Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

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BIO-3950 Master Thesis in Biology, Northern populations and Ecosystems

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Supervisors

Rolf A. Ims, UiT – The Arctic University of Norway

Dorothee Ehrich, UiT – The Arctic University of Norway

Siw Turid Killengreen, UiT – The Arctic University of Norway

Ester Ruth Unnsteinsdóttir – Icelandic Institute of Natural History

UNIVERSITY OF TROMSØ

Cover photo by

Jennifer Carbonell, arctic fox (*Vulpes lagopus*) in Hornstrandir, Iceland, summer 2016

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Abstract

Identifying the food resources for a species is one of the basic steps towards understanding population dynamics. The arctic fox is the only terrestrial carnivore on Iceland, and the population had been increasing until recently. Therefore, it is of great importance to know what factors regulate the population growth and which resources support it to understand why the population fluctuates. In this study, stable isotope analysis of arctic fox collagen from Iceland was performed, which revealed what arctic foxes were consuming in their first year of life. The samples used were from 1979 to 2011, period of steady increase of the population. The isotopic signatures were separated between three periods of time (1979-1989, 1990-1999, 2000-2011), two habitats (coastal and inland) and sexes (female and male). The results showed that the diet of young arctic foxes had changed over the study period, as well as a difference in use of resources within and between foxes utilizing different habitats. The results suggested that the main prey items for foxes living in coastal habitats were marine resources while rock ptarmigan was a main resource for inland foxes, even though foxes in both habitats displayed a varied diet. It could be noted that coastal foxes displayed more isotopic changes between periods than inland foxes, and that males living at the coast had more variation on isotopic signatures in comparison with females. From this, it could be suggested that coastal habitats have more availability of different resources and that probably males disperse more than females. These results show how a generalist predator shifts use of resources over the time.

Keywords: *Vulpes lagopus*, arctic fox, stable isotope analysis, diet, Iceland, population dynamics

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1. Introduction

High latitude environments are dynamic entities where populations of many species vary over time (Pálsson et al. 2015), due to temporal variability in their resources, and at present changes associated with climate warming (Post et al. 2009). One of the most important environmental factor influencing reproduction in mammals and hence fluctuation in population is food availability (Bronson 1989; Elmhagen et al. 2000). The relationship between food availability and population growth is crucial for predator population dynamics (Angerbjörn et al. 2004b). To understand what causes animal populations to fluctuate is of great importance to applied ecology, such as conservation, management and resource use (Unnsteinsdottir et al. 2016), since changes in resources could destabilize predator-prey dynamics (and the food web) and impact populations even to the extreme point of extinction (Huxel and McCann 1998; Roth 2003).

The arctic fox, *Vulpes lagopus*, is a medium sized canid with a circumpolar distribution in the northern hemisphere (Dalerum et al. 2012). It is one of the smallest member of the family *Canidae* and has developed many morphological adaptations to cope with the harsh environmental conditions of the Arctic tundra, an area in which it is endemic (Blix 2005). Arctic foxes have shown two main life-history strategies, in most of its range they operate as specialist predators towards lemmings (*Lemmus* and *Dicrostonyx* spp.) and voles (*Myodes* and *Microtus* spp.), and as a generalist predator in areas where these small rodents are absent (Eide et al. 2012; Angerbjörn et al. 2004b). Lemming populations fluctuate dramatically between years, resulting in large inter-annual changes in food availability (Stenseth and Ims 1993; Tannerfeldt and Angerbjörn 1998; Angerbjörn et al. 1999; Strand et al. 1999). Such large inter-annual fluctuation in lemming populations also causes variation in the recruitment of fox cubs each year (Angerbjörn et al. 2004b). However, arctic foxes also live in areas without lemmings or voles such as High Arctic Svalbard and Iceland. There, they act as opportunistic generalist predators and scavengers (Eide et al. 2012; Eide et al. 2005). In these areas, arctic foxes have access to both inland and coastal habitats and resources, resulting in a stable annual food availability

(Angerbjörn et al. 2004a; Hersteinsson and Macdonald 1996). Therefore, leading to small litter sizes and regular breeding (Braestrup 1941; Hersteinsson 1984; Dalerum et al. 2012).

The sizes of the artic fox population is presently regarded as large and stable (Angerbjörn and Tannerfeldt 2014), with the exception of Mednyi Island (Russia) and Fennoscandia (Fuglei and Ims 2008). Nevertheless, the arctic fox is a climate change flagship species, and is retracting and/or decreasing in the southern part of its range in relation with regional warming (Mclaughlin 2009). Climate change is likely to affect arctic fox populations in at least the following ways: Habitat loss, rapidly decreasing sea ice, human expansion, increased competition with southern species and changes in prey abundance (Mclaughlin 2009). Due to all these different threats it is believed that arctic islands may be the safest refuge for arctic fauna in the future (Fuglei and Ims 2008), because of less connectivity to invasive southern species (fauna and flora).

In Iceland, the arctic fox maintains large and highly viable population along the constantly ice-free coasts (Fuglei and Ims 2008), even though numbers have been decreasing during the last past few years (Unnsteinsdóttir 2014). Here 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; Kühn 2015). The hunting data suggest a sharp fall in the arctic fox population all over Iceland from the 1950s into the 1970s attributed to a decrease in rock ptarmigan (*Lagopus muta*) numbers and to excessive hunting (there was an extermination campaign set in 1950's) (Angerbjörn et al. 2004a; Hersteinsson 1987; Hersteinsson et al. 1989; Pálsson et al. 2016). Since the 1970's, however, there was a steady increase in the population for thirty years with a decline from 2008 (Fig. 1). Therefore, it is unlikely that fox hunting is the primary cause of the variation in population size over the last decades (Unnsteinsdóttir et al. 2016), since the fox hunting law was changed and regulated in the 1990's (Angerbjörn et al. 2004a). Furthermore, unlike many other areas, where arctic foxes occur, there are no cyclic rodents on Iceland (Hersteinsson 1992), which could cause short term changes in fox abundance. Changes in arctic fox population size in Iceland are thought to be due to the combined impact of changes in carrying capacity

(determined by food resources), climate and hunting; the latter being the main cause of fox mortality (Pálsson et al. 2015; Unnsteinsdóttir et al. 2016).

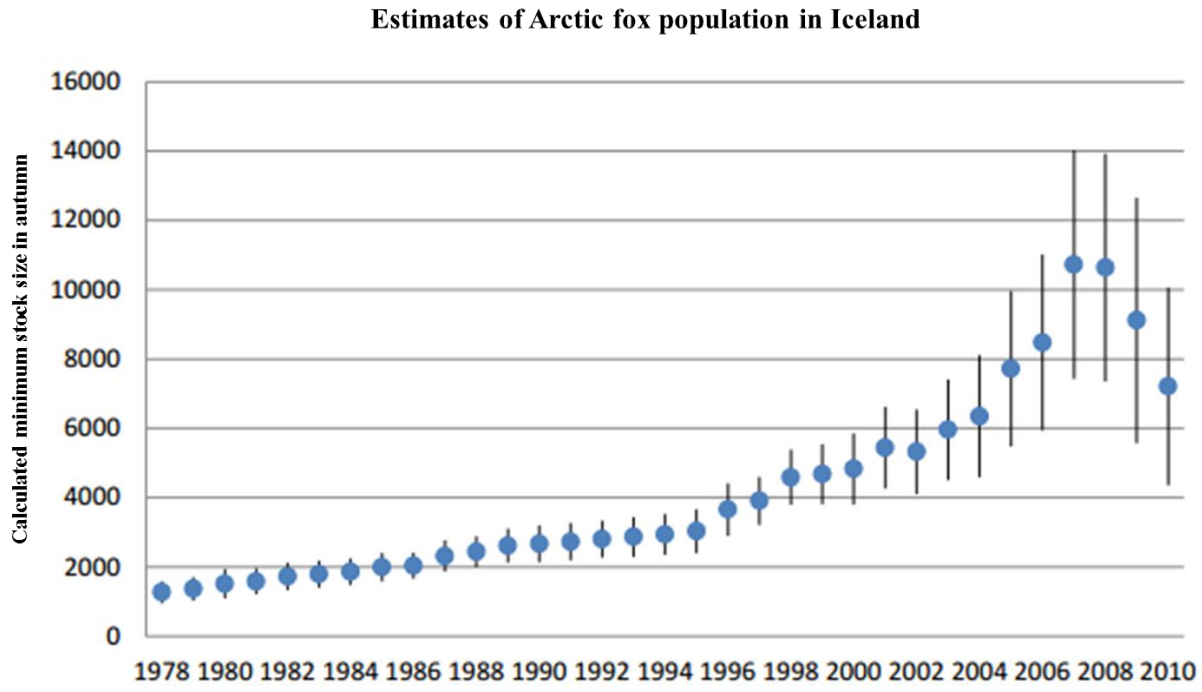

Fig 1. Estimated minimum size of the Icelandic arctic fox population at autumn each year. Vertical lines show 95% confidence interval (Unnsteinsdottir 2014).

The arctic fox is the only indigenous terrestrial carnivore mammal on Iceland (Mellows et al. 2012), and it is important to know why the population increased over such a long period and what factors were sustaining the growth. Moreover, for management of populations it is important to understand which are the main factors regulating population growth. Following the assumption of Pálsson et al. (2015) that ptarmigan is an important species for foxes in inland areas, persistent population size fluctuations in this species could lead to repercussions in the arctic fox population and its resilience. If on the other hand, seabirds are the main prey for arctic foxes living on the coast (Unnsteinsdottir et al. 2016) and sustaining the increment of abundance, this increase can lead to feedback effects on the seabird abundance. Following decreases in seabird population size could reduce the primary productivity that these contribute in the ecosystem by fertilization of the soil, and later affecting the landscape. 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 an increasing geese and wader populations. Therefore, in case that the main prey is migrating birds (Unnsteinsdottir et al. 2016 describe them as important for inland foxes), such as waders and geese, whose populations have been increasing due to climate change and subsidies by agricultural fields, the arctic fox may be important to maintain a sustainable stability by top-down effects. Or if the main factors are due to new resources benefiting from climate warming (Pálsson et al. 2015, Unnsteinsdottir et al. 2016), it could be advantageous to know what these resources are and how they could affect the dynamics of the food web.

