

# **Dietary variation in Icelandic arctic fox (*Vulpes lagopus*) over a period of 30 years assessed through stable isotopes**

Jennifer A. Carbonell Ellgutter<sup>1</sup>, Dorothee Ehrich<sup>1</sup>, Siw T. Killengreen<sup>2</sup>, Rolf A. Ims<sup>1</sup>, Ester R Unnsteinsdóttir<sup>3</sup>

---

1 Department of Arctic Biology and Marine Biology, UiT – The Arctic University of Norway, Tromsø, Norway

2 Department of Teacher Education and Education, UiT – The Arctic University of Norway, Tromsø, Norway

3 Department of Zoology, Icelandic Institute of Natural History, Reykjavik, Iceland

Corresponding author, e-mail: [shonna28@gmail.com](mailto:shonna28@gmail.com)

Conflict of Interest: The authors declare that they have no conflict of interest.

“This article does not contain any studies with human participants or animals performed by any of the authors.”

Author Contributions: J.A.C.E. processed the samples, analyzed the data and wrote the manuscript, D.E. supervised the study and with S.T.K. and E.R.U. designed the study, R.A.I. and all the authors provided editorial revision, E.R.U. provided the samples.

## **Abstract**

Identifying resources driving long-term trends in predators is important to understand ecosystem changes and to manage populations in the context of conservation or control. The arctic fox population in Iceland has increased steadily over a period of 30 years, an increase that has been attributed to an overall increase in food abundance. We hypothesized that increasing populations of geese or seabirds were driving this growth. We analyzed stable isotopes in a long-term series of collagen samples to determine the role of these different resources. The isotopic signatures of arctic foxes differed consistently between coastal and inland habitats. Whereas  $\delta^{15}\text{N}$  displayed a non-linear change over time with a slight increase in the first part of the period followed by a decline in both habitats,  $\delta^{13}\text{C}$  was stable. Stable isotope mixing models suggested that marine resources and rock ptarmigan were the most important dietary sources, with marine resources dominating in coastal habitats and rock ptarmigan being more important inland. Our results suggest that seabirds may have been driving the arctic fox population increase. The rapidly increasing populations of breeding geese seem to have played a minor role in arctic fox population growth, as rock ptarmigan were the most important terrestrial resource despite a considerable decrease in their abundance during recent decades. This study shows that a long-term population trend in a generalist predator may have occurred without a pronounced change in main dietary resources, despite ongoing structural changes in the food web, where one species of herbivorous birds increased and another decreased.

**Keywords:** *Vulpes lagopus*, stable isotope analysis, diet, Iceland, population increase

## Introduction

High latitude ecosystems are both naturally dynamic and presently subjected to long-term changes due to climate warming (Post et al. 2009). Ecosystem changes are often propagated to individual species by trophic interactions (Schmidt et al. 2017). Owing to their position at the top of food webs, predators may be especially prone to ecosystem fluctuations and change (Ehrlich et al. 2015). Changes in resource availability such as a collapse of key prey populations (Schmidt et al. 2012; Miles et al. 2015) and/or dietary shifts to lower quality prey (Reynolds et al. 2019) may drive negative population trends, whereas population increase can result from growing prey populations (Serrouya et al. 2017), or from access to new resources such as anthropogenic subsidies (Elmhagen et al. 2017). Identifying the drivers of long-term predator population trends as resulting from fluctuations in main prey or from new resources, appearing with structural changes in the food web, is important to understanding how ecosystems are impacted by climate or human activity. Such knowledge is also a prerequisite to manage predator populations both regarding conservation concerns (Ims et al. 2017) or control (Serrouya et al. 2017). A first step to understand these relationships is to study the dynamics of predator diets. While the short-term dynamics of the diet (i.e. seasonal or annual variation) are well studied in many predator species, long-term studies (i.e. at multi-decadal time scales) are rare.

The arctic fox, *Vulpes lagopus*, is a medium sized canid with a circumpolar distribution in the northern hemisphere (Berteaux et al. 2017). It has been chosen as a climate change flagship species by the International Union of Conservation of Nature (IUCN), and it is retracting and/or decreasing in the southern part of its range due to increased competition with red foxes, changes in prey abundance and to habitat loss (McLaughlin 2009; Ims et al.

2017). Due to these different threats, conducting long-term studies of the population dynamics and resource use of this species becomes crucial (Berteaux et al. 2017). Arctic foxes have been attributed to two main resource use strategies: lemming foxes and coastal foxes. Lemming foxes behave as lemming (*Lemmus* and *Dicrostonyx* spp.) specialists and their reproduction follows the resource pulses of the lemming cycle. Coastal foxes live in areas where small rodents are absent, such as in Svalbard, Iceland and on other arctic islands and feed on marine resources such as seabirds as well as on terrestrial birds or ungulate carcasses (Braestrup 1941; Angerbjörn et al. 2004a; Eide et al. 2012). They have access to both inland and coastal habitats and resources, resulting in a rather stable annual food availability (Hersteinsson and Macdonald 1996; Angerbjörn et al. 2004b) and hence little short-term variation in diet compared to arctic foxes in rodent dominated ecosystems (Elmhagen et al. 2000).

Islands may be the safest refuge for arctic fauna in a warmer future (Fuglei and Ims 2008). In Iceland, the arctic fox maintains a large population along the constantly ice-free coasts (Pálsson et al. 2016). The arctic fox is regarded as a vermin, based on supposed killing of sheep (*Ovis aries*) and damage to eider duck (*Somateria mollissima*) colonies. Fox hunting has been encouraged and legislated for since the thirteenth century, and is still coordinated and subsidized by the Wildlife Management Institute (Hersteinsson et al. 1989). The hunting data suggest a sharp fall in the arctic fox population all over Iceland from the 1950s into the 1970s and this has been attributed primarily to a decrease in rock ptarmigan (*Lagopus muta*) numbers (Hersteinsson 1987; Hersteinsson et al. 1989; Angerbjörn et al. 2004b; Pálsson et al. 2016). Since the late 1970s, however, there has been a steady increase in the fox population for thirty years, followed by a new decline since

2008 (Fig. 1). Hunting represents the main cause of mortality, but the hunting effort has been stable since the 1950s and is regulated by Icelandic law. Hunting in winter is subsidized by the municipalities, whereas in summer hunting is carried out by professional hunters. Hunting effort does thus not depend on fox abundance making hunting an unlikely driver of the population fluctuations (Pálsson et al. 2016; Unnsteinsdóttir et al. 2016).

Changes in arctic fox population size in Iceland have been attributed to changes in carrying capacity mainly determined by the abundance of food resources (Pálsson et al. 2016; Unnsteinsdóttir et al. 2016) and possibly related to climate (Hersteinsson et al. 2009). Based on prey remains at dens, Pálsson et al. (2016) conclude that the increase of the fox population was to a large extent due to increasing geese and wader populations providing resources during the breeding period. In addition, they suggested that ptarmigan is an important resource for foxes in inland areas, and that long-term population size fluctuations in this species (Nielsen 1999) could have repercussions on the arctic fox population dynamics. Several ptarmigan populations, however, have exhibited decreasing trends over the period of the arctic fox increase (Fuglei et al. 2019). Likewise, for arctic foxes living on the coast, seabirds are the main prey (Unnsteinsdóttir et al. 2016), and any increase in seabird populations could have sustained the increment in fox abundance. According to Hansen et al. (2018), the overall abundance of seabird has indeed been increasing considerably from 1970s to the end of 1990s. Here we hypothesize that the prolonged increase in the arctic fox population was related to an increase in food resources. The key driver could be either the increasing goose and wader populations, which may have partly replaced ptarmigan in the diet, or the increase in seabirds.

Diseases or parasites (Goltsman et al. 1996), interspecific competition or habitat changes could also be hypothesized to have caused the conspicuous changes in arctic fox population size. However, no infectious fox diseases such as rabies or distemper are found in Iceland (Gunnarsson et al. 1993). Moreover, arctic foxes do not have any important interspecific competitors in Iceland, and the only other terrestrial mammalian predator, the mink (*Mustela vison*) has exhibited a parallel population increase (Magnusdottir et al. 2014). There is no reason to assume an increase in habitat extent, and an increase in habitat quality would most likely be related to more available resources.

