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Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice

Abstract Consumption of marine foods by terrestrial predators can lead to increased predator densities, potentially impacting their terrestrial resources. For arctic foxes (*Alopex lagopus*), access to such marine foods in winter depends on sea ice, which is threatened by global climate change. To quantify the importance of marine foods (seal carrion and seal pups) and document temporal variation in arctic fox diet I measured the ratios of the stable isotopes of carbon ($^{13}C/^{12}C$) in hair of arctic foxes near Cape Churchill, Manitoba, from 1994 to 1997. These hair samples were compared to the stable carbon isotope ratios of several prey species. Isotopic differences between seasonally dimorphic pelage types indicated a diet with a greater marine content in winter when sea ice provided access to seal carrion. Annual variation in arctic fox diet in both summer and winter was correlated with lemming abundance. Marine food sources became much more important in winters with low lemming populations, accounting for nearly half of the winter protein intake following a lemming decline. Potential alternative summer foods with isotopic signatures differing from lemmings included goose eggs and caribou, but these were unavailable in winter. Reliance on marine food sources in winter during periods of low lemming density demonstrates the importance of the sea ice as a potential habitat for this arctic fox population and suggests that a continued decline in sea ice extent will disrupt an important link between the marine and terrestrial ecosystems.

Keywords Carbon-13 · *Alopex lagopus* · Scavenging · Stable isotope ratios

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Introduction

Many terrestrial predators forage on marine-based foods. Several canid species, for example, scavenge carcasses of marine mammals that wash onto land (Avery et al. 1987; Zabel and Taggert 1989; Rose and Polis 1998), and seabirds, mustelids, bears, and wolves may feed extensively on salmon or other marine-based fish (Hobson 1987; Ben-David et al 1997; Hilderbrand et al. 1999; Szepanski et al. 1999). This transfer of energy between ecosystems can support large numbers of primary and secondary consumers (invertebrates as well as vertebrate predators), and can lead to substantial enrichment of terrestrial primary producers (Polis and Hurd 1996; Ben-David et al 1998; Rose and Polis 1998; Anderson and Polis 1999). Thus, marine-based resources can profoundly affect the interactions among species in terrestrial food webs (Polis et al. 1997).

Arctic foxes (*Alopex lagopus*) also exploit both terrestrial and marine environments (Angerbjörn et al. 1994). Lemmings (*Dicrostonyx* and *Lemmus* spp.), which are known for their cyclic population dynamics, are the primary terrestrial prey of arctic foxes over much of their range (Chesemore 1968b; Macpherson 1969; Angerbjörn et al. 1995; Elmhagen et al. 2000). The dramatic cycles in lemming populations are often reflected in the population dynamics of arctic foxes and can have a large effect on the use of alternative foods, such as migratory birds and their eggs, by arctic foxes (Summers 1986; Greenwood 1987; Stickney 1991; Bantle and Alisauskas 1998; Strand et al. 1999; Samelius and Alisauskas 2000). Arctic foxes will also scavenge carcasses of seals killed by polar bears (*Ursus maritimus*) when the Arctic Ocean freezes in winter (Andriashek et al. 1985; Fay and Stephenson 1989) and will enter subnivean birth lairs to kill ringed seal (*Phoca hispida*) pups in spring (Smith 1976, 1987).

It has been speculated that scavenging seal carrion may be important for the survival of large numbers of arctic foxes during the winter, or that a high predation rate on seal pups may stimulate an increase in fox abun-

dance when fox densities are low (Stirling and Archibald 1977; Smith 1987; Hiruki and Stirling 1989). However, few studies have attempted to quantify the winter diet of arctic foxes, and it is not clear how important the marine environment is to many arctic fox populations, what percentage of food intake is marine-based, or how the marine proportion of the diet varies among years. Furthermore, access to seal carrion and ringed seal pups depends on sea ice, which has declined in extent during recent years as global temperatures have increased (Vinnikov et al. 1999). This decline in sea ice and increased duration of the ice-free period in the southern part of the polar bears' range has been correlated with a decrease in body condition and reproductive output of polar bears, which require sea ice to hunt seals (Stirling et al. 1999). A continued loss of sea ice may also negatively affect other terrestrial predators that forage on sea ice (Andriashek et al. 1985), and indirectly impact their terrestrial prey species. The objective of this study, therefore, was to quantify and determine seasonal and annual variation in marine diet of arctic foxes whose density is strongly affected by lemming abundance, and possibly by the seasonal opportunity to scavenge seal carcasses left by polar bears. I predicted that: (1) the diet of arctic foxes would be more marine-based in winter, when the sea ice habitat was available; and (2) the marine component of diet in winter would vary inversely with lemming abundance.

