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Variability in marine resources affects arctic fox population dynamics

JAMES D. ROTH

Department of Ecology, Evolution and Behaviour, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA

Summary

1. Terrestrial predators in coastal areas are often subsidized by marine foods. In order to determine the potential impact on terrestrial prey, the numerical response of predators to each food source must be determined.

2. In winter, arctic foxes (*Alopex lagopus*) may forage on the frozen Arctic ocean and scavenge carcasses of seals killed by polar bears (*Ursus maritimus*), but the importance of this food source and its effect on the population cycles of arctic foxes and lemmings (their primary prey) are unclear.

3. I estimated the marine component of the late winter diet of arctic foxes near Churchill, Manitoba, using stable-carbon isotope analysis, and compared these estimates to abundance of arctic foxes and collared lemmings (*Dicrostonyx richardsoni*).

4. From 1994 to 1997, fox density varied with lemming abundance, but following a decline, fox abundance began increasing before lemmings. During this increase marine foods were consumed more than in other years, with over two-thirds of food intake from marine sources.

5. Arctic and red fox (*Vulpes vulpes*) harvests in the 1980s to 1990s were correlated with published estimates of polar bear body mass, which varies with seal productivity. However, this relationship disappeared during high lemming years.

6. Thus, variation in marine productivity affects arctic fox abundance, especially when their primary prey are scarce, and this numerical response of arctic foxes to marine resources and lemmings suggests that increased predation by arctic foxes subsidized by seal carrion may delay the recovery of low lemming populations.

Key-words: allochthonous resources, indirect effects, numerical response, scavenging, stable isotope ratios

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Introduction

The flow of energy or nutrients between ecosystems can have substantial impacts on the abundance and dynamics of consumers. Because of heterogeneity in productivity and resource abundance, inputs from more productive habitats may subsidize predators or scavengers in areas of lower resources, leading to higher densities of these consumers than otherwise could occur (Polis & Hurd 1996; Polis, Anderson & Holt 1997). Coastal areas, in particular, often receive substantial inputs of energy and nutrients from the ocean, and these allochthonous inputs, or subsidies, can support large numbers of consumers that could affect the dynamics and structure of terrestrial communities (Polis *et al.* 1997; Rose & Polis 1998). Such indirect effects are not uncommon in food webs, and often are non-reciprocal as would occur if one resource is donor-controlled (Chaneton & Bonsall 2000). Food web models that include allochthonous resources have shown that small inputs of such resources could have a stabilizing influence on predator–prey dynamics, while large inputs could destabilize the food we and cause the extinction of one or more species (Huxel & McCann 1998). Yet this top-down effect of terrestrial consumers subsidized by marine foods has not been shown empirically.

Holt (1977) first pointed out that prey species that share a common predator can sometimes indirectly suppress each other by increasing the abundance of their shared natural enemy. For this indirect effect to

Correspondence: James D. Roth, Department of Biology, University of Central Florida, 4000 Central Florida Blvd, Orlando, FL 32816–2368, USA. Tel.: +1 407 823 4334. Fax: +1 407 823 5769. E-mail: jroth@ucf.edu.

occur, the predator must be primarily food limited and must have a positive numerical response to each prey. Relaxing either of these assumption tends to weaken the impact on prey (Holt 1977, 1987; Abrams & Matsuda 1996). These criteria remain in place when investigating the indirect effect of marine subsidies on the terrestrial prey of a consumer. Although rates of such allochthonous inputs have been estimated (e.g. Polis & Hurd 1996), temporal variability in the availability of marine subsidies has rarely been demonstrated. The response of consumer populations to changes in the amount of marine subsidies (the numerical response) is important to document in order to show the potential for indirect effects on the terrestrial prey of these consumers.

Arctic foxes (*Alopex lagopus*) often rely on the marine ecosystem in winter, when they scavenge carcasses of seals killed by polar bears (*Ursus maritimus*) on the polar pack ice (Andriashek, Kiliaan & Taylor 1985; Roth 2002). Polar bears specialize on seal blubber, often leaving substantial portions of seal carcasses on the sea ice, which provides a high-energy alternative food source for opportunistic foxes (Stirling & McEwan 1975). Arctic foxes also enter subnivean birth lairs of ringed seals (*Phoca hispida*) on the ice in spring to prey on the pups (Smith 1976, 1987). Seal productivity and the rate of pup predation by arctic foxes can vary between years, and may affect arctic fox densities and population dynamics (Smith 1976, 1987; Stirling, Archibald & DeMaster 1977; Hiruki & Stirling 1989). However, few studies have attempted to quantify how these marine food sources, or changes in their availability, may affect arctic fox abundance and population dynamics.

