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What Can Stable Isotope Analysis of Top Predator Tissues Contribute to Monitoring of Tundra Ecosystems?

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Abstract

Understanding how climate change and increasing human impacts may exert pressure on ecosystems and threaten biodiversity requires efficient monitoring programs. Indicator species have been proposed as useful tools, and predators and their diet may be particularly suitable. The vast and remote arctic tundra represents a good case study as shifts in ecosystem states are presently occurring, and monitoring is a major challenge. Here we assess what stable isotopes reflecting the diet of the arctic fox, a widespread and highly flexible top predator, can contribute to effective monitoring of the vertebrate prey basis of Arctic tundra. We used data collected over 2–5 years from six sites in the Eurasian Arctic and Greenland. Stable isotope signatures of arctic fox winter fur reflected both spatial and temporal variability in the composition of the vertebrate prey basis. Clear contrasts were apparent in the importance of marine resources, as well as of small rodents and their multiannual density fluctuations. Some important resources could however not be separated because of confounding isotopic signatures. Moreover, except for preferred prey, the proportions of prey in the diet may not necessarily reflect the relative importance of species in the community of available prey. Knowing these limitations, we suggest that the arctic fox diet as inferred from stable isotopes could serve as one of several key targets in ecosystem-based monitoring programs.

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Introduction

Climate change and increasing human impacts in most parts of the world exert pressures on ecosystems and threaten biodiversity. Understanding ongoing ecosystem changes and meeting the requirements of national and international conventions require efficient monitoring programs (Yoccoz 2012). Thorough studies quantitatively assessing all relevant components of ecosystems or communities can however be very resource demanding, and extremely difficult to carry out in remote areas. In such cases, the use of indicator species may be a realistic and efficient alternative (Jorgensen and others 2013). An indicator species is an organism whose characteristics such as presence, population density, reproduction, dispersion, or diet can be used as an index of attributes too difficult, inconvenient or expensive to measure for other species, processes, or environmental conditions of interest (Landres and others 1988). To be useful, an indicator should capture the complexities of the system or process it is meant to indicate, yet remain simple enough to be easily and routinely monitored (Cairns and others 1993). Predators have often been suggested as good ecological indicators owing to their position at the top of food webs and considerable evidence supports such applications (Sergio and others 2008). Thus, a lot of work has been devoted to establishing sea birds as indicators for the state of the marine ecosystem (Piatt and others 2007; Durant and others 2009). Predators may also be particularly sensitive to climate-induced ecosystem transformations (Voigt and others 2003; Springer and others 2007). Over the last decades, concerns about the use of indicators in ecological monitoring have however repeatedly been expressed and thorough quantitative validation of the relationship between the indicator and what is indicated has been called for (Cairns and others 1993; Simberloff 1998; Sergio and others 2008; Durant and others 2009; Gremillet and Charmantier 2010; Jorgensen and others 2013). Here we use an extensive data set to investigate to what extent stable isotope composition of the fur of arctic fox *Vulpes lagopus*, a medium-sized top predator, can be used as an indicator contributing to effective monitoring of Arctic tundra ecosystems.

Stable isotope ratios of predator tissues reflect the resources assimilated over a certain period and provide thus time integrated insights into trophic relationships (Inger and Bearhop 2008; Ben-David and Flaherty 2012; Layman and others 2012). They allow assessing differences in resource use between populations or individuals, as well as temporal changes in dietary composition (for example, Darimont and others 2009; Tarroux and others 2012) and have thus been used for a wide variety of applications in trophic ecology (Layman and others 2012). As potential indicator, we expect stable isotope data of a top predator to reflect the diet of the focal species in a certain food web context, as well as possible dietary shifts. This approach will indicate the presence of prey resources used, given that these prey have a distinct isotopic signature (Layman and others 2012). Without additional knowledge about the trophic ecology of the focal species it will, however, not allow inferring whether a potential prey species which is not consumed is rare/absent or just less preferred among the assemblage of prey available in the context of the specific ecosystem.

In the Arctic, climate change is more rapid than in other regions of the world and has already observable effects on terrestrial ecosystems (Gilg and others 2012; Ims and others 2013a). Changes in winter climate and snow conditions may result in dampening or loss of the multiannual high amplitude lemmings cycles (Ims and others 2008, 2011; Kausrud and others 2008; Gilg and others 2009; Korpela and others 2013) or changed dynamics of other arctic herbivores (Hansen and others 2013). As lemmings play a key role in the tundra ecosystem, both as herbivores and as main prey for a whole guild of predators (Krebs 2011), these changes may have far reaching consequences. The absence of periodic peak years is particularly detrimental for specialized predators such as snowy owls *Bubo scandiaca* or skuas *Stercorarius* spp. (Schmidt and others 2012). Moreover, as predators switch to other prey when small rodents are rare (Bety and others 2002), a fading out of the cycles can affect ground nesting birds such as geese and waders (Gilg and Yoccoz 2010; Nolet and others 2013). In the low Arctic, the small rodent community usually also comprises several species of voles (*Microtus* and *Myodes* spp.) (Dunaeva 1948; Batzli and Henttonen 1990). These species may be less sensitive than lemmings to changes in winter climate (Ims and others 2011), but food webs where they dominate differ from the typically Arctic ones (Elmhagen and others 2002; Ims and Fuglei 2005). Changes in the extent and duration of sea ice affect the climate and vegetation of coastal tundra (Post and others 2013), and are also

