effect of birth year and habitat on (a) carbon isotopes ( $\delta^{13}\text{C}$ ) and (b) nitrogen isotopes ( $\delta^{15}\text{N}$ ) from bone collagen, along with their corresponding smooth terms values.

|   | Estimate | Std. Error | t value | P                |
|---|----------|------------|---------|------------------|
| (a) $\delta^{13}\text{C}$   Formula: $\delta^{13}\text{C} \sim \text{s}(\text{Year, by} = \text{Habitat}) + \text{Habitat}$ |          |            |         |                  |
| Intercept   | 11.7720  | 0.2156     | 54.60   | <2e-16           |
| Habitat (inland)  | -5.1445  | 0.3067     | -16.77  | <b>&lt;2e-16</b> |
| (b) $\delta^{15}\text{N}$   Formula: $\delta^{15}\text{N} \sim \text{s}(\text{Year, by} = \text{Habitat}) + \text{Habitat}$ |          |            |         |                  |
| Intercept   | -18.7225 | 0.1629     | -111.88 | <2e-16           |
| Habitat (inland)  | -3.4169  | 0.2301     | -14.85  | <b>&lt;2e-16</b> |
|   | edf      | Ref.df     | F       | p-value          |
| (a) $\delta^{13}\text{C}$   Formula: $\delta^{13}\text{C} \sim \text{s}(\text{Year, by} = \text{Habitat}) + \text{Habitat}$ |          |            |         |                  |
| Coastal   | 4.338    | 5.329      | 2.472   | <b>0.0413</b>    |
| Inland  | 1.002    | 1.004      | 21.600  | <b>5.96e-06</b>  |
| (b) $\delta^{15}\text{N}$   Formula: $\delta^{15}\text{N} \sim \text{s}(\text{Year, by} = \text{Habitat}) + \text{Habitat}$ |          |            |         |                  |
| Coastal   | 1.633    | 2.022      | 0.525   | 0.5835           |
| Inland  | 4.542    | 5.562      | 1.889   | 0.0607           |

Significant effects are shown in bold.

A clear linear decrease in  $\delta^{13}\text{C}$  values was observed for inland foxes (edf = 1.002;  $p = 5.96e-06$ ; Fig 4), while coastal foxes underwent non linear variations (edf = 4.338;  $p = 0.0413$ ) with fluctuations in the start of the study period and more stable values in recent years. In contrast,  $\delta^{15}\text{N}$  ratios showed less temporal change. For coastal foxes, the values of  $\delta^{15}\text{N}$  were close to remain stable throughout the whole study period (edf = 1.633;  $p = 0.5835$ ; Fig 4) while more fluctuations were observed for inland foxes (edf = 4.542), with a noticeable increase at the end of the study period that was close to significant ( $p = 0.0607$ ).

The gam.check() function showed full convergence for both models, as well as randomly distributed residuals ( $p > 0.05$  in both cases), thus confirming the reliability of the default parameters of the program. The concurvity() function showed no evidence for concurvity between variables.

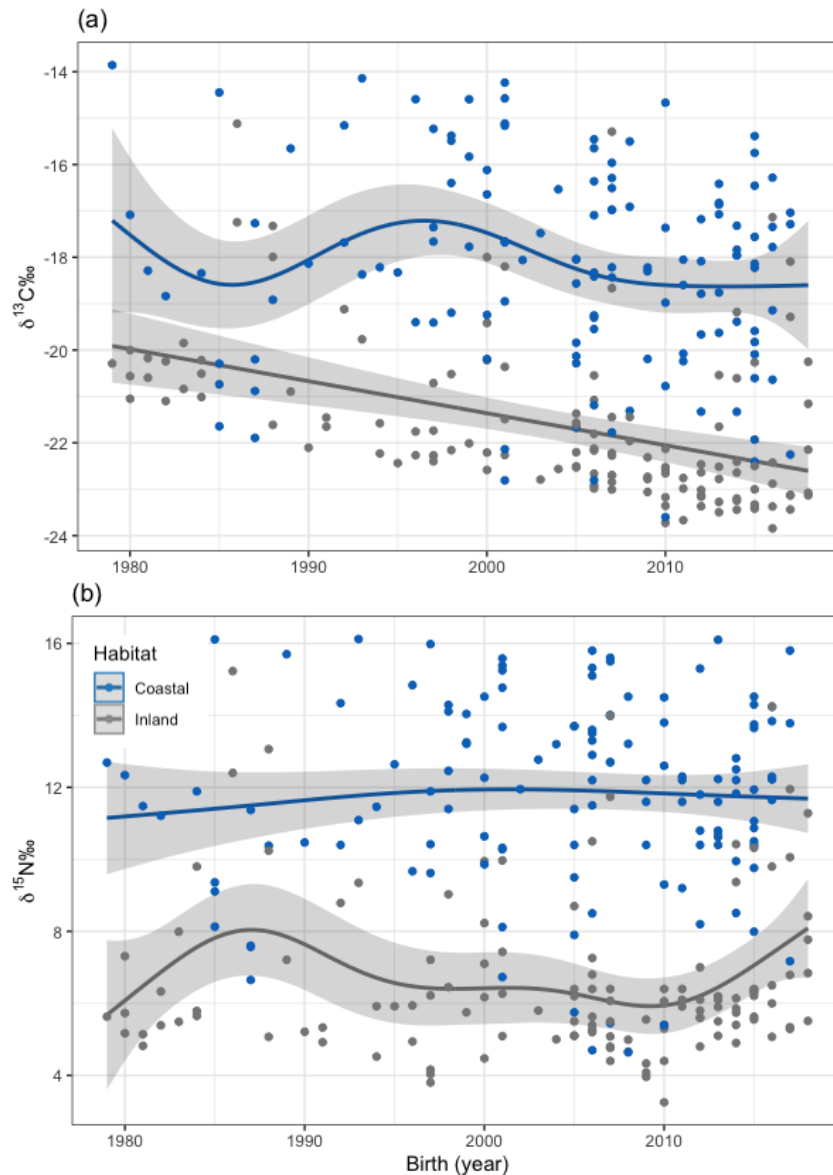
| (a)   | Number of iterations for full convergence | k' | edf  | k-index | p-value |
|---|---|----|------|---------|---------|
| $\delta^{13}\text{C}$   Formula: $\delta^{13}\text{C} \sim s(\text{Year}, \text{by} = \text{Habitat}) + \text{Habitat}$ |   |    |      |         |         |
| Coastal   | 6   | 9  | 4,34 | 1       | 0,47    |
| Inland  | 6   | 9  | 1,00 | 1       | 0,45    |
| $\delta^{15}\text{N}$   Formula: $\delta^{15}\text{N} \sim s(\text{Year}, \text{by} = \text{Habitat}) + \text{Habitat}$ |   |    |      |         |         |
| Coastal   | 7   | 9  | 1,63 | 1.01    | 0,52    |
| Inland  | 7   | 9  | 4,54 | 1.01    | 0,50    |