Arctic fox population dynamics are, however, strongly affected by microtine rodents (lemmings and voles), which are an important food source over much of their range and a well-known example of animals with population cycles (Chitty 1950; Macpherson 1969; Angerbjörn, Tannerfeldt & Erlinge 1999; Elmhagen *et al.* 2000). These lemming cycles also can indirectly affect other prey species of arctic foxes. Many Arctic-nesting birds, especially geese and waders, suffer much higher rates of nest predation when lemming numbers initially decline, lowering their breeding success (e.g. Bêty *et al.* 2002; Blomqvist *et al.* 2002). If arctic foxes also respond numerically to changes in availability of marine resources in winter, a similar indirect effect on terrestrial prey may occur. However, little research has been done on the winter foraging ecology of this species, even though it is the major furbearer and terrestrial predator throughout most of the North American Arctic (Garrott & Eberhardt 1987). Much of the evidence of the use of the sea ice by arctic foxes has been anecdotal, and the effect of variability in food abundance in this habitat on population dynamics of arctic foxes has not been documented.

Research on arctic foxes near Cape Churchill, Manitoba (58°45′ N, 94°10′ W) has documented an increase in consumption of marine foods in winter over summer and in winters following a lemming decline (Roth 2002). The objectives of this paper are to (i) examine the numerical response of arctic foxes to changes in lemming abundance and marine food intake, and (ii) determine whether arctic fox abundance varies with estimates of marine productivity and, if so, how that relationship may change with abundance of terrestrial prey.

Methods

Cape Churchill is on the west coast of Hudson Bay (Fig. 1), near the southern range boundary of arctic foxes and polar bears (Banfield 1977). The study area is characterized by numerous relic sand or gravel beach ridges created by isostatic rebound following glacial retreat, interspersed with many shallow lakes or ponds (Ritchie 1957; Dredge 1992). Vegetation is characteristic of low Arctic coastal tundra (Jefferies, Jensen & Abraham 1979), but the boreal forest begins about 20 km inland from Cape Churchill. Large fluctuations in lemming abundance occur regularly, although the amplitude of these cycles apparently declined in recent decades (Scott 1993), and harvest records imply that the local arctic fox population also cycles regularly and dramatically (Roth 2002). Harvest numbers of red fox (*Vulpes vulpes*), which can exclude arctic foxes from den sites and can be important predators and competitors in areas where the two species overlap (Hersteinsson & MacDonald 1992; Tannerfeldt, Elmhagen & Angerbjörn 2002), fluctuate similarly but with a smaller amplitude (Manitoba Natural Resources, unpubl. data). The failure of this arctic fox population to respond numerically to an exponential increase in numbers of nesting lesser snow geese (*Chen caerulescens*), which are an important summer food source (Bahr 1989), suggests that the primary limiting factor is food abundance during winter (Roth 2002), when migratory birds are absent and most caribou (*Rangifer tarandus*) move inland below the tree line (M. Campbell unpubl data; see also Abraham & Thompson 1998).

The relative density of arctic fox in this area was estimated using annual den surveys from 1994 to 1997. Arctic fox dens in tundra areas are often very conspicuous because of the lush vegetation that results from soil enrichment and disturbance, and therefore are visible from long distances (Macpherson 1969; Garrott, Eberhardt & Hanson 1983). Because of the short life expectancy (3–4 years) and large litters (averaging 8–12 in Canada), den occupancy, reflecting reproduction, is commonly used to determine population trends of arctic foxes (e.g. Macpherson 1969; Eberhardt, Garrott & Hanson 1983a). In the study area, numerous well-drained beach ridges provide abundant denning habitat along the coast, whereas the peat lowlands of the inland sedge meadows offer few upland features to support denning activity (Bahr 1989). Terrain maps were used to find these areas of suitable den habitat