likely to modify the access to marine resources constituting an important source of subsidies for terrestrial arctic predators (Gauthier and others 2011). All these changes are characterized by strong spatial heterogeneity due to spatial variation in many of the underlying processes as well as in the climate itself (Ims and others 2013a). Moreover, regionally important biotic and anthropogenic drivers interact with these climate-induced processes. For instance, goose populations have increased dramatically in some areas mostly due to improved feeding conditions in wintering areas (Jefferies and Drent 2006). In northern Fennoscandia, growing populations of semi-domestic reindeer have created additional resource subsidies for predators in winter in the form of reindeer carcasses, which lead to an increase in predator numbers, in particular generalist species (Henden and others 2014). Considering ongoing changes in the Arctic and the dramatic and possibly unexpected developments in the near future with further climate change, the recent Arctic Biodiversity Assessment concluded that monitoring across circumpolar areas must be developed (Meltofte and others 2013), and first steps toward the alignment of monitoring efforts in the Arctic have been taken, for instance, through the development of the Circumpolar Biodiversity Monitoring Program (Ferguson and others 2012; Christensen and others 2013; Ims and others 2013b).

The arctic fox, the only terrestrial mammalian predator endemic to the Arctic, has been chosen as one of 10 climate change flagship species by IUCN (Sillero-Zubiri and Angerbjörn 2009) to ''highlight climate change's disruptive effects on interactions between species.'' It is a widespread species with a circumpolar distribution in tundra areas, including most arctic islands. Except in northern Fennoscandia, where it is critically endangered, the arctic fox is a common species (Angerbjørn and others 2008). It has both been found to impact (Croll and others 2005) and be impacted (Killengreen and others 2007) by the state of tundra ecosystems. It has been characterized as an opportunistic specialist because it preys preferentially on small rodents, in particular lemmings (*Lemmus* and *Dicrostonyx* spp.), but can use other terrestrial or marine resources when small rodents are scarce (Elmhagen and others 2000; Giroux and others 2012; Tarroux and others 2012). Arctic fox reproduction has been used as a proxy for small rodent dynamics in Sweden (Elmhagen and others 2011), but arctic foxes occur also in areas where small rodents are absent, such as on the high arctic Svalbard archipelago (Fuglei and others 2003; Eide and others 2004) or on Kolguev Island (Angerbjorn and others 1999). Given the wide distribution of this species, its relative commonness and specific prey preferences combined with large dietary flexibility, we hypothesize that the diet of the arctic fox as inferred from stable isotope analysis could be used as a ''blue print'' of the state of the prey basis in vertebrate tundra food webs.

Here we specifically ask what can be inferred from stable isotope data of arctic foxes and their prey and how this information is related to important spatio-temporal variability in the structure of the tundra food web. Major aspects of spatial variation are the role of marine subsidies, terrestrial subsidies such as ungulate carrion, and the presence and composition of the small rodent community and other potential prey species such as ptarmigan, geese, and hare. Temporal variation has both a short-term and a long-term component. The short-term component is governed by the lemming cycles with resource peaks every 3–5 years or reindeer carrion peaking during severe winters (Hansen and others 2013). The long-term component represents trends of change over decades such a retreating sea ice (Post and others 2013) or steadily increasing populations of geese (Jefferies and Drent 2006). To qualify as a useful indicator the isotope signatures of arctic fox should reflect most of this variability in a predictable manner. Therefore, we also discuss which of these aspects are poorly reflected by the stable isotope approach and why.

Materials and Methods

Study Sites

This study was initiated by the International Polar Year project *Arctic predators* (2007–2010; Ehrich and others 2011) which established collaborations between Norwegian and Russian tundra monitoring sites as well as with other monitoring programs in the Arctic. Six study sites were chosen to cover important variability in the tundra ecosystem and for their contrasting food web structures known from previous monitoring. The sites represented most of the bioclimatic subzones of the Arctic (Walker and others 2005) from the high arctic Svalbard archipelago in subzone A and B to Varanger Peninsula (hereafter Varanger), which lays at the border of subzone E to subarctic birch forest and mountain tundra (Figure 1; Table 1). The sites also covered a gradient in vegetation types from high arctic tundra dominated by herbs, prostrate dwarf shrubs, rushes, and cryptogams to the lush

shrub tundra of the low Arctic (Walker and others 2005). Longitudinally the sites were spread over the whole Eurasian Arctic from Wrangel Island (hereafter Wrangel) in the east to Svalbard in the west, and included Zackenberg on eastern Greenland. The climate was thus characterized by different degrees of continentality from the very oceanic Svalbard to more continental sites located in Russia.