In order to understand the importance of the different resources to arctic fox population is the diet and how it changes in time and space. There are many ways to study the diet of arctic foxes, such as direct observations, stomach dissection, feces composition, description of food remains (Angerbjörn et al. 1994), fatty acid analysis and stable isotope analysis (Ben-David and Flaherty 2012; Ehrich et al. 2015; Kelly 2000). The latter has become more important for ecological studies (Ben-David and Flaherty 2012) because it allows to trace resources within and between animals, plants and microbes, at scales ranging from the individual to the community level (Newsome et al. 2012). Whereas direct methods such as stomach contents or feces dissection provide snapshot information about diet on a specific day, the stable isotope ratios of predator tissues, reflect the resources assimilated over a certain period (Inger and Bearhop 2008; Ben-David and Flaherty 2012; Layman et al. 2012).

Stable isotope analysis is useful to assess the foraging ecology and habitat preferences of living and extinct species because stable isotope ratios in animal tissues vary with diet, habitat, and environmental conditions (West et al. 2006; Crowley et al. 2010). The isotopic composition of carbon (^{13}C relative to ^{12}C) and nitrogen (^{15}N relative to ^{14}N) is typically determined in samples from consumers and resources to make inferences about the diet (Ben-David and Flaherty 2012; Phillips 2012). The diet of individuals or populations can be inferred based on the principle that ‘you are what you eat’, meaning that the isotopic ratios in the consumer’s tissues reflect the mixture of the isotopic ratios present in the different food items consumed (DeNiro and Epstein 1978, 1981) with a slight enrichment (Kelly 2000). Carbon and nitrogen

isotopes are well suited to distinguish between terrestrial and marine protein intake (Chisholm et al. 1983; Angerbjörn et al. 1994; Kelly 2000). Purely marine-based consumers are enriched in ^{13}C compared to strictly terrestrial consumers, while the organisms with mixed diets have intermediate signatures (Chisholm eta al. 1982; Schoeninger and DeNiro 1984; Roth 2002). The same tendency is displayed by nitrogen isotopes, showing higher N^{15} values for marine resources (Kelly 2000).

In this study, stable isotope data from bone collagen were used to determine whether and how the diet of the arctic fox in Iceland changed over a period of 30 years that included the population's strong increase since 1980 (Fig. 1). Dietary changes could give an understanding of which main resources were supporting the population growth. It was also investigated if there were any differences between foxes living in coastal areas and inland areas as been shown in many studies (e.g. Angerbjörn et al. 1994; Dalerum et al. 2012; Hersteinsson and MacDonald 1996; Pálsson et al. 2016) and if signatures differed between females and males. Finally, the main food resources in this study were compared to the ones Pálsson et al. (2015) instated as important resources during the population increase based on prey item remains on dens.

2. Materials and Methods

Study area

Iceland is an island in the North Atlantic Ocean, close to the Arctic circle (63ºN20-66ºN30; 13ºW30’-24ºW30’), with a total area of 103,000km^2. The climate is highly variable due to its position in the middle of the North Atlantic, at a point where contrasting cold and mild ocean and air currents meet. The island is influenced climatically by a branch of the Gulf Stream, with average July temperatures of 10.6ºC and average January temperatures just below freezing (Halldorsson 2003; Ogilvie 2012).

Most of the interior of the country is not inhabited and consists of sandy deserts, mountains and glaciers (Ogilvie 2012). Western Iceland has a higher proportion of productive seashores than northern, eastern and southern Iceland combined (Hersteinsson et al. 2009). Thus, for arctic foxes, Iceland can be divided into two main habitats, coastal (western Iceland) and inland (the rest of the country, termed eastern Iceland), according to available resources (Hersteinsson et al. 2009; Pálsson et al. 2015) (Fig. 2). As the coast is ice-free all year round (Dalerum et al. 2012), arctic foxes in coastal habitats have a more stable availability of food resources from season to season. In contrast, inland habitats experience substantial fluctuations in food resources (Dalerum et al. 2012). The resources available to foxes living in coastal areas can be carcasses of marine mammals and birds, crustaceans and other invertebrates, fish, waders, eider duck. Areas close to sea bird cliffs, can provide plenty of resources during summer, which is the breeding season (Hersteinsson 1984; Hersteinsson and Macdonald 1996; Hersteinsson, Yom-Tov, and Geffen 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). Foxes, both inland and coastal, feed on sheep (Hersteinsson and Macdonald 1996), cattle (*Bos taurus*), reindeer (*Rangifer tarandus*) or horse (*Equus ferus caballus*) carcasses (some left behind by the foxhunters, who use them as bait). In winter, both types of foxes can depend on ptarmigan (mainly inland), cache items (Hersteinsson

et al. 1989) and a small proportion of rodents (Helgason 2008), while foxes close to the coast still have marine resources available.

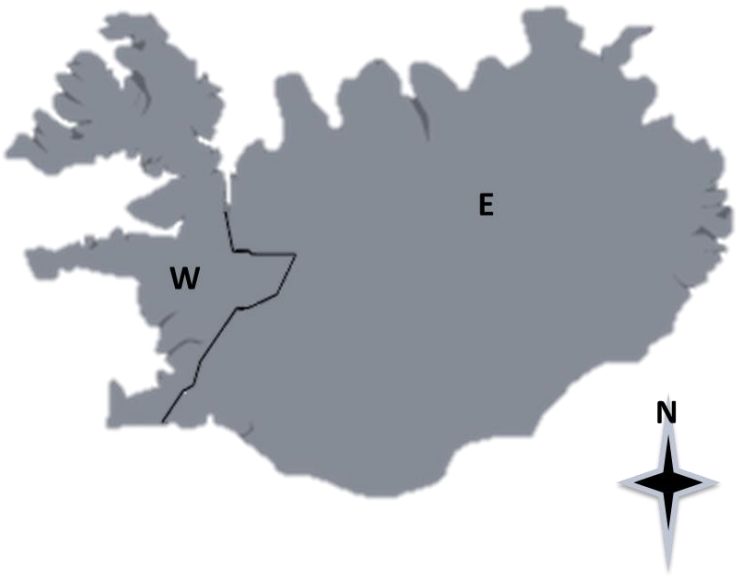

Fig 2. Map of Iceland displaying the division between West and East Iceland. For the purpose of this study West is considered as coastal habitat and east as inland habitat, since more foxes derive their food directly and indirectly from marine resources in western Iceland than in eastern Iceland (Pálsson et al. 2015).

Arctic fox sample collection and preparation for stable isotopes analysis

Fox hunting is allowed in Iceland due to the damage that foxes cause on Eider duck farms and to the presumed killing of sheep. The collection of bones used in this study was obtained from carcasses voluntarily donated by foxhunters from all over Iceland (Fig. 3) 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 day, and a database containing year and location the fox was culled (West-coast, East-inland (Fig. 2)), sex and age.

Age was determined by counting annual cementum lines of canine tooth roots (Allen and Melfi 1985; Unnsteinsdottir et al. 2016) at the Icelandic Institute of Natural History in Reykjavik.

Foxes culled in three different time periods were selected (1980-1989, 1990-1999 and 2000-2010), covering the time of population increase (Fig. 1). From each time period, 11 adult males and 11 adult females were chosen randomly, from coastal and inland areas, resulting in 44 lower jaws in total per period (Appendix A).

Fig 3. Bone Collection at The Icelandic Institute of Natural History.

Bone collagen, which is a metabolically inactive tissue, does not resorb or turnover after the animal is fully grown, so its stable isotope ratio reflects the diet of the individuals during the limited period of growth (Roth 2002), which means around the first year of life for the arctic fox.

To do stable isotope analysis 1 to 1.2mg of collagen needs to be extracted from the bones. Collagen extraction was done following the standard method based on Brown et al. (1998) and modified in Richards and Hedges (1999), by drilling four holes in the jaws using a 3.5mm drill bit. The bone powder obtained was kept in glass test tubes previously labelled with the sample number (Fig. 4). The powder was decalcified by adding 0.25M hydrochloric acid (HCl) to the tubes and properly mixed using a stirring rod. The tubes were left at room temperature for three days covered by tin foil. The samples were shaken daily using a cap to cover the tubes. On the third day, because the samples were still producing bubbles when stirred, the acid was pipetted away and replaced with new 0.25M HCl and mixed properly using the cap. The tubes were covered with tin foil and left at room temperature for two more days. After this period, making use of a vacuum pump and disposable fiber glass filters, the acid was filtered away and the samples were rinsed with distilled water. The solid left behind was placed in Eppendorf tubes and left to dry in an oven at 60^{o}C for 24 hours with the lid open.

Fig 4. Labelled tubes for samples of bone powder from Icelandic arctic foxes.

After that, a carbide bead was placed inside each vial and the samples were pulverized using a grinding machine (TissueLyser II-QIAGEN) for 2 minutes at a frequency of 20 per second.

Fat was extracted by adding a 2:1 chloroform and methanol solution to the vials inside the fume hood. The samples were left in the solution for 15 minutes, shaking them a couple of times. Afterwards, the samples were centrifuged for 5 minutes at the speed of 13rpm (revolutions per

minute) employing the Centrifuge 5415D (Eppendorf). Finally, the supernatant was discarded and the fat extraction procedure was repeated. The samples were left to dry inside the fume hood for 24 hours.

The collagen was dissolved by adding 0.01M HCl to the vials and leaving them at 57^{o}C for 24 hours while shaking them a couple of times. The fluid was pipetted away and placed in new Eppendorf tubes, then left to freeze at -80^{o}C for two hours. After that, the tubes were opened and covered by parafilm which was perforated four times by a thin needle. The frozen collagen was placed in a freeze drier and left for around 18 hours. The collagen obtained (Fig. 5) was weighed (1-1.2mg), packed in small tin foil cups, placed in a 96-well sample tray and sent to SINLAB-Stable Isotopes in Nature Laboratory at the Canadian Rivers Institute for the stable isotopes analysis of carbon and nitrogen.