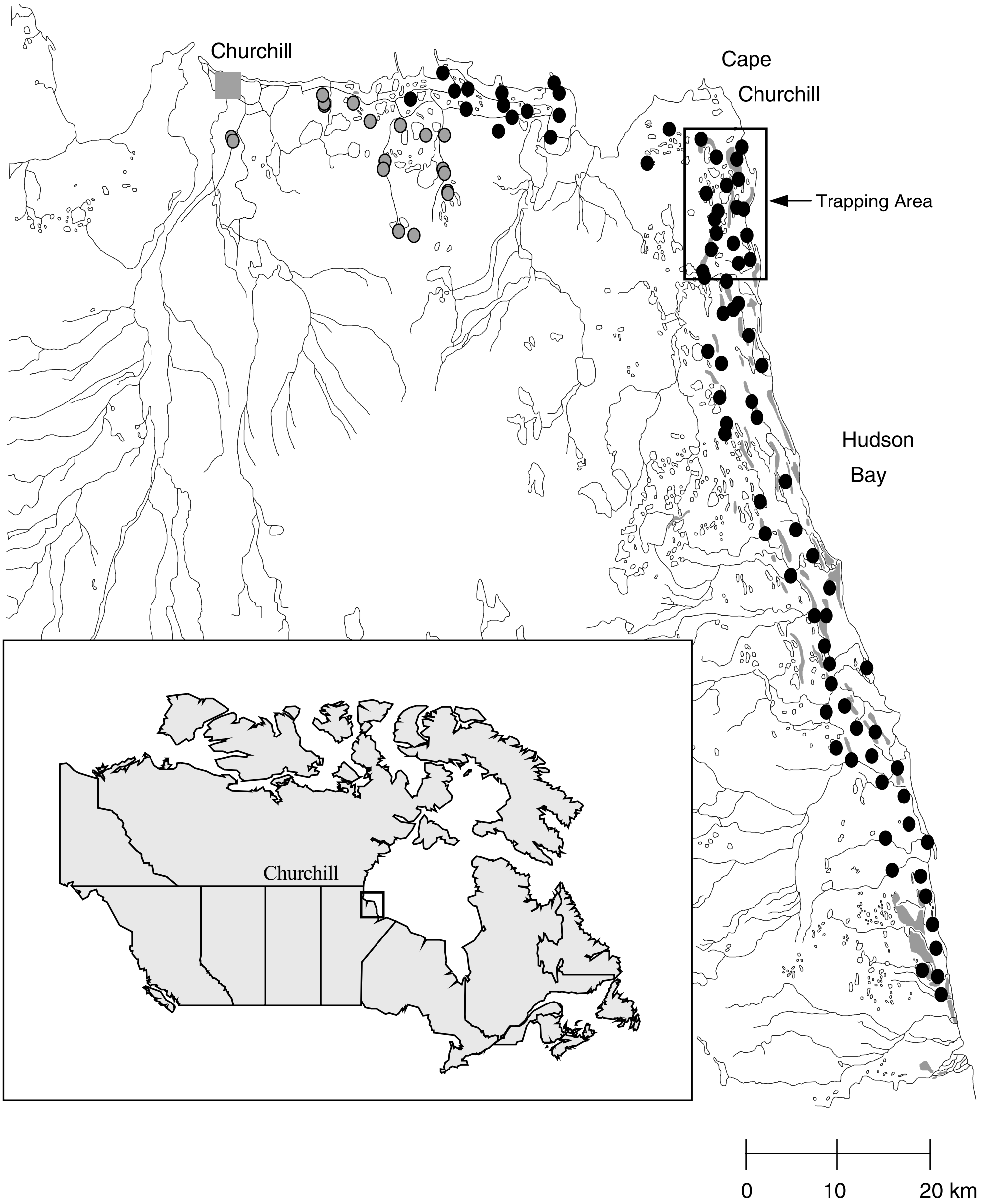

Fig. 1. Study area near Cape Churchill, Manitoba, Canada (58°45′ N, 94°10′ W), indicating den locations for arctic foxes (black circles) and red foxes (grey circles), and trapping area (rectangle).

(Smith, Smits & Slough 1992), mostly well-defined beach ridge complexes that ran parallel to the coast within 10 km of Hudson Bay. These beach ridge complexes were systematically surveyed on foot (west of Cape Churchill) or from the air (south of Cape Churchill) in August each year to locate dens and determine occupancy (several *ad hoc* surveys of the marshy inland tundra areas revealed no dens). Upland forested areas within 25 km of the town of Churchill were also systematically searched for dens. Occupied dens had recently excavated burrow entrances, worn vegetation, tracks, scats, and/or abundant prey items (Macpherson 1969; Garrott *et al.* 1983). In occupied dens visited on the ground, the presence of the animals or shed hair in burrow entrances determined which fox species occupied the den. No tundra dens located from the air appeared to be inhabited by red foxes, and this observation was verified by additional surveys of every den by snowmobile in May 1996 and 1997, as well as close visual inspection of several of these dens each August. The proportion of dens occupied in August provided an index of annual fox abundance, which was compared to an estimate of lemming density each year determined by mark–recapture methods (Roth 2002).