Arctic foxes are present at all sites and common at five of them. They are rare in Varanger as elsewhere in Fennoscandia. The food web at the different sites differed considerably with regards to small rodent assemblages, multiannual dynamics, availability of other terrestrial resources, and access to marine subsidies (Table 1). On Wrangel and at Mys Vostochny on western Taimyr (hereafter Taimyr) two species of lemmings (see Table 1 for scientific species names) exhibit population cycles with characteristic peak years, although some recent changes in the dynamics have been recorded. On Wrangel, the cycle period has increased from 5 years in the 1980s to nearly 8 years in the 1990s and 2000s, but high peak densities are still observed (Menyushina and others 2012). On Taimyr, peak years were still observed in the 2000s, but with some 3-year cycles not developing into lemming peaks (Feige and others 2012; Nolet and others 2013). On Varanger, the small rodent community consists of lemmings and voles. The voles exhibit regular 4–5 years cycles (Ims and others 2011), and lemmings reached peak densities in 2007 and in 2010–2011 (Killengreen and others 2013). At the low arctic Erkuta tundra monitoring site on southern Yamal (hereafter Yamal) the small rodent

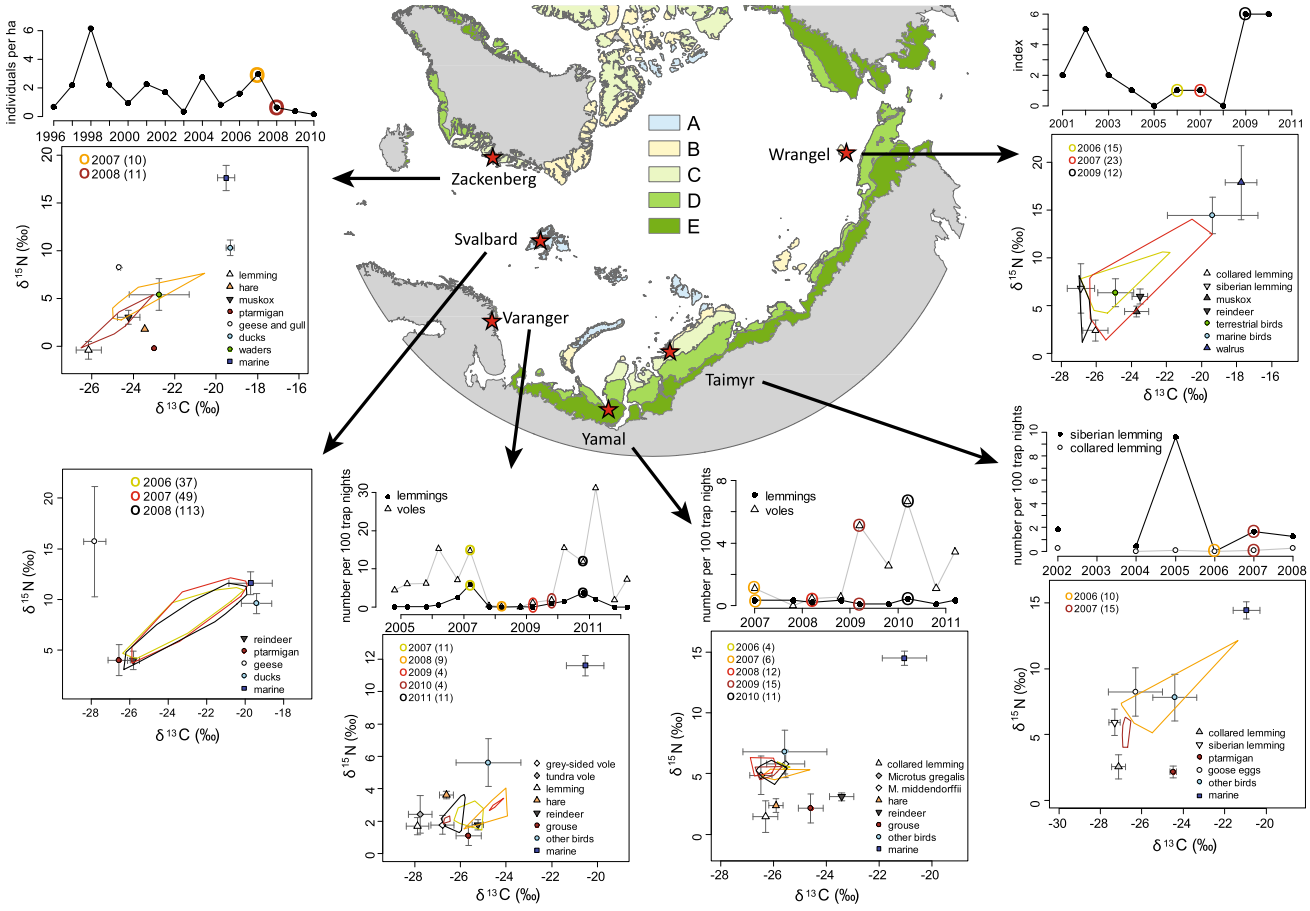

Figure 1. Map with the six study sites. For each study site, stable isotope signatures of arctic fox fur collected in summer are shown on isotopic biplots for carbon (*x*-axis) and nitrogen (*y*-axis). *Colors* indicate samples from different years, and minimum spanning polygons surround the samples from each year. Sample sizes for each year are given in *parenthesis* in the legend of the figures. The arctic fox isotope values have been corrected for discrimination according to the average factor determined by Lecomte and others (2011). Stable isotope signatures of main prey groups are shown as means with standard deviation. Small rodent dynamics for the years of sample collection are presented for five of the study sites; small rodents are lacking on Svalbard.