**Table 2** Outputs from (a) gam.check() and (b) concurvity() functions to test for the fit of the generalized additive models estimated with the default parameters of the gam() function in the mgcv package.

| (b)   | para      | Coastal      | Inland       |
|---|-----------|--------------|--------------|
| $\delta^{13}\text{C}$   Formula: $\delta^{13}\text{C} \sim s(\text{Year}, \text{by} = \text{Habitat}) + \text{Habitat}$ |           |              |              |
| worst   | 0.5267907 | 0.0609179754 | 0.0298197051 |
| observed  | 0.5267907 | 0.0007345651 | 0.0001485778 |
| estimate  | 0.5267907 | 0.0027127661 | 0.0021545252 |
| $\delta^{15}\text{N}$   Formula: $\delta^{15}\text{N} \sim s(\text{Year}, \text{by} = \text{Habitat}) + \text{Habitat}$ |           |              |              |
| worst   | 0.5267907 | 0.060917975  | 0.029819705  |
| observed  | 0.5267907 | 0.011275836  | 0.001576367  |
| estimate  | 0.5267907 | 0.002712766  | 0.002154525  |

The dietary composition of coastal foxes remained stable throughout the study period (Fig 5a) and the model converged well with respect to the discrimination factor chosen as reference (supplementary material; C, D). However, despite the convergence, the maximum correlation between seabirds and alternative marine resources was very high (-0.89) in the coastal habitat, indicating that the distinction between these two prey groups was hardly possible. Thereby, the results regarding coastal foxes' diet must be taken with caution.

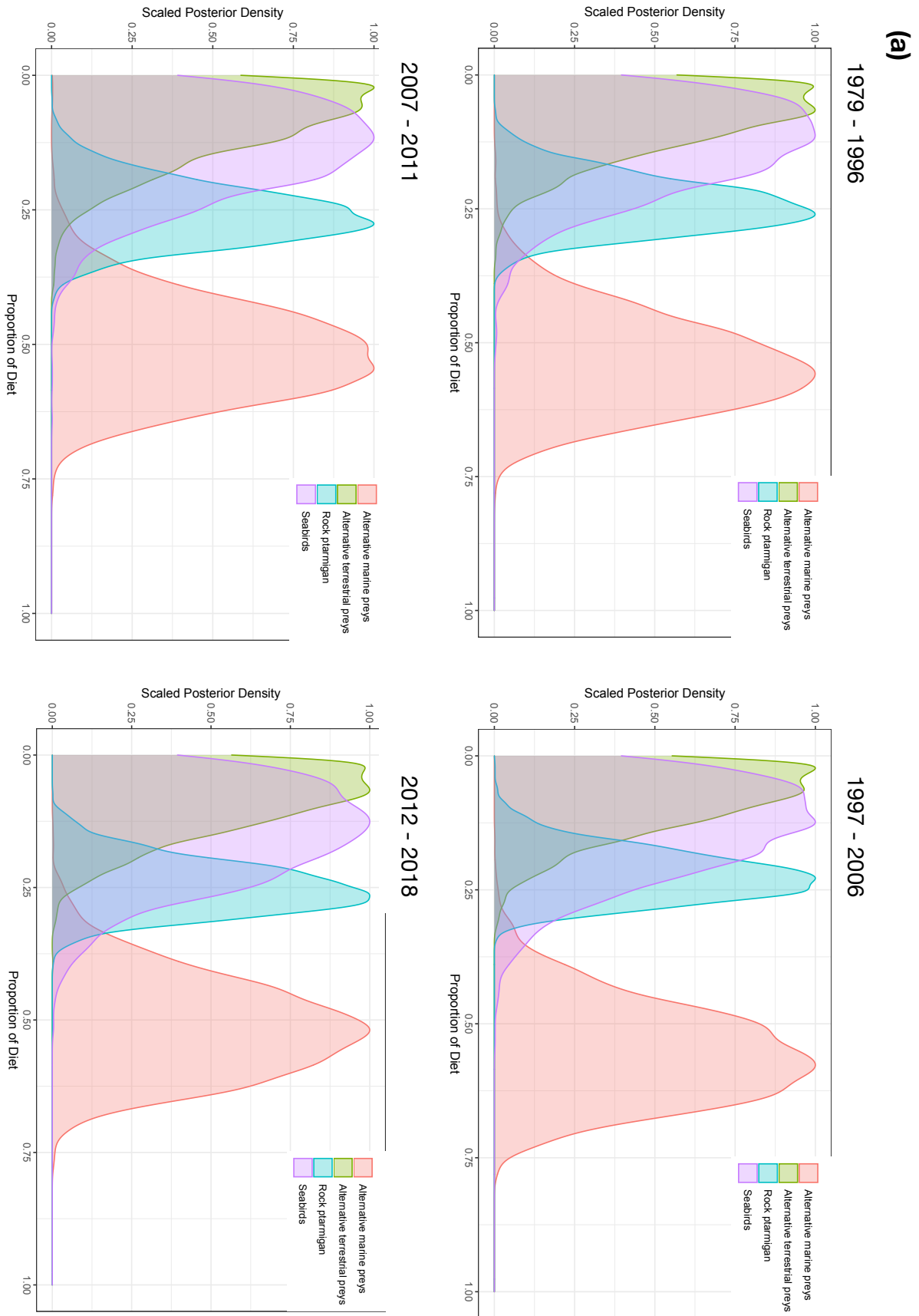
As expected, marine preys were very important for coastal foxes and composed more than half of their diet, while ptarmigans composed roughly one quarter. The proportion of seabirds was lower than expected, overlapping with terrestrial preys, and both of these resources' credibility intervals did not exclude 0. Inland foxes had a more variable diet with respect to the different periods (Fig 5b) and the model converged with the discrimination factor chosen as reference (supplementary material; C, D). Ptarmigans were always the most used resource, but their proportion varied over time, representing up to three fourth of the diet during the decline phase. During this particular period, all the other resource groups overlapped.



