FOXES AND FOOD SUBSIDIES: ANTHROPOGENIC FOOD USE BY RED AND ARCTIC FOXES,

AND EFFECTS ON ARCTIC FOX SURVIVAL, ON THE ARCTIC COASTAL PLAIN OF ALASKA

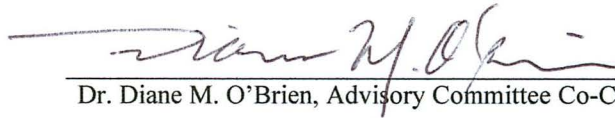By

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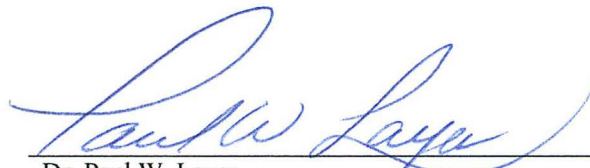
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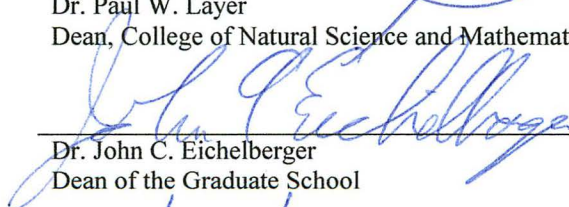
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AND EFFECTS ON ARCTIC FOX SURVIVAL, ON THE ARCTIC COASTAL PLAIN OF ALASKA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Garrett A. Savory, B.S.

Fairbanks, Alaska

December 2013

Abstract

Food subsidies have the potential to impact wildlife on the Arctic Coastal Plain of Alaska. Red foxes (*Vulpes vulpes* (L., 1758)) expanded their range into Arctic regions during the 20th century, and the availability of anthropogenic foods may have contributed to their success and persistence in the Arctic. Arctic foxes (*Vulpes lagopus* (L., 1758)) are also known to forage on anthropogenic foods in Prudhoe Bay and to forage on marine mammals on the sea ice, but it is unknown whether these strategies benefit survival of arctic foxes. This thesis examined: 1) the importance of anthropogenic foods to the diets of red and arctic foxes in Prudhoe Bay, and 2) the factors with the greatest effect on arctic fox survival, including access to food subsidies in Prudhoe Bay and on the sea ice. For the first study, stable isotopes of red and arctic fox tissues were used to infer late summer, late winter, and lifetime (for red fox only) diets. The contribution of anthropogenic foods to the diets of both species was low in late summer (~10%) but high in late winter (49%, 95% credible interval = 38-57%, of red fox diets and 37%, 95% credible interval = 29-44%, of arctic fox diets). Estimates of lifetime diet in red foxes revealed high levels of anthropogenic food use, similar to the winter diet. To characterize the extent of competition for food resources, dietary niche overlap was examined between both species by comparing isotopic niche space. Both fox species had little isotopic niche overlap but may have greater overlap between their ecological dietary niches. Availability and consumption of anthropogenic foods by red foxes, particularly in winter, may partially explain their year-round presence in Prudhoe Bay. For the second study, nest survival models and satellite collar data were used to evaluate whether multiple factors affected survival of adult and juvenile foxes. Site and sea ice use had two times more support than the other factors. Three groups of foxes were identified based on capture location and sea ice use, which corresponded to different survival rates: Prudhoe Bay foxes, NPR-A foxes that used sea ice during more than eight 2-week periods during the winter (seven 2-week periods for juveniles), and NPR-A foxes that did not use sea ice. Both adult and juvenile foxes at Prudhoe Bay had modestly higher annual survival rates, 0.50 (90% CI 0.31-0.69) and 0.04 (90% CI 0.0-0.08) respectively, than foxes at NPR-A that did not use sea ice, 0.40 (90% CI 0.18-0.62) and 0.01 (90% CI 0.0-0.04) respectively. NPR-A foxes that used sea ice extensively had the highest survival rates. Food subsidies may have far-reaching effects on red and arctic foxes on the Arctic Coastal Plain of Alaska.

Dedication

To the memory of my grandfather, Lester E. Savory Sr. (1923-2013).

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General Introduction

In the Arctic, food subsidies have the potential to impact wildlife by affecting species composition, interactions, and fitness. Two species that appear to be affected by food subsidies on the Arctic Coastal Plain of Alaska (Coastal Plain) are the arctic fox (*Vulpes lagopus* (L., 1758)) and the red fox (*Vulpes vulpes* (L., 1758)). The distribution and abundance of these two species appears to be changing (Sanzone et al. 2009; A. Stickney pers. comm.), possibly in response to the availability of anthropogenic food near human development.

Historically arctic foxes were the only abundant, widespread fox species on the Coastal Plain (Bee and Hall 1956). Arctic foxes are adapted to the extreme conditions in the arctic: they have a small compact body with short legs; reduced muzzle and ear length; deep, thick fur; countercurrent heat exchange in their paws; fur-covered foot pads; high body fat; and reduced metabolism in winter (Prestrud 1991). They are adapted to extremely low food conditions during the winter by having a decreased metabolic rate in winter relative to summer (Fuglesteg et al. 2006). In addition to these characteristics, increased availability of anthropogenic food associated with resource development, particularly in winter, may have contributed to increases in density, reduced movements, and reduced home range size in or near developed areas (Ballard et al. 2000, Pamperin 2008, Lehner 2012).

The red fox has a much broader distribution. It is the most wide spread wild canid on Earth and occupies a wide variety of habitats ranging from deserts, to forests, to human-altered habitats, farmland and urban centers (Larivière and Pasitschniak-Arts 1996). The northern range of red foxes historically extended only to the southern limit of the Arctic in North America and Eurasia potentially due to low habitat productivity, i.e. low food density (Hersteinsson and Macdonald 1992) and/or the severity and length of winter in the Arctic (Bartoń & Zalewski 2007). Since the early 20th century, the range of the red fox has expanded northward into arctic tundra habitat in Eurasia and in eastern Canada (MacPherson 1964, Chirkova 1968, Hersteinsson and Macdonald 1992, Kiener and Zaitsev 2010). In Alaska, reports of red fox occurrence along river valleys and in the northern foothills on the Brooks Range go back over 100 years but they were generally uncommon on the Coastal Plain (Nelson 1887, Bee and Hall 1956, Chesemore

1967, Eberhardt 1977). Red foxes were first observed in Prudhoe Bay, the largest oilfield on the Coastal Plain, in 1988 and have since become more common (A. Stickney, pers. comm.). The use of anthropogenic food may have facilitated red fox expansion at Prudhoe Bay.

Both red and arctic fox have been shown to consume anthropogenic foods in the Arctic. Direct observation, analysis of scat samples, and analysis of stable isotope data demonstrate that arctic fox utilize anthropogenic foods when they are available (Eberhardt 1977, Eberhardt et al. 1983, Lehner 2012). In the 1970s-80s arctic foxes were observed foraging at garbage dumpsters, soliciting food handouts from workers, and foraging near work camps in the Prudhoe bay oil fields (Eberhardt 1977, Eberhardt et al. 1982, Garrott et al. 1983). Garbage has been observed in red fox scats collected from the northern foothills of the Brooks Range during summer months, along with small mammals, birds, and insects (Eberhardt 1977). The garbage likely came from work camps during the construction of the Trans-Alaska Pipeline in the 1970s. Despite management procedures to reduce wildlife access to garbage in towns such as Barrow and in Prudhoe Bay, red and arctic foxes continue to forage at garbage accumulation sites (Pamperin et al. 2006, pers. obs.). The level of use and the consequences of using anthropogenic foods by red and arctic foxes is not well understood. Previous diet studies have primarily focused on summer diet; however, we would expect that foxes would rely more heavily on anthropogenic foods in winter than summer. Currently, few data exist for arctic fox winter diet and we are unaware of any data that exists on red fox winter diet on the Coastal Plain. The costs or benefits of the use of anthropogenic foods and other resources found in developed sites in terms of survival or reproduction of arctic or red foxes is not known.

Whether anthropogenic food subsidies increase the fitness of mesopredators in developed areas may depend on variation in their natural food (Bateman and Fleming 2012; Fischer et al. 2012). The primary prey of arctic foxes, lemmings (*Lemmus sp.* and *Dicrostonyx sp*) (Chesemore 1967; Eberhardt 1977; Garrott et al. 1983), are highly cyclic (Pitelka and Batzli 2007, Krebs et al. 2011), and may not provide adequate sustenance for foxes when prey populations are low. Arctic foxes forage widely in winter. Winter movements of arctic foxes can include several months on sea ice (Pamperin et al. 2008, Tarroux et al. 2010, Lehner 2012) to scavenge polar bear (*Ursus maritimus* Phipps, 1774) kills (Smith 1976, Roth

2002) and to hunt ringed seal pups (*Pusa hispida* (Schreber, 1775)). Although arctic foxes are highly efficient at locomotion (Fuglei and Øritsland 2003), a fox traveling extensively in pursuit of food is likely to use more energy and may have less fat reserves than a fox that does not need to travel as far (Underwood 1971). To offset the energetic costs of foraging during periods when food is scarce, arctic foxes cache food when it is in high abundance to feed on later (Samelius et al. 2007, Careau et al. 2008). In developed areas anthropogenic foods, like cached foods, can provide an alternative and reliable food source, just on a larger scale.