There are many ways to study the diet of predators, such as direct observations, stomach content analysis, feces dissection, description of prey remains on dens (Angerbjörn et al. 1994), fatty acid analysis and stable isotope analysis (Kelly 2000; Ben-David and Flaherty 2012; Ehrich et al. 2015). Whereas direct methods such as stomach contents or feces dissection provide snapshot information about diet on a specific day and prey remains on dens provide information representative for the breeding season, the stable isotope ratios of predator tissues reflect the resources assimilated over a longer time period (Inger and Bearhop 2008; Ben-David and Flaherty 2012; Layman et al. 2012). Stable isotope ratios can also be determined from bones, fur or feathers, opening possibilities to assess long-term dietary trends based for example on museum collections (Reynolds et al. 2019).

In this study, we used stable isotope signatures from a time series of bone collagen samples to determine the main resources used by arctic fox in Iceland over a period of 30 years covering the population's strong increase since 1980. We hypothesized that 1) the rapidly growing goose population may have been an important new resource driving the

increase of arctic foxes, particularly in inland areas, replacing the declining ptarmigan. In this case, we would expect to see a change in diet over the study period. Alternatively, 2) the increasing seabird populations may have supported the arctic fox growth. As seabirds have always been a major resource for the arctic fox in Iceland, in this case we would not expect any important change in diet. Because previous studies have shown that foxes use different resources in coastal and inland habitats (e.g. Angerbjörn et al. 1994; Hersteinsson and MacDonald 1996; Dalerum et al. 2012; Pálsson et al. 2016), we also investigated whether possible change in resource use were different between the two habitats. The long-term population growth in the Icelandic arctic fox, which is unusual for endemic northern apex predators, represents an interesting case also in a more general context. Structural alterations of food webs, potentially with bottom-up effects on apex predators, currently happen in many ecosystems driven by rapid environmental change. For instance, goose populations are increasing in many areas of the Arctic (Ims et al. 2013), but little is known about the long-term consequences of this increase for predator populations.

## **Materials and Methods**

### *Study Area*

Iceland is an island in the North Atlantic Ocean, close to the Arctic circle (63°20'-66°30'N; 13°30'-24°30'W), with a total area of 103,000 km<sup>2</sup>. The island is influenced climatically by a branch of the Gulf Stream, with average July temperatures of 10.6°C and average January temperatures just below freezing (Ogilvie 2012). Most of the interior of the country is not inhabited by humans and consists of sandy deserts, mountains and glaciers. Western Iceland has a higher proportion of productive seashores than northern, eastern and southern Iceland combined and supports most of the large seabird colonies (Hersteinsson et al.

2009). As the coast is ice-free all year round (Dalerum et al. 2012), arctic foxes in coastal habitats have access to more stable food resources over the year. In contrast, inland habitats experience substantial seasonal fluctuations in resources (Dalerum et al. 2012). The resources available to foxes in coastal areas can be carcasses of marine mammals and birds, crustaceans and other invertebrates, fish, waders or eider ducks. Areas close to seabird cliffs provide plenty of resources during the breeding season in summer (Hersteinsson 1984; Hersteinsson and Macdonald 1996; Hersteinsson et al. 2009). Inland foxes depend mostly on migrating birds (geese, waders and passerines) or resident birds such as ptarmigan (Hersteinsson 1984; Angerbjörn et al. 1994; Hersteinsson and Macdonald 1996; Hersteinsson et al. 2009). All foxes may occasionally feed on sheep (Hersteinsson and Macdonald 1996) and reindeer (*Rangifer tarandus*) carcasses. Cattle (*Bos taurus*) and horse (*Equus ferus caballus*) carcasses can be used as baits by foxhunters. In winter, foxes from both habitats use ptarmigan, cached items (Hersteinsson et al. 1989) and a small proportion of rodents (Helgason 2008), while foxes close to the coast in addition have access to marine resources.

#### *Arctic fox samples*

The collection of bones used in this study was obtained from carcasses voluntarily donated by foxhunters from all over Iceland and kept by the Icelandic Institute of Natural History in Reykjavik. The collection consists of skulls and lower jaws of adult arctic foxes (one-year-old or more) from 1979 to present. For each fox, we determined the distance from the coast of the culling location. In accordance with Dalerum et al. (2012), foxes were classified as *coastal* when culled less than 3 km from the shoreline. All other foxes were classified as *inland*. This classification assumed that foxes were sedentary, and that the



culling location reflected the area where the fox has been growing up, which may not be the case for a highly mobile predator such as the arctic fox (Angerbjörn et al. 2004b). Age was determined by counting annual cementum lines of canine tooth roots (Allen and Melfi 1985; Unnsteinsdóttir et al. 2016) at the Icelandic Institute of Natural History in Reykjavik and used to determine the year of birth for each fox. For the present study, we selected foxes born in between 1979 and 2008, covering the time of a more than threefold increase in estimated population size (Fig. 1). From each decade, 22 adult males and 22 adult females were selected for analysis, resulting in  $3 \times 44 = 132$  lower jaws in total. In order to achieve an even spatial distribution, half of the individuals of each sex in each decade were chosen from Western and from Eastern Iceland (Fig. 2) respectively. Individuals to analyze were chosen among all available individuals in each category (area, sex and decade) using a random number selection procedure.

Collagen was extracted from lower jaws following a standard method based on Brown et al. (1998) and modified according to Richards and Hedges (1999). The collagen obtained was weighed (1-1.2mg), packed in small tin foil cups, 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.

Bone collagen has a very slow isotopic turnover after the animal is fully grown. Thus, although it can reflect the lifetime average dietary intake in long-lived species, it is biased towards the period of most rapid growth (Libby et al. 1964; Tieszen et al. 1983; Roth 2003). Arctic foxes grow until the age of 8-9 months, and after that growth is insignificant (Hersteinsson et al. 2009). Therefore, and because in this study 86% of the foxes were between one and two years old when they were culled, we assumed that the

stable isotope signatures of the collagen represented the diet during the first year of life (Online Resources 1).

### *Prey samples*

Muscle samples of prey preserved in ethanol were obtained from The Icelandic Institute of Natural History in Reykjavik, Iceland. Ethanol storage has been shown to have a negligible effect on dietary estimates based on stable isotopes (Javornik et al. 2019). Three or more samples from each of the following species were collected in 2015: ptarmigan, eider duck, wood mouse (*Apodemus sylvaticus*), greylag goose (*Anser anser*), golden plover (*Pluvialis apricaria*), whimbrel (*Numenius phaeopus*), sheep, horse, cattle and kittiwake (*Rissa tridactyla*). The muscle samples were prepared for stable isotopes analysis according to standard methods (Ehrich et al. 2011) and analyzed at SINLAB as for the fox collagen samples. Additional prey signatures of starfish (*Asteria rubens*), redshank (*Tringa totanus*), common snipe (*Gallinago gallinago*), black guillemot (*Cepphus grille*), were provided by Rannveig Magnusdottir (unpublished data). Number of prey samples, isotopic signatures and approximate dates of collection are given in Online Resources 1.