Fig 5. Collagen isolated from jaws of Icelandic arctic foxes (top left), illustration of samples weighing (right) and packing for stable isotope analysis (bottom left).

Prey sample preparation for stable isotopes analysis

Muscle from prey samples preserved in ethanol was obtained from The Icelandic Institute of Natural History in Reykjavik, Iceland. Three samples from each of the following were obtained: Eider Duck, Wood Mouse (*Apodemus sylvaticus*), Greylag goose (*Anser anser*), Golden Plover (*Pluvialis apricaria*), Whimbrel (*Numenius phaeopus*), Sheep, Horse, Cattle and Kittiwake (*Rissa tridactyla*).

A small amount from the muscle was cut up in tiny pieces and placed in Eppendorf tubes previously labelled. These samples were left to dry in the oven at 60^{o}C for 48 hours with the lid open. Afterwards, for obtaining a homogenized powder, the samples were pulverized in the grinding machine for 3 minutes at a frequency of 20 per second, with a carbide bead inside. 1 to 1.2mg of the powder obtained was weighed, packed in tin foil cups, placed in a sample tray and sent to the laboratory for the stable isotopes analysis.

The isotopic measurements were performed at SINLAB-Stable Isotopes in Nature Laboratory at the Canadian Rivers Institute. The stable isotope ratios are expressed using δ values (in ‰), with the international reference being V-PDB (Vienna Peedee Belemnite) for δ^{13}C values and atmospheric nitrogen (AIR) for δ^{15}N values (Jürgensen et al. 2017).

Statistical analysis

All statistical analysis was performed using the software R 3.3.2 for Windows (R Core Team 2016). The isotopic signatures of organisms reflect the ratios of heavy to light isotopes of the resources they consume, modified by a discrimination factor, which reflects the physiological processes (i.e., enzymatic reactions) they employ in assimilating these resources and discarding their products (Ben-David and Flaherty 2012). The δ^{13}C and δ^{15}N values, obtained from the

stable isotope analysis, were corrected for discrimination. Signatures are dependent on the species, ecology and age, assimilation ability and even the tissue that is sampled (Ben-David and Flaherty 2012; Lecomte et al. 2011) which have different fractionation processes (Dalerum and Angerbjörn 2005). Because there is no study which determined the specific discrimination for arctic fox bone collagen, the arctic fox discrimination for fur ($\delta^{13}C_{hair}$ 2.18±0.44 and $\delta^{15}N_{hair}$ 3.34±0.69) and for muscle ($\delta^{13}C_{muscle}$ 0.37±0.76 and $\delta^{15}N_{muscle}$ 1.79±0.41) (Lecomte et al. 2011) were employed. These values were adjusted to collagen using a correlation factor determined for the wolf ($\delta^{13}C_{collagen\text{-}keratin}$ 0.4 and $\delta^{15}N_{collagen\text{-}keratin}$ 0.3, $\delta^{13}C_{collagen\text{-}muscle}$ 1.5 and $\delta^{15}N_{collagen\text{-}muscle}$ -0.5) (Crowley et al. 2010) with the formula (the same used for $\delta^{15}N$ and for muscle):

$$\delta^{13}C_{collagen} = \delta^{13}C_{hair} + \delta^{13}C_{collagen\text{-}keratin\ correction}$$

(Bocherens et al. 2014).

In the following, the discrimination factors based on the muscle and the fur estimates are referred as muscle and fur discrimination respectively.

The isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ of arctic fox collagen and prey muscle were compared graphically. The prey muscle signatures were corrected previously for lipid content using the normalization equation of (Ehrich et al. 2011), due that lipid is depleted in ^{13}C relative to other tissues and muscle can be a lipid-rich tissue (Kelly 2000). Additional prey signatures were given by Rannveig Magnusdottir (unpublished data) and the rock ptarmigan signatures values where from Varanger Peninsula, Norway (Ehrich et al. 2015). Finally, the isotopic signatures of arctic fox were graphically compared between the two habitats and sexes through the years.

The uncorrected isotopic values were analyzed using the function lm in R, to estimate the changes over the study period and to examine whether the habitat (coastal or inland) and the sex of the foxes had an influence on the stable isotope signature. The response variables used in the models were the $\delta^{13}C$ and $\delta^{15}N$, while period when each fox was born (1979-1989, 1990-1999,

2000-2011), the year of birth, habitat and sex were used as fixed effects. The year of birth of every fox was obtained by subtracting the age of each individual fox from the year in which it was hunted (information provided with the samples). To see which model fitted the best, AICc (Akaike Information Criterion corrected for small sample sizes) was employed. AICc was used to determine whether it was better to employ the periods as a factor variable or continuous time using the arctic foxes year of birth (compared models can be seen in Table 1 together their respective AICc). 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 to see if this created a noticeable change.

Bayesian stable isotope mixing models, implemented in the package MixSIAR (Francis et al. 2011; Moore and Semmens 2008; Stock and Semmens 2013), were used to estimate the proportions of the contribution of the different prey to the arctic fox diet. MixSIAR allows including fixed and random effects in the estimation of dietary proportion. The model was ran separately for coastal females, coastal males, inland females and inland males using first the continuous time and second the period as fixed effects to see how the diet changed over time. Both muscle and fur discriminations were used separately for comparison. The potential prey items were grouped depending on the similarity of their isotopic signature, to facilitate the interpretation of results. Five groups were created: Marine (starfish, eider duck, whimbrel, kittiwake, black guillemot), Farm (horse, sheep), Waders (red-shank, common snipe, golden plover), Greylag goose and Ptarmigan. Even though whimbrel is a wader, it was placed as marine source because its signature was closer to the marine resources. It has to be considered that there were only three prey sample for whimbrel, which could misrepresent the isotopic signature of the whole whimbrel population. Cattle was excluded because the signature was far away from the other farm animals, so it was better to reduce errors. The sculpin was not included because there was no literature supporting it as an important prey for Icelandic arctic foxes. The arctic char was not accounted for because as Hersteinsson and Macdonald (1996) explain, it is just an occasional resource. Finally, the wood mouse was excluded because the signature was overlapping with the wader signature, which would make it impossible to tell which one was been eaten. Furthermore, the rodents are seen as a tiny proportion in the arctic fox diet (Helgason

2008), while the waders are believed to be an important prey in the last decades (Pálsson et al. 2016).

MixSiar was employed according to the recommendations of the manual by Stock and Semmens (2013). The Gelman-Rubin diagnostic is displayed as a result in for every run, to see if the model converged. The models were ran between “long” (300,00 iterations) and “extreme” (3,000,000 iterations) length of chains to finally get accurate estimates for the posterior distribution (convergence of the diagnostic).

3. Results

Graphical analysis of stable isotopes signatures

The mean values of $\delta^{13}C$ and $\delta^{15}N$ for female coastal foxes were -19.99 and 7.86‰ (SD=2.29, SD=2.50) and for male coastal foxes -19.96 and 7.92‰ (SD=2.63, SD=3.40), respectively. The mean value of $\delta^{13}C$ and $\delta^{15}N$ for female inland foxes were -22.84 and 3.60‰ (SD=1.61, SD=2.73) and for male inland foxes -22.31 and 3.90‰ (SD=2.11, SD=3.16), correspondingly (Appendix B). There was no difference between the mean values of males and females. The inland foxes tended to display lower isotopic signatures both for $\delta^{13}C$ and $\delta^{15}N$, even though there were some foxes which exhibited a different pattern (Fig. 6). Moreover, it can be noticed that at the end of the study period the female coastal foxes showed slightly higher isotopic signatures than the male coastal foxes (more apparent in $\delta^{15}N$). Additionally, the isotopic signatures of coastal foxes and inland foxes were different during the study period (Fig. 6).

The isotope signatures of the foxes were compared graphically with the signatures of the possible prey with their respective standard deviation (Fig. 7 using muscle discrimination, for fur discrimination see Appendix C). From the visual comparison it seems that coastal foxes consumed a mixture of marine and terrestrial food, while the inland foxes were slightly closer to terrestrial prey. It can be seen that the isotopic signatures of the foxes do not fall exactly into the polygon delimited by the signatures of the possible prey used in this study. The visual overview also indicates that one of the main resources for inland foxes is the rock ptarmigan, and for the coastal foxes the eider duck.