Materials and methods

Study area

The study was based near Cape Churchill, Manitoba, (58° 45′N, 94°10′W) on the west coast of Hudson Bay. This area is characterized by numerous well-drained sand or gravel beach ridges separated by peat lowlands with many shallow lakes and ponds (Ritchie 1957; Bahr 1989). The vegetation is characteristic of low Arctic coastal tundra, dominated by different species of willow (Jefferies et al. 1979; Johnson 1987). The climate of the area is strongly influenced by Hudson Bay, which is frozen for 7–8 months of the year and exerts a cooling effect on the coast (Rouse 1991). This area is near the southern edge of the distribution of both arctic foxes and polar bears (Banfield 1977).

Harvest records from the Churchill area imply that the local arctic fox population cycles regularly and dramatically (Walter 1996). The density of collared lemmings (*Dicrostonyx richardsoni*) near Churchill also fluctuates regularly (Scott 1993). In summer over 200 species of migratory birds nest in and around the area, including a large and expanding colony of lesser snow geese (*Chen caerulescens*) at La Pérouse Bay (Jehl and Smith 1970; Cooke et al. 1995). A caribou (*Rangifer tarandus*) herd that summers near Cape Churchill moves below tree line during winter (M. Campbell, unpublished data), as does a neighboring herd that migrates each year between tundra summer habitats and boreal forest winter habitats (Abraham and Thompson 1998). The density of polar bears near Cape Churchill in autumn is among the highest in the world, with large aggregations forming near the coast while bears wait for the sea ice to form (Derocher and Stirling 1990). As the use of seal remains by arctic foxes in winter may be affected by relative abundance of polar bears (Macpherson 1969), the arctic foxes in this area clearly have an opportunity to follow polar bears onto the sea ice in winter to scavenge seal carcasses.

Methods

I measured the ratio of stable-carbon isotopes ($^{13}C/^{12}C$) in arctic fox hair to estimate protein intake from marine and terrestrial sources. Consumers of purely marine-based food sources are enriched in ^{13}C compared to strictly terrestrial consumers, and organisms with mixed diets have intermediate signatures (Chisholm et al. 1982; Schoeninger and DeNiro 1984). Although C_3 plants and C_4 plants also have distinct carbon-isotope signatures, only C_3 species occur in the Arctic (Tieszen and Boutton 1989). However, the tissues of migratory birds potentially could reflect carbon input from other ecosystems (Alisauskas and Ankney 1992). Stable isotope analysis of bone collagen has been used to determine individual and regional dietary variation in other arctic fox populations (Angerbjörn et al. 1994), but because of the short life expectancy (3–4 years), the turnover rate of bone collagen is too slow to infer seasonal or yearly variation in the arctic fox diet (Tieszen and Boutton 1989). Metabolically inactive tissues like hair do not resorb or turnover, so their stable isotope ratios reflect the diet of individuals during a limited period of growth. Arctic foxes molt twice per year, with the spring molt occurring between March and June while the autumn molt starts in September and continues into November (Johansson 1960; Chesemore 1970). Since the ice-free period of Hudson Bay, when seals are not available to polar bears, generally lasts from July to November (Stirling et al 1999), I assumed that the brown summer pelage would reflect diet at the end of winter and the white winter pelage would reflect diet at the end of summer.