### *Statistical analysis*

All statistical analyses were performed using the software R 3.3.2 for Windows (R Core Team 2016). The stable isotope ratios were expressed using the standard  $\delta$  notation (in ‰), with the international reference being the Vienna Peedee Belemnite for  $\delta^{13}\text{C}$  values and atmospheric nitrogen for  $\delta^{15}\text{N}$  values (Jürgensen et al. 2017). The relationship between the arctic fox signatures for each habitat and the different potential prey was assessed graphically. The isotopic signatures of organisms are similar to those in the resources they

consume, modified by a species and tissue specific discrimination factor (Ben-David and Flaherty 2012). Because the discrimination for arctic fox bone collagen has not been determined experimentally, we applied several different discrimination factors to assess how robust our results were to this uncertainty. Specifically, we used estimates for wolf collagen (Fox-Dobbs et al. 2007), red fox collagen (Krajcarz et al. 2018), and arctic fox fur and muscle (Crowley et al. 2010; Lecomte et al. 2011). Because none of them resulted in a plot where the fox values were within the polygon delimited by the prey values, we determined an additional arbitrary discrimination factor, which places the arctic fox signatures closer to prey signatures (referred to as *fit*; Online Resources 1). For the plots (Fig. 3), we used the values from arctic fox fur ( $\Delta^{13}\text{C} = 2.58 \pm 0.44$  and  $\Delta^{15}\text{N} = 3.64 \pm 0.69$ ) (Lecomte et al. 2011). Because lipids are depleted in  $^{13}\text{C}$  relative to other tissues and muscle can be a lipid-rich tissue (Kelly 2000), the prey muscle signatures were corrected for lipid content using the normalization equation of Ehrlich et al. (2011). Since the Industrial Revolution, there has been a decrease of  $\delta^{13}\text{C}$  in the biosphere due to an increase of anthropogenic  $\text{CO}_2$  (the Suess effect; Keeling 1979; Reynolds et al. 2019). The raw  $\delta^{13}\text{C}$  data were corrected for this effect using a mean rate of  $\delta^{13}\text{C}$  change of  $-0.026\text{‰}$  per year, which is close to atmospheric estimates and to mean estimates for Atlantic waters (Olsen 2006). All fox and prey isotopic ratios were corrected to levels, which correspond to the first year of the study.

The temporal changes in arctic fox isotopic values were analyzed using linear models. We used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  as response variables, while the year each fox was born (from 1979 to 2008; time) and habitat (coastal or inland) were used as explanatory variables. For each stable isotope ratio, we assembled four candidate models. We compared

a model including the additive effect of time and habitat to a model with and interaction between the two. In addition, to account of a possible non-linear effect of time, we included a quadratic term for time both as additive effect, and in an interaction with habitat (Online Resource 1). Models were compared using Akaike's Information Criterion corrected for small sample sizes ( $\Delta AICc$ ). Models with a difference in  $AICc$  of  $<2$  were considered equally adequate (Burnham and Anderson 2002) and the simpler models were chosen following Occam's Razor (Dunbar 1980) (Online Resource 1). The fit of the selected model was assessed graphically by looking at the distribution of the residuals. Finally, the parameters from the selected models were estimated including and excluding some influential values identified in the graphical assessment of the residuals.

The proportions of different resources in the diet of arctic foxes over time were estimated using Bayesian stable isotope mixing models, as implemented in the package MixSIAR (Stock et al. 2018). Because mixing models perform best with a moderate number of potential sources, and in order to use clearly distinct sources, the potential prey items were grouped according to the similarity of their isotopic signatures. Five groups of resources were created: Marine (starfish, eider duck, whimbrel, kittiwake, black guillemot), Farm (horse, sheep), Terrestrial (red-shank, common snipe, golden plover, wood mouse), Greylag goose and Rock ptarmigan. Even though whimbrels are waders, they were placed in the marine group because their signature was closer to the marine resources. Cattle was excluded because the signature was far away from the other farm animals. Greylag goose and Rock ptarmigan were kept as distinct groups, because they were focal species for our research questions. Time was included as a continuous covariate and the analyses were run separately for inland and coastal foxes. To account for uncertainty in the arctic fox bone

collagen discrimination factor, we used large standard errors in the estimation as recommended by Savory et al. (2014) (SD of  $\Delta^{13}\text{C} = 1.0\text{‰}$  and  $\Delta^{15}\text{N} = 1.0\text{‰}$ ) and repeated the analysis with each of five different discrimination factors (Online resource). We ran the analysis according to the recommendations in the MixSIAR manual and used equally likely proportions for all dietary components as prior, 1,000,000 MCMC replicates (500,000 burn-in) and a Residual\*Process error. Convergence of the estimation was checked based on Gelman-Rubin Diagnostic and Geweke Diagnostic. Despite long runs, the analyses did not converge well using time as a continuous covariate (Online Resource 1). Therefore, we ran this analysis also using a factor for three discrete time periods corresponding to each of the three decades over which the samples were collected (1979-1989; 1990-1999; 2000-2008).

## **Results**

### *Temporal and spatial variation in isotopic values*

The isotopic signatures of the prey species displayed the typical gradient from low values for both ratios in terrestrial species to higher values in marine species (Fig. 3). The lowest  $\delta^{15}\text{N}$  values were observed for rock ptarmigan, whereas the lowest  $\delta^{13}\text{C}$  values, although with higher  $\delta^{15}\text{N}$ , were observed for domestic herbivores, horses and sheep. Geese were intermediate between ptarmigan and farm animals, while waders were isotopically more heterogenous. The common snipe had values close to the terrestrial herbivores, cattle and wood mouse, whereas the whimbrel had marine signatures and the redshank occupied an intermediate position (Fig.3). Isotopic signatures were obtained for a total of 130 arctic fox samples. The isotope ratios of both coastal and inland foxes spread over the whole gradient of prey signatures from terrestrial species to marine species. As expected, there was a

tendency for more coastal foxes towards marine resources and more inland foxes towards terrestrial resources (Figure 3).

For  $\delta^{13}\text{C}$ , the most parsimonious linear model was the simplest model consisting of a linear effect of time in addition to habitat. The model including a quadratic effect of time received a slightly lower AICc score than the simplest model ( $\Delta\text{AICc} = 0.52$ ), but this difference did not support the inclusion of the quadratic term (Table 1). The selected model showed a clear effect of habitat on  $\delta^{13}\text{C}$ , which was on average 2.37‰ (SE = 0.41,  $p < 0.001$ ) lower for inland foxes than for coastal foxes, but no effect of time (-0.04‰ per year, SE = 0.02,  $p = 0.13$ ; Fig. 4; Table 2).

For  $\delta^{15}\text{N}$ , the best model according to AICc included a quadratic effect of time in addition to habitat. It revealed a significant concave curvilinear response of  $\delta^{15}\text{N}$  to time with parameter estimates of  $-0.01\% \text{ time}^2$  (SE = 0.00) + 0.28 time (SE = 0.14). After a slight increase in the beginning of the study period, there was a decrease in  $\delta^{15}\text{N}$  after the middle of the period. In addition, there was a clear effect of habitat as in  $\delta^{13}\text{C}$ . In inland foxes,  $\delta^{15}\text{N}$  was on average 3.48‰ (SE = 0.56,  $p < 0.001$ ) lower than in coastal foxes. There was no indication that this difference has changed over the study period ( $\Delta\text{AICc}$  for a model with an interaction between time and habitat was 1.97; Fig. 4; Table 2).

#### *Inference about diets based on mixing models*

The mixing models including time as a continuous covariate did not converge well, but for models with time included as three distinct periods, convergence diagnostics were satisfactory for some of the discrimination factors used (Online Resources 1). For both habitats, good convergence and unimodal posterior probability distributions were obtained

using the discrimination factor for arctic fox fur (Lecomte et al. 2011). Marine resources and rock ptarmigan were the two main prey groups in the diet of the arctic fox in Iceland, both in coastal and inland habitats (Fig. 5). As expected, marine resources were more important for coastal foxes, where they represented about two thirds of the diet, whereas ptarmigan represented about one quarter (Fig. 5; Online Resources 1). For inland foxes, ptarmigan were the most important resource representing approximately half of the diet. Marine resources were somewhat less important, but 95% posterior credibility intervals of predicted diet proportion overlapped to some degree with ptarmigan. Greylag geese, farm animals and other terrestrial resources were much less important in both habitats and their credibility intervals did not exclude 0.

Overall, dietary proportions varied little over the three time periods and credibility intervals for all resources overlapped largely between time periods. The suggested shifts in dietary proportions indicated a slight increase in the proportion of marine resources in the second period for coastal foxes, followed by a slight decrease in the third period in agreement with the results from the linear model for  $\delta^{15}\text{N}$ . In the last period, there was a slight increase of ptarmigan. For inland habitats, the suggested dynamics were opposite, with a slight increase of the proportion of ptarmigan in the second period and the third period with a decrease in the use of marine resources. The estimations using other discriminations factors were largely congruent with these results and revealed only very minor shifts in dietary proportions over time. The arbitrary fit discrimination factor suggested a somewhat higher contribution of greylag goose to the diet in all periods for both inland and coastal foxes, whereas the discrimination factor for arctic fox muscle (Lecomte et al. 2011) resulted in a

higher proportion of marine resources and a lower proportion of ptarmigan in the diet of coastal foxes (Online Resources 1).