In Chapter 1, we examined stable isotope ratios of red and arctic fox tissues to determine the influence of anthropogenic foods in late summer and late winter diet of foxes, and red fox lifetime diet, from Prudhoe Bay. We collected tissues (hair, red blood cells, muscle and bone) from live and dead foxes from Prudhoe Bay in April and May in 2011 and 2012. Due to different metabolic turnover rates, stable isotopes in different tissues can represent diet over different time periods (Phillips and Eldridge 2006). We used stable isotope analyses of winter coat hair to infer diet during late summer, as the winter hair of both fox species is grown prior to the start of winter in September and October (Chesemore 1967, Maurel et al. 1986). We analyzed red and arctic fox red blood cells and muscle tissue to infer late winter diet. Red blood cells and muscle have similar turnover rates and isotope ratios; therefore, we used them interchangeably as measures of winter diet 1-2 months prior sampling (Roth and Hobson 2000, Lecomte et al. 2011). Bone collagen has a slow turnover period (Tieszen et al. 1983) so we used it to infer red fox lifetime diet. From the stable isotope data, we used a Bayesian dietary mixing model in SIAR (Stable Isotope Analysis in R; Parnell et al. 2010) to estimate the relative proportions of four food items (anthropogenic foods, lemmings, voles and eggs) in fox diet. We expected that red fox would have a greater proportion of anthropogenic foods in the diet than arctic fox. We also characterized the extent of dietary niche overlap between the two fox species using a model of isotopic niche space (Newsome et al. 2007).

In Chapter 2 we investigated how access to food subsidies at a developed site and on the sea ice affects the survival of arctic foxes on the Coastal Plain. We used satellite telemetry data from foxes captured in Prudhoe Bay, a developed site, and near Teshekpuk Lake, an undeveloped site in the National

Petroleum Reserve-Alaska (NPR-A), to determine if site, sea ice use, travel rate, season, sex, and age influenced survival. We estimated survival using nest survival models in program MARK (White and Burnham 1999) and determined the best approximating models by information-theoretic methods (Burnham and Anderson 2002). To obtain arctic fox survival estimates, we model-averaged the best approximating models. We expected arctic fox survival to be higher in Prudhoe Bay than in NPR-A because access to anthropogenic food waste could increase food availability and reduce the energy requirements for obtaining food in winter, thereby improving fox body condition.

This study will add to our understanding of how resource development is potentially impacting red and arctic foxes on the Coastal Plain, in order to effectively and appropriately manage these fox populations. This is important because changes in red and arctic fox abundance on the Coastal Plain will likely have ramifications for other wildlife species and for humans. Increases in red or arctic fox abundance may negatively impact avian species of conservation concern; for example red foxes, have been observed killing threatened species such as the spectacled eider (*Somateria fischeri* (Brandt, 1847)) (A. Stickney pers. comm.; B. Lawhead pers. comm.). Increased inter- or intra-specific interactions due to increased density or frequenting sites such as dumpsters and landfills that contain anthropogenic foods could increase the spread of zoonotic diseases such as rabies, thereby increasing human and wildlife disease exposure (Hueffer et al. 2011). Increased red fox abundance could also negatively affect arctic fox populations through behavioral changes or competition for or exclusion from resources such as food, and den sites. This is evidenced by the larger, more aggressive red fox dominating interspecific interactions (Rudzinski et al. 1982, Korhonen et al. 1997) and observations of red foxes killing arctic foxes (Frafjord et al. 1989, Pamperin et al. 2006, Sanzone et al. 2009). Exclusion from resources has been documented in Prudhoe Bay where all monitored active breeding dens in the 1990s were occupied by arctic fox, but since 2010 the majority has been occupied by red foxes (Sanzone et al. 2009; Stickney pers. comm.). Exclusion of arctic fox by red fox has also been observed in Fennoscandia where arctic fox have not been observed denning within 8 km of red foxes in lowland habitat that was previously occupied by arctic foxes (Tannerfeldt et al.

2002, Frafjord 2003, Selås and Vik 2007). This study examines red and arctic fox diets, and creates an important baseline for monitoring interactions between these species.

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Chapter 1

Anthropogenic food use and niche overlap between red and arctic foxes in Prudhoe Bay, Alaska. [*]

Abstract

This study examined the importance of anthropogenic foods to the diets of red (*Vulpes vulpes* (L., 1758)) and arctic foxes (*Vulpes lagopus* (L., 1758)) in Prudhoe Bay, Alaska. Red foxes expanded their range into Arctic regions during the 20th century when the growing availability of anthropogenic foods may have contributed to the success and persistence of this species in the Arctic. We collected red and arctic fox tissues during late winter and used stable isotope analysis to infer diet during late summer and late winter, estimating late summer diet from hair samples, late winter diet from red blood cell and muscle samples, and lifetime diet (for red fox only) from bone collagen. While the contribution of anthropogenic foods in late summer to both species' diets was low (~10%), the contribution in late winter was higher and varied between species (49%, 95% credible interval = 38-57%, of red fox diets and 37%, 95% credible interval = 29-44%, of arctic fox diets). Estimates of lifetime diet in red foxes based on bone collagen revealed high levels of anthropogenic food use, similar to the winter diet. Both red and arctic foxes had a high proportion of lemmings in their diet; however, red foxes were more specialized on lemmings while arctic foxes had a more diverse diet including bird eggs and/or voles. To characterize the extent of competition for food resources we examined dietary niche overlap between both species by comparing ellipses characterizing isotopic niche space. Both fox species had little isotopic niche overlap but may have greater overlap between their ecological dietary niches. Availability and consumption of anthropogenic foods by red foxes, particularly in winter, may partially explain their year-round presence in Prudhoe Bay.

Keywords: Vulpes vulpes, *Vulpes lagopus*, red fox, arctic fox, Arctic Coastal Plain, disturbance ecology, stable isotope mixing model, interspecific competition

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Introduction

In the Arctic, red foxes (*Vulpes vulpes* (L., 1758)) historically had a limited distribution with little overlap into the range of arctic foxes (*Vulpes lagopus* (L., 1758)) (Hersteinsson and Macdonald 1992). During the 20th century, red foxes expanded their range into Arctic regions of Canada and Eurasia (MacPherson 1964, Chirkova 1968, Hersteinsson and Macdonald 1992, Kiener and Zaitsev 2010). During this range expansion, red foxes were not abundant north of the Brooks Range in northern Alaska, and they were more often observed in the foothills and in river corridors rather than on the Arctic Coastal Plain (hereafter referred to as the Coastal Plain) (Bee and Hall 1956, Chesemore 1967). However, red foxes occasionally were observed in high numbers on the Coastal Plain; for example, in Barrow during the 1920s (Brower 1942), shortly after domestic reindeer (*Rangifer tarandus* (L., 1758)), were introduced to the area (Sonnenfeld 1959). Reindeer offal and wolf-killed carcasses were likely a rich food subsidy to red foxes during that time. This hypothesis is supported by Hersteinsson and Macdonald (1992) who concluded that sparsely distributed food in northern regions was one of the major limitations to widespread settlement of red foxes.

Construction of the Prudhoe Bay oil fields in the 1970s changed the Coastal Plain landscape and made anthropogenic foods available to foxes and other species. At that time, only arctic foxes were known to have established den territories in the Prudhoe Bay area (Eberhardt 1977), and they were observed foraging on anthropogenic food waste and soliciting food from people (Eberhardt 1977, Eberhardt et al. 1982, Garrott et al. 1983). In 1988 red foxes were first observed in Prudhoe Bay, and later, in the early 1990s, they were observed breeding in dens formerly used by arctic foxes (A. Stickney personal communication, 2011). By 2010, the majority of monitored dens with breeding foxes were occupied by red foxes (Sanzone et al. 2009, A. Stickney personal communication, 2011). The larger red fox can dominate and outcompete arctic fox for forage and den sites (Rudzinski et al. 1982, Korhonen et al. 1997, Angerbjörn et al. 2013), and at least one instance of a red fox killing an arctic fox has been observed in Prudhoe Bay (Pamperin et al. 2006). Ecological factors favoring the expansion of red foxes into Prudhoe Bay are

unclear, but the availability of a food subsidy, anthropogenic foods, has likely contributed to their success and persistence there.

Use of anthropogenic foods by red fox could increase fox densities and the spread of zoonotic diseases, which are concerns for human and wildlife health. Diseases such as rabies could be spread more quickly in developed areas as a result of higher densities of both red and arctic foxes, and of foxes interacting at sites such as dumpsters and landfills (Hueffer et al. 2011). Red foxes would also have the potential to have a greater impact on prey populations than arctic foxes, if population densities were equal, because they are larger and require more energy than arctic foxes (Hersteinsson and Macdonald 1992).

This study examines the importance of anthropogenic foods to the late summer and late winter diets of both red and arctic foxes, and to the lifetime diet of red foxes, in Prudhoe Bay, Alaska. Stable isotopes in different tissues represent different time periods of diet, due to variable rates of tissue turnover (Phillips and Eldridge 2006). We captured and collected foxes during late winter/early spring and used stable isotope data from analysis of their winter coat hair to infer diet during late summer, as the winter hair of both fox species is grown before winter begins in September and October (Chesemore 1967, Maurel et al. 1986). We used stable isotope data from analysis of red blood cells and muscle samples to infer late winter diet. Red blood cells and muscles have similar turnover rates and isotope ratios; therefore, we use them interchangeably as measures of the winter diet over the 1-2 months prior to sampling (Roth and Hobson 2000, Lecomte et al. 2011). We also analyzed the stable isotopic composition of bone collagen in red foxes, as an averaged measure of lifetime diet (Tieszen et al. 1983). We described the use of anthropogenic foods in the diet using Bayesian dietary mixing models, with the expectation that red fox would have a greater proportion of anthropogenic foods in their diet compared to the native arctic fox. To characterize competition for food resources between red and arctic foxes, we also examined dietary niche overlap using stable isotope data. The isotopic composition of an animal is a reflection of available dietary items it consumes in its habitat, and thus its niche (Layman et al. 2007). Thus, metrics describing the isotopic distribution of individuals of a species have been proposed as an indirect measure of niche-space (Newsome et al. 2007).