I collected hair from arctic foxes near Cape Churchill from 1994 to 1997. The hair collected in the first year included samples grown in the summer of 1993 and samples grown in winter of 1994. Likewise, hair collected the 3 following years included hair samples grown the previous summer. Arctic fox carcasses were collected from local trappers during trapping seasons (November–March of 1993–1994, 1994–1995 and 1996–1997) or other researchers in the spring (April–June of 1994–1997; Walter 1996). Pelted foxes usually had some hair remaining around the anus or on the feet, and samples were clipped from these areas with scissors. Arctic foxes were also live-trapped at den sites (1994–1996), and hair samples were clipped with scissors from the thigh or neck of each adult captured. Both winter and summer hair were collected from animals that were molting. I extracted a lower canine tooth from each fox carcass to estimate age using counts of cementum layers (Bradley et al. 1981). An x-ray was first taken of each tooth to distinguish juveniles by the size of the pulp cavity (Grue and Jensen 1976), and tooth sectioning and age analysis were performed on teeth from adults by Matson's Laboratory (Milltown, Mont.). Individuals born the previous spring were considered subadults.

I collected eggs from nests of Canada geese (*Branta canadensis*) and lesser snow geese in June 1996 (ten nests per species, one egg per nest), since geese and their eggs can be important food sources to these arctic foxes in summer (Bahr 1989). Eggs from other species were salvaged from nests that had been abandoned or failed to hatch and additional avian samples, representing known foods of arctic foxes, were salvaged opportunistically from active fox dens. Samples of caribou muscle were obtained from native hunters in the fall of 1995 and the spring of 1997, and from a carcass found on the coast in July 1996. I also measured the stable-carbon isotope ratios of polar bear hair collected from free-ranging polar bears near Cape Churchill in a separate study (M. Ramsay, unpublished data). Since polar bears feed exclusively from marine sources (Ramsay and Hobson 1991), the hair of arctic foxes feeding exclusively from marine sources would be expected to have a similar isotopic composition, assuming similar fractionation patterns between diet and tissues of the two species.

I estimated the abundance of small mammals in the area using mark-recapture methods on three trapping grids (9×8 with 10 m between grid points) established at different areas of lichen-heath tundra. The minimum distance between grids was 1.4 km, well beyond the maximum distance usually traveled by collared lemmings within their home range (0.47 km; Tuchscherer 1990). Two Sherman live traps baited with oats and peanut butter were placed

within 2 m of each grid point, near fresh burrows if possible, and set continuously for 1 week at each grid in late June–early August in 1994–1997. Traps were checked twice daily (more frequently in hot weather) and animals were individually dye-marked for identification. Toe clipping was also used in the first field season to ensure that dye marks were retained throughout the trapping period. I estimated the population size for each grid using the Schnabel method (Krebs 1989), and calculated density assuming a 5-m strip (half the distance between grid points) around each grid. These densities were averaged over the three grids for each year. Samples for stable isotope analysis were obtained from three accidental trap deaths and seven lemmings collected in June 1994 by the Royal Ontario Museum. Seasonal variation in isotopic signatures of lemmings is not expected because summer and winter foods of lemmings are similar (Shelford 1943). The handling protocol for arctic foxes and lemmings was approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol no. 9404004). Collection of goose eggs was approved by the University of Saskatchewan Committee on Animal Care and Supply (protocol ID 960031).

Hair samples were cleaned with soap and water to remove surface oils and debris, dried at 90 C, and homogenized with scissors. Eggs were homogenized in a Waring blender after removing the shells. Egg and muscle samples were then freeze-dried and powdered with mortar and pestle. The carbon isotope ratios of lipids differ substantially from other compounds (DeNiro and Epstein 1978; Tieszen et al. 1983), and variations in lipid concentration can significantly influence $\delta^{13}C$ measurements (Rau et al. 1992). Therefore, I removed lipids from egg and muscle samples using a Soxhlet apparatus with chloroform solvent for at least 8 h. Chloroform was then removed by evaporation in a drying oven. Stable-carbon isotope ratios were measured on a continuous flow isotope ratio mass spectrometer in the Stable Isotope Facilities at the Department of Soil Sciences, University of Saskatchewan. Stable-carbon isotope signatures are expressed as parts per thousand (‰) relative to the Pee Dee Belemnite standard as follows: $\delta^{13}C = [(R_{sample}/R_{standard})-1]\times10^3$, where R is the ratio $^{13}C/^{12}C$. Measurement accuracy (as reported by the Stable Isotope Facility) was within 0.3‰.