The body mass of polar bears in western Hudson Bay was used to indicate relative abundance of marine resources available to arctic foxes. Polar bear body mass can vary among years and increases with marine productivity and availability of seals (Stirling *et al.* 1977; Smith 1987; Derocher & Stirling 1995; Stirling & Lunn 1997). Because of the polar bears' habit of selectively feeding on seal blubber, bears will very probably leave more seal remains when hunting conditions are favourable and they are in better condition, and environmental conditions leading to increased foraging success of polar bears should also increase the arctic fox's ability to hunt seal pups. Therefore, polar bear body mass should be positively correlated with the amount of seal carrion available to scavengers on the sea ice. Female polar bears with cubs use their fat reserves to nurse young (Ramsay & Stirling 1988), and therefore their physical condition may be most sensitive to variation in prey availability. Thus, published estimates of mean body mass of females with cubs (Derocher & Stirling 1995) were compared to numbers of foxes harvested from 1979 to 1993 (no harvest data were available for the 1990–91 trapping season). Red foxes also may forage on the sea ice (Andriashek *et al.* 1985), so harvest numbers of both arctic fox and red fox were compared with polar bear body mass. Separate comparisons were also conducted for years when lemmings were abundant and years when they were not abundant (Scott 1993; Walter 1996).

Stable-carbon isotope analysis was used to estimate the proportion of the arctic fox diet acquired from marine vs. terrestrial sources. The ratio of the stable isotopes of carbon ($^{13}C/^{12}C$) differs in marine and terrestrial systems, providing a quantitative estimate of the amount of protein intake from each source (e.g. Chisholm, Nelson & Schwarcz 1982; Roth 2002). Samples of liver, muscle and bone (a tibia) were collected from arctic fox carcasses removed from a portion of the study area (Fig. 1) in April and May of 1994–97 in a separate study (Walter 1996). The rates of carbon turnover in these tissues suggest that stable isotope ratios of liver may reflect diet assimilated over the previous week, whereas muscle tissue provides dietary information from the previous two months (Tieszen *et al.* 1983; Hobson & Clark 1992). Muscle samples collected in April and May, soon after arctic foxes pair up at den sites, should thus reflect the arctic fox diet in late winter (February–April). A lower canine tooth was extracted from each fox carcass and X-rayed to distinguish juveniles from adults by the size of the pulp cavity (Grue & Jensen 1976). Individuals born the previous spring were considered subadults. Although arctic and red foxes are harvested by local fur trappers, most trapping near Churchill occurs on land in late fall and early winter, and trappers may take a higher proportion of young or inexperienced individuals (Smirnov 1968). Furthermore, arctic foxes may become nomadic in winters when local foods are scarce, returning to den sites in spring for breeding (Chesemore 1968; Garrott & Eberhardt 1987). Thus, the fox harvest may not be a random sample of the fox population, and soft tissues from these foxes may not reflect an unbiased estimate of the marine component of winter diet. The samples used in this study were collected at the end of winter when the foxes had returned to den sites for breeding, and should be a better representation of the entire population.

Liver and muscle samples were freeze-dried and powdered with mortar and pestle. Bone samples were scraped clean of muscle and other tissues, and broken open and scraped to remove marrow and fat. To extract collagen, bone samples were ground to approximately 1 mm, demineralized with 0·25 N HCl, refluxed at 90 °C overnight, filtered under vacuum, and dried. The carbon isotope ratios of lipids differ substantially from other compounds (DeNiro & Epstein 1978; Tieszen *et al.* 1983), and variations in lipid concentration can significantly influence $\delta^{13}C$ measurements (Rau *et al.* 1992). Therefore, lipids were removed from muscle and collagen samples using a Soxhlet apparatus with chloroform solvent for at least 8 h. Samples were then rinsed with distilled water and dried. Stable-carbon isotope ratios were measured on a continuous flow isotope ratio mass spectrometer at the Stable Isotope Facilities in the Department of Soil Sciences, University of Saskatchewan. Stable-carbon isotope ratios are expressed as parts per thousand (‰) relative to the Pee Dee Belemnite (PDB) standard as $\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R is the ratio $^{13}C/^{12}C$. Measurement precision was < 0·3‰.