Table 1. Ecosystem Characteristics of the Six Study Sites

Site	Bioclimatic subzone	Lemmings	voles	Other terrestrial resources	Marine resources and sea ice	References
Wrangel 71.3°N, 180°E	B	***Dicrostonyx vinogradovii*** and ***Lemmus sibiricus portenkoi***	–	Snow geese colony *Anser caerulescens*, waders, carrion of reindeer *Rangifer tarandus* and muskox *Ovibos moschatus*	Stable sea ice cover, presence of polar bears and seals, as well as sea birds	Menyushina and others (2012)
Taimyr 74.1°N, 86.7°E	C	*Dicrostonyx torquatus* and ***Lemmus sibiricus***	–	Geese *Anser albifrons* and *Branta bernicla*, waders, rock ptarmigan *Lagopus muta*, passerines (reindeer and hare *Lepus timidus* are rare)	Stable sea ice cover, presence of polar bears and seals	De Raad and others (2011), Nolet and others (2013)
Yamal 68.2°N, 69.1°E	E	*Dicrostonyx torquatus* and *Lemmus sibiricus*	***Microtus middendorffii***, ***Microtus gregalis***	Hare, willow ptarmigan *Lagopus lagopus*, waterfowl (ducks and geese), waders, passerine, carrion of domestic reindeer	Closest sea is the narrow Baidaratskaya Bay. Stable sea ice cover	Ehrich and others (2012), Sokolov and others (2012), Sokolova and others (2014)
Varanger 70.5°N, 29.5°E	E-subarctic	***Lemmus lemmus***	***Microtus oeconomus***, ***Myodes rufocanus***	Willow ptarmigan, rock ptarmigan, waterfowl, waders, passerine, geese, hare – all at rather low densities; carrion of semi-domestic reindeer	No sea ice	Ims and others (2013b), Killengreen and others (2013)
Svalbard 78°N, 16°E	A–B	small local population of introduced *Microtus levis*	–	Rock ptarmigan, geese *Anser brachyrhynchus* and *Branta leucopsis*, reindeer carrion	Strong year to year variability in extent and stability of sea ice. Presence of polar bears and seals. Sea bird colonies	Fuglei and others (2003), Eide and others (2012), Hansen and others (2013)
Zackenberg 74.5°N, 21°W	C	***Dicrostonyx groenlandicus***	–	Rock ptarmigan, arctic hare *Lepus arcticus*, waders, geese *Branta leucopsis and Anser brachyrhynchus*, carrion of muskox	Stable sea ice cover. Presence of seals and polar bears	Meltofte and others (2008), Schmidt and others (2012)

For small rodents, the dominant species in the community are indicated in bold.

community is dominated by two species of voles (Sokolova and others 2014). Lemmings of both genera are present, but their abundance has been very low for more than a decade. The voles exhibit multiannual density fluctuations of moderate amplitude. At Zackenberg, collared lemming is the only species of small rodents (Schmidt and others 2008). Previously populations were cyclic, however, without reaching very high densities, but recently the cycles have collapsed and populations have remained at low densities during more than a decade (Schmidt and others 2012). On Svalbard, small rodents are absent from the autochthonous fauna altogether. Species and abundances of other terrestrial prey such as waterfowl, ptarmigan, hare, and ungulates also vary considerably. On Wrangel, there is a large colony of snow geese, but ptarmigan and hare are absent, whereas the two latter species are abundant at Erkuta, and present in lower numbers in Taimyr, Zackenberg, and Varanger. Reindeer and/or muskox, whose carcasses can provide important resources for foxes (Fuglei and others 2003; Eide and others 2004; Killengreen and others 2011) are present at all sites, but at very different densities. Access to marine resources varies also considerably between sites.

Sample Collection and Laboratory Analyses

Samples of arctic fox winter fur were primarily collected in the entrances of dens during den surveys in summer (June–August). The fur shed in spring reflects the diet during the period when the foxes were molting to winter fur during early fall of the previous year. All fur samples from dens were examined under a microscope to confirm that they were from arctic foxes. A few winter fur samples were found independently of dens or collected from carcasses. Samples from Svalbard were obtained from foxes collected from trappers in the frame of a monitoring program of the Norwegian Polar Institute (trapped between December and March).

We collected muscle samples of most potential prey for arctic foxes at each site. As an opportunistic predator, arctic fox can feed on a wide variety of resources (Hersteinsson and Macdonald 1996; Elmhagen and others 2002; Eide and others 2005; Shtro 2009; Goltsman and others 2011). Potential prey included thus all species of small rodents, medium-sized terrestrial mammals such as hare, large herbivores such as reindeer and muskox, birds, as well as marine resources including mammals, birds, and a few fish. For birds (sea birds, waterfowl, ptarmigan, waders, and passerines) both muscle and eggs were collected as arctic foxes cache eggs and use them later in the year, making eggs a possible resource at the end of the summer (Samelius and others 2007; Careau and others 2008). Stable isotope data for prey from Taimyr and partly from Varanger have been published previously in Feige and others (2012) and Killengreen and others (2011), respectively. Samples of small rodents were obtained from snap-trapping carried out in the frame of a monitoring program or specifically for the purpose of this study (Wrangel). Samples of other species were largely obtained opportunistically, for instance, from prey remains found on dens or on raptor nests, or from carcasses. Some samples were obtained from local hunters. All prey samples were collected in summer—close to the time when the winter fur of the arctic foxes has been growing. Samples were stored and analyzed for stable isotope composition according to standard methods as described in Appendix.

