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Dietary variation in arctic foxes *(Alopex lagopus)* – an analysis of stable carbon isotopes

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Abstract We used stable carbon isotopes to analyse individual variation in arctic fox diet. We extracted collagen from bones (the lower jaw), and measured stable carbon isotopes. The foxes came from three different localities: Iceland, where both microtines and reindeer are rare; west Greenland, where microtines are absent; and Sweden, where scat analyses showed the primary food to be microtine rodents and reindeer. The Icelandic samples included foxes from both coastal and inland habitats, the Swedish sample came from an inland area, and the Greenland sample from coastal sites. The spatial variation in the isotopic pattern followed a basic division between marine and terrestrial sources of protein. Arctic foxes from inland sites had $\delta^{13}C$ values of –21.4 (Iceland) and –20.4‰ (Sweden), showing typical terrestrial values. Coastal foxes from Greenland had typical marine values of –14.9 ‰, whereas coastal foxes from Iceland had intermediate values of –17.7‰. However, there was individual variation within each sample, probably caused by habitat heterogeneity and territoriality among foxes. The variation on a larger scale was related to the availability of different food items. These results were in accordance with other dietary analyses based on scat analyses. This is the first time that stable isotopes have been used to reveal individual dietary patterns. Our study also indicated that isotopic values can be used on a global scale.

Key words Carbon isotopes · Arctic fox · Diet · Bone Collagen

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Introduction

In the analysis of mammalian diet, the most commonly used methods are analysis of stomach contents, faecal pellets or food remains. This gives a picture of the last meal at a specific time, but might not be typical of the overall diet. To obtain a more general picture of the diet one can collect faecal pellets or food remains over longer periods, but it is then often difficult or impossible to obtain information about individual variation in diet. In contrast, an analysis of stable isotopes will provide in-formation about the average diet of individuals over a longer period (DeNiro and Epstein 1978a), even a life-time in a relatively short-lived animal such as a fox. DeNiro and Epstein (1981) showed in a laboratory study, and Vogel (1978) in a field study, that an animal's diet is isotopically reflected in its tissues. Further, Tieszen et al. (1983) showed that different tissues have different carbon turnover times. Metabolically active tissues (e.g. liver) have faster carbon turnover than less metabolically active tissues (e.g. bone). They therefore recommend isotope analysis of bone collagen, which has a very long turnover time, in combination with an analysis of faeces and/or stomach contents for dietary studies in animals.

Carbon isotopes are used in dietary studies to distinguish between terrestrial and marine protein intake, for which a difference of c. 7‰ is expected between the two extremes (Chisholm et al. 1983). This difference is due to fractionation between the marine and the atmospheric carbon reservoir. Carbon isotopes have also been used to distinguish between consumers of C3 and C4 plants, where the isotopic difference is due to different photosynthetic pathways in the plants (Smith and Epstein 1971). There are no C4 plants in this part of the world, so expected end values for terrestrial C3 plant consumers would be –21 to –22‰, as seen in numerous studies (e.g.

DeNiro and Epstein 1978b; Vogel 1978; Chisholm et al. 1983; Schoeninger et al. 1983; Hobson 1987; Bada et al. 1990; Bocherens 1990). Hence, an expected end value for a marine protein consumer would be −12 to −13‰ as seen in Greenlandic eskimos (Tauber 1981) or in seals (Schoeninger and DeNiro 1984).

Previous dietary studies on animals using stable carbon isotopes include a wide range of applications using different species from different geographical areas. Dietary differences between (1) trophic levels (Welch and Parson 1993) or food webs (Rau et al. 1983; Peterson and Fry 1987; Schell and Ziemann 1988; Sholto-Douglas et al. 1991); (2) species (DeNiro and Epstein 1978b; Vogel 1978; Ambrose and DeNiro 1986; Hobson 1987; Bocherens 1990; Ramsay and Hobson 1991); and (3) populations (van der Merwe et al. 1990; Vogel et al. 1990; Alisauskas and Hobson 1993) have been discussed.

Here we will use information from an analysis of stable carbon isotopes in arctic fox (*Alopex lagopus*) to examine individual and spatial variation in its diet. We will compare these results with data on arctic fox diet from faecal analyses and prey remains at fox dens. This is thus the first time an analysis of stable isotopes has been combined with data from faeces to reveal dietary patterns for a mammal species.