The $\delta^{13}C$ values of liver and muscle were corrected for isotopic fractionation using values calculated for red fox (0·6‰ for liver, 1·1‰ for muscle; Roth & Hobson 2000). Estimates of diet-collagen fractionation in carnivores vary between no enrichment (Krueger & Sullivan 1984) and 4·5‰ (Lee-Thorp, Sealy & van der Merwe 1989), and therefore an intermediate value of 2·0‰ was used. If arctic foxes adopt one of two distinct winter foraging strategies, either on land or on the sea ice, then the distribution of stable carbon isotope ratios each year would be bimodal. Therefore, I used the Kolmogorov–Smirnov test to determine whether the distribution of $\delta^{13}C$ values departed from normality. To control for annual dietary variation, I used two-way analysis of variance to examine the effect of sex or age class on $\delta^{13}C$ (Zar 1999).

Results

A clear distinction between arctic and red fox den sites was observed, as red fox dens were limited to forested areas or the transition zones between boreal forest and tundra (Fig. 1). A total of 88 arctic fox natal den sites were located (58, 22, 4 and 4 new dens found in 1994–97, respectively). Nineteen of these dens were within an area where fox densities were manipulated (Walter 1996), so these dens were excluded in calculations of den occupancy, and other dens whose fate was unknown at the end of the breeding season were also excluded. Arctic fox den occupancy differed among years (Fig. 2a; $\chi^2 = 57{\cdot}98$, d.f. = 3, $P < 0{\cdot}0001$). The same pattern occurred using only unmanipulated dens that were first located in 1994 (occupancy rates of those 39 dens were 80%, 9%, 27% and 54% in 1994–97, respectively). Another 19 dens of red fox were located within forested areas in the western part of the study area, and the pattern of red fox den occupancy generally followed that of arctic foxes (Fig. 2a). Den occupancy of the two fox species were correlated ($r = 0{\cdot}976$,

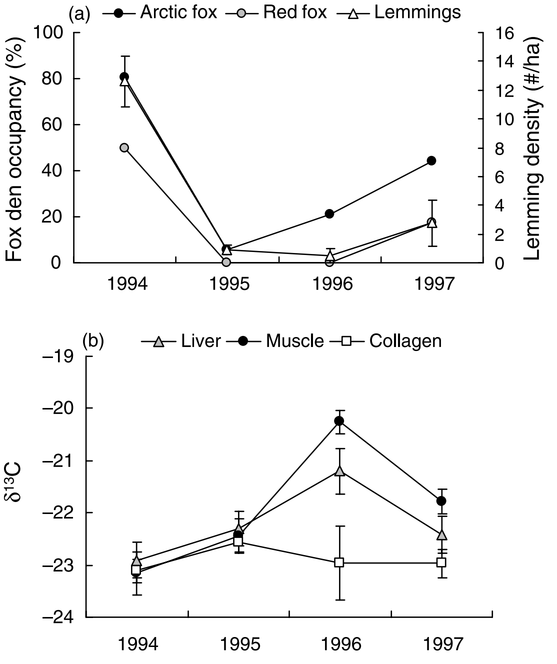

Fig. 2. Annual variation in (a) abundance of foxes and lemmings near Churchill, Manitoba, and (b) mean δ^{13}C values (± SE) of arctic fox tissues. Den occupancy was determined from 31, 54, 62 and 66 arctic fox dens and 14, 18, 17 and 17 red fox dens in 1994–97, respectively. Lemming densities are average (± SE) Schnabel estimates from three trapping grids each summer (Roth 2002). Isotopic signatures have been corrected for differential diet-tissue fractionation.

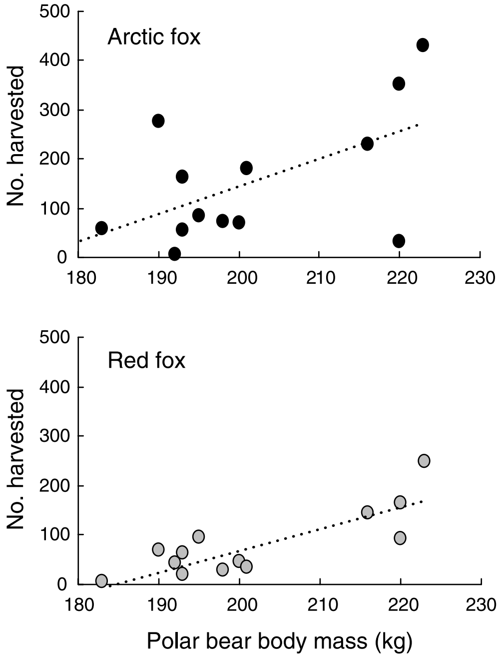

Fig. 3. Relationship between number of arctic fox and red fox harvested near Churchill, Manitoba, and the body mass of polar bears (females with cubs) in western Hudson Bay (polar bear data from Derocher & Stirling 1995).