Data Analysis

All analyses were carried out in R version 2.15.2 (R Core Team 2013). The year to year variation in arctic fox isotope signatures was assessed graphically by plotting individual values for each year and sites. Values were corrected for isotopic discrimination—the difference in isotope ratios between consumer tissue and resource resulting from different metabolic rates of the isotopes—according to the average discrimination factors determined for arctic fox by Lecomte and others (2011). Mean signatures for the main prey groups were included as reference on the plots. As samples of marine resources were not available for Taimyr and Varanger, we used samples from other places in the same region, that is, the Barents Sea (Svalbard) and the Kara Sea (Yamal), respectively. A few outliers were excluded (see Appendix for details on prey signature averaging).

To explicitly relate the observed changes in fox isotopic values to changes in diet, we used stable isotope mixing models as implemented in a Bayesian framework in the R package Stable Isotope Analysis in R (SIAR) version 4.2 (Parnell and others 2010). Mixing models allow estimating the proportional contribution of sources to a mixture and thus the proportion of different resources in the diet of a consumer. The performance of mixing models improves when the prey isotopic signatures are sufficiently different from each other (Layman and others 2012). Therefore, prey species for each site were visually assembled into 3–5 groups, aiming at minimizing overlap in isotopic signature among groups (avoiding usually overlap in ±1 standard