The arctic fox is a circumpolar small carnivore. It is distributed over the tundra, north of and above the tree line, in both Eurasia and North America, and on islands and along coasts in the Arctic. The arctic fox is considered to be an opportunistic omnivore (Hersteinsson 1984; Garrott and Eberhardt 1987). In inland areas such as Fennoscandia (Collett 1912; Østbye et al. 1978), Canada (Macpherson 1969), and Siberia (Bannikov 1970), the dominant food is lemmings and voles. In these areas arctic foxes are also known to scavenge on carcasses of reindeer/caribou (*Rangifer tarandus*). In coastal areas, e.g. in Iceland, they feed on invertebrates, seabirds and seal carcasses (Hersteinsson 1984), but also on eggs and birds on islands with dense bird colonies in Alaska and Svalbard (Fay and Stephenson 1989; Frafjord 1993). Sometimes they even follow polar bears (*Ursus maritimus*) over the pack ice for left-overs (Bannikov 1970).

We studied variation in diet in one area where both microtine rodents and reindeer are common, Sweden (Angerbjörn et al. 1991); in another area where reindeer are present but microtines absent, west Greenland (Birks and Penford 1990); and in a third area where both are absent or rare, Iceland (Hersteinsson 1992).

Methods

Sample preparation and measurement

Fleshy parts on the jaw bones were removed and all bones were boiled for at least 1 h before drying and drilling. We drilled one or two holes in the lower jaw and extracted collagen from the bone powder according to Brown et al. (1988). In addition, we extracted lipids after demineralisation using a modified version of the method of Kates (1980). The carbon isotopic values of lipids have been shown to differ from those of bone collagen by as much as 7‰ (Smith and Epstein 1971; DeNiro and Epstein 1978a; Vogel 1978; Lidén et al. 1994). It is therefore necessary to make absolutely certain that all lipids are removed prior to isotope analysis. After lipid extraction and evaporation of the solvents (chloroform/methanol), we freeze-dried the samples overnight, prior to the final collagen extraction steps. Stable carbon isotopes were measured on a VG Isotech Prism mass spectrometer with a measurement uncertainty of less than 0.1‰. The results are reported with respect to the PDB standard (PeeDee Belemnite Carbonate, a marine carbonate).

Study sites and material

Iceland

The arctic fox is found all over Iceland. It is heavily persecuted on account of the damage it can do to eider (*Somateria mollissima*) colonies where farmers harvest eider down from nests, and because of purported predation on lambs in spring and summer. Local authorities employ foxhunters each spring to kill foxes occupying known breeding dens. The jaws in this study and information on food remains at dens were provided by these hunters. Food habits have also been determined at all seasons in a coastal area of northwestern Iceland (Hersteinsson 1984).

It is convenient to divide the country into two major habitat types, coastal and inland (Hersteinsson 1984, 1989). In coastal habitats the foxes have access to what the sea brings ashore in addition to many species of birds. In inland areas, the ptarmigan (*Lagopus mutus*) and carcasses of sheep and in some areas reindeer are important food species. There are bird cliffs in coastal areas of the country, particularly in the northwest, and also in some inland areas where colonies of fulmars, in particular, breed. Overall, food abundance and population densities of arctic foxes are higher in coastal areas than further inland, and the blue morph, which is well camouflaged when foraging on the shoreline in all seasons, is more common on the coast than the white morph, while in inland regions the frequencies of the colour morphs are more equal (Hersteinsson 1989).

Sweden

The arctic fox is distributed over the northern part of Fennoscandia, in mountains and on tundra above the tree line. They are also known to conduct long migratory movements (Pullianen 1965) and are regularly found along the coasts of the Bothnian Gulf and Norway. The foxes in Fennoscandia undergo drastic fluctuations in numbers, following their main prey species, the Norwegian lemming (*Lemmus lemmus*) and several species of voles (*Microtus* spp., *Clethrionomys* spp.; Angerbjörn et al. 1991). Domestic reindeer, on which the foxes scavenge, are also frequent in the area. The arctic fox population has been very small for about 75