**Figure 4** Isotopic signatures in (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  of foxes from both habitats are plotted according to their year of birth. Lines have been generated with generalized additive models, along with the 95% confidence interval.

Marine preys were more important during the two first periods of growth, composing a third of the diet and reduced to a fourth during the second period. The proportion of seabirds and terrestrial preys was very low and the credibility intervals of these resources did not exclude 0. Terrestrial preys seemed to be more important during the last growth phase, and represented over a fourth of the diet. Marine preys were slightly less used, and the ptarmigans only composed half of the diet.

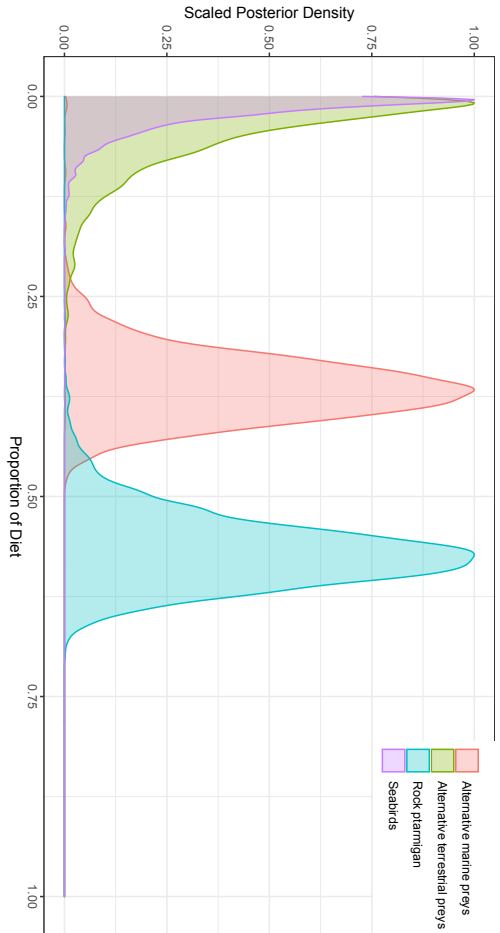
The sensitivity analysis using different discrimination factors showed no convergence for any other model (supplementary material; C).



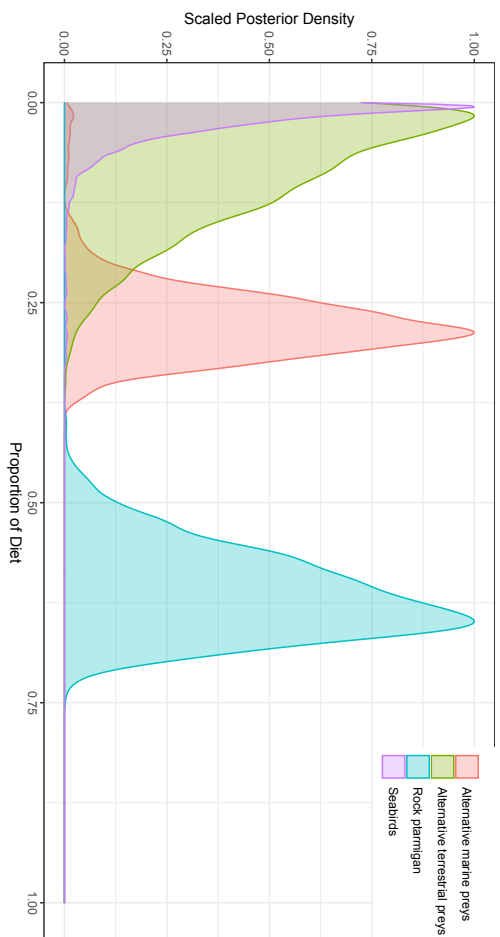
**Figure 5** MixSIAR (stable isotope mixing models) estimates showing the scaled posterior density of the proportion of the different prey groups in the diet of (a) coastal and (b) inland foxes.

(b)