Materials and Methods

Study Site and Sample Collection

This study was conducted in Prudhoe Bay, Alaska, USA (70˚15'N, 148˚22'W). The Coastal Plain, including Prudhoe Bay, is characterized by flat treeless tundra. Prudhoe Bay has extensive infrastructure, including oil wells, pipelines, roads and buildings, summing to approximately 88 km^2 in total surface area (Gilders and Cronnin 2000). Thousands of people work in Prudhoe Bay to support oil extraction activities. Food is imported and any food not consumed by people is disposed of in dumpsters and ultimately at a landfill in Prudhoe Bay. Dumpsters and the landfill are designed to be restrictive to bear (*Ursus spp.*) access. Despite these precautions, food waste is accessible to foxes at dumpsters due to the dumpster doors not being closed and food waste not making it completely into the dumpster; and at the landfill due to gaps in the fence, snow drifting over the fence, and gates not always being closed (personal observation).

A total of ten red and ten arctic foxes were captured in April and May 2011 and 2012 for collection of hair and blood samples. In addition to sampling live foxes, we opportunistically sampled hair, muscle, and bone samples from nine red and three arctic foxes that were killed in 2010 – 2012 for harvest or control purposes and donated to this study. A full complement of tissue samples could not be collected from several foxes due to sampling constraints, including early recovery from anaesthesia, which prohibited blood sampling, and donated carcasses either lacking a pelt or having a collection date outside of the April/May time frame (which prohibited assessment of late summer and late winter diets, respectively). Thus, our study totals included 13 measurements of late summer diet and 13 measurements of late winter diet in red foxes, 10 measurements of late summer diet and 11 measurements of late winter diet in arctic foxes, and eight measurements of lifetime diet of red foxes.

Fox Capture and Sampling Methods

We used #1 ½ softcatch footholds (Oneida Victor Inc. Ltd., Euclid, OH, USA) and cage traps (model 208, Tomahawk Live Trap Company, Tomahawk, WI, USA) to capture foxes. Traps were set in

areas with high fox activity or sign throughout the Prudhoe Bay area, including near dens, dumpsters, and at the landfill, and were checked at least twice a day. Foxes captured in the foothold traps were restrained using animal graspers (Tomahawk Live Trap Company, Tomahawk, WI, USA) to safely inject with anaesthetics. Foxes captured in cage traps were transferred to a restraint module (Tomahawk Live Trap Company, Tomahawk, WI, USA) for injection of anaesthetics. Foxes were anaesthetised with a mixture of ketamine and xylazine: 60-100 mg of ketamine and 10 mg of xylazine for red foxes, and 20-40 mg of ketamine and 10 mg of xylazine for arctic foxes. Foxes were muzzled while anaesthetised.

We shaved a small section on each fox's neck so we could withdraw 4 mL of blood from the jugular vein. The hair from the shaved section was collected, placed in a coin envelope, and stored at -20 ˚C. The blood was drawn into an EDTA vial, centrifuged to separate the red blood cells from the plasma, and stored at -20 ˚C. The EDTA vials would not have significantly affected red blood cell $\delta^{13}C$ or $\delta^{15}N$ values (Wilkinson et al. 2007). Once recovered from the effects of anaesthesia, foxes were released near the capture site. Hair samples were collected from donated fox carcasses using similar methods. Muscle samples from carcasses were taken from either the jaw or leg, placed into plastic bags, and stored at -20 ˚C. Bone samples were taken from either the mandible or leg bones by using a Dremel tool (Dremel, Racine, Wisconsin, USA) to cut a ~35 mg piece from the bone. Fox capture and sample collection was approved by University of Alaska Fairbanks Institutional Animal Care and Use Committee (#230160-5) and by Alaska Department of Fish and Game (Scientific Permits 11-123 and 12-119).

Specimen Preparation and Analysis

Red blood cell and muscle tissue was either lyophilized or dried in an oven at 60 ˚C for at least 24 hours. Once dried, muscle samples were homogenized using a mortar and pestle. Hair samples were cleaned using three successive 30-minute rinses with sonication in deionized water, a 2:1 mixture of methanol/chloroform, and deionized water; and then homogenized using a ball mill.

Bone samples were sonicated in deionized water to remove debris, soaked in chloroform for two 8 hour sessions to remove lipids, rinsed with deionized water, and air-dried. To separate the collagen and mineral portions of the bone, samples were demineralized by soaking in an HCl-H_2O solution until they became translucent and then rinsed with deionized water. To separate collagen from other proteins and organic compounds, the bone samples were gelatinized by placing the collagen samples in a culture tube with an HCl-H_2O solution (pH = 3.0 - 4.0) and heating at 70 ˚C, under a stream of nitrogen, to dissolve the collagen. After centrifugation the supernatant was lyophilized to retrieve the collagen.

Between 0.1 and 0.5 mg of red blood cell, muscle, hair, and collagen samples were placed in tin capsules, which were crushed and loaded into an autosampler. Samples were analyzed for stable carbon and nitrogen isotopes at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks, using continuous-flow isotope ratio mass spectrometry with a Costech ECS4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA) interfaced to a Finnigan Delta Plus XP isotope ratio mass spectrometer via the Conflo III interface (Thermo Fisher Scientific, Waltham, MA, USA). Isotope ratios were expressed in δ notation as per mil (‰) abundance of heavy isotope relative to a standard:

$$\delta X = ((R_{sample}/R_{standard})-1) \times 1000‰,$$

where X = ^{13}C or ^{15}N and R_{sample} and $R_{standard}$ are the ratios of heavy to light isotope of the sample and the standard, respectively. Standards are Vienna - Pee Dee Belemnite for $\delta^{13}C$ values and atmospheric N for $\delta^{15}N$ values. These standard values are measured using a laboratory standard (peptone) calibrated against several certified reference materials. The laboratory standard was also measured after every 10th sample to evaluate precision and accuracy of analyses. Precision was within 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$, and accuracy was within 0.02‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Statistical Analysis

We tested whether the $\delta^{13}C$ and $\delta^{15}N$ values of fox red blood cells/muscle and hair differed by species, by season, or by the interaction of species and season using MANOVA with Pillai's trace statistic.

Univariate normality, outliers, and homogeneity of variance for $\delta^{13}C$ and $\delta^{15}N$ values were first checked with residual plots and boxplots. Multivariate outliers were checked with a Q-Q plot of Mahalanobis distances.

To evaluate the proportions of natural and anthropogenic foods in red and arctic fox diets, we used a mixing model in the SIAR package (Stable Isotope Analysis in R; Parnell et al. 2010) in program R (v.3.0.0, R Development Core Team 2013). SIAR uses a Bayesian statistical framework to estimate the proportion of selected dietary endpoints in the diet, where each dietary endpoint is a particular food or a specified food group. We report the mode and 95% credible interval for the proportion of each dietary endpoint in the diet, as follows (mode; 95% credible interval) (Parnell et al. 2010).

We selected four dietary endpoints based on literature review of red and arctic fox diet: i) lemmings (*Lemmus sibiricus* (Kerr, 1792) and *Dicrostonyx groenlandicus* (Traill, 1823)), ii) voles (*Microtus oeconomus* (Pallas, 1776)), iii) eggs (an average of shorebird and goose), and iv) anthropogenic foods (Table 1). The three natural food categories were selected based on prior fox diet studies from the Coastal Plain, which showed that these were the most common foods found in fox scat (Chesemore 1967, Eberhardt 1977, Garrott et al. 1983). The isotopic values for these endpoints were taken from the literature or from unpublished analysis of samples collected on the Coastal Plain (Table 1). We used an integrated isotopic endpoint for anthropogenic foods based on analysis of hair samples (using the 2 mm closest to the scalp) from six workers at the Prudhoe Bay oil field that had been resident at Prudhoe Bay for at least two weeks (Lehner 2012). Human hair isotope ratios were adjusted to account for the isotopic fractionation between diet and human hair, estimated to be 1.4 for $\delta^{13}C$ values (Schoeller et al. 1986) and 5.2 for $\delta^{15}N$ values (O'Connell et al. 2012).

Using mixing models to estimate diet requires that fox tissue $\delta^{13}C$ and $\delta^{15}N$ values be adjusted to account for diet to tissue isotope fractionation (DeNiro and Epstein 1978, 1981). We used values from Roth and Hobson (2000) for red foxes (red blood cells: $\Delta\delta^{13}C = 0.7‰$ and $\Delta\delta^{15}N = 2.6‰$; muscle: $\Delta\delta^{13}C = 1.1‰$ and $\Delta\delta^{15}N = 3.3‰$; and hair: $\Delta\delta^{13}C = 2.6‰$ and $\Delta\delta^{15}N = 3.2‰$) and from Lecomte et al. (2011) for arctic foxes (red blood cells: $\Delta\delta^{13}C = 0.5‰$ and $\Delta\delta^{15}N = 1.8‰$; muscle: $\Delta\delta^{13}C = 0.4‰$ and $\Delta\delta^{15}N = 1.8‰$;

and hair: $\Delta\delta^{13}C = 2.2‰$ and $\Delta\delta^{15}N = 3.3‰$). No fractionation estimate of fox bone collagen exists so we used the mean fractionation estimates ($\Delta\delta^{13}C = 1.0‰$ and $\Delta\delta^{15}N = 3.6‰$) calculated from wolf (*Canis lupus* L., 1758) bones (Bocherens and Drucker 2003). Adjusted stable isotope ratios were used in all analyses due to different fractionation values between tissues and species.