## **Discussion**

Over the 30 years period of population increase of the Icelandic arctic fox population, the stable isotope ratios of carbon varied little. For nitrogen, on the contrary, a slight increase in  $\delta^{15}\text{N}$  was followed by a clear decrease. Although the isotopic signatures differed significantly between coastal and inland foxes, there was no statistical support for differences in temporal trends of isotopic values between the habitats. While the analysis of the isotopic ratios themselves suggested possible dietary shifts during the period of population growth, the estimation of dietary proportions from isotopic mixing models indicated that the major resources, marine resources and rock ptarmigan, had remained the same, and their proportions in the diet showed only minor changes over time.

Pálsson et al. (2016) suggested that an increase in goose numbers, increased use of marine resources and probably waders caused the rise of the fox population over the decades after 1980. Populations of greylag geese, but also of pink-footed (*Anser brachyrhynchus*) and barnacle geese (*Branta leucopsis*) have experienced a strong increase in Iceland during the last decades making them a potential emerging resource for local predators, which could have replaced to some extent the declining year-round resident ptarmigan population. Contrary to these expectations corresponding to our first hypothesis, our data did not indicate increasing use of geese by inland arctic foxes. The initial increase in  $\delta^{15}\text{N}$  while  $\delta^{13}\text{C}$  remains constant could be compatible with a shift from ptarmigan to geese in inland foxes, but towards the end of the period there was a clear decrease in  $\delta^{15}\text{N}$ , which would rather be compatible by an opposite switch back to ptarmigan. Moreover, the



mixing model results suggested that geese played a minor role in the diet of arctic foxes during the whole study period, while rock ptarmigan remained the most important terrestrial prey. Because of their negative population trend (Fuglei et al. 2019), it is, however, unlikely, that ptarmigan have been driving the arctic fox growth. The collagen isotopes analyzed here reflect the resources used by young foxes over first 8-9 months of their life, whereas Pálsson's results were based on prey remains at den. Dalerum et al. (2012) reported that the diet of adult foxes differs somewhat of the diet of juveniles. Moreover, geese are only present on Iceland in summer, therefore they may be a resource used only during a short time and represent only a small part of the total resources used by a growing fox, despite their high relative abundance in prey remains. Moreover, eggs of geese and samples of other goose species (barnacle goose or pink-footed goose), were not included in this study, leaving the possibility that these could still be a resource for young foxes.

Marine resources provided the main part of the diet of coastal foxes but were important throughout the study period for inland foxes as well. According to the findings of Dalerum et al. (2012), coastal habitats in Iceland are generally more heterogeneous than the inland, and with access to seabird colonies and productive coastlines they provide more stable year-round resources. The mixture of terrestrial and marine isotopic signatures displayed by coastal and inland foxes show that they have access to both marine and terrestrial resources in both habitats. As arctic foxes are quite mobile animals, dispersing around 10-30 km, and sometimes much more, from their natal ground after a few months (Angerbjörn et al. 2004a; Angerbjörn et al. 2004b, Pamperin et al. 2008, Tarrowx et al. 2010, Fuglei and Tarrowx 2019), this was indeed expected. It is rather surprising that we

observed a consistent difference in average isotopic ratios in arctic foxes, which were culled only a few kilometers from the coast.

For arctic foxes at the coast, in western Iceland, seabirds are the main prey, and any increase in seabird populations could have supported an increase in the fox population without a change in diet (Unnsteinsdóttir et al. 2016). Harvesting data of puffin (*Fratercula arctica*) and other seabirds in Iceland show that these populations have been increasing considerably from the 1970s to the end of the 1990s but have declined rather rapidly since about the year 2000 (Hansen et al. 2018). Our isotopic data, showing a high proportion of marine resources in coastal foxes over the whole study period, but also to a certain degree in inland foxes, are compatible with our second hypothesis that seabirds and marine resources have been the main driver of the population increase. A constant proportion of marine resource use is indeed suggested by the stable  $\delta^{13}\text{C}$  ratios throughout the study period. The fox population growth based on rich marine resources might have spilled over into inland habitats through individuals dispersing from the coast to inland habitats. As western Iceland harbors most of the highly productive coastal habitats (Hersteinsson et al. 2009), whereas inland habitats are more typical for eastern Iceland, this process could also explain the slightly delayed onset of arctic fox population growth observed in eastern Iceland. If seabirds and marine resources in general were the main driver of the fox increase, the decline in  $\delta^{15}\text{N}$  observed in the later part of the study period could be explained by two processes. First, the  $\delta^{15}\text{N}$  values of seabirds in the southern Atlantic have been shown to decrease in recent decades with 0.48 ‰ per decade due to changes in the underlying food web and a diet shift from fish to dietary items at lower trophic levels (Reynolds et al. 2019). Ecosystem changes affecting the availability of prey are also one

of the likely causes for seabird decline in the north Atlantic (Fauchald et al. 2015) and may well be associated to a decrease in trophic level of prey species, resulting in lower  $\delta^{15}\text{N}$  values in the seabirds, and lower  $\delta^{15}\text{N}$  values in arctic foxes. Second, when seabirds decline in abundance, arctic foxes may increasingly feed on marine resources from lower trophic levels such as eider ducks, waders, crustaceans and other invertebrates, or fish.

Helgason (2008) studied the winter diet of Icelandic arctic foxes through analyses of scats and stomach contents and showed that foxes consumed large proportions of big mammals. However, the isotopic signatures in this study did not show any important contribution of this prey group to the diet of arctic foxes, which could be related to the fact that the main period of growth of foxes, which is reflected in the collagen, is in summer and fall. In addition, stomach contents are affected by the baits used by hunters, which consist often of large mammal carcasses such as horses.

Regarding the results from our mixing model analyses, it must be noticed that the signatures of the foxes did not exactly fit with the prey signatures. This could be due to prey signatures having seasonal fluctuations not covered well in our samples or because the discrimination factors used were not accurate, as they had not been estimated for collagen in arctic foxes. Nevertheless, many possible discrimination values were tested to increase the sensitivity of our analysis. Moreover, not all the possible prey species were sampled for study, as we lacked notably goose eggs, barnacle geese and pink-footed geese, crustaceans, lamb, etc., which could have provided a more comprehensive picture. Finally, our prey samples did not cover the temporal extent of the arctic fox samples. The assumption that the prey signatures were stable over time is supported for example by the findings of Barrett et al. (2011), who documented that stable isotope signatures in cod from

several areas in the North Sea were nearly constant over centuries. But, as mentioned above, changes in marine food webs may also have caused changes in some dietary sources. All this may have caused some biases in the diet estimation.

## **Conclusion**

Using a long time series of isotopic signatures reflecting the diet of young individuals, we were able to investigate which food resources may have been the drivers of the prolonged increase of the Icelandic arctic fox population. We found evidence that the population growth may have been supported mainly by the increase of seabird populations and other marine resources, which have been a major component of the diet during the whole period. This study should be elongated until present, to observe if the recent decrease in arctic fox population could be related to the decrease in seabird population in Iceland. Rapidly growing goose populations, which potentially represent a new major resource for arctic predators, appeared much less important. The important changes driving the fox population were thus not the structural changes in the terrestrial food web, where one species of herbivorous birds increased and another decreased, but fluctuations in the abundance of the main resource for this population, the marine resources.

## **Acknowledgements**

This study was supported and financed by UiT, which provided extra funds for the flights to Iceland. We are grateful to the Icelandic Institute of Natural History for providing the fox mandibles. Thanks to Þorvaldur Björnsson for collecting the muscle prey samples, to Rannveig Magnusdottir for providing unpublished stable isotope data, to Sissel Kaino for

aiding and guidance during laboratory procedures, and to Arnaud Tarrow for comments on an earlier version of the manuscript.