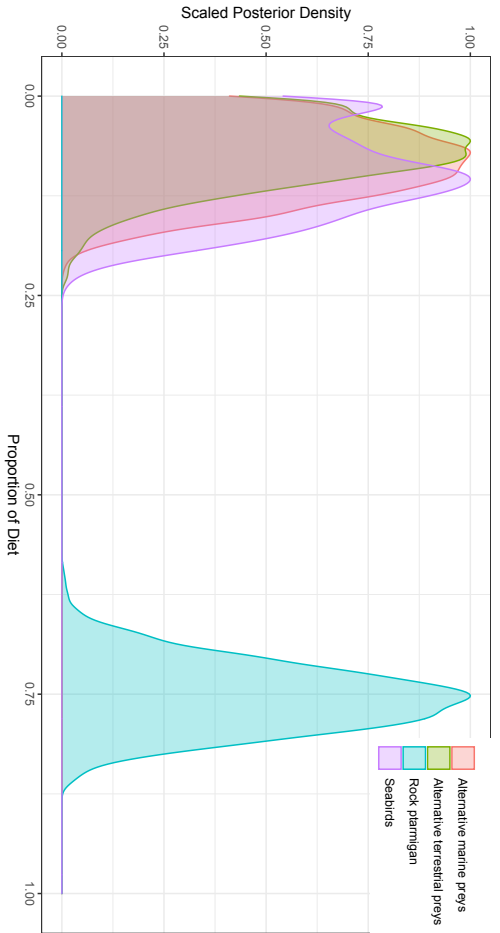
1979 - 1996



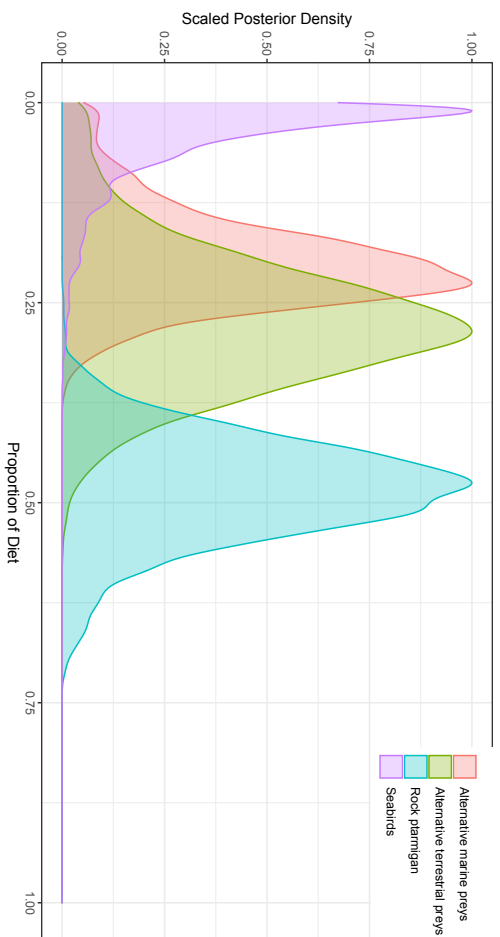
1997 - 2006



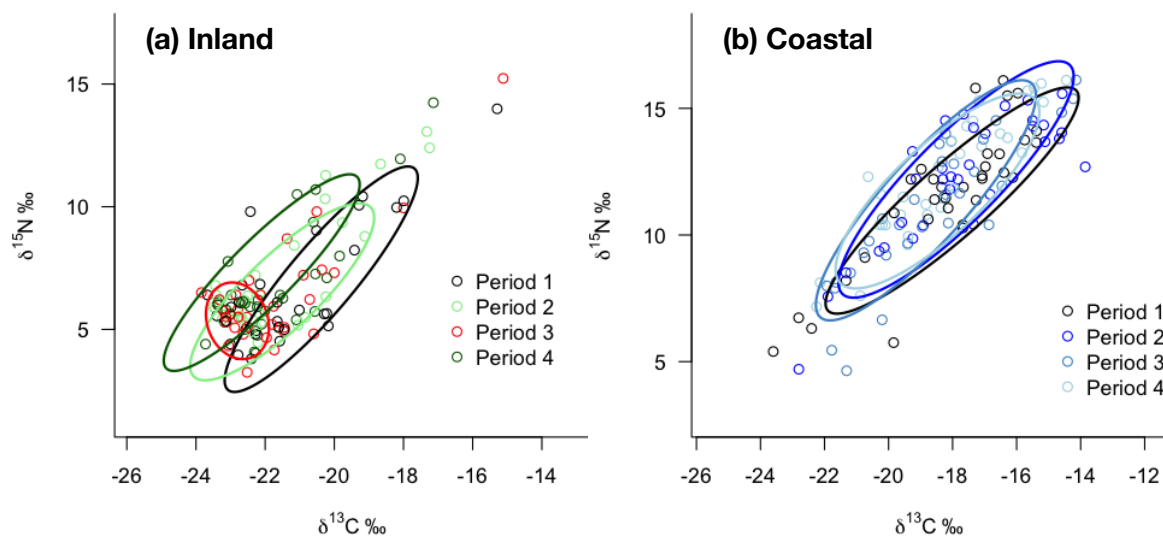
2007 - 2011



2012 - 2018



As for the mixing models, the variations in the isotopic niche breadths were more visible for inland foxes (Fig 6a). The niches shifted towards lower  $\delta^{13}\text{C}$  values over time and kept a similar width until the decline phase when the niche shrank considerably. Coastal foxes' niches remained stable and overlapped during the different periods (Fig 6b). The niche breadths of coastal foxes were globally greater than the ones of inland foxes (supplementary material; E).



**Figure 6** Standard ellipses representing the isotopic niches breadth from (a) inland and (b) coastal foxes during four different periods.

## 4. Discussion

### 4.1 Variations in resource use

The results confirmed the marked differences in diet between coastal and inland foxes, with coastal foxes having overall more marine signatures than inland foxes. The temporal trends in isotopic values gave a first insight in the dynamics of these differences. The significant decrease in the stable isotope ratio of carbon among inland foxes suggested a shift towards more terrestrial preys, and was combined with a slight increase in nitrogen ratios at the end of the study period. Coastal foxes, on the opposite, showed no statistical evidence for changes in nitrogen ratios, and the changes in carbon ratios they underwent during the beginning of the study had a low statistical support, and were likely due to the small amount of individuals sampled during the first years of the study. These differences between a rather stable diet at



the coast and more fluctuations in inland habitats are in agreement with the estimations of dietary composition from isotopic mixing models as well as the isotopic niche breadths, which showed important changes in the resource use of inland foxes while coastal foxes seemed to have a rather stable diet and constant niche width throughout the years.

Earlier diet studies based on prey remains at dens and scat content analysis suggested that seabirds such as fulmars or alcids were an important resource, especially for coastal foxes but also for some inland foxes that could access to nesting fulmars and gulls colonies further away from the coast (Hersteinsson 1984, Angerbjörn & al. 1994, Pálsson & al. 2016). Surprisingly, no support was found for a major use of seabirds regardless of the habitat. Even though we need to keep in mind the high correlation between seabirds and marine resources observed for coastal foxes, which made the distinction between these two sources hardly possible in the mixing model analysis, this result contrasts with previous founding. Although the three seabird species used in this study are on the decline in Iceland (Skarphéðinsson 2018, Icelandic Institute of Natural History unpublished data), the mixing model results suggested that the proportion of seabirds in foxes' diet remained rather low and constant throughout the different periods. This resource being available only seasonally, it is likely that the results are slightly underestimated since isotopes from bone collagen reflect the lifetime dietary intake of foxes. However, prey remains at dens results might also be biased towards only part of the population, i.e breeding pairs. Dalerum & al. (2012) reported the existence of a difference between the diet of coastal adult and juvenile foxes, with juveniles foxes having enriched carbon and nitrogen rates. He suggested that cubs were mostly fed with marine resources, which could explain the apparent greater importance of seabirds in prey remain at dens studies than in my results.