To determine effects of sex, age, or source of the samples on the stable-carbon isotope ratios of winter and summer hair I controlled for differences among years using 2-way ANOVAs. $\delta^{13}C$ values of potential prey species were compared using a t-test corrected for unequal variances (t'; Snedecor and Cochran 1989). To determine the effect of changes in lemming density on arctic fox diet I calculated the correlation coefficient (Pearson) relating the $\delta^{13}C$ values of both winter and summer hair with average lemming density each year. For winter hair, lemming density from the previous summer was used. To calculate the percentage of arctic fox diet that was derived from marine resources I assumed the $\delta^{13}C$ values of lemming and ringed seal muscle reflected the terrestrial and marine endpoints, respectively, and corrected for isotopic fractionation between winter diet and summer hair using fractionation values determined for red fox (Roth and Hobson 2000). To test whether two distinctive foraging strategies (terrestrial vs. marine based) are used by different segments of the population in winter, which would be indicated by a bimodal distribution of $\delta^{13}C$ values, I compared the stable carbon isotope ratios of summer hair to a normal distribution using the Kolmogorov-Smirnov test.

Results

Collared lemmings were the only small mammal species captured. The estimated density of lemmings varied significantly over the course of the study ($F_{3,11}=17.5$, $P=0.002$), with peak numbers in 1994 [Tukey's honestly significant difference (HSD)=4.9, $P<0.05$], very few in 1995 and 1996, and a non-significant increase in 1997 (Fig. 1a).
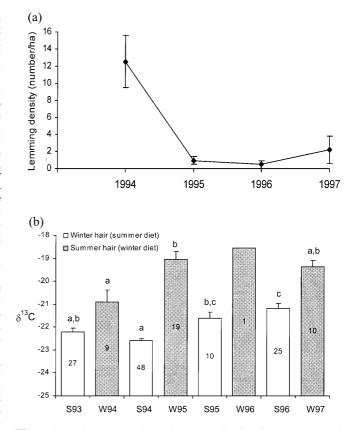

Fig. 1 Annual changes in **a** lemming density in summer and **b** stable-carbon isotope ratios (mean±SE) of arctic fox hair from Cape Churchill, Manitoba. Lemming densities are average (±SE) Schnabel estimates from three trapping grids. Winter (*W*) hair values reflect diet at the end of the previous summer (*S*), and summer hair values reflect late winter diet; thus, axis labels reflect the season in which the pelage was grown. *Different letters* denote significant differences (*P*<0.05) among years for each season, and *numbers on the bars* indicate sample sizes

Lemming muscle tissue had $\delta^{13}C$ values typical for a terrestrial C_3 herbivore (approximately –25‰, Table 1). Caribou muscle was enriched in ^{13}C over lemmings by 3.4±0.4‰ (mean±SE difference; $t'=7.72$, $df=3.2$, $P=0.004$). Results from the avian samples varied (Table 1), reflecting terrestrial C_3 inputs (ptarmigan, several shorebirds), marine inputs (eider, loon), or a substantial C_4 input acquired prior to or during migration (Canada goose). Canada goose eggs were significantly enriched in ^{13}C compared to snow goose eggs ($t'=4.08$, $df=9.7$, $P=0.0024$), and eggs of both Canada goose ($t'=5.94$, $df=9.2$, $P=0.0002$) and snow goose ($t'=8.13$, $df=15.3$, $P<0.00005$) were enriched relative to lemmings. Gosling muscle from Canada and snow geese did not differ from each other or from muscle of lemmings (Kruskal-Wallis test: $H_{16}=3.89$, $P=0.14$). For both Canada geese ($H_{16}=11.0$, $P=0.0003$) and snow geese ($H_{16}=10.5$, $P=0.0006$), adults were enriched in ^{13}C compared to goslings, and eggs were intermediate.

Hair samples were analyzed from 29, 49, 10 and 25 arctic foxes in 1994–1997, respectively. The source of the samples (local trappers, other researchers, or live-

Table 1 Stable-carbon isotope ratios of potential prey items (mean±SE, sample sizes *in parentheses*)