We evaluated the dietary niches and potential for competition over food resources between red and arctic foxes using isotopic models for characterizing niche overlap (Jackson et al. 2011). We used the SIAR package in program R to fit standard ellipses corrected for small sample size (SEA_C) to the stable isotope data to calculate areas of "isotope niche space" for late summer and late winter diets in both red and arctic foxes. A standard ellipse describes the points around the mean of a bivariate distribution that are analogous to the mean ± one standard deviation (SD) for univariate data. From the SEA_C's, we calculated the area of isotopic overlap as described by Jackson et al. (2011), and percent of overlap (% overlap = area of overlap / group 1 SEAc + group 2 SEA_C − area of overlap, where group = red or arctic fox SEA_C in either late summer or late winter), between species and seasons. Although this metric is not equivalent to ecological niche space per se, it does provide an objective measure of the extent of dietary overlap between species when the diet consists of multiple, isotopically-distinct foods (Jackson et al. 2011).

Results

The $\delta^{13}C$ and $\delta^{15}N$ values of red and arctic fox tissues are presented in Table 2. Both $\delta^{13}C$ and $\delta^{15}N$ values varied significantly by species ($F_{[2,42]} = 11.0$, $P < 0.001$) and by season ($F_{[2,42]} = 35.6$, $P < 0.001$). The interaction between species and season was marginally non-significant for $\alpha = 0.05$ ($F_{[2,42]} = 2.8$, $P = 0.07$). The $\delta^{13}C$ and $\delta^{15}N$ values for red and arctic fox tissues (winter = red blood cells or muscle, summer = hair) are corrected for fractionation and plotted with food items in Figure 1.

The mixing model analysis in SIAR revealed major differences in the proportion of dietary items in fox diet between seasons as well as between species (presented as mode, 95% credible interval) (Figure 2). During late summer, both red and arctic foxes used lemmings heavily, although use by red foxes (75%,

58-87%) was greater than that by arctic foxes (50%, 34-67%). Anthropogenic foods made up a small portion of the late summer diet for both red (10%, 4-17%) and arctic foxes (12%, 6-20%). Voles and eggs were a small component of late summer diet in red foxes. In arctic foxes, voles were a moderate component of the late summer diet (18%, 0-41%) and eggs were a small component. Due to the isotopic similarity between voles and eggs, the model had some difficulty distinguishing between them; consequently, the estimated use for both diet items were inversely related to each other (r = -0.67).

Fox diet during late winter differed considerably from that of late summer for both species (Figure 2). There was a substantial decrease in the proportion of lemmings in both red and arctic fox diets, although lemming use by red foxes (38%, 18-52%) was still higher than that by arctic foxes (13%, 0-31%). Use of anthropogenic foods was higher for red foxes (49%, 38-57%) than by arctic foxes (37%, 29-44%). There was evidence for egg use (30%, 2-45%) and some vole use (22%, 0-45%) by arctic foxes during the late winter, although estimated use of these diet items was again collinear (r = -0.66). Red foxes had little to no vole or egg use in their late winter diets.

The lifetime diet of red foxes as estimated from analyses of bone collagen was similar to their diet during late winter. The proportion of lemmings in their diet was 37% (11-51%). Use of anthropogenic foods was 52% (40-60%). There appeared to be little to no use of voles or eggs.

SEA_C's were smaller for both red and arctic foxes in late summer (red fox: $2.03‰^2$; arctic fox: $1.32‰^2$) than in late winter (red fox: $4.68‰^2$; arctic fox: $3.94‰^2$) (Figure 3). Isotopic niche overlap estimated that there was relatively little overlap between red and arctic fox diets in either late summer (area of overlap = $0.31‰^2$; 10% overlap) and in late winter (area of overlap = $0.62‰^2$; 8% overlap) (Figure 3). Within each species there was no seasonal overlap of isotope niche space.

Discussion

We found that red foxes living in Prudhoe Bay consumed anthropogenic food resources year-round, with about a five-fold greater use of anthropogenic foods in late winter than in late summer.

Estimates of lifetime diet based on bone collagen support substantial use of anthropogenic foods throughout their lifespan; therefore, the availability and the consumption of these foods by red foxes may at least partially explain their year-round presence in Prudhoe Bay. In addition to anthropogenic foods, the red fox in our study were highly specialized on lemmings. This suggests the use of anthropogenic food would be particularly important to red foxes in years when lemmings are in the low phase of their cycle.

Like red foxes, arctic foxes used anthropogenic foods more heavily in the winter; however, arctic fox diets were more diverse than red fox diets during both seasons, including greater use of voles and/or eggs. Our estimates of lemming and garbage use by arctic foxes during late summer are similar to prior estimates from Prudhoe Bay. Eberhardt (1977) found that garbage debris occurred in 0-13%, and lemming remains occurred in 35-50%, of arctic fox scat collected during August and September of 1974 and 1975. Arctic foxes, during the same study, were found to have moderate use of eggs and very low use of voles (Eberhardt 1977). Considering that our estimates of vole and egg consumption were collinear, arctic foxes in our study may have actually consumed mostly eggs rather than voles.

There is a long history of human activity providing food subsidy to red foxes on the Coastal Plain and other Arctic regions, with concomitant increases in red fox abundance. In Barrow, Alaska, during the winter of 1927-28, local resident Charles Brower noted an atypical peak in the red fox population in this way: "an unusual influx of red foxes made white ones {arctic foxes} scarce" (Brower 1942). At that time the domestic reindeer population, introduced in this region in 1897 as a food and income source for the people of Barrow, neared 15 000 – 20 000 (Sonnenfeld 1959). Although there were an indeterminate number of red foxes in Barrow at that time, it is plausible that a red fox population with an apparently higher density was maintained by scavenging from reindeer offal piles and wolf-killed carcasses. The Barrow reindeer industry collapsed in the 1950s (Sonnenfeld 1959) and red foxes are currently uncommon in Barrow. In northern Fennoscandia, increasing reindeer husbandry and the availability of reindeer carcasses and offal may have contributed to red fox range expansion and exclusion of arctic foxes during the 20th century (Killengreen et al. 2011, Angerbjörn et al. 2013). Gallant et al. (2012) suggest that access to anthropogenic food was the primary reason the red fox population could expand and persist on the

Coastal Plain of Yukon Territory. Our finding of high levels of anthropogenic food use by red foxes resident in Prudhoe Bay is consistent with this hypothesis.

It is unknown why red foxes are currently present in elevated densities in Prudhoe Bay but not in Barrow. In Barrow, anthropogenic food is currently available to scavenging wildlife at the landfill and at offal piles from subsistence hunter's harvests (personal observation; B. Person, personal communication). One possibility is that the Dalton Highway, which originates south of the Brooks Range and terminates in Prudhoe Bay, facilitated red fox expansion northward by providing foxes the opportunity to forage on hunter's caribou offal piles (B. Person, personal communication) and food handouts from people. Eberhardt (1977) found that red fox scat in the foothills of the Brooks Range along the Dalton Highway during the summer of 1974 and 1975 had a 6% occurrence of garbage debris in it. It is unknown what facilitated red fox expansion to Barrow in the 1920s; one plausible scenario is that red foxes could have followed wolves northward to the domestic reindeer located at Barrow and foraged opportunistically at wolf kill sites along the way.

Despite the accumulated evidence that red fox utilize anthropogenic foods in northern areas where they have expanded their range, it remains unclear whether they require anthropogenic foods to survive and reproduce in these locations or whether they are using anthropogenic foods opportunistically. This could be tested by removing anthropogenic foods from the landscape. In Israel, elimination of access to anthropogenic food waste at two villages caused severe declines in red fox survival (Bino et al. 2010). If red foxes rely on anthropogenic foods to overwinter in Prudhoe Bay, limiting access to sites where anthropogenic foods are most readily available could be an effective management tool for controlling or eliminating the local red fox population.

Our dietary analyses using mixing models suggested considerable overlap in food resources between red and arctic foxes; however, an isotopic niche model suggested that dietary niche overlap was low. Although the niche model has fewer assumptions than mixing models (Parnell et al. 2010, Jackson et al. 2011), inferences relating isotopic niche to ecological dietary niche can be difficult to interpret (Bearhop et al. 2004, Newsome et al. 2007, Flaherty and Ben-David 2010). In our system, small differences in

anthropogenic food intake may have disproportionate effects on estimated isotopic niche difference because anthropogenic foods are so isotopically distinct from the rest of the diet ($\Delta\delta^{13}C \geq 8$). It is also possible that niche area was underestimated due to the relatively small sample sizes in this study (Syväranta et al. 2013). Alternatively, our mixing models may have overestimated dietary overlap between red and arctic foxes by omitting minor dietary items, as the number of diet items that could practically be included in our mixing model was limited by small sample size. When combined, the mixing and niche overlap models show a scenario in which the two fox species have similar use of abundant resources (anthropogenic foods and lemmings) but differ enough in the use of these and less common foods that their foraging niches are moderately distinct.

Although arctic foxes are known to venture on the sea ice to forage on seal pups and carcasses during winter (Smith 1976, Stirling and Archibald 1977, Roth 2003), we did not include marine foods as a dietary endpoint in this study, for two reasons: i) telemetry data from arctic foxes in Prudhoe Bay show no use of sea ice, which is required for access to seal carcasses and pups (Pamperin 2008, Lehner 2012), and ii) preliminary mixing models that included ringed seal (*Pusa hispida* (Schreber, 1775)) as a dietary endpoint found no contribution to either red or arctic fox diets, consistent with the low tissue $\delta^{15}N$ values found in this study. We therefore omitted ringed seal from our estimations of diet because the inclusion of this item significantly increased the uncertainty with which the contribution of other dietary items was estimated.