$P = 0·024$, $n = 4$ years), and each was correlated with mean lemming density (arctic fox $r = 0·933$, $P = 0·067$; red fox $r = 0·982$, $P = 0·018$). Remains of arctic fox in winter colouration were found at two of the seven active red fox dens in 1994, although whether these were depredated or scavenged was unclear.

δ^{13}C values were measured in tissues from 50 arctic fox carcasses (17, 20, 5, and 8 in 1994–97, respectively). The overall sex ratio was 1 : 1 and did not vary among years ($\chi^2 = 2·97$, d.f. = 3, $P = 0·40$). Likewise, the proportion of subadults (47%, 45%, 0% and 25% in 1994–97, respectively) did not vary among years ($\chi^2 = 4·65$, d.f. = 3, $P = 0·20$). Liver, muscle, and collagen values for each individual were highly correlated (liver muscle, $r = 0·832$, $P < 0·001$, $n = 49$; liver collagen, $r = 0·400$, $P = 0·005$, $n = 48$; muscle collagen, $r = 0·361$, $P = 0·011$, $n = 49$). There were no differences in δ^{13}C values between adults and subadults for liver ($F_{1,42} = 0·002$, $P = 0·97$), muscle ($F_{1,43} = 0·30$, $P = 0·63$), or collagen ($F_{1,42} = 0·01$, $P = 0·93$). Likewise, there were no differences between males and females for liver ($F_{1,41} = 2·39$, $P = 0·16$), muscle ($F_{1,42} = 0·42$, $P = 0·53$), or collagen ($F_{1,42} = 1·44$, $P = 0·29$). Therefore, sex and age classes were pooled for further comparisons.

The δ^{13}C values differed among years for muscle (Fig. 2b; analysis of variance, $F_{3,46} = 6·06$, $P = 0·0014$), but there were no differences among years for liver ($F_{3,45} = 2·12$, $P = 0·11$) or collagen ($F_{2,45} = 1·01$, $P = 0·40$). Muscle samples from 1996 were significantly enriched in ^{13}C compared to 1994 and 1995 (Tukey HSD, $P = 0·001$ for 1994 and $P = 0·016$ for 1995), and no other pairwise comparisons were significant. When lemming abundance was used as a covariate, lemmings significantly influenced muscle δ^{13}C values ($F_{1,48} = 7·10$, $P = 0·010$), marginally affected liver ($F_{1,47} = 3·60$, $P = 0·064$), but did not affect collagen ($F_{1,47} = 1·95$, $P = 0·17$). The distribution of δ^{13}C values for each tissue did not differ from normality ($Z < 1·14$, $P > 0·14$ for liver, muscle and collagen each year), indicating there were not two distinct foraging strategies adopted by arctic foxes.

Using the muscle data corrected for isotopic fractionation, the proportion of arctic fox diet in late winter from seals (mean $\delta^{13}\text{C} = -18·1‰ \pm 0·04$ SE, Ramsay & Hobson 1991) and lemmings (mean $\delta^{13}\text{C} = -24·6‰ \pm 0·07$ SE, Roth 2002) was calculated. The average marine intake varied from 22% in 1994 (abundant lemmings) to 67% in 1996 (the second year of very low lemming densities). This analysis assumes that lemmings and seals are the only dietary source for these foxes in late winter, as these food sources do appear to constitute the primary component of the diet of arctic foxes in this population during winter (Roth 2002).