Table 1 Mean values of $\delta^{13}C$ (‰) for arctic fox bones from Greenland, Iceland and Sweden. One-way ANOVA for differences between locations was $F(3,22) = 26.4$, $P<0.0001$. There were differences between all samples except between the Icelandic inland and the Swedish inland

Location	Habitat	$\delta^{13}C$	95% C I	SD	*n*
Greenland	coastal	−14.9	−13.6 −16.3	1.04	4
Iceland	coastal	−17.7	−16.8 −18.6	1.68	8
Iceland	inland	−21.4	−20.3 −22.6	0.52	6
Sweden	inland	−20.4	−19.4 −21.3	1.24	8

years in Fennoscandia and its existence is threatened due to low population density (Hersteinsson et al. 1989; Angerbjörn et al. 1991; Tannerfeldt et al. 1994).

Of the Swedish sample, seven foxes came from the Scandian mountains and one from a forested area closer to the coast of the Bothnian Gulf. Five of these foxes are roadkills from the collections of the Museum of Natural History in Stockholm, and the other three foxes belong to the Swedish Arctic Fox Project, having died of natural causes in the Vindelfjällens nature reserve (Angerbjörn et al. 1991).

Greenland

Due to the massive ice cap covering Greenland, most arctic foxes here are found close to the coast. However, Braestrup (1941) distinguished between inland foxes, predominantly of the white colour morph, and coastal foxes of the blue colour morph. In contrast to the northern and eastern coast of Greenland, no lemmings or voles are found on the west coast of Greenland (Braestrup 1941; Birks and Penford 1990), but herds of caribou are present, as well as several species of birds, e.g. geese, ducks, passerines, and ptarmigan, and also seabirds. All four foxes from Greenland were shot by hunters and came from the collections of the Museum of Natural History in Stockholm. They were all reported to be from coastal areas in the west, but the exact locations are not known.

Results

Iceland

The isotopic pattern for arctic foxes from Iceland followed a basic division between marine and terrestrial sources of protein (Fig. 1). Foxes from inland sites showed typical terrestrial values of $\delta^{13}C$ from –20.8 to –22.5‰, with a mean of –21.4‰. The coastal foxes, on the other hand, had a mean $\delta^{13}C$ value of –17.7‰, showing an intermediate isotope signature. However, one coastal fox from the north-east and one from the south-west, the only fox of the white colour morph among the coastal foxes, had more terrestrial isotope values (–19.2‰ and –21.0‰, respectively). Excluding those two terrestrial values, the range of coastal foxes was from –15.7 to –17.9‰.

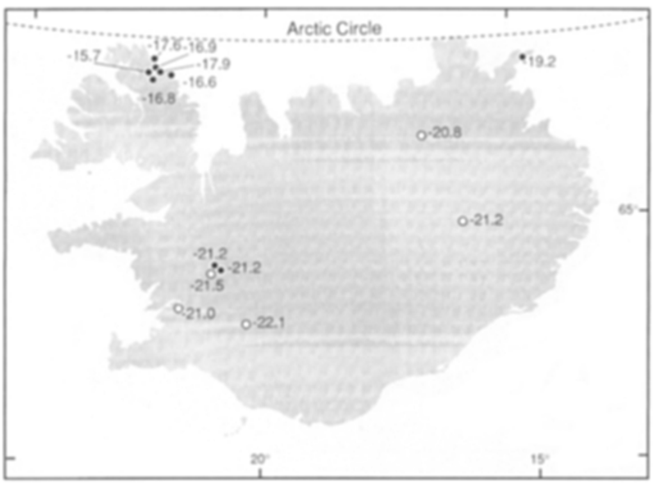

Fig. 1 A map of Iceland showing localities for the arctic foxes and $\delta^{13}C$ values for bone collagen (‰). White and blue colour morphs are shown by *open* and *closed symbols* respectively