In summary, we found that both red and arctic foxes in Prudhoe Bay use anthropogenic foods, particularly in late winter when 49% of red fox diet and 37% of arctic fox diet was attributed to anthropogenic foods. Even if this behaviour is opportunistic, it suggests future development on the Coastal Plain could facilitate further population increases and range expansion of red foxes. We found that red and arctic foxes occupy moderately distinct dietary niches. It is unknown if arctic foxes exhibited a moderately different niche from red foxes because they were excluded from prime foraging habitat, or if red foxes were unable to fully use the dietary niche occupied by arctic foxes because they lacked the adaptations required to exploit a greater array of diet items. Managers in developed areas on the Coastal Plain, especially on

newly developed lands, should strive to minimize the availability of food waste to foxes to minimize impact to the Arctic ecosystem.

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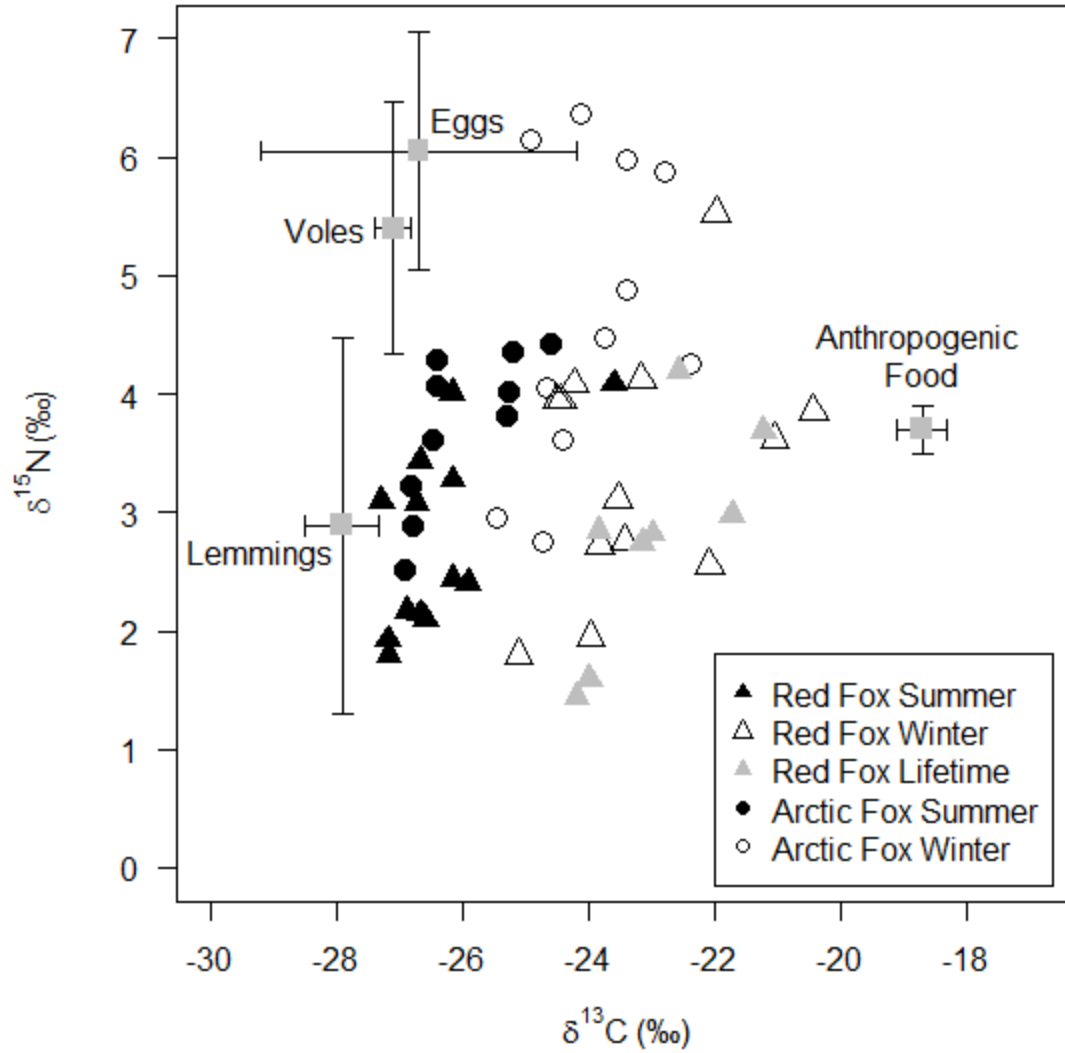Figure 1. Stable carbon and nitrogen isotope values of red and arctic fox tissues, plotted with diet items, from Prudhoe Bay, Alaska. Summer isotope ratios are from hair, winter isotope ratios are from red blood cells or muscle, and lifetime isotope ratios are from bone collagen. Fox stable isotope ratios have been corrected for fractionation to allow for direct comparison between fox species, tissues, and diet items.
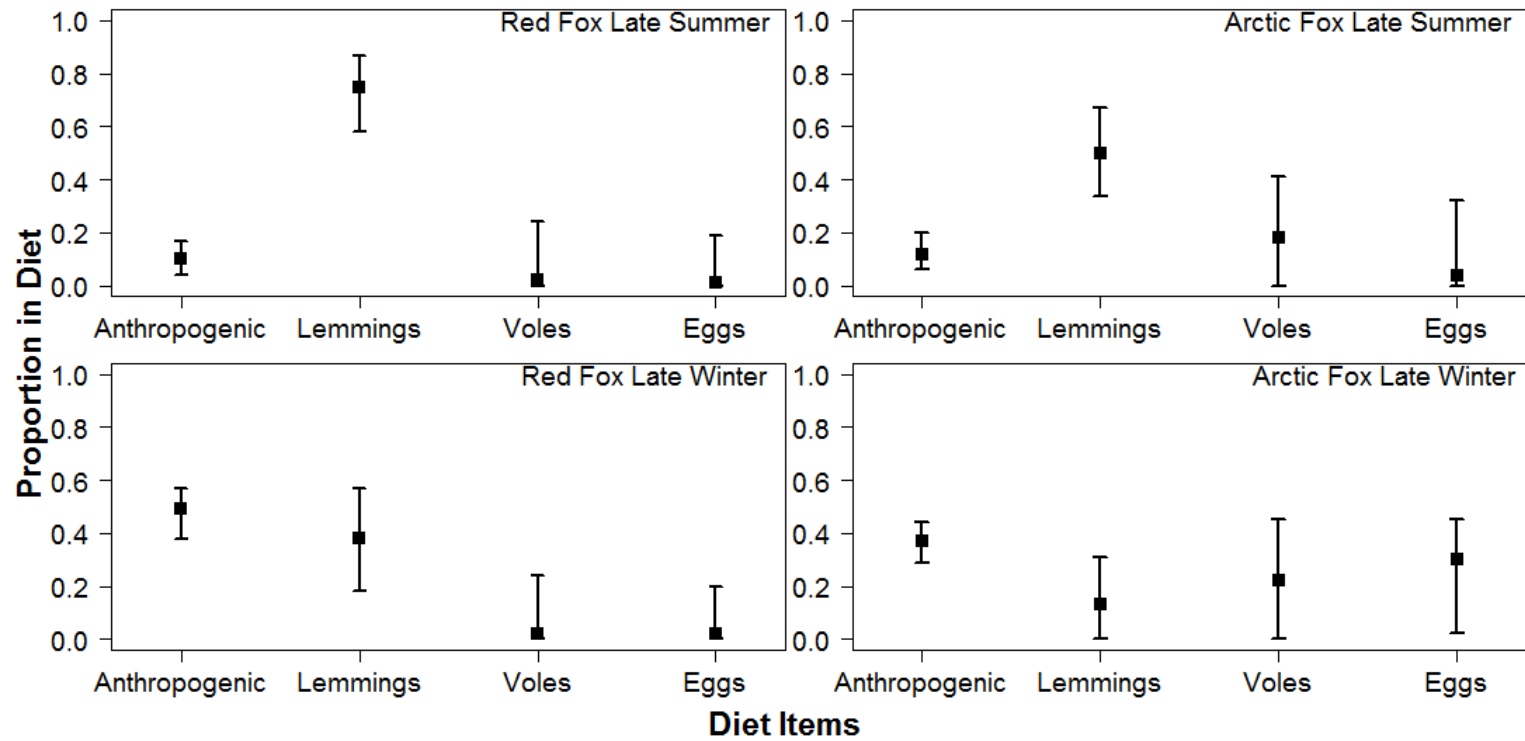
Figure 2. Proportion of diet items in red and arctic fox diets in late summer and in late winter. Squares represent mode and error bars represent 95% credible interval for each dietary proportion.