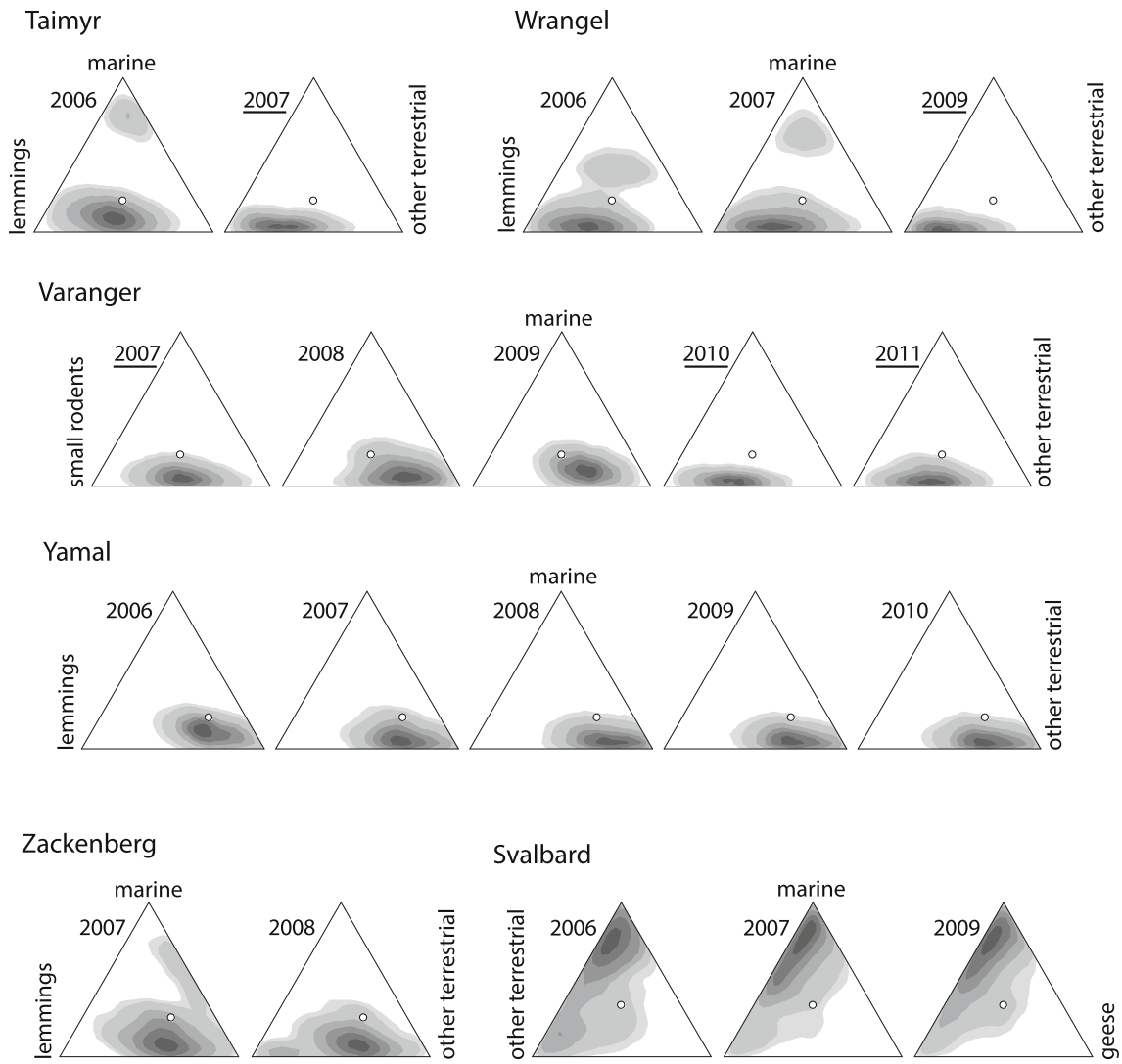

Figure 2. Year to year fluctuations in the diet of arctic foxes at six study sites. Lemming years are *underlined*. The plots show the proportion of three resource categories in the diet as posterior probability kernels which represent both individual variability and uncertainty resulting from the MCMC estimation. *Gray shades* indicate 10, 30, 50, 70, 90, and 95% posterior probability intervals, respectively, and *white circles* in the center indicate the prior with equal contributions of sources used in SIAR. For Taimyr and Wrangel, lemmings include both siberian lemmings and collared lemmings, whereas other species include all birds on Taimyr and ungulates and birds with terrestrial signatures on Wrangel. For Varanger, small rodents include norwegian lemmings, gray-sided voles and tundra voles, and other terrestrial includes birds and reindeer. For Yamal, lemmings refer to collared lemmings and other terrestrial includes voles, birds, and reindeer. At Zackenberg, lemmings refer to collared lemmings and other terrestrial to birds, muskox, and arctic hare. For Svalbard, other terrestrial refers to reindeer and rock ptarmigan (see Supplementary Material for details about prey species and grouping).

deviation intervals) as well as making groups that correspond to ecological entities such as, for instance, birds or large herbivores. We tried also as far as possible to keep lemmings as a separate group (see Appendix for groupings at each site). Using SIAR, we estimated diet proportions for each individual fox (function siarsolomcmcv4) using 1,200,000 MCMC replicates (the first 200,000 were discarded as burn in and every 1,000th replicate was saved to estimate posterior probability distributions). We used equal proportion of resources in the diet as priors, because we did not have site-specific, meaningful estimates of resource availability to create informative priors. The posterior distributions from the individual foxes were merged. Therefore, the width of the posterior distributions reflects both

the uncertainty resulting from the estimation of the individual diets and the variation between the different individuals. To make the results more comparable among sites and provide a visual summary of the suggested arctic fox diet indicator, dietary proportions were summarized on triangle plots to illustrate the shift in diet from lemmings/small rodents to terrestrial or marine alternative prey. When more than three sources were used in the mixing model, resulting proportions belonging to one side of the triangle, such as two different groups of terrestrial alternative prey, were summed.

To assess changes in the width of the trophic niche of the arctic foxes at each site, we estimated the size of the isotopic niche, which represents a proxy of the trophic niche (Newsome and others 2007). Isotopic niche width was estimated for each year and site as the size of Bayesian ellipses using SIAR (function siber.ellipses with default values) (Jackson and others 2011).

Results

In total, stable isotope signatures from 381 arctic fox samples and 711 prey specimens belonging to 78 species were obtained. Our sampling resulted in a good coverage of most potential prey species at most sites (Appendix Table S1). Although the relative positions of prey species in the isotopic space were rather constant, there were clear differences in the signatures of certain species among sites. Figure 1 shows the arctic fox signatures at each site for the different years together with signatures of main prey groups and small rodent abundance indices. Spatial variability in the vertebrate prey basis was clearly reflected in the arctic fox stable isotope data. Thus, marine resources, such as sea birds or marine mammals, were used extensively on Svalbard, and in years of low lemming densities this was also the case in Taimyr and Wrangel. Differences in the use of other resources were less apparent. Short-term temporal variation resulting from the small rodent cycle resulted in clear shifts in stable isotope signatures in Wrangel and Taimyr, the high Arctic sites where lemming populations are cyclic. In Taimyr, lemming numbers were low in 2006 but increased in fall 2007 to reach a peak with obviously high densities under the snow in late winter 2008, which was not reflected in the trapping data because trapping was carried out in summer (2–18 July) after the lemmings had crashed in spring 2008 (Feige and others 2012). The increase in density in fall 2007 was apparently sufficient for lemmings to dominate the diet of the foxes in late summer that year; therefore we refer to 2007 as a lemming year in the following, although it was not a proper peak year. In Varanger, the isotope signatures indicated a trophic position combining several terrestrial resources for the first lemming peak year in 2007. In 2010–2011, the high lemming abundance was more clearly reflected in the stable isotope signatures by a shift to lower δ^{13}C values. The position of the fox signatures from Varanger did not, however, indicate an equally strong dominance of lemmings in the diet as in Wrangel or Taimyr. At Zackenberg, lemmings exhibited only low amplitude fluctuations (Schmidt and others 2012), and these small fluctuations were not reflected by the arctic fox isotope signatures. The apparent shift of the arctic fox signatures toward lemmings in 2008 (Figure 1), the year with lower lemming abundance, was mainly due to a single fox with low δ^{13}C and δ^{15}N in that year. In Yamal, where vole cycles had low amplitude and collared lemming densities were stable and low, arctic fox signatures varied little over the years. They were also temporally stable in Svalbard, where foxes cannot include small rodents in their diet, but the availability of other terrestrial resources such as reindeer carcasses may vary from year to year.