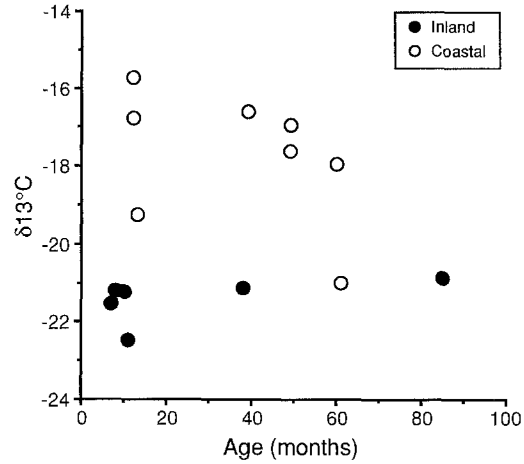

Fig. 2 $\delta^{13}C$ values for bone collagen (‰) for inland and coastal Icelandic foxes against their age (years)

Fig. 3 The diet of arctic foxes in different areas: inland Iceland, coastal Iceland and inland Fennoscandia. The different food species have been categorized into three groups, viz. of marine, intermediate and terrestrial origin

There was considerable variation in the $\delta^{13}C$ value between individuals. The coastal foxes from Iceland

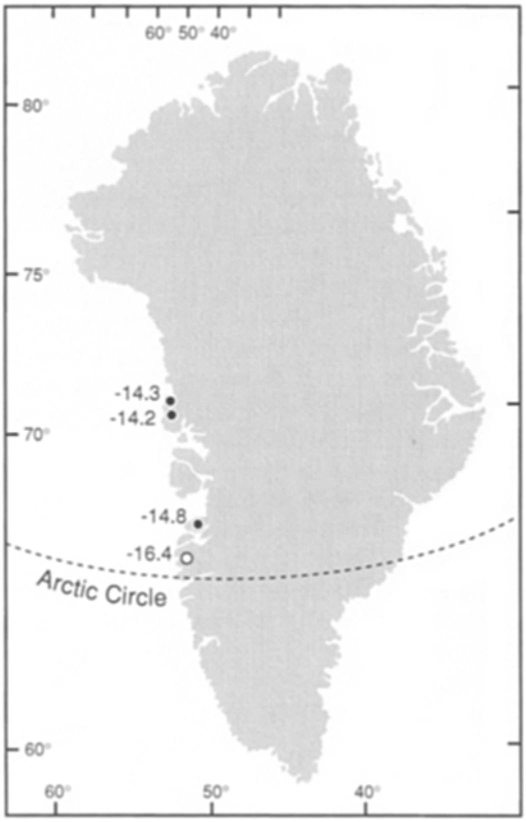

Fig. 4 $\delta^{13}C$ values for bone collagen (‰) from arctic foxes from northern Sweden

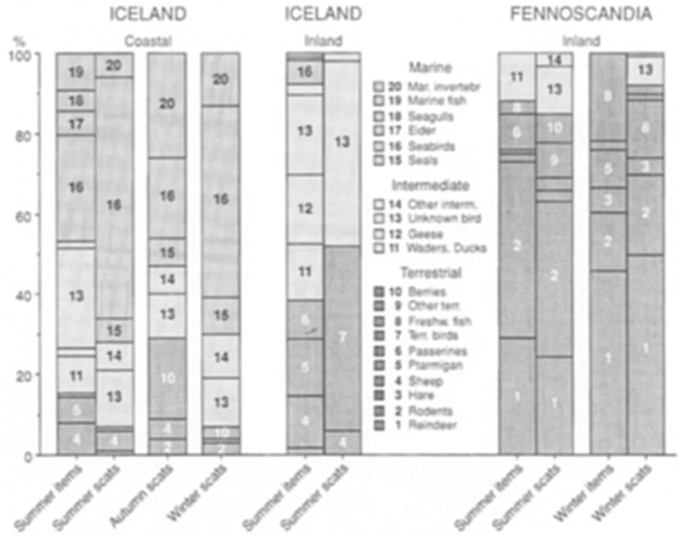

Fig. 5 $\delta^{13}C$ values for bone collagen (‰) for arctic foxes on Greenland. White and blue colour morphs are shown by *open* and *closed symbols* respectively

came from different areas (Fig. 1) and had significantly higher variance in $\delta^{13}C$ values than inland foxes from Iceland [coastal SD = 1.68, versus inland SD = 0.52; $F(7,5) = 8.78$, $P<0.05$]. When we look at the subsample from the north-west (NW) and compare its variance with the inland subsample from the south-west, we still get a higher variance in the coastal sample [coastal SD = 0.78, versus inland SD = 0.18, $F(5,2) = 18.8$, $P = 0.05$] suggesting a more diverse diet in terms of marine and terrestrial protein at coastal than at inland sites.