## References

Allen DH, Melfi RC (1985) Improvements in techniques for ageing mammals by dental cementum annuli. *Proc Iowa Acad Sci* 92(3):100-102

Angerbjörn A, Hersteinsson P, Lidén K, Nelson E (1994) Dietary variation in arctic foxes (*Alopex lagopus*)—an analysis of stable carbon isotopes. *Oecologia* 99:226–232  
doi:10.1007/BF00627734

Angerbjörn A, Hersteinsson P, Tannerfeldt M (2004a) Consequences of resource predictability in the arctic fox—two life history strategies. In: MacDonald DW, Siller-Zubiri C (eds) *Biology and conservation of wild canids*. Wildlife conservation research unit, University of Oxford, UK

Angerbjörn A, Hersteinsson P, Tannerfeldt M (2004b) Arctic fox (*Alopex lagopus*). In: Sillero-Zubiri C, Hoffmann M, Macdonald DW (eds) *Canids: foxes, wolves, jackals and dogs*. Status survey and conservation action plan. IUCN/SSC Canid specialist group, Gland, Switzerland, and Cambridge, UK

Barrett JH, Orton D, Johnstone C, Harland J, Van Neer W, Ervynck A, Roberts C, Locker A, Amundsen C, Enghoff IB, Hamilton-Dyer S, Heinrich D, Hufthammer AK, Jones AKG, Jonsson L, Makowiecki D, Pope P, O’Connell TC, de Roo T, Richards M (2011) Interpreting the expansion of sea fishing in medieval Europe using stable isotope analysis of archaeological cod bones. *Journal of Archaeological Science* 38(7):1516-1524  
doi:10.1016/j.jas.2011.02.017

Ben-David M, Flaherty EA (2012) Stable isotopes in mammalian research: a beginner's guide. *J Mammal* 93:312-328 doi:10.1644/11-MAMM-S-166.1

Berteaux D, Thierry A-M, Alisauskas R, Angerbjörn A, Buchel E, Doronina L, Ehrich D, Eide NE, Erlandsson R, Flagstad Ø et al. (2017) Harmonizing circumpolar monitoring of arctic fox: benefits, opportunities, challenges and recommendations. *Polar Research* 36:2 doi:10.1080/17518369.2017.1319602

Braestrup FW (1941) A study on the arctic fox in Greenland: immigrations, fluctuations in numbers based mainly on trading statistics. *København: Reitzels* 131:1-101

Brown TA, Nelson DE, Vogel JS, Southon JR (1998) Improved collagen extraction by modified Longin method. *Radiocarbon* 30(2):171-177

Crowley BE, Carter ML, Karpanty SM, Zihlman AL, Koch PL, Dominy NJ (2010) Stable carbon and nitrogen isotope enrichment in primate tissues. *Oecologia* 164:611-626 doi:10.1007/s00442-010-1701-6

Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York

Dalerum F, Perbro A, Magnúsdóttir R, Hersteinsson P, Angerbjörn A (2012) The influence of coastal access on isotope variation in Icelandic arctic foxes. *PloS One* 7 (3): e32071 doi:10.1371/journal.pone.0032071

Dunbar MJ (1980) The blunting of Occam's Razor, or to hell with parsimony. *Can J Zool* 58(2):123-128 doi:10.1139/z80-016

Ehrich D, Tarrow A, Stien J, Lecomte N, Killengreen S, Berteaux D, Yoccoz NG (2011)

Stable isotopes analysis: modelling lipid normalization for muscle and eggs from arctic mammals and birds. *Methods Ecol Evol* 2:66-76 doi:10.1111/j.2041-210X.2010.00047.x

Ehrich D, Ims RA, Yoccoz NG, Lecomte N, Killengreen ST, Fuglei E, Rodnikova AY, Ebbinge BS, Menyushina IE, Nolet BA et al. (2015) What can stable isotope analysis of top predator tissues contribute to monitoring of tundra ecosystems? *Ecosystems* 18:404-416 doi:10.1007/s10021-014-9834-9

Eide NE, Stien A, Prestrud P, Yoccoz NG, Fuglei E (2012) Reproductive responses to spatial and temporal prey availability in a coastal arctic fox population. *J Anim Ecol* 81:640-648 doi:10.1111/j.1365-2656.2011.01936.x

Elmhagen B, Tannerfeldt M, Verucci P, Angerbjörn A (2000) The arctic fox (*Alopex lagopus*): an opportunistic specialist. *J Zool Lond* 251:139-149 doi:10.1111/j.1469-7998.2000.tb00599.x

Elmhagen B, Berteaux D, Burgess R, Ehrich D, Gallant D, Henttonen H, Ims R, Killengreen S, Niemimaa J, Norén K, Ollila T, Rodnikova A, Sokolov A, Sokolova N, Stickney A, Angerbjörn A (2017) Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research* 36, sup1 doi:10.1080/17518369.2017.1319109

Fauchald P, Anker-Nilssen T, Barrett RT, Bustnes JO, Bårdsen B-J, Christensen-Dalsgaard S, Descamps S, Engen S, Erikstad KE, Hanssen SA, Lorentsen S-H, Moe B, Reiertsen TK, Strøm H, Systad GH (2015) The status and trends of seabirds breeding in Norway and Svalbard. NINA Report 1151. 84 pp

Fox-Dobbs K, Bump JK, Peterson RO, Fox DL, Koch PL (2007) Carnivore-specific stable

isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. *Can J Zool* 85:458-471 doi:10.1139/Z07-018

Fuglei E, Ims RA (2008) Global warming and effects on the arctic fox. *Science Progress* 91(9296):175–91 doi:10.3184/003685008X327468

Fuglei E, Henden JA, Callahan CT, Gilg O, Hansen J, Ims RA, Isaev AP, Lang J, McIntyre CL, Merizon RA et. al. (2019) Circumpolar status of Arctic ptarmigan: Population dynamics and trends. *Ambio* doi:10.1007/s13280-019-01191-0

Goltsman M, Kruchenkova EP, Macdonald DW (1996) The Mednyi Arctic foxes: treating a population imperiled by disease. *Oryx* 30(4):251-258 doi:10.1017/S0030605300021748

Gunnarsson E, Hersteinsson P, Adalsteinsson S (1993) Rannsóknir á sjúkdómum í íslenska melrakkanum (Studies on diseases in the Icelandic arctic fox). In: Hersteinsson P, Sigbjarnarsson G (eds) *Villt íslensk spendýr* (e. Reykjavík, Wild Icelandic Mammals), Hið íslenska náttúrufræðifélag, pp 49–58

Hansen ES (2018)

<https://www.arcticbiodiversity.is/index.php/program/presentations2018/422-135-year-time-series-of-atlantic-puffin-production-is-negatively-correlated-to-sea-surface-temperature-population-control-by-temperature-dependent-survival-of-ectotherm-sandeel-prey-erpur-hansen-1> (accessed 30.05.2019)

Helgason HH (2008) Fæða refa (*Vulpes lagopus*) á hálendi Íslands að vetrarlagi. Námsverkefni Háskóli Íslands (In Icelandic)



Hersteinsson P (1984) The behavioural ecology of the arctic fox (*Alopex lagopus*) in Iceland. PhD thesis, Oxford: University of Oxford, UK

Hersteinsson P (1987) Calculations of the size of the arctic fox population. *Wildl Manage News, Iceland* 3(1):25-54 (In Icelandic with English Summary)

Hersteinsson P (1992) Demography of the arctic fox (*Alopex lagopus*) population in Iceland. In: McCullough DR, Barrett RH (eds) *Wildlife 2001: populations*. Elsevier, London, pp 954-964 doi:10.1007/978-94-011-2868-1\_73

Hersteinsson P, Angerbjörn A, Frafjord K, Kaikusalo A (1989) The arctic fox in Fennoscandia and Iceland: management problems. *Biological Conservation* 49:67–81 doi:10.1016/0006-3207(89)90113-4

Hersteinsson P, Macdonald DW (1996) Diet of arctic foxes (*Alopex lagopus*) in Iceland. *J Zool* 240:457–474 doi:10.1111/j.1469-7998.1996.tb05298.x

Hersteinsson P, Yom-Tov Y, Geffen E (2009) Effect of sub-polar gyre, north atlantic oscillation and ambient temperature on size and abundance in the Icelandic arctic fox. *Global Change Biology* 15(6):1423–33 doi:10.1111/j.1365-2486.2008.01765.x