Species	Eggs	Muscle (juveniles)	Muscle (adults)
Birds			
Lesser snow goose (*Chen caerulescens*)	–23.4±0.13 (11)	–24.4±0.16 (3)	–22.0±0.74 (3)
Canada goose (*Branta canadensis*)	–20.6±0.67 (10)	–24.4±0.07 (4)	–15.8±0.07 (3)
Willow ptarmigan (*Lagopus lagopus*)	–23.4±0.11 (3)		–23.5±0.24 (2)
Whimbrel (*Numenius phaeopus*)	–23.3±0.29 (3)		
Dunlin (*Calidris alpina*)	–23.5±1.0 (2)		
Lesser yellowlegs (*Tringa flavipes*)	–26.6 (1)	–26.8 (1)	
Hudsonian godwit (*Limosa haemastica*)	–25.1 (1)		
Short-billed dowitcher (*Limnodromus griseus*)	–24.3 (1)		
Golden plover (*Pluvialis dominica*)	–22.4 (1)		
Least sandpiper (*Calidris pusilla*)	–22.4 (1)		
Common eider (*Somateria mollissima*)			–18.8 (1)
Pacific loon (*Gavia pacifica*)			–18.1 (1)
Mammals			
Collared lemming (*Dicrostonyx richardsoni*)			–24.6±0.07 (10)
Caribou (*Rangifer tarandus*)			–21.3±0.43 (4)
Ringed seal (*Phoca hispida*)[a]			–18.1±0.04 (27)

[a] from Ramsay and Hobson (1991)

trapped) had no effect on $\delta^{13}C$ values of winter hair ($F_{2,102}=0.78$, $P=0.46$). Likewise, the $\delta^{13}C$ values did not differ between sexes (winter hair $F_{1,102}=0.54$, $P=0.46$; summer hair $F_{1,32}=1.85$, $P=0.18$) or between adults and subadults (winter hair $F_{1,99}=0.77$, $P=0.38$; summer hair $F_{1,31}=1.18$, $P=0.29$) for either season.

Isotope ratios of fox hair varied seasonally, with summer pelage (reflecting winter diet) significantly enriched in ^{13}C compared to winter pelage ($F_{1,141}=71.8$, $P<0.0001$), indicating a greater use of marine foods during the winter (Fig. 1b). There were also differences between years for both winter hair ($F_{3,106}=19.2$, $P<0.0001$) and summer hair ($F_{3,35}=4.42$, $P=0.0098$; Fig. 1b). Winter hair was depleted in ^{13}C in year 2 of the study compared to both year 3 (Tukey's HSD for unequal n, $P=0.03$) and year 4 ($P=0.0001$), and in year 1 compared to year 4 ($P=0.0002$). Thus, winter hair was least enriched in ^{13}C in the second year, intermediate in the first year and most enriched in the last 2 years (Fig. 1b). Summer hair was more enriched in ^{13}C in year 2 compared to year 1 (Tukey's HSD for unequal n, $P=0.02$) and slightly enriched in year 4 compared to year 1 ($P=0.08$; insufficient sample size precluded statistical comparison of summer hair from the third year). The $\delta^{13}C$ values of both winter and summer hair were negatively correlated with lemming density (winter hair $r=-0.62$, $P<0.0001$, $n=83$; summer hair $r=-0.52$, $P=0.0007$, $n=39$). Estimates of marine-derived protein in the winter diet increased from 17% to 46% following the initial decline in lemmings between the first 2 years, and decreased slightly to 40% the last year.

Hair samples from ten free-ranging adult polar bears near Cape Churchill had a mean $\delta^{13}C$ value of –16.0±0.1 SE. Hair is approximately 2.6‰ enriched in ^{13}C relative to diet for red fox (Roth and Hobson 2000), and assuming a similar diet-tissue fractionation factor for arctic foxes the isotope ratios of hair from foxes feeding entirely on lemmings should be about –22‰. Thus, hair of arctic foxes feeding from both terrestrial and marine sources should range between –22‰ and –16‰. The measured range of all hair samples was –23.6‰ to –16.7‰, indicating that both food sources were used. However, the distribution of $\delta^{13}C$ values of arctic fox hair did not differ from normality in any year ($Z<0.9$, $P>0.44$ for each year).