The subsample of coastal foxes from north-west Iceland also showed lower $\delta^{13}C$ values with age [Fig. 2, $b = -0.031$, $t(5) = -2.82$, $P<0.05$], but no such effect was detected for inland sites [$b = 0.01$, $t(5) = 1.27$, $P = 0.27$], or from the whole coastal sample [$b = -0.033$, $t(7) = -1.14$, $P = 0.30$]. This implies that the observed age effect was dietary rather than physiological. Thus, young coastal foxes had a more marine diet than older coastal foxes. However, we found no differences between the sexes for the Icelandic foxes (ANOVA: $F(1,12) = 0.59$, $P = 0.47$).

Food remains found at dens in coastal and inland Iceland are shown in Fig. 3. It is clear that the diet during summer is very different in inland and coastal Iceland. Various marine birds, such as fulmar (*Fulmarus glacialis*), guillemots, eider and seagulls, in addition to marine fish, are prominent among food remains at coastal dens in summer, while terrestrial and intermediate food types like ptarmigan, passerines and geese predominate at inland dens. The remains of lamb carcasses are found in both habitat types.

Similar data are not available for winter diet, but the results of a scat analysis in a coastal area in Iceland (Hersteinsson 1984) suggest that during winter, spring and summer around 80% of the prey items taken by coastal foxes are of marine origin. In the autumn this proportion is lower, around 50–60% (Fig. 3).

Inland foxes, however, are believed to depend heavily on ptarmigan in winter, as well as cached geese, waders and passerine birds together with eggs of different species. Sheep carcasses are also exploited in winter, as are reindeer carcasses in eastern Iceland (Hersteinsson 1984). In some inland areas of Iceland the arctic fox has access to nesting fulmars and gulls, species which are more generally associated with coastal habitats (Fig. 3).

Sweden

In Sweden, seven of eight individuals came from inland sites and showed typical terrestrial values, ranging from –20.3 to –22.2‰ (Fig. 4). The only fox closer to the coast, at a salmon-bearing river, had a value of –18.1‰, thus showing some influence of marine protein. The diet of arctic foxes in Sweden is dominated by lemmings and voles, temporarily depending on the status of the vole cycle (A. Angerbjörn, unpublished). Reindeer and birds are the second most important food items. In another area in Fennoscandia, northern Finland at an inland site (Fig. 3), food remains at dens and scats collected over a number of years showed that the fox diet consisted of reindeer and microtines followed by fresh water fish during winters (A. Kaikusalo and A. Angerbjörn, unpublished).

Greenland

Three of the four individuals from Greenland showed typical marine values of $\delta^{13}C$, –14.2 to –14.8‰ (Fig. 5). The fourth fox, the only white one, showed some influence of terrestrial protein, –16.4‰. In a study discussing summer diet on Greenland, Møller-Nielsen (1991) reported a pair of coastal foxes that lived entirely on marine fish from rock pools. Braestrup (1941) reported that the diet of coastal foxes in west Greenland included molluscs, crabs, small fishes, eiders and other birds, and seal carcasses. The diet of foxes at an inland site (Birks and Penford 1990) was dominated by reindeer during winter and spring and by insects and birds (mostly passerines) during summer.

Discussion

The arctic fox shows a spatial variation in diet which can be divided into two components, variation between habitats, and local individual variation within each habitat.

First, we found the largest variation in $\delta^{13}C$ between different areas. The inland foxes from Sweden and Iceland had typical terrestrial values (–20.4 and –21.4‰ respectively), whereas those from coastal Greenland had typical marine values (–14.9‰). The coastal foxes from Iceland on the other hand had intermediate values (–17.7‰). [The value from a sample of an Alaskan arctic fox of –20.6‰ given by Schoeninger and DeNiro (1984) must be interpreted as coming from inland Alaska.] A diet consisting of terrestrial protein only should generate $\delta^{13}C$ values of –21 to –22‰ (Schoeninger et al. 1983), while the end value for a 100% marine diet would be –12 to –13‰ (Tauber 1981). However, the protein in arctic fox diet can be of both terrestrial origin, as for reindeer (–27.7‰ muscle) or lemmings (–26.1‰ muscle, Schell and Ziemann 1988), or of marine origin as for seals (–12.3‰, Schoeninger and DeNiro 1984) and marine fish (–14.6‰, Sholto-Douglas et al. 1991). Prey species that should have intermediate $\delta^{13}C$ values are shore birds, gulls (–15.0‰, Hobson 1987), ducks (–17.6‰ for muscle, Tietje and Teer 1988), that spend their winters feeding on marine shore lines, but breed in inland areas of the Arctic.