Ims RA, Ehrich D, Forbes BC, Huntley B, Walker DA, Wookey PA, Berteaux D, Bhatt US, Bråthen KA, Edwards ME et. al. (2013) Terrestrial ecosystems. In: *Arctic biodiversity assessment: status and trends in Arctic biodiversity*. Conservation of Arctic Flora and Fauna, Akureyri pp. 560, 348-440

Ims RA, Killengreen ST, Ehrich D, Flagstad Ø, Hamel S, Henden JA, Jensvoll I, Yoccoz NG (2017) Ecosystem drivers of an Arctic fox population at the western fringe of the

Eurasian Arctic. Polar Research 36, sup1 doi:10.1080/17518369.2017.1323621

Inger R, Bearhop S (2008) Applications of stable isotopes analyses to avian ecology. *Ibis* 150(3):447-61 doi:10.1111/j.1474-919X.2008.00839.x

Javornik J, Hopkins III JB, Zavadlav S, Levanič, Lojen S, Polak T, Jerina K (2019) Effects of ethanol storage and lipids on stable isotope values in a large mammalian omnivore. *Journal of Mammalogy* 100(1):150-157 doi:10.1093/jmammal/gyy187

Jürgensen J, Drucker DG, Stuart AJ, Schneider M, Buuveibaatar B, Bocherens H (2017) Diet and habitat of saiga antelope during the late Quaternary using stable carbon and nitrogen isotope ratios. *Quaternary Science Reviews* 160:150-161 doi:10.1016/j.quascirev.2017.01.022

Krajcarz MT, Krajcarz M, Bocherens H (2018) Collagen-to-collagen prey-predator isotopic enrichment ( $\Delta^{13}\text{C}$ ,  $\Delta^{15}\text{N}$ ) in terrestrial mammals - a case study of a subfossil red fox den. *Palaeogeography, Palaeoclimatology, Palaeoecology* 490:563–570 doi:10.1016/j.palaeo.2017.11.044

Keeling CD (1979) The Suess Effect:  $^{13}\text{C}$ - $^{14}\text{C}$  Interrelations. *Environment International* 2:229-300

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA, Post DM, Bearhop S (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev* 87:545-62 doi:10.1111/j.1469-185X.2011.00208.x

Lecomte N, Ahlstrøm Ø, Ehrich D, Fuglei E, Ims RA, Yoccoz G (2011) Intrapopulation

variability shaping isotope discrimination and turnover: experimental evidence in arctic foxes. PLoS ONE 6(6): e21357 doi:10.1371/journal.pone.0021357

Libby WF, Berger R, Mead J, Alexander G, Ross J (1964) Replacement rates for human tissue from atmospheric radiocarbon. Science 146:1170-1172 doi:10.1126/science.146.3648.1170

Mclaughlin M (2009) Arctic foxes and climate change out-foxed by Arctic warming. IUCN Red List

Miles WTS, Mavor R, Riddiford NJ, Harvey PV, Riddington R, Shaw DN, Parnaby D, Reid JM (2015) Decline in an Atlantic Puffin Population: Evaluation of Magnitude and Mechanisms. PLoS ONE 10(7): e0131527 doi:10.1371/journal.pone.0131527

Nielsen OK (1999) Gyrfalcon predation on ptarmigan: numerical and functional responses. J Anim Ecol 68: 1034-1050 doi:10.1046/j.1365-2656.1999.00351.x

Ogilvie AEJ (2012) Encyclopedia of global warming & climate change, Iceland. SAGE Publications doi:10.4135/9781452218564.n361

Olsen A, Omar AM, Bellerby RGJ, Johannessen T, Ninnemann U, Brown KR, Olsson KA, Olafsson J, Nondal G, Kivimäe C et. al. (2006) Magnitude and origin of the anthropogenic CO<sub>2</sub> increase and <sup>13</sup>C Suess effect in the Nordic seas since 1981. Global Biogeochemical Cycles 20:GB3027 doi:10.1029/2005GB002669

Pálsson S, Hersteinsson P, Unnsteinsdóttir ER, Nielsen ÓK (2016) Population limitation in a non-cyclic arctic fox population in a changing climate. Oecologia, online open doi:10.1007/s00442-015-3536-7

Pamperin NJ, Follmann EH, Person BT (2008) Sea-ice use by arctic foxes in northern Alaska. *Polar Biol* 31:1421-1426 doi:10.1007/s00300-008-0481-5

Post E, Forchhammer MC, Bret-Harte MS, Callghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hicks DS, Høye TT et. al. (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science* 11;325(5946):1355-8 doi:10.1126/science.1173113

R Core Team (2016) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://www.R-project.org/>

Reynolds S, Hughes B, Wearn C, Dickey R, Brown J, Weber N, Weber S, Paiva V, Ramos J (2019) Long-term dietary shift and population decline of a pelagic seabird-A health check on the tropical Atlantic? *Global Change Biology* 25:1383-1394 doi:10.1111/gcb.14560

Richard MP, Hedges REM (1999) Stable isotopes evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic coast of Europe. *J Archaeol Sci* 26:717-722 doi:10.1006/jasc.1998.0387

Roth JD (2003) Variability in marine resources affects arctic fox population dynamics. *J Anim Ecol* 72:668-676 doi:10.1046/j.1365-2656.2003.00739.x

Savory GA, Hunter CM, Wooller MJ, O'Brien DM (2014) Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. *Can J Zool* 92:657-663 doi: dx.doi.org/10.1139/cjz-2013-0283

Schmidt NM, Ims RA, Høye TT, Gilg O, Hansen LH, Hansen J, Lund M, Fuglei E, Forchhammer MC, Sittler B (2012) Response of an arctic predator guild to collapsing

lemming cycles. Proceedings of the Royal Society B-Biological Sciences 279: 4417–4422  
doi:org/10.1098/rspb.2012.1490

Schmidt NM, Hardwick B, Gilg O, Høye TT, Krogh PH, Meltofte H, Michelsen A, Mosbacher JB, Raundrup K, Reneerkens J et. al. (2017) Interaction webs in arctic ecosystems: determinants of arctic change? *Ambio* 46:12-25 doi:10.1007/s13280-016-0862-x

Serrouya R, McLellan BN, van Oort H, Mowat G, Boutin S (2017) Experimental moose reduction lowers wolf density and stops decline of endangered caribou. *Peerj* 5. Retrieved from [Go to ISI://WOS:000411954600006](https://doi.org/10.7717/peerj.3736) doi:10.7717/peerj.3736

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6. e5096 doi:10.7717/peerj.5096

Tarroux A, Berteaux D, Bêty J (2010) Northern nomads: ability for extensive movements in adult arctic foxes. *Polar Biol* 33:1021-1026 doi:10.1007/s00300-010-0780-5

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for  $\delta^{13}\text{C}$  analysis of diet. *Oecologia* 57:32-37 doi:10.1007/BF00379558

Unnsteinsdóttir ER, Hersteinsson P, Pálsson S, Angerbjörn A (2016) The fall and rise of the Icelandic arctic fox (*Vulpes lagopus*): a 50-year demographic study on a non-cyclic arctic fox population. *Oecologia*, online open doi:10.1007/s00442-016-3635-0

Unnsteinsdóttir ER (2014) A decline in the Icelandic arctic fox population [Press release].