Discussion

The seasonal differences in the stable-carbon isotope ratios of arctic fox hair indicated the diet was much more marine in winter, as expected if the sea ice provided access to marine resources. In addition, between-year variation in the winter diet of arctic foxes was related to lemming abundance. Summer hair was least enriched in ^{13}C in the first year of the study, reflecting a more terrestrial (C_3) diet the winter that lemmings were most abundant. When lemmings declined, the marine input in the arctic fox diet increased, as reflected in the higher ^{13}C content of hair grown in late winter. Thus, the importance of the sea ice as an alternative habitat for arctic foxes in winter was a function of the abundance of their terrestrial prey, and in years of low lemming abundance the sea ice provided nearly half of the protein input of arctic foxes, on average. Other studies have documented a similar decrease in the occurrence of small mammals in the winter diet of arctic foxes when rodent densities decline, increasing the importance of alternative food sources (Macpherson 1969; Fay and Stephenson 1989). The occurrence of marine mammal carrion in arctic fox stomachs has been correlated with the amount of subcutaneous fat, suggesting how important this food source can be for maintaining body condition in winter (Anthony et al. 2000). A similar importance of marine foods dur-

ing rodent declines has been shown for other carnivores. For example, American marten (*Martes americana*) in southeast Alaska consume carcasses of spawning Pacific salmon in the fall when vole abundance declines (Ben-David et al. 1997).

Arctic foxes are often nomadic in winter, dispersing from their summer home ranges in the fall. Distinctive seasonal movements can occur, as arctic foxes in tundra areas often move toward the coast in the fall and then return to inland den sites in spring (Dementyeff 1958; Chesemore 1968a; Shilyaeva 1968; Garrott and Eberhardt 1987). In years of food scarcity these movements may include large-scale migrations (Elton 1949; Dementyeff 1958; Shilyaeva 1968; Wrigley and Hatch 1976; Eberhardt and Hanson 1978), which may be male-biased (Dementyeff 1958; Bannikov 1970) or age-related, although whether subadults (Shilyaeva 1968; Hiruki and Stirling 1989) or adults (Dementyeff 1958; Wrigley and Hatch 1976) are primarily responsible for these observations is unclear. Thus, the two foraging options that arctic foxes have in winter, to follow polar bears onto the sea ice and scavenge or to stay on land to hunt lemmings, might be adopted by different segments of the population. Yet I found no evidence of a bimodal distribution of stable isotope ratios, and there were no differences in use of marine resources among different age or sex classes. The use of the sea ice does, however, appear to depend on the abundance of terrestrial prey, since stable isotope ratios of arctic fox hair were related to lemming abundance. Arctic foxes may prefer to forage on land in winter as long as terrestrial resources are sufficient because resources on the sea ice are patchily distributed and unpredictable (Ferguson et al. 2000). Potential differences in energy content of lemmings vs. seal carcasses or pups, as well as fox body condition, may also affect this foraging decision.

Seasonal variation occurs in hair length and pigmentation, fat deposition, and energy requirements of arctic foxes (Underwood 1971, 1981; Prestrud and Nilssen 1992). If the difference in ^{13}C content in summer and winter hair reflected physiological differences in arctic foxes during each season, sex or age differences might be expected, especially in the summer pelage, which develops during mating, gestation and the start of lactation (Dementyeff 1958). However, few structural differences exist between summer and winter guard hairs (Russell and Tumlison 1996) and I found no differences in δ^{13}C between males and females or between adults and subadults. Although nutritional stress can affect nitrogen stable-isotope ratios, it does not seem to affect carbon (Hobson et al. 1993). Thus, it appears that marine food sources do become important to arctic foxes in this area during winter when the abundant summer foods (migratory birds and caribou) have disappeared and the sea ice habitat becomes available.

Arctic foxes may consume some cached avian foods in winter and spring when nesting birds are absent (Fay and Stephenson 1989; Stickney 1991; Frafjord 1993; Bantle and Alisauskas 1998; Anthony et al. 2000), and
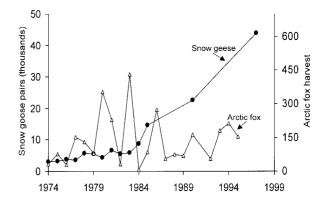