Arctic foxes from the west coast of Greenland used only marine protein, but coastal foxes in Iceland used protein with a marine signature, such as seal carcasses and fish, protein with a mixed signature, such as seabirds and ducks, and also protein with a terrestrial signature, such as sheep and ptarmigan. There is certainly potential for the same variation in Greenland, with a division between coast-living foxes feeding on marine protein (Møller-Nielsen 1991), and inland foxes (Braestrup 1941; Birks and Penford 1990) living on terrestrial protein such as ptarmigan and reindeer.

A comparison between Sweden and inland Iceland reveals the same terrestrial isotopic signature, despite differences in diet (microtines and reindeer vs ptarmigan and sheep). To be able to distinguish between these two diets, an analysis of, for example, trace elements would be needed.

Second, the local variation in isotopic values within each habitat was noticeable for all areas. In Sweden, one fox from close to a salmon-bearing river showed the influence of marine protein. The fourth fox from Greenland, the only white fox, showed that arctic foxes also feed on terrestrial food sources in west Greenland. Further, this fits well with the observations made by Braestrup (1941) that white foxes in Greenland originate mainly in inland habitats. Although samples from inland Iceland were from different parts of the country, they showed very low variation. The available food sources with a partly marine origin in these inland areas were ducks and waders, but these prey species seem to be of minor importance according to isotopic values.

The Icelandic coastal foxes on the other hand, with a diet intermediate between terrestrial and marine food sources, had isotopic values with a higher variance, suggesting a more diverse diet than inland foxes in terms of terrestrial or marine origin of the protein. Food remains and scat analysis indicated a higher dependence on marine resources than the isotopic values, especially for some individuals. However, food remains at dens and scat analysis give biased data with respect to size of prey species, and they give no information on variance between individuals. Furthermore, they do not provide information about the diet for an individual over the longer term. This illustrates the advantage of using isotopes in dietary studies and the problems of drawing conclusions based on scat analysis or food remains alone.

A possible explanation for the higher variation in coastal areas could be that arctic foxes defend their territories against conspecific intruders (Hersteinsson and Macdonald 1982), which means that only those individuals with territories at the coastline have continuous access to food on the beach. Since these areas have a predictable renewable food resource, they are very attractive (Hersteinsson 1984). Neighbours, although close to the sea, will only have occasional opportunities to feed on marine protein at the coastline. Individual variation in diet within each habitat may thus be a function of habitat heterogeneity and territoriality.

The observation that diet becomes less marine in origin with age for the coastal subpopulation might be due to a seasonal effect. Cubs are born during late spring or early summer (Hersteinsson 1984) and the availability of marine protein is higher during spring and summer (80%) than during autumn (50–60%). Since arctic foxes reach adult size during their first summer, this marine effect should slowly be diluted with an intermediate diet with age, in accordance with our observed pattern.

In this study we used stable carbon isotopes and scat analyses to investigate individual variation in the diet of arctic foxes. The combination of the two different techniques provides the opportunity to study diet both on a short- and on a long-term scale. The analyses of $\delta^{13}C$ on an individual level demonstrate that it is possible to draw conclusions about individual variation in diet. This could be most relevant in the analysis of diet for many other species, including ancient humans.

Furthermore, we used stable carbon isotopes to reveal variation in the diet of arctic foxes from different localities. There was a very good agreement of the isotopic signature, from Sweden, Iceland, Greenland, and even Alaska, with arctic fox diet deduced from other sources. This approach also has several applications in the study of vertebrate diet. If variation is found within a fairly homogeneous habitat, this would suggest that individuals utilize resources differently. But if variation is between areas and habitats, a conservative interpretation would be that there is a difference in food availability.