Numbers of both fox species harvested were significantly correlated with polar bear body mass (Fig. 3; arctic fox $r = 0·560$, $P = 0·046$, $n = 13$ years; red fox $r = 0·821$, $P = 0·001$, $n = 13$). Considering only years when lemming densities were high, however, there was no relationship (arctic fox $r = 0·098$, $P = 0·88$, $n = 5$; red fox

$r = 0{\cdot}740$, $P = 0{\cdot}15$, $n = 5$). When lemming densities were not high, the relationship was maintained (arctic fox $r = 0{\cdot}690$, $P = 0{\cdot}058$, $n = 8$; red fox $r = 0{\cdot}843$, $P = 0{\cdot}009$, $n = 8$). Although annual variation in the number of trappers was related to red fox harvest during this time ($r = 0{\cdot}816$, $P = 0{\cdot}002$, $n = 11$), trapper numbers were unrelated to arctic fox harvest ($r = 0{\cdot}484$, $P = 0{\cdot}13$, $n = 11$), and harvest numbers for both species were unrelated to average fur prices (arctic fox $r = 0{\cdot}314$, $P = 0{\cdot}45$, n 11; red fox r 0·439, P 0·28, n 11), implying that variation in trapper effort did not significantly affect these results.

Discussion

The abundance of arctic foxes in this population is clearly related to lemming abundance, but following the large initial decline in both species, the fox population began to increase prior to the recovery of lemmings (Fig. 2a). This pattern of increase differs from most cyclic predator–prey systems, where recovery of the predator usually lags behind increases in prey abundance. With the increased arctic fox density in 1996, marine dietary inputs increased, indicated by the larger stable-carbon isotope ratios in arctic fox muscle tissue (Fig. 2b). Thus, the greater use of resources on the sea ice appears to have led to an increase in the arctic fox population, which could have increased predation pressure on lemmings and potentially delayed their recovery. Predators can delay the growth of prey populations following a decline, extending the low phase of microtine population cycles (Reid, Krebs & Kenney 1995; Boonstra, Krebs & Stenseth 1998). However, the use of the sea ice by arctic foxes appears to depend on the abundance of terrestrial prey because muscle stable isotope ratios were related to lemming abundance and the relationship between arctic fox harvest and polar bear body mass disappeared in high lemming years. Foraging on the sea ice may be a risky strategy, as resources are patchy and unpredictable (Stirling *et al.* 1977), and arctic foxes may prefer to forage on land when terrestrial resources are adequate. In fact, in winters when local foods are sufficient arctic foxes often remain in their summer home ranges (Eberhardt, Garrott & Hanson 1983b). Although access to sea ice in spring may differ among years due to the ephemeral nature of ice conditions and open leads, arctic foxes not only can swim over 2 km in sea water and across rivers and lakes (Dementyeff 1958; Strub 1992), but they also can move extraordinary distances on land and ice (up to 2300 km; Garrott & Eberhardt 1987) and have been found 800 km offshore and within 150 km of the North Pole (Wrigley & Hatch 1976). Thus, even after returning to den sites along the coast for breeding in April/May, foraging excursions onto the sea ice are certainly plausible. It seems therefore that seal availability can affect arctic fox abundance when terrestrial resources are low, but marine foods become less important when lemmings are abundant.

Elsewhere, arctic fox populations that are strongly dependent on lemmings can occasionally experience high survival rates or even increase in abundance when lemming densities are low (Sdobnikov 1958; Smirnov 1968). These Russian studies were conducted on the edge of the Arctic Ocean, where foxes would have access to the sea ice in winter. Increased seal availability could have compensated for low lemmings in some years, allowing more foxes to survive and the population to increase. Arctic fox densities have been related to subjective estimates of seal productivity (Hiruki & Stirling 1989), and high rates of seal pup predation may stimulate an increase in fox populations (Smith 1987). Certainly, supplemental winter food sources added experimentally or from human garbage can increase arctic fox survival and reproduction the following spring (Eberhardt *et al.* 1983a; Angerbjörn *et al.* 1991), and arctic foxes in Svalbard have responded numerically to increased numbers of caribou carcasses in winter (Fuglei, Oritsland & Prestrud 2003). A natural marine-based subsidy could likewise increase survival and reproduction. Neither of the two largest arctic fox harvests in Churchill followed peak lemming years, yet in both years polar bear body mass was quite high, implying that seals had been relatively accessible and compensated for low terrestrial prey abundance.