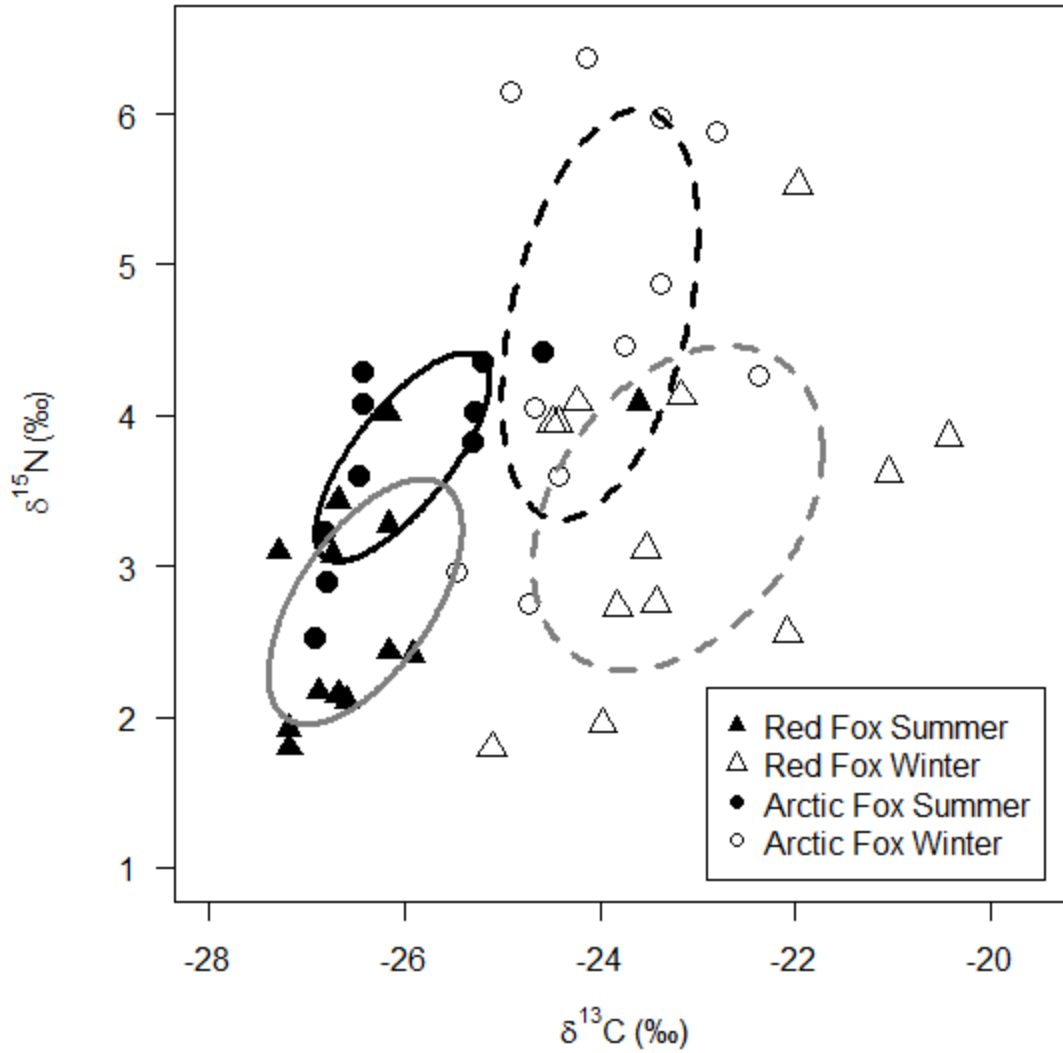Figure 3. Isotope niche space, represented by standard ellipses of carbon and nitrogen stable isotope ratios for red and arctic foxes. Grey and black lines show standard ellipses for red and arctic foxes, respectively. Solid lines and dashed lines denote isotope niche space for late summer and late winter, respectively. Stable isotope ratios have been corrected for fractionation to allow comparison.

Table 1. Stable isotope ratios of dietary endpoints used in the mixing model analysis of red and arctic fox diet in Prudhoe Bay, Alaska, USA.

Dietary Endpoint	N[*]	δ¹³C (‰) ± 1 SD	δ¹⁵N (‰) ± 1 SD
Lemmings[†]	7	-27.9 ± 0.6	2.9 ± 1.6
Voles[†]	7	-27.1 ± 0.3	5.4 ± 1.1
Eggs[‡,§]	392	-26.7 ± 2.5	6.1 ± 1.0
Anthropogenic Foods[‖]	6	-18.7 ± 0.4	3.7 ± 0.2

[*] Sample size
[†]Alaska Department of Fish and Game, unpublished data
[‡]Gauthier et al. 2003
[§]Jamieson 2009
[‖]Lehner, unpublished data

Table 2. Stable isotope ratios, not corrected for fractionation, of red and arctic fox hair, red blood cells, muscle, and bone collagen from Prudhoe Bay, Alaska, USA.

Species	Tissue[*]	Time Period	N[†]	$\delta^{13}C$ (‰) ± 1 SD	$\delta^{15}N$ (‰) ± 1 SD
Red Fox	Hair	Late summer	13	-23.8 ± 0.9	6.2 ± 0.8
	Red Blood Cells	Late winter	9	-22.4 ± 1.5	5.5 ± 0.7
	Muscle	Late winter	4	-22.4 ± 1.0	7.7 ± 0.6
	Bone Collagen	Lifetime	8	-22.0 ± 1.0	6.4 ± 0.9
Arctic Fox	Hair	Late summer	10	-23.8 ± 0.8	7.1 ± 0.6
	Red Blood Cells	Late winter	8	-23.6 ± 0.9	5.9 ± 1.0
	Muscle	Late winter	3	-23.6 ± 0.9	7.9 ± 0.2

*Hair, red blood cells, and muscle were in April/May 2011-12, and red fox bone collagen was collected over multiple months in 2010-2012
†Sample size

Chapter 2

The effect of an oil field and sea ice use on arctic fox survival on the Arctic Coastal Plain of Alaska.[*]

Abstract

Mesopredators often increase their fitness by taking advantage of anthropogenic food in developed areas. In Prudhoe Bay, Alaska, the largest oil field in northern Alaska, arctic fox (*Vulpes lagopus*) are known to forage on anthropogenic foods but it is not known if this benefits fox survival. The primary objective of this study was to determine whether arctic fox survival was higher at Prudhoe Bay than at an undeveloped area. Using nest survival models and satellite collar data we evaluated whether site, sea ice use, season, travel rate, and sex affected survival of adult or juvenile foxes. Site and sea ice use had two times more support than the other factors. Three groups of foxes were identified based on capture location and sea ice use, which corresponded to different survival rates: Prudhoe Bay foxes, NPR-A foxes that used sea ice during more than eight 2-week periods during the winter (seven 2-week periods for juveniles), and NPR-A foxes that did not use sea ice. Both adult and juvenile foxes at Prudhoe Bay had modestly higher annual survival rates, 0.50 (90% CI 0.31-0.69) and 0.04 (90% CI 0.0-0.08) respectively, than foxes at NPR-A that did not use sea ice, 0.40 (90% CI 0.18-0.62) and 0.01 (90% CI 0.0-0.04) respectively. NPR-A foxes that used sea ice extensively had the highest survival rates.

Introduction

        Mesopredators often thrive in developed areas by exploiting anthropogenic food waste that can subsidize their diet and increase fitness (Bateman and Fleming 2012; Fischer et al. 2012). For example, raccoons (*Procyon lotor*) that have access to anthropogenic food waste in urban areas occur at higher densities (Riley et al. 1998; Smith and Engeman 2002; Prange et al. 2003) and have higher survival than raccoons in rural areas (Riley et al. 1998; Prange et al. 2003). Raven (*Corvus corax*) survival (Webb et al. 2004; Webb et al. 2011) and fledging success (Kristan and Boarman 2007) is positively correlated with use of areas that have anthropogenic food. Access to anthropogenic food waste can be particularly beneficial in more extreme environments such as the Arctic where food availability can vary dramatically through prey cycles and among seasons. On the Arctic Coastal Plain of Alaska (hereafter referred to as Coastal Plain) fledging success of glaucous gulls (*Larus hyperboreus*) is positively correlated with consumption of anthropogenic foods (Weiser and Powell 2010). In addition, man-made structures also provide platforms for nesting or roosting that have been implicated as a cause of increased raven abundance around oilfields in the Coastal Plain (Backensto 2010).

        Arctic foxes (*Vulpes lagopus*) may be expected to benefit from access to anthropogenic food waste because their primary prey, lemmings (*Lemmus sp.* and *Dicrostonyx sp*) (Chesemore 1967; Eberhardt 1977; Garrott et al. 1983), are highly cyclic (Pitelka and Batzli 2007; Krebs et al. 2011) and may not provide adequate sustenance for foxes when the population of prey is low and foxes switch to alternative foods such as birds and eggs (Stickney 1991; Elmhagen et al. 2000). Arctic foxes are adapted to extremely low food conditions during the winter by having a lower metabolic rate in winter relative to summer (Fuglesteg et al. 2006). They also exhibit foraging strategies to ensure they have enough food year-round during food scarcities. Arctic foxes will venture out on the sea ice for several months (Pamperin et al. 2008; Tarroux et al. 2010) to scavenge polar bear (*Ursus maritimus*) kills (Smith 1976; Roth 2002) and to hunt ringed seal pups (*Pusa hispida*), but this can require travelling long distances (Pamperin et al. 2008; Lehner 2012). Although arctic foxes are highly efficient at locomotion (Fuglei and Øritsland 2003), a fox traveling in search of food has higher energetic demands and may have less fat reserves than a sedentary well-fed fox

(Underwood 1971). To potentially offset the energetic costs of foraging during periods when food is scarce, arctic foxes cache food when the supply is high (Samelius et al. 2007; Careau et al. 2008). In developed areas anthropogenic foods, like cached foods, can provide an alternative and predictable food source.

Arctic foxes have been shown to consume anthropogenic food at Prudhoe Bay, the largest oil field on Alaska's Coastal Plain (Eberhardt 1977; Garrott et al. 1983; Lehner 2012). During the construction of Prudhoe Bay in the 1970s, foxes were observed consuming garbage and soliciting food from people (Eberhardt 1977; Eberhardt et al. 1982; Garrott et al. 1983). Fox access to garbage has been reduced in recent years through implementation of garbage management practices aimed at reducing access to garbage by bears (Pamperin 2008) and through training oil field employees not to feed wildlife. Despite these efforts, foxes still access some garbage accumulation sites, including the landfill, and continue to solicit food from people (pers. obs.). Recent studies have estimated that 37 to 59 % of the winter diet of Prudhoe Bay arctic foxes comes from anthropogenic sources (Chapter 1, this thesis; Lehner 2012). Access to anthropogenic foods may have contributed to higher density of denning arctic foxes in Prudhoe Bay than in outlining areas (Eberhardt et al. 1983; Ballard et al. 2000) prior to recent declines thought to be related to the presence of red foxes (*Vulpes vulpes*) (Sanzone et al. 2009; A. Stickney pers. comm.) . The effect of anthropogenic foods confers on survival or productivity of foxes has not been investigated.