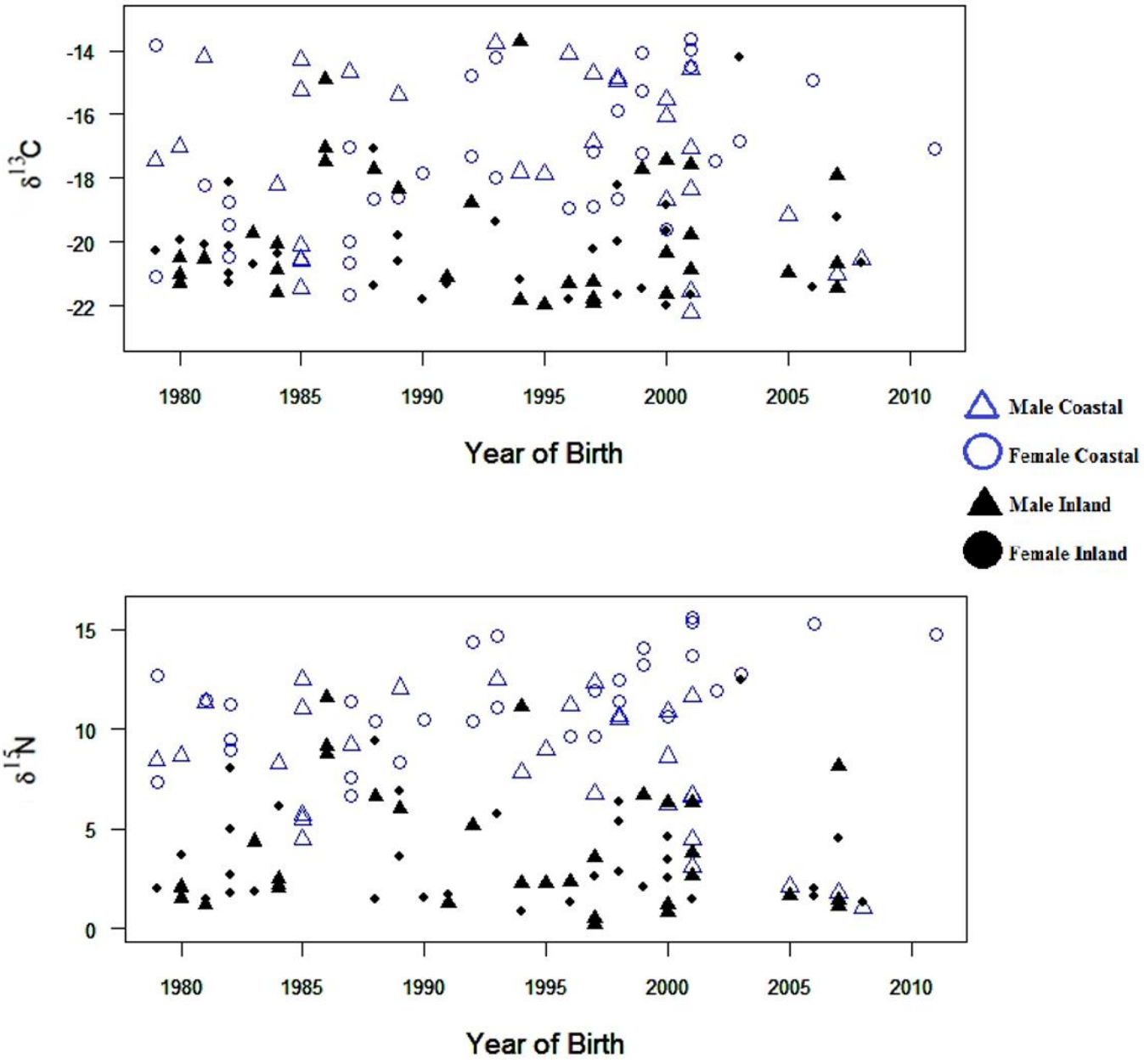

Fig 6. Graphical view of the isotopic signatures of male and female arctic fox in the different habitats during the study period (Year of birth of each fox). Where (a) displays the $\delta^{13}C$ signatures (‰) and (b) $\delta^{15}N$ signatures (‰) of the Icelandic arctic foxes.

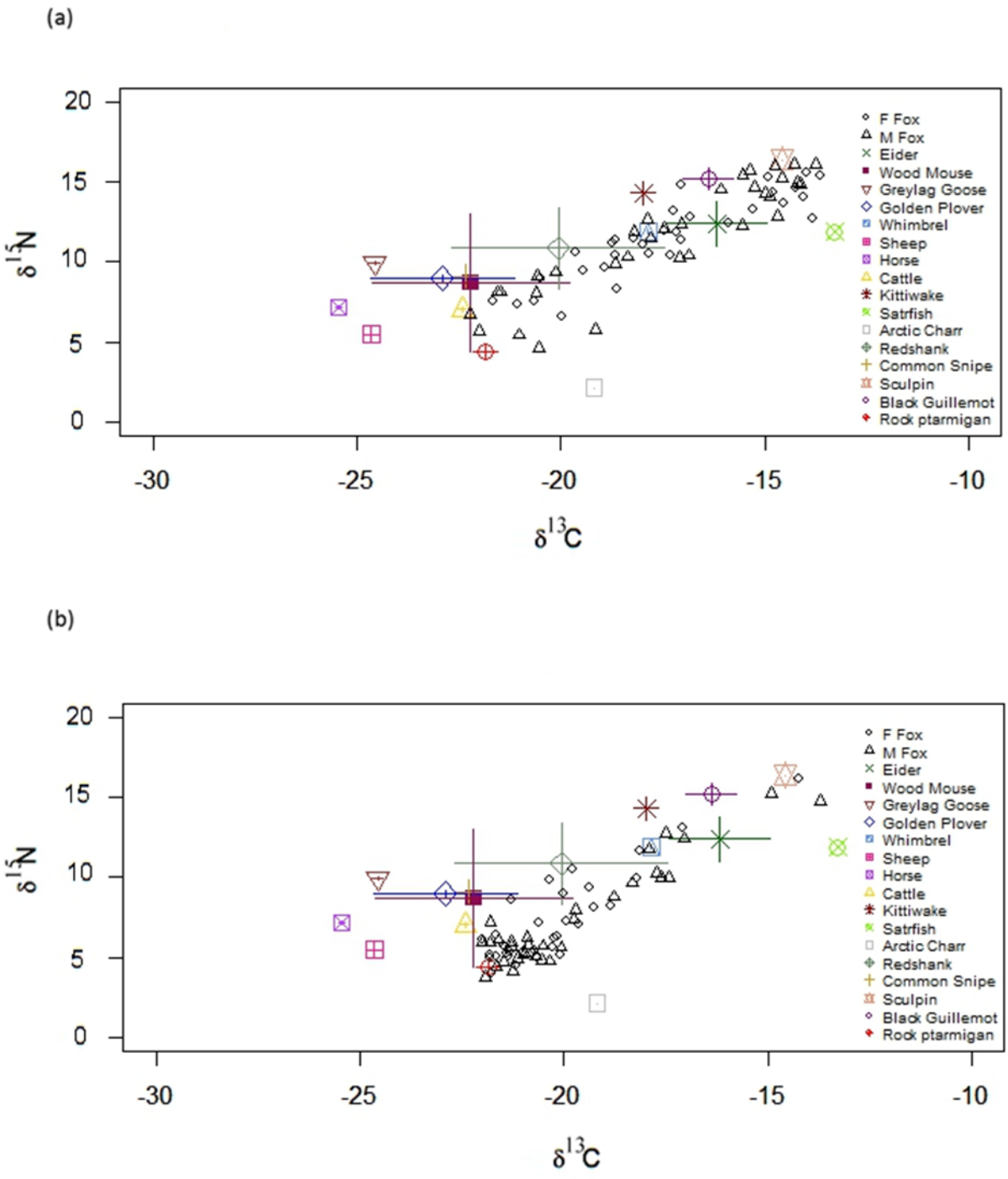

Fig 7. Graphical view of the isotopic signatures (‰) of the possible prey for Icelandic arctic foxes corrected for trophic discrimination using the factor estimated from muscle and their respective standard deviation. (a) Coastal and (b) Inland fox signatures. Female (F Fox) and Male (M Fox) arctic foxes are displayed by different symbols in each of the graphs.

Linear models

While comparing the different models, the one with the lowest AICc for both isotopes, included an interaction between period*habitat*sex (Table 1), where period referred to the three discrete time periods (1979-1989, 1990-1999, 2000-2011) and not to time as continuous variable. It has to be noticed that for $\delta^{13}C$, the model to be chosen was an interaction between period*habitat, because when ΔAICc is lower than two, the simpler model should be chosen (Hu 2007). But in order to compare between carbon and nitrogen values, the three-way model interaction was chosen. Still, both models show the same changes in diet over the study period (Table 2, Appendix D). The changes of the arctic fox signatures over the study periods can be seen in Fig. 8, where can be noticed an isotopic variation between habitats in both $\delta^{13}C$ and $\delta^{15}N$.

The coastal females had a significant increase of 2.24‰ (SE=0.82, p=0.01) in $\delta^{13}C$ and 2.62‰ (SE=1.10, p=0.05) in $\delta^{15}N$ between the second period and the intercept (first period), and 3.03‰ (SE=0.94, p=0.01) in $\delta^{13}C$ and 4.34‰ (SE=1.27, p=0.001) in $\delta^{15}N$ between the third period and the first. For the coastal males there was a significant interaction of -4.21‰ (SE=1.27, p=0.01) in $\delta^{13}C$ and -7.07‰ (SE=1.70, p=0.001) in $\delta^{15}N$ on the third period, in relation to the third period of coastal females (Table 2). This showed that coastal males in the end of the study period shifted towards less marine preys while the coastal females in the opposite direction. The coastal males relied more on marine resources in the second period, but the difference between coastal female and coastal males in the second period was not significant (p=>0.1).

A significant interaction was displayed between the inland and coastal females during the second and third period, respectively. In the second period the inland females had a decrease of -2.98‰ (SE=1.18, p=0.05) in $\delta^{13}C$ and -3.97‰ (SE=1.58, p=0.05) in $\delta^{15}N$ in relation to the second period of coastal females, and -2.87‰ (SE=1.29, p=0.05) in $\delta^{13}C$ and -4.72‰ (SE=1.73, p=0.01) in $\delta^{15}N$ decrease in the third period in relation with the third period of the coastal

females. Inland males had less pronounced changes (Table 2), and showed no great significant difference with inland females between the periods.

*Table 1. Model selection for the δ13C and δ15N responses. Time effects were fitted both as a continuous predictor ("Year"), and as a factor ("Period") with three levels in separate models. Other explanatory variables were "habitat" (coastal or inland) and sex. + 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 (ΔAICc) are presented. The selected models (i.e. the one with the lowest AICc) are shown in bold. The models which differed by less than 2 in ΔAICc to the best model are shown in italics.*

	Model	K	AICc	ΔAICc
δ13C				
	*Period * Habitat*	*7*	*573.01*	*0.46*
	Period * Sex	7	617.61	45.06
	Period * Habitat * Sex	**13**	**572.55**	**0.00**
	*Period * Habitat + Sex*	*8*	*574.27*	*1.72*
	Year * Habitat	5	577.75	5.20
	Year * Sex	5	615.59	43.04
	Year * Habitat * Sex	9	577.69	5.14
	Year * Habitat + Sex	6	579.40	6.85
δ15N				
	Period * Habitat	7	654.69	6.15
	Period * Sex	7	708.64	60.10
	Period * Habitat * Sex	**13**	**648.54**	**0.00**
	Period * Habitat + Sex	8	656.66	8.12
	Year * Habitat	5	657.26	8.72
	Year * Sex	5	706.10	57.56
	Year * Habitat * Sex	9	650.97	2.43
	Year * Habitat + Sex	6	659.35	10.81

Table 2. Results from linear models on the effects of period (1979-1989, 1990-1999, 2000-2011), habitat (inland or coastal) and sex (female or male) on (a) carbon isotope ($\delta^{13}C$), (b) nitrogen isotope ($\delta^{15}N$) in Icelandic arctic foxes. The intercept is the first period (1979-1989), coastal habitat and female, effect sizes are shown as contrasts to the intercept.