In agreement with Carbonell Ellgutter & al. (2020), who highlighted the importance of marine resources in the diet of Icelandic arctic foxes, the mixing models analysis suggested that marine preys are the main resource consumed by coastal foxes, and also seemed to be important for inland individuals, to a degree. Interestingly, our results are in line even though the prey items comprised in our marine sources are different. In contrast with Carbonell Ellgutter & al. (2020), the present study does not include seabirds as part of the marine sources in the mixing models, suggesting that preys from lower trophic levels such as eiders

and whimbrels would be the most important. It is likely that marine resources like eider ducks which are available throughout the year represent an important part of the diet of Icelandic arctic foxes. These birds are widely distributed on the coastal areas of Iceland, and their population has been steadily increasing until 2000 (Icelandic Institute of Natural History, unpublished data). They might support the fox population especially during the winter when migrant birds are absent.

The rock ptarmigan, a species also available throughout the year, appears to be the preferred terrestrial resource. They are especially important for inland foxes, and might be partly responsible for the observed decrease in carbon ratio over time. However, recent research has shown that this species has a negative population trend in Iceland (Fuglei & al. 2019), and is thus unlikely to be solely responsible for the major growth in arctic foxes' population. It is nonetheless possible that the recent decline and growth periods that occurred on a much shorter span have been influenced by ptarmigan cycles.

During the breeding season, waders and geese are increasingly available to foxes. In contrast with Pálsson & al. (2016) who suggested that these resources might have partly driven the rise in the arctic fox population, the results suggested that these prey items are of minor importance, and confirmed the results from Carbonell Ellgutter & al. (2020) who did not find support for an increased use of geese, despite isolating the greylag goose as a focal source in their mixing model analysis. However, the latest period of growth in foxes' population size showed a recrudescence in the use of alternative terrestrial resources among inland foxes. As these terrestrial preys have a higher nitrogen signature than ptarmigans, this would support the increase in nitrogen ratio observed for inland foxes during the end of the study period. The observed shift towards preys with lower carbon ratios could then be explained by the use of resources such as goose eggs in combination with the ptarmigans.

Alternatively, whimbrels, which were included in our marine preys, could have been an important resource for foxes from both habitats as they are abundant and accessible during their nesting season (Skarphéðinsson 2018). Unfortunately, the grouping used in the mixing models analysis makes it hard to determine whether or not this particular wader species was more important than the others, and no information was found in literature to either support or contest this assumption.

It seems like variations in the abundance of food sources did not result in major changes in the diet of Icelandic arctic foxes, even though it has impacted their population size. In contrast with Carbonell Ellgutter & al. (2020), no support was found in the results for temporal variations in nitrogen ratios, suggesting that foxes did not shift from seabirds to marine resources from lower trophic levels, but either acted as true generalist predators, utilizing a large number of prey items since the beginning of the study period. The results generally suggest that marine resources supported the growth in foxes' numbers, confirming the importance of marine preys for this population (Dalerum & al. 2012, Pálsson & al. 2016, Carbonell Ellgutter & al. 2020). The brutal fluctuations that occurred during the last decade may result from drastic variations in the rock ptarmigan population, which represent a very important resource for Icelandic arctic foxes.

## **4.2 Population isotopic niche breadth**

The high hunting pressure in Iceland leads to a high turnover in territorial foxes, and Unnsteinsdóttir & al. (2016) suggested that Icelandic arctic foxes engage in contest competition as they adapt their territory size in response to variations in carrying capacity.

Consequently, I predicted that arctic foxes' niche breadth would vary over time, but found no support for this hypothesis in the coastal habitat. Although the diet of coastal foxes seemed not to vary over the study period, one could assume that they have to deal with intra-specific competition since they experienced a decline in the availability of one of their favorite resource combined to an increase in the number of conspecifics. Even though we found no support for variations in their niche breadth, the apparent consistence in their isotopic niche at the population level could hide some variations at a finer scale - the individual scale.

The results from isotopic niche analysis suggested that coastal foxes globally have broader niches than inland foxes. In previous research, Dalerum & al. (2012) pointed out the same phenomenon and suggested that these wider niches were due to a diversification of individual strategies likely dictated by the local abundance of resources. The heterogeneity of coastal areas could lead to increased individual specialization of some foxes, especially since coastal foxes are more territorial (Hersteinsson 1984). This assumption would support that the fluctuations in carbon ratios observed among coastal foxes are likely to be influenced by individual variations in the diet rather than by a global shift in resource use at the population

scale. This specialization would be a way of reducing the potential dietary overlap among foxes, in response to an increasing intra-specific competition pressure (Svanbäck & Bolnick 2007). The present study did not test for individual isotopic niche breadth, however, it seems reasonable to assume that the combination of these specialized diets would result in a wide isotopic niche at the population scale, as observed in this case.

On the other hand, inland foxes showed more variations in isotopic niche space over time, as well as a marked reduction in their niche breadth during the period of decline. This fits with the increased use of rock ptarmigan observed in the mixing model results during the decline period, but also with the assumption that this specific prey item, potentially in combination with other preys with low carbon signature like goose eggs, might have partly driven the decline in carbon ratio observed among inland foxes.

This would suggest that, in contrast with coastal foxes, inland foxes' niche breadth increases as the fox population increases, and foxes would tend to diversify their diet as their preferred resource - the rock ptarmigan - is declining or less available because highly preyed upon by other conspecifics. This would follow one of the predictions from the optimal foraging theory, where a predator should add new prey items to its diet when preferred prey become scarce (Stephens & Krebs, 1986). The resulting diversification would then be more homogeneous among individuals, and lead to a more restrained increase in niche breadth than observed for coastal foxes, as we might witness here.