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Appendix Values of δ13C (0/00) for arctic foxes from different parts of the world (*f* female, *m* male)

Location	Habitat	Age	Sex	Colour	$\delta^{13}C$ (‰)	Sample
Greenland	coast		f	blue	−14.2	a606700
Greenland	coast		f	blue	−14.3	a606971
Greenland	coast		f	blue	−14.8	a609310
Greenland	coast		m	white	−16.5	a637731
Iceland	coast	61	f	white	−21.0	2876
Iceland	coast	13	f	blue	−19.2	2923
Iceland	coast	39	m	blue	−16.6	3044
Iceland	coast	12	f	blue	−15.7	3046
Iceland	coast	12	m	blue	−16.8	3048
Iceland	coast	60	f	blue	−17.9	3050
Iceland	coast	49	m	blue	−17.6	3051
Iceland	coast	49	f	blue	−16.9	3052
Iceland	inland	8	f	blue	−21.8	2947
Iceland	inland	10	f	blue	−21.2	2962
Iceland	inland	7	m	white	−21.5	2966
Iceland	inland	38	f	white	−21.1	2979
Iceland	inland	85	m	white	−20.8	3074
Iceland	inland	11	f	white	−22.5	2856
Sweden	inland		f		−18.1	815044
Sweden	inland		m		−20.4	a795013
Sweden	inland		f		−21.4	865029
Sweden	inland	3	m		−19.3	905035
Sweden	inland	3	f		−22.2	a915018
Sweden	inland				−20.5	ma710029
Sweden	inland		f		−20.3	ma785039
Sweden	inland				−20.7	c9007

References

Alisauskas RT, Hobson KA (1993) Determination of lesser snow geese diets and winter distribution using stable isotope analysis. J Wildl Manage 57:48–54

Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. Oecologia 69:395–406

Angerbjörn A, ArvidSon B, Noren E, Strömgren L (1991) The effect of winter food on the reproduction in the arctic fox, *Alopex lagopus*: a field experiment. J Anim Ecol 60:705–714

Bada JL, Peterson RO, Schimmelmann A, Hedges REM (1990) Moose teeth as monitors of environmental isotopic parameters. Oecologia 82:102–106

Bannikov AG (1970) Arctic fox in the U.S.S.R.: biological premises of productivity. IUCN New Ser 16:121–130

Birks JDS, Penford N (1990) Observations on the ecology of arctic foxes *Alopex lagopus* in Eqalummiut Nunaat, West Greenland. Medd Grönland Biosci 32:3–27

Bocherens H, Fizet M, Mariotti A (1990) Mise en evidence alimentaire vegetarien de l'ours des cavernes (*Ursus spelaeus*) par la biogeochemie isotopique (^{13}C, ^{15}N) des vertebres fossiles. C R Acad Sci Paris Ser II 311:1279–1284

Braestrup FW (1941) A study on the arctic fox in Greenland. Medd Grön 131:1–102

Brown TA, Nelson DE, Vogel JS, Southon JR (1988) Improved collagen extraction by modified Longin method. Radiocarbon 30:171–177

Chisholm BS, Nelson DE, Schwarcz HP (1983) Marine and terrestrial protein in prehistoric diets on the British Columbia coast. Curr Anthropol 24:396–398

Collett R (1912) Mammals of Norway (in Norwegian). Aschehaug, Kristiania

DeNiro MJ, Epstein S (1978a) Influence on diet on the distribution of carbon isotopes in animals. Geochim Chosmochim Acta 42:495–506

DeNiro MJ, Epstein S (1978b) Carbon isotope evidence for different feeding patterns in two *Hyrax* species occupying the same habitat. Science 201:1906–1908

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Fay FF, Stephenson RO (1989) Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. Can J Zool 67:1989–1994

Frafjord K (1993) Food habits of Arctic foxes (*Alopex lagopus*) on the western coast of Svalbard. Arctic 46:49–54

Garrott RA, Eberhardt LE (1987) Arctic fox. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild fur bearer management and conservation in North America. Ministry of Natural Resources, Ontario, pp 394–406

Hersteinsson P (1984) The behaviourial ecology of the arctic fox (*Alopex lagopus*) in Iceland. D Phil thesis, University of Oxford