The primary objective of this study was to determine if survival rates of arctic foxes were higher in the heavily developed area of Prudhoe Bay than in the National Petroleum Reserve-Alaska (NPR-A), an undeveloped site on the Coastal Plain. We expected fox survival to be higher in Prudhoe Bay because access to anthropogenic foods would increase food availability and reduce the energy requirements for obtaining food, thereby improving fox body condition. Energetic demands associated with travel while searching for winter foods are greatly reduced for foxes in Prudhoe Bay compared to foxes in NPR-A, which traveled distances six-fold further than foxes wintering at Prudhoe Bay (Lehner 2012). We also evaluated whether sea ice use, travel rate, season, or sex affected survival rates of foxes. Scavenging and hunting on the sea ice is likely to be less predictable but may provide greater rewards in terms of larger and more energy dense rations when food is obtained. Travelling greater distances in search of food would

require more energy and could be expected to reduce survival given equivalent rewards. We predicted

survival to be lower during winter than during summer because snow pack reduces access to lemmings and

migratory prey species are no longer available.

Materials and Methods

Study Area

The Coastal Plain of Alaska comprises 230,000 km^2 of flat, treeless tundra adjacent to the

Beaufort and Chukchi Seas. Sea ice connects the Coastal Plain to the polar ice cap usually from November

until June (Wendler et al. 2010). The Coastal Plain is mostly undeveloped and unsettled by humans, but

includes traditional Iñupiat subsistence hunting and fishing grounds that are still used today. It also

encompasses the NPR-A (Figure 1), a vast area (~92,300 km^2) set aside for future development and oil

extraction (BLM 2008).

Most of the current oil and gas production on the Coastal Plain occurs in an area (~6000 km^2)

commonly referred to as Prudhoe Bay, which lies adjacent to the Beaufort Sea between the Colville and

Sagavanirktok Rivers (Figure 1). The oil field began construction in 1969 and started production in 1977

after the completion of the Trans-Alaska Pipeline (Gilders and Cronnin 2000). Many facilities and

infrastructure (e.g. roads, pipelines, and buildings) have been constructed to aid oil extraction; totaling

about 88 km^2 of disturbed surface area (Gilders and Cronnin 2000). Thousands of people work in Prudhoe

Bay to support oil extraction activities. All food is shipped or trucked in and food waste is disposed of and

transferred from dumpsters to the landfill, where it may be scavenged by wildlife despite fencing around

the landfill (Pamperin et al. 2006; Sanzone et al. 2009; Weiser and Powell 2011; Lehner 2012).

Fox Capture and Collaring

Arctic foxes were captured in Prudhoe Bay (70˚15'N, 148˚22'W) and near Teshekpuk Lake

(70˚34'N, 153˚30'W) in the NPR-A (Figure 1) in August and September of 2004, 2005, and 2009. We

trapped foxes using cage traps (Model 208, 106 x 38 x 38 cm, Tomahawk Live Trap, Tomahawk,

Wisconsin, USA) baited with canned fish and set in locations with high fox activity near dens and dumpsters. In Prudhoe Bay, we used the road system to access trapping sites and checked traps three times per day. The NPR-A is roadless and we used a helicopter to deploy and check traps daily.

We transferred captured foxes from the cage trap to a restraint cage (Tru-Catch Traps, Belle Fourche, South Dakota, USA) to facilitate anesthesia. Foxes were then sedated with an injection of 7 mg/kg of ketamine hydrochloride and 3.5 mg/kg xylazine hydrochloride into muscle tissue at the hip. We affixed satellite collars to the foxes once they were anesthetized. We recorded sex, weight, and determined age class as juvenile (< 1 year old) or adult (>1 year old) by canine appearance and eruption (Macpherson 1969; Frafjord and Prestrud 1992). Foxes were allowed to recover before being released near their capture site. All fox capture and handling methods were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (Assurance Nos. 05-45 and 149496-4) and by the Alaska Department of Fish and Game (Permit Nos. 04-105, 05-007, and 09-140).

We used two models of satellite collars in this study; model A-3110, 185g, or model ST-20 TAW-4110, 185 g, Telonics, Inc., Mesa, Arizona, USA. Model A-3110 collars were used in both sites in 2004 and 2005, and in Prudhoe Bay in 2009. Model ST-20 TAW-4110 collars were used in NPR-A in 2009. The two models of satellite collars were programmed to transmit location data at different time intervals (duty cycles). The model A-3110 collars transmitted location data for four hours once every four days, the model ST-20 TAW-4110 collars for four hours once every three days. The satellite collars also contained temperature and activity sensors to aid in identifying mortality events. Batteries for both collar models were designed to be viable for one year, however some remained viable for two years.

Location data were collected by CLS America, Inc. (Largo, Maryland, USA) and retrieved through their website. Data were filtered using the Douglas Argos-Filter Algorithm version 7.03 (Douglas 2007) in SAS version 9.2 (SAS Institute Inc. 2010) to eliminate redundant locations that were simultaneously obtained by multiple satellites, and to retain only probable locations. This resulted in one location per duty cycle (every three or four days depending on the collar model) for each fox provided that at least one location passed all filter criteria. For each location we recorded whether or not the fox was

located on sea ice, which we defined as a location ≥ 5 km seaward of the coast, and fate of the individual (alive or dead). A fox was recorded as dead if the temperature sensor indicated body temperature was much lower than normal and the activity sensors indicated no movement for at least two duty cycles. Foxes whose satellite collar failed, or those that were removed from the study for a companion study, were right-censored. Juveniles were considered to become adults on 1 June the year following capture and collaring (arctic fox kits on the Coastal Plain are typically born in early June). We calculated travel rate (km 2-weeks^{-1}) as the sum of all the straight line distances between successive locations in a 2-week period. For 2-week periods where distance measures were missing due to missing locations, we estimated and replaced the missing distance measures with a mean of the distance measure from the last known interval with distance measure from the next known interval.

Survival Analysis

We used nest survival models (Dinsmore et al. 2002) to estimate arctic fox survival probabilities (S). Estimation was conducted using RMark version 2.1.4 (Laake et al. 2012) in R version 2.15.2 (R Development Core Team 2012) and Program MARK version 6.2 (White and Burnham 1999). Nest survival models estimate a daily survival rate assuming a recapture probability of one. Due to the length of the study and the frequency of mortality events we defined the daily interval in our nest survival models to be a 2-week period.

We evaluated the effect of five factors on survival: SITE, ICE, TRAVEL RATE, SEASON and SEX as defined in Table 1. We included AGE (juvenile or adult) in all models because prior studies have shown large differences in survival between juvenile and adult foxes (Hiruki and Stirling 1989; Meijer et al. 2010; Eide et al. 2012). Our candidate set included 37 models: the null model S_{AGE} and all two- and three-factor additive models (except $S_{AGE+ICE+TRAVEL\ RATE}$), two-factor interactive models, and three-factor models with one two-way interaction. We did not include any models with interactions between AGE and ICE or TRAVEL RATE, SEX and ICE or TRAVEL RATE, or ICE and TRAVEL RATE due to either lack of data, biological reasons, or high correlation among factors.

We used information-theoretic methods to determine the best approximating model and to identify factors that most affected fox survival (Burnham and Anderson 2002). We used ΔQAICc to correct for small sample size and overdispersion, which results in conservative values of QAICc (Dinsmore et al. 2002). We calculated ĉ by dividing the deviance by degrees of freedom from our most general model $S_{AGE*SEASON+SEX}$. We estimated model-averaged 2-week survival rates from all models with ΔQAICc ≤ 1. We calculated annual survival rates for foxes captured in Prudhoe Bay and NPR-A as $S^{ANNUAL} = (S^{No\ ICE})^{(26-X)} * (S^{ICE})^{X}$; where $S^{No\ ICE}$ is the model-averaged 2-week survival estimate for a fox not using the sea ice, S^{ICE} is the model-averaged 2-week survival estimate for a fox using the sea ice, and X is the number of 2-week periods a fox was on the sea ice. Foxes can use the sea ice for varying amounts of time so we calculated annual survival for foxes that used the sea ice from zero to eleven 2-week periods in a year. We calculated the variance in annual survival using the delta method and calculated 90% confidence intervals as $\bar{y} \pm 1.65 * SE$.

Results

We captured and collared 73 arctic foxes; however, two foxes died within 1 week of capture and were removed from the data set. Our data set included 81 encounter histories (Table 2). This differs from the number of unique fox captures because four juvenile and six adult foxes survived to 31 May the year following capture and were reclassified as new adults on 1 July. We right-censored seven foxes removed as part of another study and six foxes whose collars failed. Detailed methodology and analyses of movement patterns for these foxes are presented in Pamperin (2008), Pamperin et al. (2008), and Lehner (2012). The mean travel rate for foxes captured in Prudhoe Bay (17. 3 km 2-weeks^{-1}, SE 25.0) was lower than foxes captured in NPR-A (77.7 km 2-weeks^{-1}, SE 109.6). No locations on the sea ice (≥ 5 km from shore) were recorded for foxes captured in Prudhoe Bay (n=46). In contrast, five adult and three juvenile foxes captured in NPR-A were recorded traveling on the sea ice during at least one 2-week interval. On average, these foxes spent seven 2-week periods (SD = 3) on the sea ice, with one juvenile fox using the sea ice during 11 2-week periods. The mean travel rate of foxes captured in NPR-A that used the sea ice (215.4 km

2-weeks^{-1}, SE 161.2) was greater than foxes captured in NPR-A that did not use the sea ice (50.5 km

2-weeks^{-1}, SE 69.6).