### **4.3 Driver of population change**

The cleavage between coastal and inland foxes in Iceland has been previously reported genetically (Norén & al. 2009), through density dependence (Unnsteinsdóttir & al. 2016), and also through their resource use strategies (Angerbjörn et al. 1994, Hersteinsson & MacDonald 1996, Dalerum et al. 2012, Pálsson et al. 2016, Carbonell Ellgutter & al. 2020). The greater productivity and heterogeneity of coastal habitat enable these foxes to have a more stable food supply, which led here to stable dietary composition and niche breadth, highlighting a generalist predator behavior. In contrast, inland foxes displayed more variations in their diet as well as in their niche width, and the results pointed out the importance of the rock ptarmigan, suggesting that inland foxes diversify their diet during periods of growth, when their preferred prey become scarce and when the number of conspecifics increases.

As suggested by Unnsteinsdóttir 2016, the fluctuations in foxes' population size may arise from variations in carrying capacity, which is likely to vary with the changes in abundance of marine resources, and to some extent with the increased availability of seasonal resources that likely supported the recent growth of the population.

However, the variations reflected through stable isotopes remain blurry for sources with similar isotopic compositions (Newsome & al. 2007) and it is unfortunately the case in this study between seabirds and alternative marine preys. The addition of more seabirds species in the mixing models analysis like alcids or puffins could have helped the distinction between the two source groups, while it would have still be relevant for potential specialized coastal foxes. Moreover, we also lacked prey sources like the barnacle geese, the pink-footed geese, reindeers, crustaceans, etc., which could have provided a more detailed picture of the foxes' diet. Further research combining direct methods like prey remains at dens or scat dissection along with stable isotope analysis could give a more precise insight into foxes' diet, providing both seasonal and annual information about their resource use. Investigating the inter-individual differences in dietary composition thanks to stable isotope analysis of blood samples from marked individuals over several years would also be a major improvement to understand to which extent specialization is occurring in this particular population.

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## 6. Supplementary materials

**Table A** Year of birth, location and sex of the different foxes we used for this analysis.

| Birth year | Inland male samples | Inland female samples | Total Inland samples | Coastal male samples | Coastal female samples | Total coastal samples | Total samples |
|------------|---------------------|-----------------------|----------------------|----------------------|------------------------|-----------------------|---------------|
| 1979       | -                   | 1                     | 1                    | -                    | 1                      | 1                     | 2             |
| 1980       | 2                   | 1                     | 3                    | 1                    | -                      | 1                     | 4             |
| 1981       | 1                   | 1                     | 2                    | -                    | 1                      | 1                     | 3             |
| 1982       | -                   | 2                     | 2                    | -                    | 1                      | 1                     | 3             |
| 1983       | 1                   | 1                     | 2                    | -                    | -                      | -                     | 2             |
| 1984       | 2                   | 1                     | 3                    | 1                    | -                      | 1                     | 4             |
| 1985       | -                   | -                     | -                    | 4                    | -                      | 4                     | 4             |
| 1986       | 2                   | -                     | 2                    | -                    | -                      | -                     | 2             |
| 1987       | -                   | -                     | -                    | -                    | 4                      | 4                     | 4             |
| 1988       | 1                   | 2                     | 3                    | -                    | 1                      | 1                     | 4             |
| 1989       | -                   | 1                     | 1                    | 1                    | -                      | 1                     | 2             |
| 1990       | -                   | 1                     | 1                    | -                    | 1                      | 1                     | 2             |
| 1991       | 1                   | 1                     | 2                    | -                    | -                      | -                     | 2             |
| 1992       | 1                   | -                     | 1                    | -                    | 2                      | 2                     | 3             |
| 1993       | -                   | 1                     | 1                    | 1                    | 1                      | 2                     | 3             |
| 1994       | 1                   | 1                     | 2                    | 1                    | -                      | 1                     | 3             |
| 1995       | 1                   | -                     | 1                    | 1                    | -                      | 1                     | 2             |
| 1996       | 1                   | 1                     | 2                    | 2                    | -                      | 2                     | 4             |
| 1997       | 3                   | 2                     | 5                    | 2                    | 2                      | 4                     | 9             |
| 1998       | -                   | 2                     | 2                    | 2                    | 2                      | 4                     | 6             |
| 1999       | -                   | 1                     | 1                    | -                    | 3                      | 3                     | 4             |
| 2000       | 2                   | 3                     | 5                    | 3                    | 1                      | 4                     | 9             |
| 2001       | 3                   | 1                     | 4                    | 5                    | 4                      | 9                     | 13            |
| 2002       | -                   | -                     | -                    | -                    | 1                      | 1                     | 1             |
| 2003       | -                   | 1                     | 1                    | -                    | 1                      | 1                     | 2             |
| 2004       | 1                   | -                     | 1                    | -                    | 1                      | 1                     | 2             |
| 2005       | 3                   | 3                     | 6                    | 7                    | -                      | 7                     | 13            |
| 2006       | 4                   | 5                     | 8                    | 7                    | 4                      | 11                    | 19            |
| 2007       | 5                   | 4                     | 9                    | 5                    | 3                      | 8                     | 17            |
| 2008       | 1                   | 1                     | 2                    | 3                    | -                      | 3                     | 5             |
| 2009       | 1                   | 3                     | 4                    | 1                    | 2                      | 3                     | 7             |
| 2010       | 2                   | 5                     | 7                    | 4                    | 1                      | 5                     | 12            |