Hersteinsson P (1989) Population genetics and ecology of different colour morphs of arctic foxes *Alopex lagopus* in Iceland. Finn Game Res 46:64–78

Hersteinsson P (1992) Mammals of the Thingvallavatn area. Oikos 64:396–404

Hersteinsson P, Macdonald DW (1982) Some comparisons between red and arctic foxes, *Vulpes vulpes* and *Alopex lagopus*, as revealed by radio-tracking. Symp Zool Soc Lond 49:259–289

Hersteinsson P, Angerbjörn A, Frafjord K, Kaikusalo A (1989) The arctic fox in Fennoscandia and Iceland: management problems. Biol Conserv 49:67–81

Hobson KA (1987) Use of stable isotope analysis to estimate marine and terrestrial protein content in gull diets. Can J Zool 65:1210–1212

Kates M (1980) Techniques of lipidology; isolation, analysis and identification of lipids, 2nd edn. Elsevier, Amsterdam

Lidén K, Takahashi C, Nelson DE (1994) The effect of lipids and the use of NaOH in stable carbon isotope analysis. J Arch Sci (in press)

Macpherson AH (1969) The dynamics of Canadian arctic fox populations. Can Wildl Serv Rep Ser 8:1–49

Merwe NJ van der, Lee-Thorp JA, Thaderay JF, Hull-Martin A, Kruger FJ, Coetzees H, Bell RH, Lindeque M (1990) Source-area determination of elephant ivory by isotopic analysis. Nature 346:744–746

Møller-Nielsen S (1991) Fishing arctic foxes on a rocky island in west Greenland. In: Angerbjörn A, Hersteinsson P (eds) Arctic fox biology: abstracts from the first international arctic fox meeting. Scientifur 16:79

Østbye E, Skar H-J, Svalastog D, Westby K (1978) (in Norwegian) Arctic fox and red fox on Hardanger vidda: den ecology, distribution and population status. Medd Norsk Viltforsk 4:1–66

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Pulliainen E (1965) On the distribution and migrations of the arctic fox (*Alopex lagopus* L.) in Finland. Aquilo Ser Zool 2:35–40

Ramsay MA, Hobson KA (1991) Polar bears make little use of terrestrial food webs: evidence from stable carbon isotope analysis. Oecologia 86:598–600

Rau GH, Mearns AJ, Young DR, Olson RJ, Schafer HA, Kaplan IR (1983) Animal $^{13}C/^{12}C$ correlates with trophic levels in pelagic food webs. Ecology 64:1314–1318

Schell DM, Ziemann PJ (1988) Natural carbon isotope tracers in arctic aquatic food webs. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Springer, Berlin Heidelberg New York, pp 230–251

Schoeninger MJ, DeNiro MJ (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochim Cosmochim Acta 48:625–639

Schoeninger MJ, DeNiro MJ, Tauber H (1983) Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. Science 220:1381–1383

Sholto-Douglas AD, Field JG, James AG, Merwe NJ van der (1991) $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios in the southern Benguela ecosystem: indicators of food web relationships among different size-classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. Mar Ecol Prog Ser 78:23–31

Smith BN, Epstein S (1971) Two categories of $^{13}C/^{12}C$ ratios for higher plants. Plant Physiol 47:298–301

Tannerfeldt M, Angerbjörn A, ArvidSon B (1994) The effect of summer feeding on juvenile Arctic fox survival – a field experiment. Ecography 17:97–107

Tauber H (1981) Diet in prehistory. In: Egevang R (ed) The creative human (in Danish). National Museum, Copenhagen, pp 112–116

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissue: implications for the analysis of diet. Oecologia 57:32–37

Tietje WD, Teer JG (1988) Winter body condition of northern shovelers on freshwater and saline habitats. In: Weller M (ed) Waterfowl in winter. University of Minnesota Press, Minneapolis, pp 353–376

Vogel JC (1978) Isotopic assessment of the dietary habits of ungulates. S Afr J Sci 74:298–301

Vogel JC, Talma AS, Hall-Martin AJ, Viljoen PJ (1990) Carbon and nitrogen isotopes in elephants. S Afr J Sci 86:147–150

Welch DW, Parsons TR (1993) $\delta^{13}C$-$\delta^{15}N$ values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* ssp.). Fish Oceanogr 2:11–23