The importance of donor-controlled resources (like carrion) in food web dynamics is not always recognized (Polis & Strong 1996), but carrion can have a big impact on predator population dynamics and predator–prey interactions. Like arctic foxes, other predators (e.g. red fox and dingos) may switch to consuming carrion when their primary prey decline (Catling 1988; Thompson 1992; Hewson 1984), and when carrion inputs are regular this ability to switch foraging strategies may stabilize predator populations. For example, snowshoe hare declines in Alberta have little effect on numbers of coyotes in agricultural areas, which switch to consuming farm carrion, but cause a large decrease in coyotes that live in forest habitats where alternative foods are scarce (Todd 1985). Likewise, coyotes in Manitoba are largely unaffected by snowshoe hare cycles because they scavenge large ungulates killed by wolves (Paquet 1991). Yet changes in carrion availability can also affect the abundance and dynamics of predators and their prey. The increase in carrion biomass following the reintroduction of wolves to Yellowstone National Park has benefitted coyotes, bears, eagles and ravens (Crabtree & Sheldon 1999), whereas the elimination of large predators (e.g. bear, wolf and lynx) in Scandinavia reduced the amount of carrion available to small predators, which may have amplified the population cycles of their prey (Engan & Engan 1995). In the ocean, carrion is important to a wide variety of generalist predators that exploit it opportunistically, and there is evidence that the massive accumulation of human-generated carrion in the sea has profoundly altered community structure in marine environments (Britton & Morton 1994). Thus, the interaction between scavenging and predation can have a large influence on population dynamics and food webs, and the numerical response of arctic foxes in this study to changes in availability of marine carrion suggests that such interactions between ecosystems can have a similarly strong effect on food web structure and dynamics.

The tissue differences in $\delta^{13}C$ for some years highlight the importance of choosing a tissue type appropriate to the question being addressed. The enrichment in 1996 of muscle (2-month average diet) compared to liver (1 week) indicates that the overall late-winter diet included more marine foods than the week prior to capture at den sites, after arctic foxes would have returned from their nomadic winter foraging to meet mates and begin breeding. Bone collagen stable isotope ratios were much less variable among years and indicated a lower marine component on average (Fig. 2b). These collagen values probably reflected diet mostly during the animal's first summer, because although bone collagen can reflect the lifetime average dietary intake in long-lived species, it is biased toward the period of greatest growth (juvenile arctic foxes reach adult body size in August–September; Frafjord 1994). Stable isotope ratios of arctic fox collagen may reflect individual and regional dietary variation (Angerbjörn *et al.* 1994), but the turnover rate is too slow to infer short-term (less than several years) temporal variation in diet (Tieszen & Boutton 1989) and may miss diet shifts outside the main season of growth. Because Hudson Bay is generally frozen from November through June (Stirling & Lunn 1997), stable isotope ratios of muscle tissues collected in spring appear to be the best indication of the diet of arctic foxes in late winter.

The numerical response of arctic foxes to changes in the abundance of marine-based carrion (Fig. 3), in addition to their terrestrial prey, suggests that other species in the terrestrial food web can be affected by variation in marine productivity. This effect would be similar to the effect of lemming cycles on nesting birds. When lemmings decline, many arctic-nesting birds suffer higher rates of nest predation and lower reproductive success (e.g. Greenwood 1987; Summers, Underhill & Syroechkovski 1998; Bêty *et al.* 2002; Blomqvist *et al.* 2002). Changes in abundance of arctic foxes through other mechanisms can have similarly dramatic effects on nesting birds (e.g. Anthony, Flint & Sedinger 1991; Birkhead & Nettleship 1995). Thus, variation in marine foods may have a similar indirect effect on both nesting birds and microtine rodents. This effect would be greater on lemmings in coastal areas and could disrupt a pattern of regular population cycles that might otherwise occur in such areas, resulting in irregular fluctuations with occasional irruptions (e.g. Predavec *et al.* 2001). Because of the wide-ranging influence that lemming cycles can have on the reproduction, population size and/or migration patterns of many arctic predators (e.g. hawks, owls and jaegers; Pitelka, Tomich & Treichel 1955; Wiklund, Kjellen & Isakson 1998), any impact on the timing or magnitude of the lemming cycle could have cascading effects on the terrestrial food web. However, although predation may be an important influence on the population cycles of lemmings and voles (Andersson & Erlinge 1977; Hansson 1984), clearly other factors such as harsh environmental conditions or availability of quality resources may affect lemming populations (Banfield 1977; Reid & Krebs 1996), and it is beyond the scope of this paper to conclusively determine the primary forces driving lemming cycles. Yet predator–prey population cycles are often affected by a combination of top-down and bottom-up forces (Krebs *et al.* 1995), and increased predation by arctic foxes subsidized by marine resources certainly could negatively impact their prey species, representing an important link between the marine and terrestrial ecosystems.

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