| Birth year | Inland male samples          | Inland female samples | Total Inland samples | Coastal male samples          | Coastal female samples | Total coastal samples | Total samples                   |            |
|------------|------------------------------|-----------------------|----------------------|-------------------------------|------------------------|-----------------------|---------------------------------|------------|
| 2011       | 2                            | 1                     | 3                    | 1                             | 3                      | 4                     | 7                               |            |
| 2012       | 4                            | 2                     | 6                    | 3                             | 2                      | 5                     | 11                              |            |
| 2013       | 3                            | 3                     | 6                    | 2                             | 4                      | 6                     | 12                              |            |
| 2014       | 3                            | 4                     | 7                    | 4                             | 2                      | 6                     | 13                              |            |
| 2015       | 4                            | 2                     | 6                    | 5                             | 7                      | 12                    | 18                              |            |
| 2016       | 3                            | 2                     | 5                    | 3                             | 2                      | 5                     | 10                              |            |
| 2017       | 1                            | 4                     | 5                    | 2                             | 1                      | 3                     | 8                               |            |
| 2018       | 3                            | 2                     | 5                    | -                             | -                      | -                     | 5                               |            |
|            | <b>Total inland samples:</b> |                       | <b>127</b>           | <b>Total coastal samples:</b> |                        | <b>129</b>            |                                 |            |
|            |                              |                       |                      |                               |                        |                       | <b>Total number of samples:</b> | <b>256</b> |

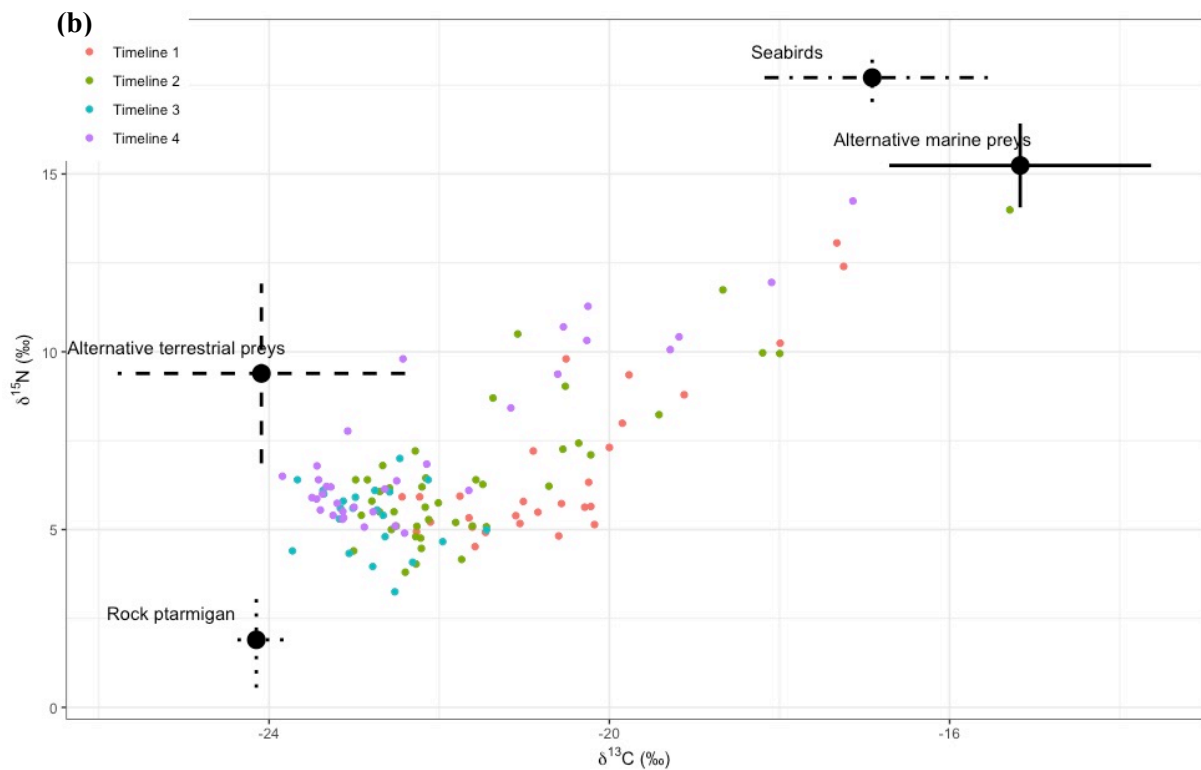
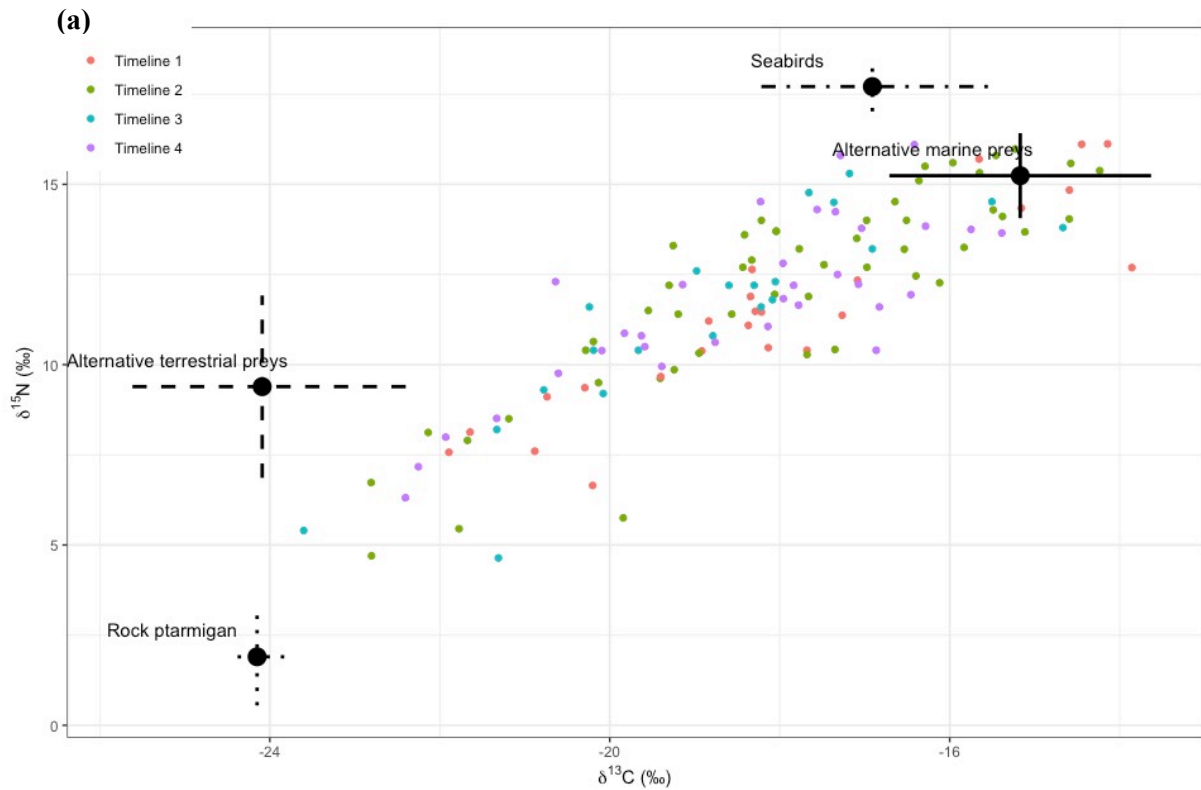
**Table B** Summarizing table of Carbonell Ellgutter & al. (2020) extraction along with the extraction carried out in the present study.