Retrieved from [http://www.ni.is/sites/ni.is/files/atoms/files/Stofnmat-a-refum\\_oktober-2014.pdf](http://www.ni.is/sites/ni.is/files/atoms/files/Stofnmat-a-refum_oktober-2014.pdf) (In Icelandic)

**Table 1** Candidate models considered for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  as response variables. Explanatory variables were time and habitat (coastal and inland). + indicates additive effects and \* indicates and interaction. For each model the number of parameters (K), AICc and the difference in AICc to the best model ( $\Delta\text{AICc}$ ) are presented. The selected models (i.e. the one with the lowest AICc) are shown in bold. Models which differed by less than 2 in  $\Delta\text{AICc}$  from the best model, and were chosen because they were simpler than the best model, are shown in italics and bold

	<b>Model</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>
$\delta^{13}\text{C}$	<b>Time+habitat+I(Time<sup>2</sup>)</b>	<b>5</b>	<b>585.94</b>	<b>0</b>
	<i>Time+habitat</i>	<i>4</i>	<i>586.46</i>	<i>0.52</i>
	Time*habitat+I(Time <sup>2</sup> )	6	588.13	2.19
	Time*habitat	5	588.60	2.66
$\delta^{15}\text{N}$	<b>Time+habitat+I(Time<sup>2</sup>)</b>	<b>5</b>	<b>670.80</b>	<b>0</b>
	Time*habitat+I(Time <sup>2</sup> )	6	672.76	1.97
	Time+habitat	4	674.62	3.83
	Time*habitat	5	676.49	5.69

**Table 2** Parameter estimates from linear and quadratic models assessing the effects of time and habitat (inland or coastal) on (a) carbon isotope ( $\delta^{13}\text{C}$ ), (b) nitrogen isotope ( $\delta^{15}\text{N}$ ) from bones of Icelandic arctic foxes. The intercept is the coastal area, effect sizes are shown as contrasts to the intercept

	<b>Value</b>	<b>Std. Error</b>	<b>t value</b>	<b>P</b>
<b>(a) <math>\delta^{13}\text{C}</math> Fixed effect</b>				
Intercept	<b>-17.52</b>	<b>0.49</b>	<b>-36.09</b>	<b>&lt;0.001</b>
Time	-0.04	0.02	-1.53	0.13
Habitat Inland	<b>-2.37</b>	<b>0.41</b>	<b>-5.79</b>	<b>&lt;0.001</b>
<b>(b) <math>\delta^{15}\text{N}</math> Fixed effect</b>				
Intercept	<b>9.96</b>	<b>0.95</b>	<b>10.53</b>	<b>&lt;0.001</b>
Time	<b>0.28</b>	<b>0.14</b>	<b>2.05</b>	<b>0.04</b>
I(Time^2)	<b>-0.01</b>	<b>0.00</b>	<b>-2.44</b>	<b>0.02</b>
Habitat Inland	<b>-3.48</b>	<b>0.56</b>	<b>-6.15</b>	<b>&lt;0.001</b>



**Fig. 1** Estimated population size (estimates based on age-cohort analysis and hunting statistics), with standard error bars of the arctic fox in Iceland from 1978 to 2011 (from Unnsteinsdóttir 2014). Dots represent foxes born in each year and vertical lines the three different decades.

**Fig. 2** Map of Iceland displaying the division between West and East Iceland. For the purpose of this study coastal habitat was defined within 3km of the shore, while inland as all terrain more than 3km from the shoreline. The dark gray represents the areas where the foxes were culled.

**Fig. 3** The isotopic signatures (‰) of the possible prey for Icelandic arctic foxes corrected for trophic discrimination (discrimination factor estimated for arctic fox fur; Lecomte et al. 2011) are plotted with their respective standard deviation together with the signature of each analyzed arctic fox. Symbols distinguish between foxes culled in coastal and inland habitat

**Fig. 4** Isotopic signatures of Inland and Coastal foxes are plotted according to year of birth of each fox. Lines show trends as predicted by the most parsimonious linear and quadratic models (continuous line for Inland and dashed line for Coastal). (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  isotopic signature (‰)

**Fig. 5** MixSIAR (Stable isotope mixing model) results showing the scaled posterior probability density of the proportion of the prey groups in the diet of coastal and inland foxes

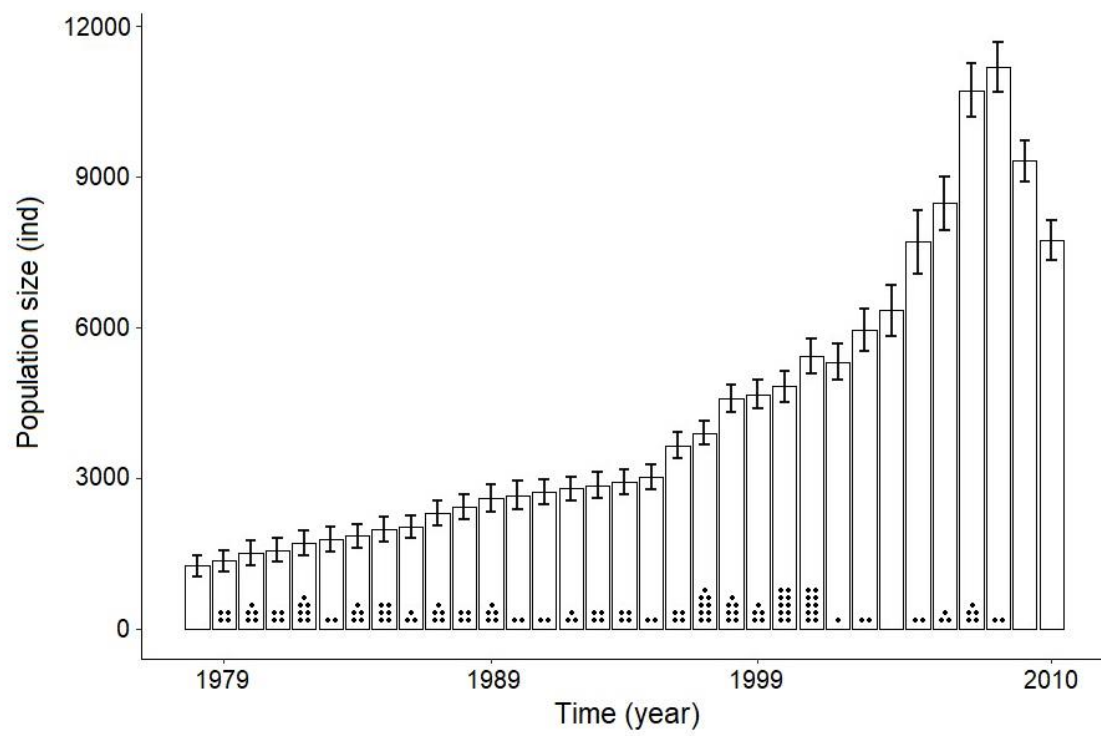


Fig. 1

[Escriba aquí]



Fig. 2

[Escriba aquí]

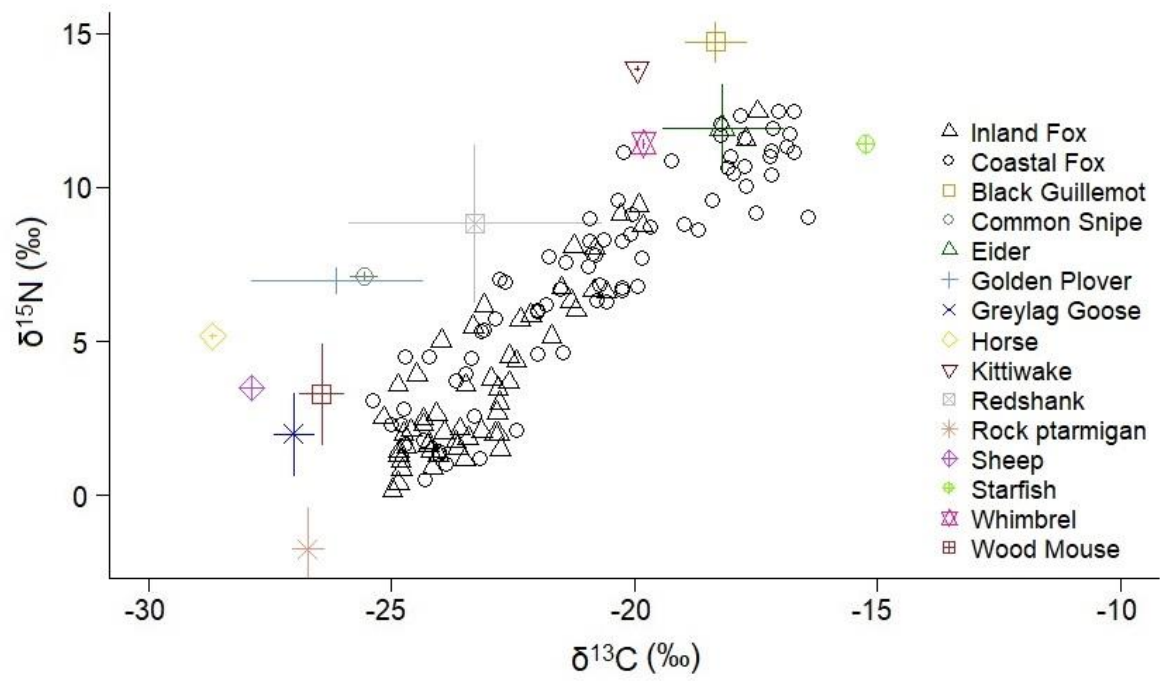


Fig. 3

[Escriba aquí]