	Value	Std. Error	t value	P	
(a) δ13C Fixed effect					
Intercept	**-19.03**	**0.59**	**-32.10**	**<2e-16**	*******
Period 2	**2.24**	**0.82**	**2.72**	**0.007**	******
Period 3	**3.03**	**0.94**	**3.23**	**0.002**	******
Habitat Inland	-1.03	0.82	-1.25	0.213	
SexM	1.60	0.84	1.90	0.059	**.**
Period 2:Habitat Inland	**-2.98**	**1.18**	**-2.53**	**0.013**	*****
Period 3:Habitat Inland	**-2.87**	**1.29**	**-2.22**	**0.028**	*****
Period 2:SexM	-0.43	1.25	-0.35	0.731	
Period 3:SexM	**-4.21**	**1.27**	**-3.31**	**0.001**	******
Habitat Inland:SexM	-0.85	1.16	-0.73	0.466	
Period 2:Habitat Inland:SexM	0.35	1.73	0.20	0.842	
Period 3:Habitat Inland:SexM	3.50	1.78	1.97	0.051	**.**
(b) δ15N Fixed effect					
Intercept	**9.42**	**0.79**	**11.86**	**<2e-16**	*******
Period 2	**2.62**	**1.10**	**2.38**	**0.019**	*****
Period 3	**4.34**	**1.26**	**3.46**	**0.001**	*******
Habitat Inland	-1.63	1.10	-1.48	0.142	
SexM	**2.69**	**1.12**	**2.39**	**0.018**	*****
Period 2:Habitat Inland	**-3.97**	**1.58**	**-2.52**	**0.013**	*****
Period 3:Habitat Inland	**-4.72**	**1.73**	**-2.72**	**0.007**	******
Period 2:SexM	-0.99	1.67	-0.59	0.554	
Period 3:SexM	**-7.07**	**1.70**	**-4.15**	**6.24E-05**	*******
Habitat Inland:SexM	-2.23	1.56	-1.43	0.155	
Period 2:Habitat Inland:SexM	1.27	2.32	0.55	0.585	
Period 3:Habitat Inland:SexM	**6.17**	**2.38**	**2.59**	**0.011**	*****

Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

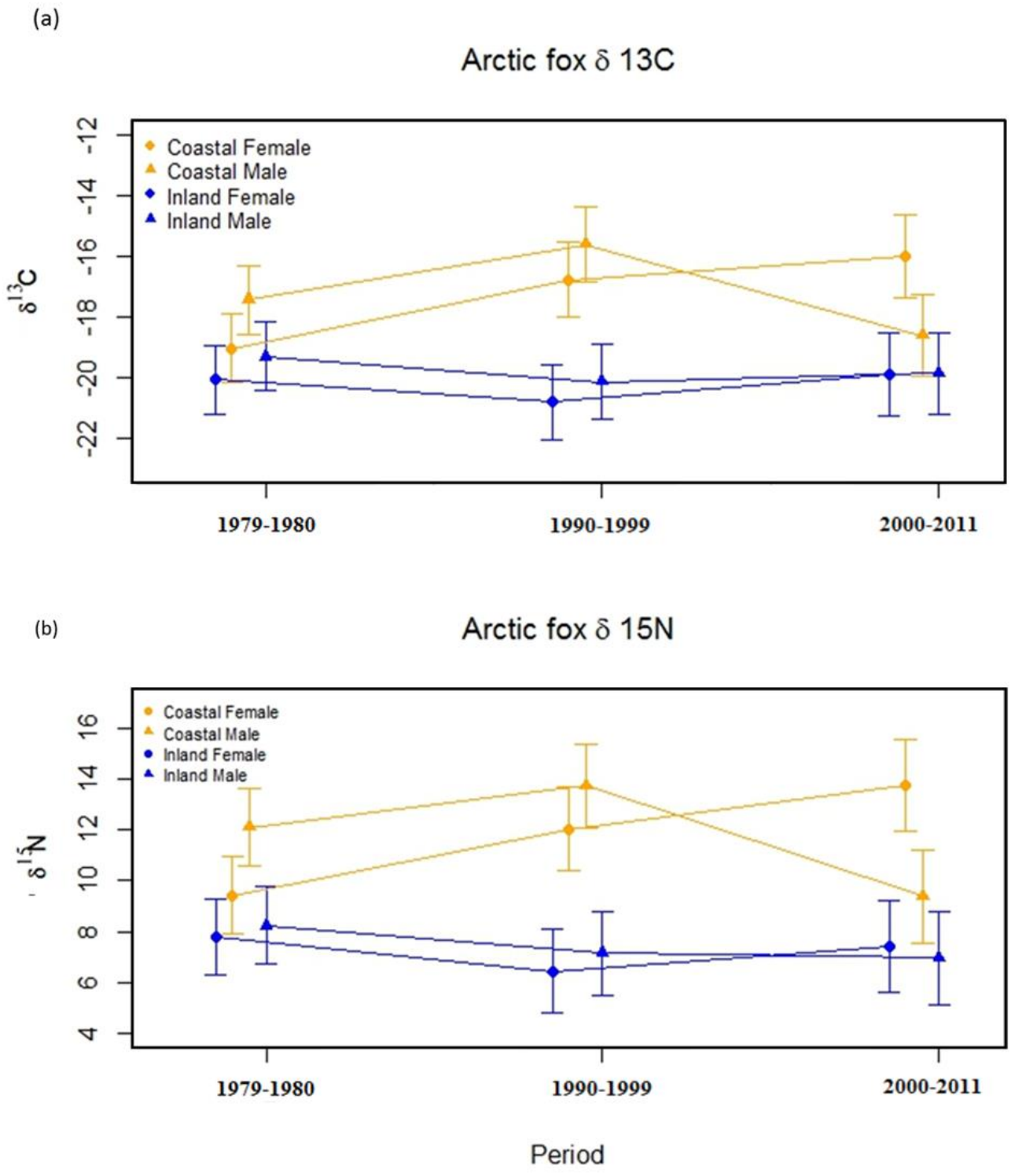

Fig 8. Predictions of (a) $\delta^{13}C$ and (b) $\delta^{15}N$ isotopic signature (‰) with 95% confidence intervals from the best linear models (Table 3).

Mixing models

The main intention for using stable isotope mixing model (MixSIAR), was to get the composition of the young arctic fox diet in respect with period (1979-1989, 1990-1999, 2000-2011) and continuous time as fixed factors. But for the latter, no matter how long the models were run, the diagnostic showed that runs did not converge. Therefore, these models were not included in the results (Appendix E). The MixSIAR estimates based on the two different discrimination factors (muscle and fur), both showed similar overall tendencies in diet (Appendix F), but it was decided to use the muscle discrimination as main results since the signatures fell closer to the prey groups (Fig. 7). Furthermore, because the proportion of marine and rock ptarmigan were more distinct estimates based on the muscle discrimination and there is more important contribution from waders (Mean=0.05-0.13) (Appendix F).

The results based on the muscle discrimination obtained from the mixing models showed that marine and rock ptarmigan were the two main prey groups contributing the overall variation in the diet (Fig. 9). Furthermore, these models supported the results from the linear models (Table 2, Fig. 8). That is, the coastal females had more marine contribution to their diet in the end of the study period (Credible Intervals (CI)=0.79-0.97, Mean=0.89) than in the beginning (CI=0.45-0.67, Mean=0.56), while coastal males had a slight decrease in marine resources from the first period (CI=0.58-0.84, Mean=0.72) to the third (CI=0.45-0.80, Mean=0.63). Moreover, the inferred dietary changes for the inland foxes were less pronounced than for the coastal foxes (Fig. 9, Appendix F).

Waders displayed a constant contribution to the diet of female and male foxes living inland from the first period (CI=0.01-0.32, Mean=0.12; CI=0.01-0.31, Mean=0.11, respectively) to the last (CI=0.00-0.62, Mean=0.13; CI=0.003-0.302, Mean=0.09). At the same time, for female foxes living in coastal areas, waders did not represent a big proportion of the diet, decreasing from the first period (CI=0.00-0.29, Mean=0.09) to the third (CI=0.00-0.11, Mean=0.03). For coastal males, wader's contribution increased from the initial period (CI=0.01-0.25, Mean=0.09)

to the last (CI=0.00-0.39, Mean=0.10) (Fig. 9, Appendix F). All the other prey groups (graylag goose and farm), displayed mean proportions lower than 0.1 (Fig. 9).