Resource use inferred from mixing model analyses showed patterns that were largely similar to those inferred from the plots of isotopic signatures (Figure 2; posterior distributions of the dietary proportions for all sources as estimated using SIAR are presented in Appendix Figure S1). Where lemming populations were fluctuating, the proportion of lemmings was higher in lemming years whereas the proportion of alternative resources, both terrestrial and marine, increased in low years (Taimyr, Wrangel, and Varanger). In sites with more stable small rodent populations (Zackenberg, Yamal) and in Svalbard, the diet composition of the arctic fox remained more stable over the years. Marine resources dominated in Svalbard in all years, whereas their use was temporally variable in Taimyr and Wrangel, and of little importance at the three other sites, where alternative terrestrial preys were more important. In Varanger, the proportion of birds (excluding ptarmigan) increased in low rodent years, but the proportion of reindeer and ptarmigan was inferred to be rather high in all years. Because of similar isotope values, neither proportions of reindeer or ptarmigan nor proportions of Norwegian lemmings or tundra voles could be estimated separately at this site (Appendix Figure S1, Appendix). However, as ptarmigan numbers are at present low in Varanger (Henden and others 2011; Ehrich and others 2012), it is likely

that this result reflects mostly the importance of reindeer carcasses in the diet. The diet of arctic foxes from Yamal was inferred to be dominated by voles and birds, which could not be separated because of large overlap in isotope values, whereas reindeer and willow ptarmigan were less important (Appendix Figure S1). Note that hares in Yamal had isotope values that could not be separated from collared lemmings and were therefore excluded from the mixing model analysis (Appendix: Supplementary methods 2, Yamal). The distributions of posterior probabilities, which reflect both the estimation uncertainty and the variation between individuals in the population, indicate that all temporal shifts in population dietary proportions were small (mostly overlapping 75% posterior probability intervals—PPI). The choices made when grouping prey into categories did influence the results somewhat, in particular because of the prior of equal contributions of all sources used throughout. General trends as described above where however apparent in all analyses.

The size of the isotopic niche, used as a proxy for the trophic niche, varied considerably among years in Taimyr and Wrangel, but less so at the other sites (Appendix Figure S2). The 95% PPI for the niche size in 2006 and 2007 did not overlap in Taimyr and the same was the case for 2007 and 2009 in Wrangel. In these sites, the niche was thus significantly smaller in years with moderate to high abundance of lemmings. This result corresponds to the expectations based on the ecology of the arctic fox as an opportunistic specialist, behaving as a lemming specialist in such years and as a generalist in lemming trough years. In Varanger, where two lemming peaks occurred during the study period, the relation of niche size of the foxes to lemming abundance was not as clear, as the largest niche was estimated in 2010 (a year with high lemming abundance in fall; Figure 1), but 75% PPI were overlapping. The absolute size of the isotopic niche cannot be compared between the sites as it depends on the signatures of the different prey species.

Discussion

The present study is based on internationally coordinated sampling of a top predator, the arctic fox, and its potential resources in the same biome, but across highly contrasting ecosystems states. This gave us a unique possibility to assess which components of the structure of the food web were reflected by predator stable isotopes and to what extent such data could contribute to monitoring programs as an indicator. We found that stable isotope signatures of arctic fox winter fur reflected both spatial and temporal variability in the prey basis of this predator across the circumpolar Arctic. Clear spatial contrasts were apparent in the importance of marine resources, which dominated the diet of the arctic fox on Svalbard, were used as alternative resources on Taimyr and on Wrangel, but had little importance in the three other sites, even though these localities were situated near the coastline. The results also suggested that the importance of terrestrial resources such as ungulate carcasses and birds varied among sites. Moreover, there was clear spatial variability in the short-term temporal dynamics of the stable isotope signatures, as well as of inferred resource use and isotopic niche width. This variability corresponded to a large extent to what we expected based on observed small rodent community composition and dynamics, and knowledge of the dietary preferences of arctic foxes. Thus, in lemming years in high arctic ecosystems (Taimyr and Wrangel) foxes fed mainly on lemmings, whereas in years with low lemming numbers their isotopic niche was larger and indicated a switch to a variety of terrestrial and marine alternative prey. Also in low arctic/alpine Varanger the arctic fox signatures followed the small rodent cycle to some extent, but not as clearly as in the high Arctic. In Svalbard, where small rodents are absent, and in Zackenberg, where the lemming cycles have faded out, there were as expected almost no changes in fox diet among years. Although not directly assessed by our study, our results make it likely that important long-term temporal trends of change as observed in the tundra food web (for example, fading out of lemming cycles, or major changes in the abundance or distribution of species; Ims and others 2013a) would also be reflected by the stable isotope data.

To a certain extent we can thus conclude that the stable isotope signatures of arctic fox fur do reflect large scale spatial variation and year to year fluctuations in the resources available to this predator. Several important aspects of this variation are, however, not well reflected by our approach. These limitations are related on the one hand to technical limitations of stable isotope analysis and on the other hand to the trophic ecology of predators, notably the context dependent variability of their dietary preferences.