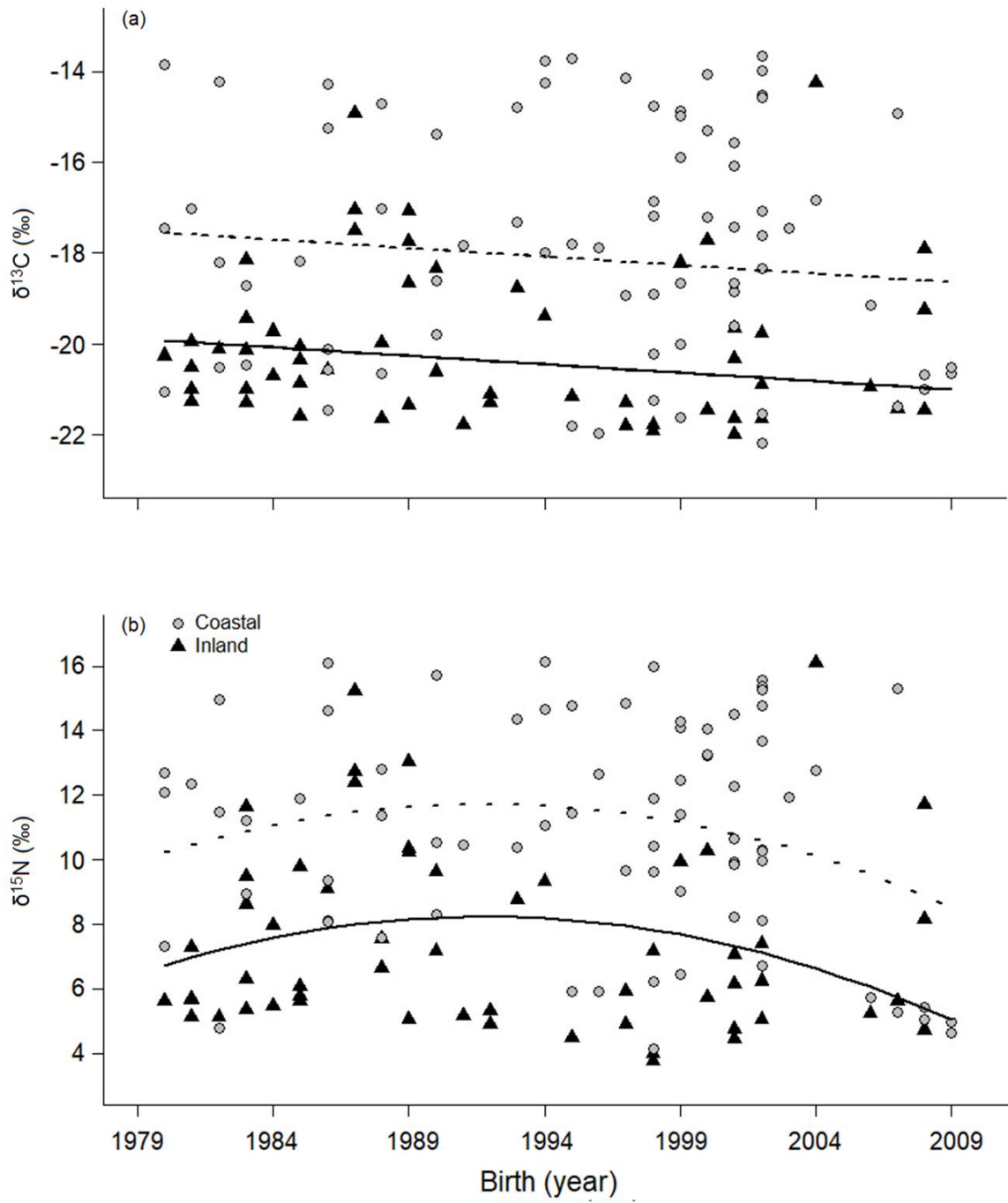


Fig. 4

[Escriba aquí]

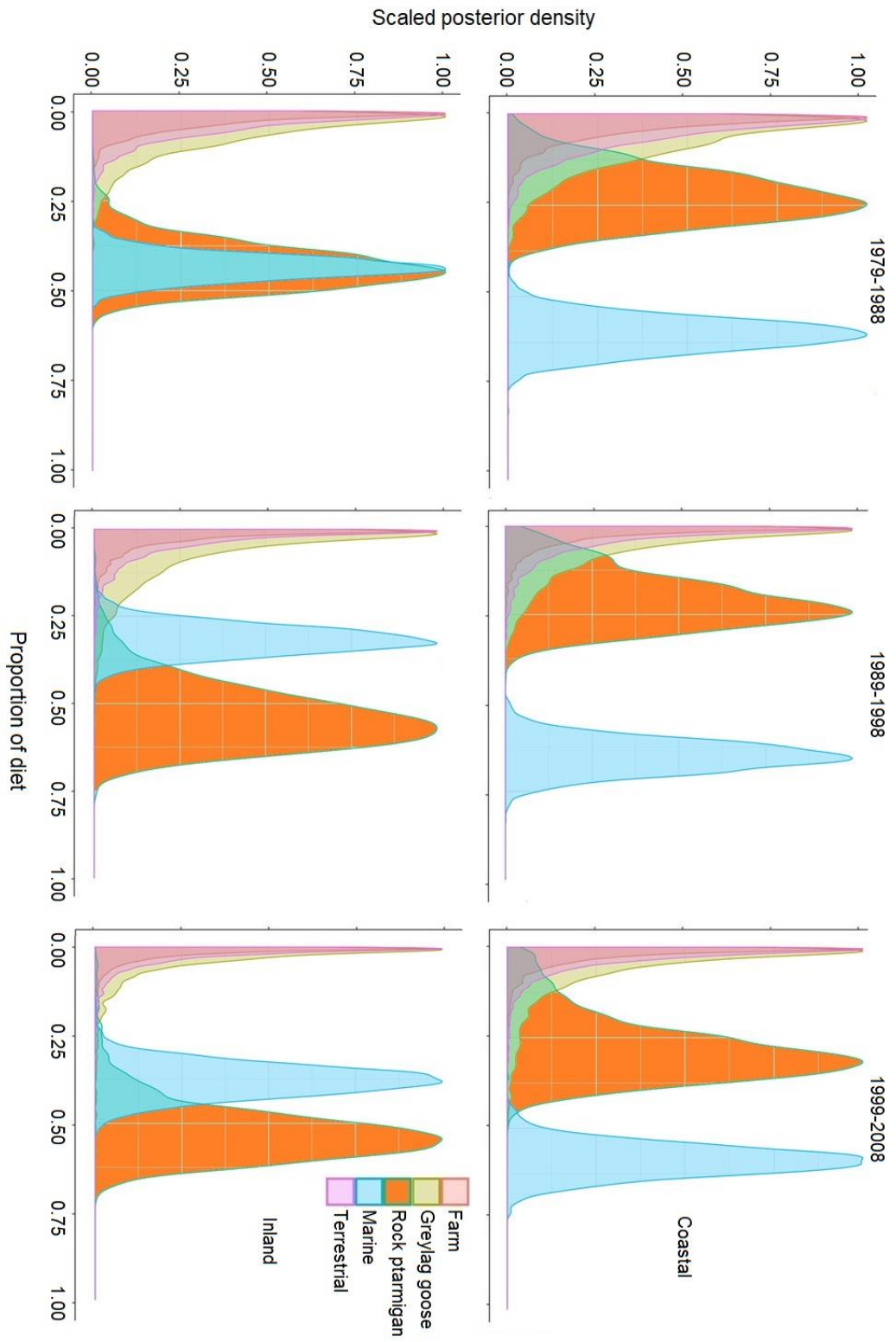


Fig. 5

[Escriba aquí]