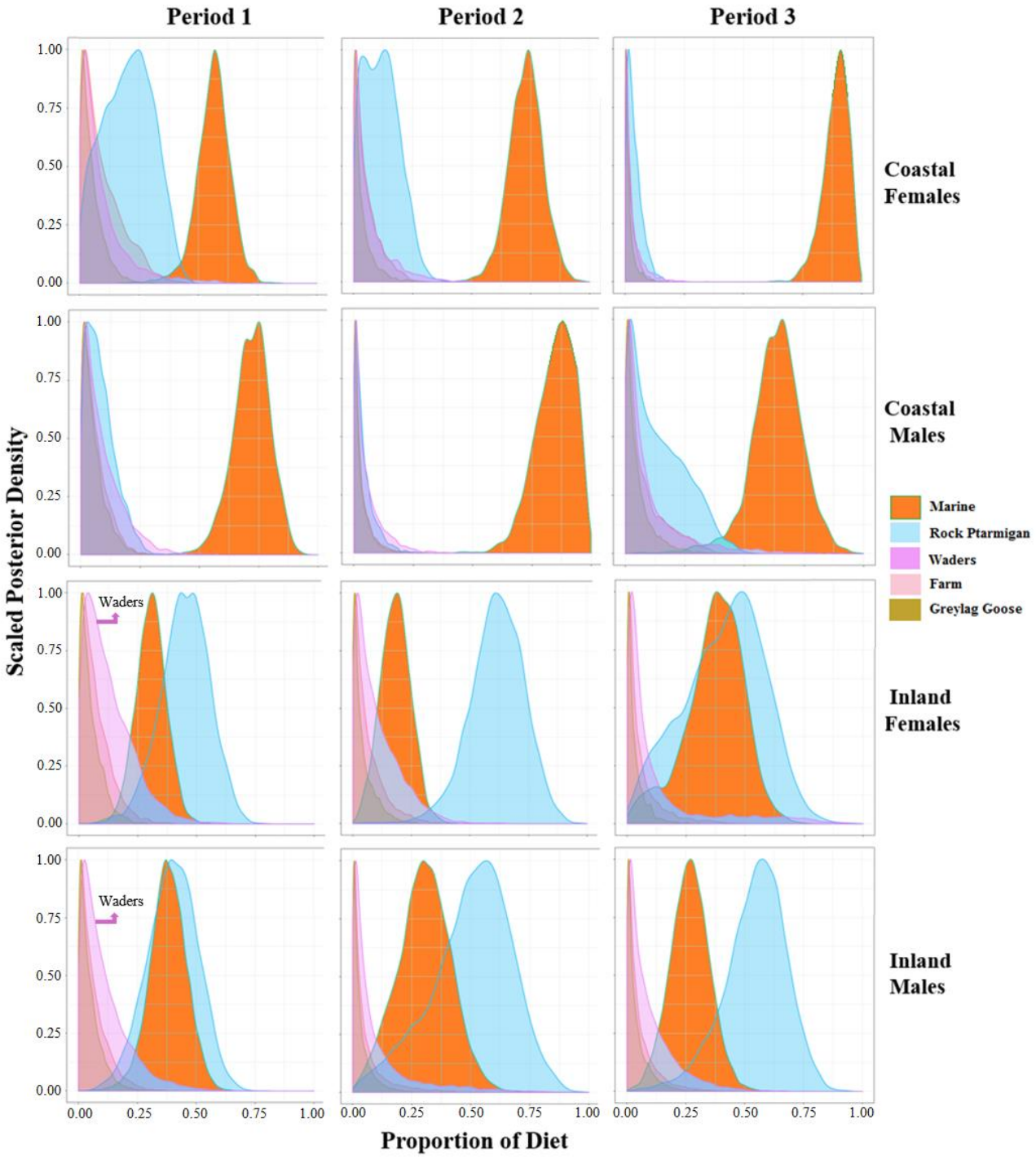

Fig 9. MixSIAR (Stable isotope mixing model) results showing the scaled posterior probability density of the proportion of the prey groups in the diet of the four categories (coastal female, coastal male, inland female and inland male) of Artic foxes. The marine, rock ptarmigan and waders are the ones with proportions higher that 0.1 (Appendix F).

4. Discussion

The present study is based on stable isotope analysis of arctic fox collagen and of the potential food resources for arctic foxes, over a period of steady increase of the fox population. This gave an opportunity to discern whether the prey used by young foxes changed over time and if diet varied between sexes and between foxes using different habitats. The results showed that there was a change in isotopic signature over the study period as well as a difference in resources within and between foxes utilizing different habitats over the time. Furthermore, the mixing model suggested the marine resources are main prey item for coastal foxes and rock ptarmigan for inland foxes in Iceland.

The stable isotope signatures of the Icelandic arctic foxes varied over the period of population increase. The variation over time was not linear for all the foxes, these years of constant increase on the population were employed as three discrete time periods (1979-1989, 1990-1999, 2000-2011) and not as continuous effect. Changes were stronger in foxes living in coastal areas and not as pronounced amongst the ones living inland. In accordance with the findings of Dalerum et al. (2012), coastal habitats are generally more heterogeneous than the inland, with access to seabird colonies and productive coastlines, resulting in more variation in isotopic signatures. Besides, the definition of coastal and inland territories in this study is as described by Pálsson et al. (2016), were all of western Iceland is considered coastal and all eastern Iceland as inland. Therefore, it could be assumed that both inland and coastal foxes, have a possibility to obtain marine and terrestrial resources, and this is in accordance to the results which displayed a mixture of terrestrial and marine prey. Still, they indicated a stronger contribution of rock ptarmigan to the diet of inland foxes and of marine resources to the diet of coastal foxes. This could be explained because western Iceland has more productive seashores than eastern Iceland (Unnsteinsdottir et al. 2016). It also confirms the result that coastal foxes exhibited stronger shifts in diet between periods than inland ones, due to easier access to both types of resources. Another explanation for the mixture of prey resources in different habitats is that foxes are quite mobile and they disperse between 10-30km (some individuals can disperse further (Pamperin et al. 2008; Tarroux et al. 2010)) from their natal ground after a few months (Angerbjörn et al. 2004a; Angerbjörn et al. 2004b), which could create the heterogeneity in the

signature values of their resources. Moreover, it has been suggested in red foxes (*Vulpes vulpes*) that younglings have a higher variation in isotopic signatures than adult foxes, due to juvenile dispersal (Killengreen et al. 2011). This could mean that arctic foxes shot in one habitat did not necessarily were born there, which could explain the mixture of isotopic signatures in arctic foxes culled at both habitats (Fig. 6, Fig. 7).

The linear model showed that inland foxes of both sexes had similar signatures during the time periods and the mixing model suggested the rock ptarmigan as main prey, followed by marine resources and a smaller but steady contribution of waders. As Pálsson et al. (2016) describes, the ptarmigan population decreased around the 1950s, and since the 1980's the ptarmigan population still fluctuates but with lower amplitude than before. The low ptarmigan population at the start of the study, could explain the contribution of marine resources to the diet of foxes living inland, due to their need for an alternative prey. The constant contribution of waders to the diet over the periods implied that this type of prey is a reliable part of the diet to the foxes living inland.

The differences expressed between male and female coastal foxes in the linear model was larger than for the inland ones. Variability in resources is higher in coastal territories, which could explain the differences between the foxes in this habitat (Fig. 6). The observed differences between the sexes is uncertain, although it could be related to sex-specific life history strategies. Food availability, intraspecific competition and dominance relations are the factors for why and when adults and pups leave the dens (Frafjord 1992). It could be that males tend to wander faster and further away from the territory, due to the tension of having a dominant male already in the area. Furthermore, it is known that the common trend among fox species is for juvenile males to disperse to avoid inbreeding (Kamler et al. 2004; Kitchen et al. 2005). While juvenile females tend to remain philopatric (Angerbjörn et al. 2004b; Kamler et al 2004; Kitchen et al. 2005), because it avoids the high costs of dispersal, and it could help to acquire experience in raising the young, increase fitness and inherit a portion of natal territory (Kamler et al. 2004). Therefore, the stronger changes of males in isotopic signatures could be due to higher dispersal which would lead to availability of different resources. However, if the dispersal is the explanatory reason for coastal males having higher temporal variability of diet, the same pattern would be expected for

males living inland. The lack of big changes in the signatures of inland males could be due that eastern Iceland is a much larger area (Fig. 2) and with less productive shores (Unnsteinsdottir et al. 2016), which could reduce the opportunities to shift so often to different resources.

The strong significant difference displayed in the third period between males and females living at the coast, could be related to the carrying capacity of the habitat. In the third period the population has increased steadily for over two decades (Fig. 1), which could place pressure on the males to disperse further away from their territories in search for females, territories and food resources. It can be that male foxes killed in the coast came from inland habitats (less productive area (Hersteinsson et al. 2009)), which could explain the less marine isotopic signatures of coastal males in the last period.

Pálsson et al. (2016) suggested that the recent decline of the arctic fox population in Iceland was mainly due to a reduction of ptarmigan, and that the increase in geese numbers, use of marine resources and probably waders caused the slow rise of the fox population over the decades after 1980. The results in this study showed no sign of geese as main prey, while waders were present in the arctic fox diet in a small proportion. Still, the main contributors to the signatures of the arctic fox were the ptarmigan and marine resources. It could be that geese are a preferred prey for adult foxes and because this study only showed the isotopic signature of foxes when young, it could reflect that in this stage of their life foxes do not use geese as a resource. It has to be taken into consideration that geese overwinter outside Iceland, and maybe geese as resource is not available when young foxes are developing. Furthermore, eggs of geese were not included in this study, leaving the possibility that these could still be a resource for young foxes. Approximate values Giroux et al. (2012) and Ehrich et al. (2015) show an isotopic signature of goose eggs closer to the signatures of the arctic foxes than the graylag goose. This supports, the possibility of goose eggs as a resource for young arctic foxes. Besides, it can be that adult foxes choose eggs as food for themselves and not as resource to take back to the den. As Dalerum et al. (2012) suggested by their results, adult foxes adopted different strategies for selecting resources to consume compared to resources to bring back to feed their offspring.

Male arctic foxes have been shown to be significantly heavier and to have longer mandibles than females (Hersteinsson et al. 2009), which could explain some of the difference in isotopic signatures between sexes. Meaning, that the development of the bone collagen could differ between males and females, and therefore creating a slight variation of isotopic signatures.

Helgason (2008) studied the winter diet of Icelandic arctic foxes through analyses of scats and stomach contents and showed that foxes consumed a large proportions of big mammals. Large mammals were thus, expected to be present in the diet of the arctic foxes (used as bait by foxhunters and farm animals dying on the field). However, the isotopic signatures in this study did not show any big contribution of this prey group to the diet of arctic foxes, which could be related to age preference in diet.