| Extraction                       | Sample-span | Icelandic counties represented | Total Inland samples | Total Coastal samples | Total number of samples |
|----------------------------------|-------------|--------------------------------|----------------------|-----------------------|-------------------------|
| Carbonell Ellgutter & al. (2020) | 1979-2008   | 7 (see Figure 2)               | 52                   | 54                    | 106                     |
| Present study                    | 2003 - 2018 | 2 (see Figure 2)               | 75                   | 75                    | 150                     |

**Table C** Overview of the runs performed in mixSIAR. Foxes were analyzed separately depending on their habitat and time was included as a categorical (four periods) covariate. I used a combination of five different discrimination factors based on the values from arctic fox fur (Lecomte & al. 2011), modified according to Crowley & al. (2010) +/- 2 standard deviation to test the sensitivity of the results. Convergence was assessed based on the Gelman-Rubin (Gel.) and Geweke (Gew.) diagnostics. The runs that did not converge or that did not result in unimodal posterior distributions for dietary proportions (Unim.) were discarded. The maximal correlation between two sources is given (Cor.). Sources are abbreviated as Ptarmigan – P, Alt. terrestrial – T, Alt. Marine – M, Seabirds – S. Mean posterior estimates of dietary proportions are given with 95% credibility intervals for the models which had satisfactory convergence diagnostics (in bold).

| Run   | Convergence |      |       |           | Estimates with 95% posterior interval |           |                  |          |             |
|---|-------------|------|-------|-----------|---------------------------------------|-----------|------------------|----------|-------------|
|   | Gel.        | Gew. | Unim. | Cor.      | Perio                                 | Ptarmigan | Alt. terrestrial | Seabirds | Alt. marine |
| inland ( $\Delta 13C = 1.7$ ; $\Delta 15N = 2.26$ )                             | yes         | no   | yes   | -0.57 M-P |                                       |           |                  |          |             |
| inland ( $\Delta 13C = 1.7$ ; $\Delta 15N = 5.02$ )                             | no          | yes  | yes   | -0.76 M-P |                                       |           |                  |          |             |
| <b>inland (<math>\Delta 13C = 2.58</math>; <math>\Delta 15N = 3.64</math>)</b>  | yes         | yes  | yes   | -0.65 M-P | 1                                     | 0.568     | 0.046            | 0.023    | 0.363       |
|   |             |      |       |           | 2                                     | 0.614     | 0.082            | 0.028    | 0.276       |
|   |             |      |       |           | 3                                     | 0.754     | 0.069            | 0.095    | 0.081       |
|   |             |      |       |           | 4                                     | 0.485     | 0.271            | 0.051    | 0.193       |
| inland ( $\Delta 13C = 3.46$ ; $\Delta 15N = 2.26$ )                            | yes         | no   | yes   | -0.81 T-P |                                       |           |                  |          |             |
| inland ( $\Delta 13C = 3.46$ ; $\Delta 15N = 5.02$ )                            | yes         | no   | yes   | -0.59 T-P |                                       |           |                  |          |             |
| coastal ( $\Delta 13C = 1.7$ ; $\Delta 15N = 2.26$ )                            | yes         | no   | no    | -0.89 S-M |                                       |           |                  |          |             |
| coastal ( $\Delta 13C = 1.7$ ; $\Delta 15N = 5.02$ )                            | yes         | no   | yes   | -0.73 M-P |                                       |           |                  |          |             |
| <b>coastal (<math>\Delta 13C = 2.58</math>; <math>\Delta 15N = 3.64</math>)</b> | yes         | yes  | yes   | -0.89 S-M | 1                                     | 0.242     | 0.086            | 0.135    | 0.537       |
|   |             |      |       |           | 2                                     | 0.223     | 0.085            | 0.139    | 0.553       |
|   |             |      |       |           | 3                                     | 0.257     | 0.094            | 0.140    | 0.509       |
|   |             |      |       |           | 4                                     | 0.249     | 0.089            | 0.150    | 0.512       |
| coastal ( $\Delta 13C = 3.46$ ; $\Delta 15N = 2.26$ )                           | yes         | no   | no    | -0.97 S-M |                                       |           |                  |          |             |
| coastal ( $\Delta 13C = 3.46$ ; $\Delta 15N = 5.02$ )                           | yes         | no   | no    | -0.90 S-M |                                       |           |                  |          |             |

**Table D** Isospace plots generated by MixSIAR on the convergent runs for (a) coastal and (b) inland habitats. The discrimination factor used for this model was based on the values from arctic fox fur (Lecomte & al. 2011), modified according to Crowley & al. (2010). Foxes were rather well distributed in the polygon delimited by the prey values, and except from seabirds and alternative marine preys that had close isotopic signatures, the prey groups were distinct.



**Table E** Standard ellipse area determined with the SIBER package for (a) coastal and (b) inland foxes over the four periods.