A major limitation of stable isotope analysis is that this approach only reflects changes in resource use among resources which have distinct isotopic signatures (Newsome and others 2007). In our dataset, this clearly hampers the possibility to infer ecologically important changes in the diet of arctic

foxes. Thus, in Yamal the signatures of hares and collared lemmings overlap to a large extent, as do the signatures of *Microtus* voles with those of passerine birds and waders. A possible diet shift from lemmings and voles to alternative prey could thus go undetected, if the foxes switch to hares or waders and passerines, respectively. The observed stability at this site may thus reflect stability in food web composition and resource use, or undetected switching between prey with identical signatures. A similar confounding of prey species was observed in Varanger and on Svalbard for ptarmigan and reindeer, limiting inference regarding the extent to which arctic foxes benefit from reindeer carcasses—an important question for future management in Varanger (Killengreen and others 2013). Data from an additional isotope may have solved some of the problems encountered with confounded prey signatures, and could have increased the precision of dietary proportions estimated by the mixing model. Sulfur is another element which is used in dietary studies, but results from a few recent studies indicate that it is unlikely that including δ^{34}S would have solved the problems in our study system. Values of δ^{34}S clearly distinguish marine resources from terrestrial and freshwater resources (Richards and others 2003; Touzeau and others 2014). The difference between marine and terrestrial prey is already well characterized by δ^{13}C in our system and the role of freshwater resources for arctic foxes is minor. Moreover, δ^{34}S signatures of terrestrial herbivores tend to exhibit large intraspecific variability and little distinction between species (Sayle and others 2013; Resano-Mayor and others 2014; Touzeau and others 2014) making it unlikely that they will increase resolution among the different herbivores in tundra ecosystems.

The variability in isotopic discrimination factors represents another important source of inexactitude when inferring diet from stable isotope data (Galvan and others 2012). Lecomte and others (2011) showed that there can be large differences in the magnitude of discrimination within a single captive arctic fox population, and that discrimination can depend on the type of resource used. In wild animals from a large geographic area, it is likely that differences in discrimination factors are at least as large. In our data, the discrimination factors of Lecomte and others (2011) may not have been appropriate for Varanger, where the arctic fox signatures appear less depleted in δ^{13}C than their potential prey in all years (Figure 1) although we were careful in adjusting both the spatial and temporal distribution of prey sampling (Appendix: Supplementary methods 2, Varanger). Even assuming that reindeer and possibly ptarmigan play a more important role in the diet of this population than previously assumed (Elmhagen and others 2002), as indicated by the stable isotope mixture analysis, the arctic fox signatures seem misplaced relative to the prey signatures (Figure 1) lowering confidence in the diet inference for this site.

Assuming that stable isotopes would provide an accurate picture of the spatio-temporal variability of the arctic fox diet, how would this information be related to prey availability at the respective sites? Our results suggest that knowledge of the arctic fox diet faithfully reflects the multiannual fluctuations in lemming populations. As it is known that arctic foxes behave as lemming specialists when lemmings are available (Elmhagen and others 2000), their diet reliably reflects changes in this key component of the food web. Lemming cycles of the amplitude of those clearly reflected in our data (Taimyr, Wrangel, Varanger) are however a conspicuous phenomenon, which an informed visitor to a tundra site would usually be able to record during a short stay without having to resort to analyses of arctic fox fur.

The arctic fox diet reflects also to a certain extent the presence of other potential prey species at each site. But the use of alternative prey is much more variable between sites, and depends both on the availability of these resources and the relative dietary preferences of the predator in the respective food web context. Although a consumed prey must be present, prey that is not consumed can either be rare/absent or not preferred in the specific context. The realized diet depends also on the accessibility of the resources, which may be affected, for instance, by competitors, as is the case for reindeer carcasses in Varanger, which are used mainly by the competitively dominant red fox (Hamel and others 2013). These complex interactions in the food web make it difficult to have a robust and stable relationship between diet as an indicator and the available prey assemblage it should indicate. A similar difficulty in the application of ecological indicator species has been highlighted for seabirds by Gremillet and Charmantier (2010), who show how shifts in the plastic responses of seabirds to environmental change limit their usefulness as indicators. Consequently, it is not clear whether the diet of a specialist or a generalist predator would provide a better indicator. An indicator based on the diet of a specialist is likely to have a narrow focus. A perfect generalist consuming resources proportionally to

their availability would indeed reflect the state of the prey community, but this is probably rare. In real food webs multiple interactions and individually variable nonlinear responses are likely to complicate the relationship between prey community and diet.

Although stable isotope data of arctic fox fur reflect several important aspects of prey availability in the vertebrate tundra food web, there are limitations that are cumulated because the approach consists of two levels of indirect inference. Altogether we show that this approach may provide a useful contribution to monitoring of the state of tundra food webs when taking into account what it reflects and what not. It could be integrated as one variable into a set of state variables (Lindenmayer and Likens 2011) chosen according to model-based derivation of the most likely process-relations between state variables in the system to be monitored (Ims and others 2013b). Several state variables representing the demographic and trophic dynamics of the arctic fox should be an integral part of such a monitoring scheme for changes in the tundra food web, as arctic foxes are one of the prominent arctic predators with important functions in the ecosystem. In addition, as Gremillet and Charmantier (2010) recently concluded for seabirds, arctic foxes could also be used as sentinel or flagship species capable of attracting the attention of the public or politicians to important transitions in the tundra ecosystem, such as the fading out of lemming cycles, loss of marine subsidies to the terrestrial food web, or influx of new competitively dominant predators that restrict arctic fox resource use.

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