Another factor to be considered, is the changes in the climate over the last decades. Temperature rise could be beneficial to arctic foxes living in Iceland, since they lack competitors and it means longer breeding and growing periods of their resources (Pálsson et al. 2016). Moreover, as Herteinsson and Macdonald (1996) mention, arctic foxes also use crowberries, seaweed and insects as food resource, which could be found more often with less harsh climatic conditions. If these resources were to be added to the possible prey isotopic signatures, it could explain further the shifts in diet over the time, even though the importance of these resources for young foxes is not known.

It has to be noticed that the signatures of the foxes do not exactly fit with the prey signatures, which could be because the discrimination used was just an approximation from the arctic fox discrimination factor and the difference between discrimination in muscle and collagen determined for wolves, due to the lack of information about the true discrimination on collagen for the arctic fox. This could create a biased overview of the prey resources on the diet of the arctic foxes in this study. Still, the main distinction between marine and terrestrial resources is not affected. Furthermore, it has to be taken into account that the rock ptarmigan signatures were taken from another area (Varanger) and not from Iceland. But previous studies have shown that there is not a big difference between the signatures of resources in different areas (Ehrich et al. 2015).

5. Conclusion

In Iceland, arctic foxes act as generalist predators, where coastal foxes show more variation in diet over time probably due to more availability of resources in the area. The main resources for foxes in this study were ptarmigan and marine resources, which could give an idea for further studies of the reason the population is decreasing over the last years.

This study gives an indication of the prey items that foxes have utilized in the last decades, but is recommended to do further investigations to get a wider idea of the population dynamics. For instance, would be suggested to perform diet studies using different methods, as direct observations. Moreover, it would be needed behavioral studies to understand why males and females have different diets. In addition, the use of telemetry to obtain information about the dispersal of the young or migrations of the adults could give a better understanding of the dynamics of the arctic fox population in Iceland.

It would also be important to elongate the study to periods were the population of arctic foxes was in decline (before 1980's or after 2009), to be able to infer whether the changes in the diet affect the population. Furthermore, would be beneficial to add more prey items, as geese eggs, to further comparison with other studies.

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7. Appendix

Appendix A

Table A. Samples of arctic fox jaws taken from The Icelandic Institute of Natural History collection.

Sample No.	ID Iceland	period	sex	habitat
1	368	1980-1989	female	inland
2	480	1980-1989	female	inland
3	610	1980-1989	female	inland
4	696	1980-1989	female	inland
5	956	1980-1989	female	inland
6	1103	1980-1989	female	inland
7	2444	1980-1989	female	inland
8	2509	1980-1989	female	inland
54	1120	1980-1989	female	inland
55	1122	1980-1989	female	inland
56	1494	1980-1989	female	inland
9	478	1980-1989	male	inland
10	562	1980-1989	male	inland
11	698	1980-1989	male	inland
12	875	1980-1989	male	inland
13	1051	1980-1989	male	inland
14	1213	1980-1989	male	inland
15	1410	1980-1989	male	inland
16	2491	1980-1989	male	inland
57	1493	1980-1989	male	inland
58	1502	1980-1989	male	inland
59	1722	1980-1989	male	inland
17	443	1980-1989	female	coastal
18	878	1980-1989	female	coastal
19	1007	1980-1989	female	coastal
20	1265	1980-1989	female	coastal
21	2468	1980-1989	female	coastal
60	652	1980-1989	female	coastal
61	1871	1980-1989	female	coastal
62	1893	1980-1989	female	coastal
63	2094	1980-1989	female	coastal
64	2102	1980-1989	female	coastal
65	2189	1980-1989	female	coastal
22	435	1980-1989	male	coastal
23	660	1980-1989	male	coastal
24	1002	1980-1989	male	coastal
25	1173	1980-1989	male	coastal
26	1334	1980-1989	male	coastal
27	2095	1980-1989	male	coastal
66	815	1980-1989	male	coastal
67	1275	1980-1989	male	coastal
68	1276	1980-1989	male	coastal
69	1631	1980-1989	male	coastal
70	2512	1980-1989	male	coastal
28	4323	1990-1999	female	inland
29	4926	1990-1999	female	inland
30	5111	1990-1999	female	inland
31	6306	1990-1999	female	inland
71	2578	1990-1999	female	inland
72	2938	1990-1999	female	inland
73	3145	1990-1999	female	inland
74	3867	1990-1999	female	inland
75	4282	1990-1999	female	inland
76	5678	1990-1999	female	inland
77	5793	1990-1999	female	inland
32	4842	1990-1999	male	inland
33	5112	1990-1999	male	inland
78	3118	1990-1999	male	inland
79	3614	1990-1999	male	inland
80	3831	1990-1999	male	inland
81	4279	1990-1999	male	inland
82	4723	1990-1999	male	inland
83	4835	1990-1999	male	inland
84	4960	1990-1999	male	inland
85	4961	1990-1999	male	inland
86	5097	1990-1999	male	inland
34	4356	1990-1999	female	coastal
35	4652	1990-1999	female	coastal
36	5010	1990-1999	female	coastal
37	5290	1990-1999	female	coastal
38	5626	1990-1999	female	coastal
39	6120	1990-1999	female	coastal
87	2882	1990-1999	female	coastal
88	3179	1990-1999	female	coastal
89	3680	1990-1999	female	coastal
90	4054	1990-1999	female	coastal
91	5136	1990-1999	female	coastal
40	4358	1990-1999	male	coastal
41	4518	1990-1999	male	coastal
42	4831	1990-1999	male	coastal
92	3019	1990-1999	male	coastal
93	3334	1990-1999	male	coastal
94	3664	1990-1999	male	coastal
95	4072	1990-1999	male	coastal
96	5262	1990-1999	male	coastal
97	5318	1990-1999	male	coastal
98	5378	1990-1999	male	coastal
99	5429	1990-1999	male	coastal
43	5980	2000-2009	female	inland
44	6267	2000-2009	female	inland
45	6731	2000-2009	female	inland
100	6504	2000-2009	female	inland
101	6632	2000-2009	female	inland
102	7057	2000-2009	female	inland
103	8261	2000-2009	female	inland
104	8518	2000-2009	female	inland
105	8641	2000-2009	female	inland
106	8783	2000-2009	female	inland
107	9150	2000-2009	female	inland
46	6262	2000-2009	male	inland
47	6482	2000-2009	male	inland
108	6502	2000-2009	male	inland
109	6720	2000-2009	male	inland
110	6735	2000-2009	male	inland
111	6798	2000-2009	male	inland
112	7026	2000-2009	male	inland
113	8519	2000-2009	male	inland
114	8620	2000-2009	male	inland
115	8757	2000-2009	male	inland
116	8850	2000-2009	male	inland
48	6113	2000-2009	female	coastal
49	6251	2000-2009	female	coastal
50	6614	2000-2009	female	coastal
51	6751	2000-2009	female	coastal
117	6977	2000-2009	female	coastal
118	7100	2000-2009	female	coastal
119	7102	2000-2009	female	coastal
120	7322	2000-2009	female	coastal
121	7843	2000-2009	female	coastal
122	8461	2000-2009	female	coastal
123	9643	2000-2009	female	coastal
52	6464	2000-2009	male	coastal
53	6704	2000-2009	male	coastal
124	6825	2000-2009	male	coastal
125	6949	2000-2009	male	coastal
126	6956	2000-2009	male	coastal
127	6974	2000-2009	male	coastal
128	6982	2000-2009	male	coastal
129	7038	2000-2009	male	coastal
130	8305	2000-2009	male	coastal
131	8552	2000-2009	male	coastal
132	9139	2000-2009	male	coastal

Appendix B

Table B. Mean values of $\delta^{13}C$ and $\delta^{15}N$ (‰) for Icelandic arctic fox bones.

Zone	Sex	Mean C	SD C	Mean N	SD N
Coastal	Female	-19.99	±2.29	7.86	±2.50
Coastal	Male	-19.96	±2.63	7.92	±3.40
Inland	Female	-22.84	±1.61	3.60	±2.74
Inland	Male	-22.31	±2.11	3.90	±3.16