Fig. 2 Abundance of lesser snow geese (no. of nesting pairs) and arctic foxes (harvested by local fur trappers) near Cape Churchill, Manitoba. Snow goose data are from Cooke et al. (1995) and R. Rockwell (personal communication), and fox harvest data are from the Manitoba Department of Natural Resources

some of these foods may be enriched in ^{13}C because of reserves acquired during migration (e.g., Canada goose eggs). Although an increased reliance on these caches in winters when lemming numbers are low might produce a similar pattern of changes in stable-carbon isotope ratios, this hypothesis is less likely for several reasons. Some authors have observed that cached prey often seem to be eaten more during summer or autumn than in winter or spring, and that their importance in winter may have been exaggerated (Frafjord 1993; Birks and Penford 1990). Additionally, the large-scale fall migrations of arctic foxes that may be triggered when lemmings decline often occur in areas of abundant summer-nesting birds (Elton 1949; Dementyeff 1958; Shilyaeva 1968; Wrigley and Hatch 1976), implying that cached food supplies are not sufficient to sustain large numbers of foxes over winter.

Furthermore, the snow goose colony at La Pérouse Bay has been increasing at a rate of 8% annually over the past 30 years (Cooke et al. 1995), yet the number of arctic foxes harvested by local trappers has not increased ($r=0.32$, $P=0.13$; Fig. 2). During this time there were no significant changes in average fur prices ($r=0.13$, $P=0.63$) or the number of trappers ($r=0.05$, $P=0.82$), implying harvest was not affected by a change in trapper effort. Thus, even with this exponential increase in summer food abundance over the past 30 years, the arctic fox population has not shown a numerical response, suggesting that winter food abundance is a limiting factor that cannot be compensated for by food caches.

The summer diet of arctic foxes also was affected by changes in lemming populations, as the difference among years in ^{13}C content of winter hair (reflecting summer diet) among years was related to lemming abundance. The isotopic signatures of winter hair grown during the lemming high in 1994 (and collected in the second year of the study) are consistent with a diet composed entirely of lemmings, assuming the same diet-hair fractionation values determined for red fox (Roth and Hobson 2000). Lemmings were moderately abundant in 1993 (Walter

1996), and the carbon isotope ratios of hair grown that summer were intermediate to hair produced at high lemming densities (1994) and in years with very few lemmings (1995 and 1996). Thus, the importance of lemmings in the summer arctic fox diet reflected their abundance.

Other foods that are slightly enriched in ^{13}C compared to lemmings (Table 1) became more important in summers with lower lemming densities. Goose eggs and goslings, which are common summer prey even in years when rodents are abundant (Bahr 1989; Stickney 1991), likely were the most important alternative foods, as adult geese are rarely taken because of their large body size (Bahr 1989; Samelius and Alisauskas 2000). The enriched δ^{13}C values of nesting geese and their eggs reflected the use of energy and nutrient reserves acquired on wintering grounds and during migration (Ankney et al. 1991; Alisauskas and Ankney 1992), which apparently were more important for Canada geese than snow geese (Table 1). Caribou calves, which can be preyed on by arctic foxes (Prestrud 1992), are another potential food source, and calf carcasses occasionally have been found near fox dens at Cape Churchill (Walter 1996; personal observation). The higher δ^{13}C values of caribou compared to lemmings (Table 1) were consistent with a diet of lichens, which are an important food of caribou (Scoter 1967) and are enriched by 3–4‰ over other tundra vegetation (Schell and Ziemann 1989). Because of the low variation in δ^{13}C among prey items (Table 1), it is impossible to distinguish exactly which alternative prey became most important in summer during lemming lows. However, during peak lemming abundance, the stable-carbon isotope ratios of fox hair reflect the dominance of lemmings in the summer diet of arctic foxes.

The high marine component of arctic fox diet in winter, when access to seal carrion was provided by the sea ice, demonstrates the importance of the sea ice as an alternative habitat for this population, especially during periods of low lemming density. Because of this importance, there is the potential for an indirect effect of marine resources on other terrestrial prey species of the arctic fox. If arctic foxes are able to maintain a higher density because of this marine foraging strategy, terrestrial prey species could suffer increased rates of predation. Arctic foxes can have a large impact on the distribution and abundance of many arctic-nesting birds (Larson 1960), but changes in the availability of resources on the sea ice may affect their interactions with their prey. Climatic changes that affect the behavior of predators can have cascading effects on lower trophic levels (Post et al. 1999), and the likely continued decline in the extent of sea ice in the next several years (Vinnikov et al. 1999) could affect terrestrial species not only through the abiotic effects of climate change, but also by disrupting an important link between the marine and terrestrial food webs provided by this mobile predator.

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