Appendix C

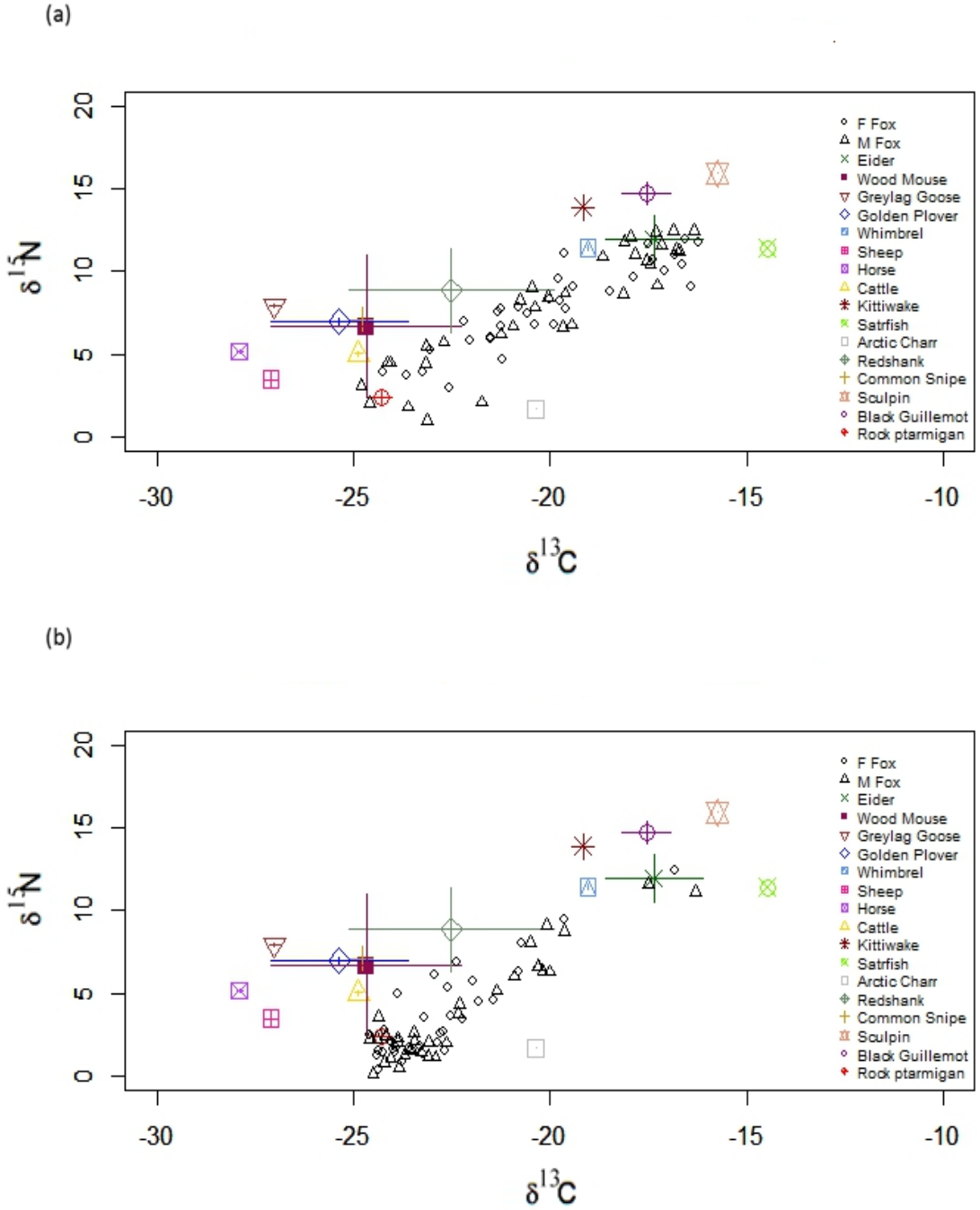

Fig C. Graphical view of the isotopic signatures (‰) of the possible prey for Icelandic arctic foxes corrected for trophic discrimination using the factor estimated from fur and their respective standard deviation. (a) Coastal and (b) Inland fox signatures. Female (F Fox) and Male (M Fox) arctic foxes are displayed separately in each of the graphs.

Appendix D

Table D. Results from linear models on the effects of period (1979-1989, 1990-1999, 2000-2011), habitat (inland or coastal) on (a) carbon isotope ($\delta^{13}C$), (b) nitrogen isotope ($\delta^{15}N$) in Icelandic arctic foxes. The intercept is the first period (1979-1989), coastal habitat.

	Value	Std. Error	t value	P	
δ13C Fixed effect					
Intercept	**-18.23**	**0.43**	**-42.14**	**<2e-16**	***
Period 2	**1.89**	**0.63**	**2.98**	**0.004**	**
Period 3	0.72	0.65	1.10	0.273	
Habitat Inland	**-1.46**	**0.60**	**-2.43**	**0.017**	*
Period 2:Habitat Inland	**-2.68**	**0.89**	**-3.02**	**0.003**	**
Period 3:Habitat Inland	-0.92	0.91	-1.00	0.318	.

Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Appendix E

*Table E. MixSIAR (Stable isotope mixing model) global results with predicted diet proportions (5th to 95th credible intervals) of each potential group prey in the continuous time compared to $\delta^{13}C$ and $\delta^{15}N$ mixture values for Icelandic Arctic fox. Mean values are in parentheses and the highest group prey contribution values are in **bold***

		Farm	Greylag Goose	Marine	Rock Ptarmigan	Waders
Coastal Female	**Fur**	0.004-0.279(0.092)	0.004-0.284(0.097)	**0.016-0.306(0.113)**	**0.053-0.477(0.234)**	**0.158-0.760(0.464)**
	Muscle	0.002-0.226(0.061)	0.002-0.231(0.063)	**0.021-0.930(0.619)**	0.003-0.268(0.079)	**0.002-0.690(0.178)**
Coastal Male	**Fur**	NA	NA	NA	NA	NA
	Muscle	NA	NA	NA	NA	NA
Inland Female	**Fur**	**0.004-0.302(0.101)**	0.003-0.263(0.088)	**0.031-0.389(0.176)**	**0.077-0.809(0.415)**	**0.009-0.581(0.220)**
	Muscle	**0.005-0.278(0.101)**	0.004-0.259(0.091)	**0.086-0.419(0.252)**	**0.088-0.626(0.335)**	**0.010-0.595(0.221)**
Inland Male	**Fur**	**0.009-0.422(0.149)**	**0.007-0.406(0.138)**	**0.071-0.701(0.352)**	**0.003-0.419(0.117)**	**0.023-0.591(0.245)**
	Muscle	**0.011-0.481(0.185)**	**0.008-0.443(0.160)**	**0.099-0.685(0.343)**	0.001-0.113(0.031)	**0.040-0.618(0.281)**

*Table F. MixSIAR (Stable isotope mixing model) results with predicted diet proportions (5th to 95th credible intervals) of each potential group prey in the three discrete periods compared to $\delta^{13}C$ and $\delta^{15}N$ mixture values for Icelandic Arctic fox. Mean values are in parentheses and the highest group prey contribution values are in **bold***

			Farm	Greylag Goose	Marine	Rock Ptarmigan	Waders
Coastal Female	**Fur**	**Period 1**	0.002-0.152 (0.044)	0.001-0.090(0.030)	**0.263-0.441(0.352)**	**0.364-0.632(0.516)**	0.003-0.170(0.058)
		Period 2	0.001-0.116(0.032)	0.001-0.082(0.023)	**0.425-0.613(0.514)**	**0.241-0.500(0.385)**	0.001-0.167(0.046)
		Period 3	0.001-0.108(0.030)	0.001-0.098(0.026)	**0.581-0.796(0.688)**	**0.082-0.318(0.202)**	0.001-0.193(0.053)
	Muscle	**Period 1**	0.005-0.262(0.095)	0.002-0.139(0.048)	**0.449-0.673(0.564)**	**0.031-0.370(0.203)**	0.004-0.294(0.090)
		Period 2	0.002-0.164(0.052)	0.001-0.123(0.035)	**0.611-0.848(0.730)**	**0.011-0.246(0.118)**	0.002-0.231(0.065)
		Period 3	0.001-0.068(0.022)	0.000-0.066(0.018)	**0.790-0.965(0.891)**	0.004-0.103(0.040)	0.001-0.111(0.030)
Coastal Male	**Fur**	**Period 1**	0.003-0.173(0.059)	0.003-0.143(0.048)	**0.408-0.652(0.531)**	**0.093-0.412(0.258)**	**0.006-0.296(0.103)**
		Period 2	0.001-0.143(0.043)	0.001-0.149(0.041)	**0.499-0.814(0.652)**	**0.031-0.342(0.171)**	0.003-0.307(0.093)
		Period 3	0.001-0.227(0.052)	0.001-0.093(0.028)	**0.231-0.539(0.394)**	**0.097-0.642(0.440)**	0.002-0.420(0.085)
	Muscle	**Period 1**	0.003-0.154(0.057)	0.003-0.150(0.052)	**0.581-0.843(0.719)**	0.007-0.199(0.083)	0.005-0.253(0.088)
		Period 2	0.001-0.094(0.028)	0.001-0.112(0.031)	**0.701-0.962(0.848)**	0.002-0.128(0.041)	0.001-0.178(0.052)
		Period 3	0.002-0.261(0.076)	0.002-0.171(0.050)	**0.454-0.800(0.634)**	**0.005-0.352(0.140)**	**0.003-0.388(0.100)**
Inland Female	**Fur**	**Period 1**	0.003-0.158(0.054)	0.002-0.102(0.035)	**0.089-0.272(0.181)**	**0.502-0.788(0.658)**	0.004-0.208(0.072)
		Period 2	0.001-0.153(0.045)	0.001-0.094(0.027)	0.020-0.174(0.090)	**0.615-0.920(0.783)**	0.001-0.184(0.055)
		Period 3	0.001-0.088(0.025)	0.001-0.059(0.017)	**0.026-0.307(0.154)**	**0.536-0.926(0.756)**	0.001-0.173(0.048)
	Muscle	**Period 1**	0.004-0.189(0.069)	0.003-0.137(0.050)	**0.200-0.413(0.306)**	**0.274-0.615(0.451)**	**0.009-0.316(0.123)**
		Period 2	0.002-0.194(0.060)	0.001-0.139(0.042)	**0.078-0.288(0.183)**	**0.416-0.794(0.616)**	**0.004-0.285(0.100)**
		Period 3	0.002-0.217(0.057)	0.001-0.107(0.033)	**0.122-0.549(0.370)**	**0.103-0.661(0.410)**	**0.004-0.617(0.130)**
Inland Male	**Fur**	**Period 1**	0.002-0.139(0.045)	0.002-0.099(0.033)	**0.118-0.346(0.234)**	**0.454-0.764(0.619)**	0.004-0.209(0.069)
		Period 2	0.001-0.105(0.028)	0.001-0.073(0.020)	**0.026-0.255(0.128)**	**0.593-0.927(0.777)**	0.001-0.171(0.046)
		Period 3	0.001-0.137(0.037)	0.001-0.091(0.025)	**0.038-0.259(0.143)**	**0.561-0.890(0.739)**	0.001-0.194(0.055)
	Muscle	**Period 1**	0.004-0.179(0.062)	0.003-0.140(0.048)	**0.251-0.508(0.381)**	**0.217-0.568(0.399)**	**0.007-0.310(0.109)**
		Period 2	0.001-0.221(0.055)	0.001-0.122(0.035)	**0.113-0.484(0.304)**	**0.185-0.751(0.504)**	**0.003-0.433(0.103)**
		Period 3	0.002-0.182(0.053)	0.001-0.139(0.040)	**0.131-0.405(0.268)**	**0.309-0.739(0.545)**	0.003-0.302(0.094)