Two models had ΔQAICc values <1; $S_{AGE+SITE+ICE}$ and $S_{AGE+ICE}$ (Table 3). The summed QAICc

factor weights for ICE and SITE were similar and each had about two times more support than any other

factor (Figure 2). A capture location in Prudhoe Bay (β = 0.050, 90% CI = 0.018 – 0.983; logit scale) and

use of sea ice (β = 1.778, 90% CI = 0.069 – 3.488; logit scale) both had a positive effect on 2-week survival

rates but the effect was greater for sea ice use. As a result, model-averaged estimates of 2-week survival

rates were highest for adult foxes captured in NPR-A that used sea ice (0.993, 90% CI 0.957-0.999, n = 5),

followed by adult foxes captured in Prudhoe Bay that did not use sea ice (0.974, 90% CI 0.955-0.985, n =

19), and lowest for adult foxes captured in NPR-A that did not use the sea ice (0.965, 90% CI 0.937-0.981,

n = 12: Figure 3). The same pattern was observed for juveniles. Model-averaged 2-week survival estimates

for juveniles captured in NPR-A that used sea ice were similar to estimates for adult survival rates,

although the confidence intervals overlapped.

The annual survival probability of adult (0.40, 90% CI 0.18-0.62) and juvenile (0.01, 90% CI 0.0-

0.04) foxes captured in NPR-A did not exceed the annual survival probability of adult and juveniles foxes

captured in Prudhoe Bay, 0.50 (90% CI 0.31-0.69) and 0.04 (90% CI 0.0-0.08) respectively, unless the

NPR-A foxes traveled on the sea ice during at least eight 2-week periods for adults (0.50, 90% 0.29-0.71)

or seven 2-week periods for juveniles (0.04, 90% CI 0.0-0.08;Figure 4).

Discussion

In our study, both location and sea ice use affected arctic fox survival. No previous studies have

compared arctic fox survival between developed and undeveloped sites or in relation to their use of sea ice.

The results suggest that foxes captured in NPR-A had lower survival rates than foxes in Prudhoe Bay

unless they spent extended periods offshore on the sea ice. There is some ambiguity in interpretation of the

results because of uncertainty in model selection (i.e. small differences in ΔQAICc values), and

overlapping confidence intervals or survival estimates among models. However, given the evidence which includes the top ranked model having informative parameters and the value of summed factor weights for SITE and ICE compared to the other factors, some generalizations can be concluded about arctic fox foraging strategies and how each strategy can affect fox survival.

It appears that the differences in survival rates for arctic foxes in NPR-A and Prudhoe Bay correspond to differences in area used in winter (Pamperin 2008; Lehner 2012) and amount of anthropogenically sourced food in the diet (Lehner 2012). Foxes in NPR-A used a large area in winter (10,041 km^2 (Pamperin 2008) to 17,250 km^2 (Lehner 2012); 50% fixed kernel distributions). Considering that energy use by arctic fox increases with muscular activity (Underwood 1971; Fuglei and Øritsland 2003), it is likely that foxes in NPR-A expend more energy foraging for food than foxes in Prudhoe Bay which had a smaller area used in winter (23 km^2 (Pamperin 2008) to 151 km^2 (Lehner 2012); 50% fixed kernel distributions). Because anthropogenic food is a reliable and abundant food source, foxes in Prudhoe Bay appeared to employ a strategy that resulted in having a low risk of not locating food with a high reward of obtaining high food quantities, which corresponded to a moderately higher survival rate. The relatively high proportion of anthropogenic foods in their diet suggests this was a moderate to high reward strategy. Foxes in NPR-A that did not use the sea ice employed a potentially more energetically expensive strategy, and also had a lower potential for reward of food obtained. The balance of risk to reward for this strategy would depend on the abundance of lemmings, their primary food source. At the peak of a lemming cycle this would be a moderate risk, moderate return strategy, whereas at periods of low lemming abundance it would be a moderate risk and low return strategy. In our study, this moderate risk, moderate to low reward strategy resulted in a slightly lower survival rate.

Arctic foxes that foraged on the sea ice appeared to have an elevated survival rate compared to foxes that stayed on land in NPR-A. Food on the sea ice, such as seals, can be distributed unevenly (Stirling and Øritsland 1995) which could make the risk to arctic foxes of not encountering food high. Arctic foxes likely followed the marine mammal distribution off the northern coast of Alaska, as evident by their wide movement patterns on the sea ice (Pamperin et al. 2008; Lehner 2012). However, the reward for this

strategy would be the potential for large meals of high energy foods (Smith 1976). The relatively higher survival rate for these foxes suggests this high risk is balanced by the high reward of food resources: a high risk, high reward strategy. This supports studies that suggest that scavenging polar kills and hunting seal pups on the sea ice is an effective survival strategy for arctic foxes especially when terrestrial food availability is low (Chesemore 1967; Smith 1976; Stirling and Archibald 1977; Hiruki and Stirling 1989; Roth 2002; Roth 2003).

Our estimated annual survival rate for NPR-A adult arctic foxes, regardless of sea ice use, appeared to be lower than previous estimates of arctic fox survival in undeveloped regions of North America: 0.55 (foxes aged 1.5 to 4.5 years) in what is now Nunavut, Canada (Macpherson 1969); 0.58 on Banks Island, Northwest Territories, Canada (Hiruki and Stirling 1989); and 0.75 on St. Lawrence Island, Alaska (Fay and Rausch 1992). However, those estimates were calculated by life-table analyses and the differences in methodology make direct comparisons difficult to interpret. Our estimates of annual survival rates of juvenile foxes in Prudhoe Bay and NPR-A (0.04 and 0.01, for no sea ice use respectively) were similar to juvenile fox survival estimates from Banks Island in some years (0.03 - 0.07) but much lower than pooled estimates of survival rate from all years (0.23) (Hiruki and Stirling 1989). In both our study and the Hiruki and Stirling (1989) study, annual estimates of juvenile survival rate were very low. We caution that our juvenile survival estimates may have been lower than true survival because some of the juvenile foxes may have been handicapped by added weight of the satellite collar. On average, the collar weight (185 g) was about 7% of juvenile fox weight (mean = 2690 g, SD = 530); however, with five juvenile foxes, collar weight was about 11% of their weight (mean = 1740 g, SD = 30), which is slightly above the recommended maximum collar to body weight proportion of 10% (Sikes et al. 2011).

We do not know of another study that estimated arctic fox survival rates at a developed site with which we can compare our results. However, a similar study of kit foxes (*Vulpes macrotis*) found higher survival in a developed area compared to an undeveloped area of an oil field, although it was attributed to reduced coyote (*Canis latrans*) presence rather than access to anthropogenic foods or other resources (Cypher et al. 2000). In contrast, arctic fox presence and den occupancy were found to be negatively

correlated with the presence of human structures in Norway, but this was attributed to an increase in red fox presence (Selås et al. 2010).

Differences in survival between sites and among foraging strategies were modest. Several factors that we did not measure may have contributed to variation in our survival estimates. One potential factor affecting survival of foxes in Prudhoe Bay is an apparent increase in the local red fox population in the 2000s (Sanzone et al. 2009; A. Stickney pers. comm.). Red foxes can outcompete arctic foxes for forage and den territory (Rudzinski et al. 1982; Korhonen et al. 1997) and have been observed killing arctic foxes (Pamperin et al. 2006); therefore arctic foxes in Prudhoe Bay could experience both direct and indirect effects of interspecific competition with red foxes. These circumstances would lead to reduced arctic fox survival as has been suggested by Selås et al. (2010). Similarly, lemming abundance, which was not measured during this study, could have had a major effect on fox survival. If lemming abundance was moderate to high arctic foxes may not have received as great of a benefit from either anthropogenic food in Prudhoe Bay, or from foraging for marine mammals on the sea ice as they would have during low lemming abundance. Additionally, lemming abundance could have differed between the study sites making direct comparison more difficult.

Reductions in lemming populations have been observed in Fennoscandia, Greenland, and Wrangel Island: where dampened amplitude and a lengthening period between peaks have been observed in the lemming cycles (Gilg et al. 2009; Ims et al. 2011; Elmhagen et al. 2011; Menyushina et al. 2012). The decline of arctic foxes in Fennoscandia is attributed to decreased lemming abundance (Angerbjörn et al. 2013) and arctic fox and lemming abundance has been shown to covary at Cape Churchill, Manitoba, Canada (Roth 2003). Declines in lemming abundance or reductions in the frequency or intensity of peak abundances will increase the risk and reduce the rewards of a no ice use foraging strategy for foxes in undeveloped areas. The southern Beaufort Sea polar bear population is expected to decline in response to reduced summer sea ice (Hunter et al. 2010). If this projection holds true, use of sea ice in winter will become an even riskier strategy because scavenging opportunities may decline and any survival benefit over a sedentary strategy will be reduced.

Our estimates of arctic fox survival are the first to compare survival between developed and undeveloped areas and first to estimate survival in relation to sea ice use. We found that arctic foxes in Prudhoe Bay, a developed area, had higher survival than foxes in NPR-A, an undeveloped area, unless the foxes in NPR-A used sea ice extensively in winter. Our results imply survival consequences of three different foraging strategies. Future studies should investigate how lemming cycles affect survival of terrestrially foraging arctic foxes in undeveloped areas in comparison to arctic foxes that forage on anthropogenic foods or marine mammals.

Acknowledgements

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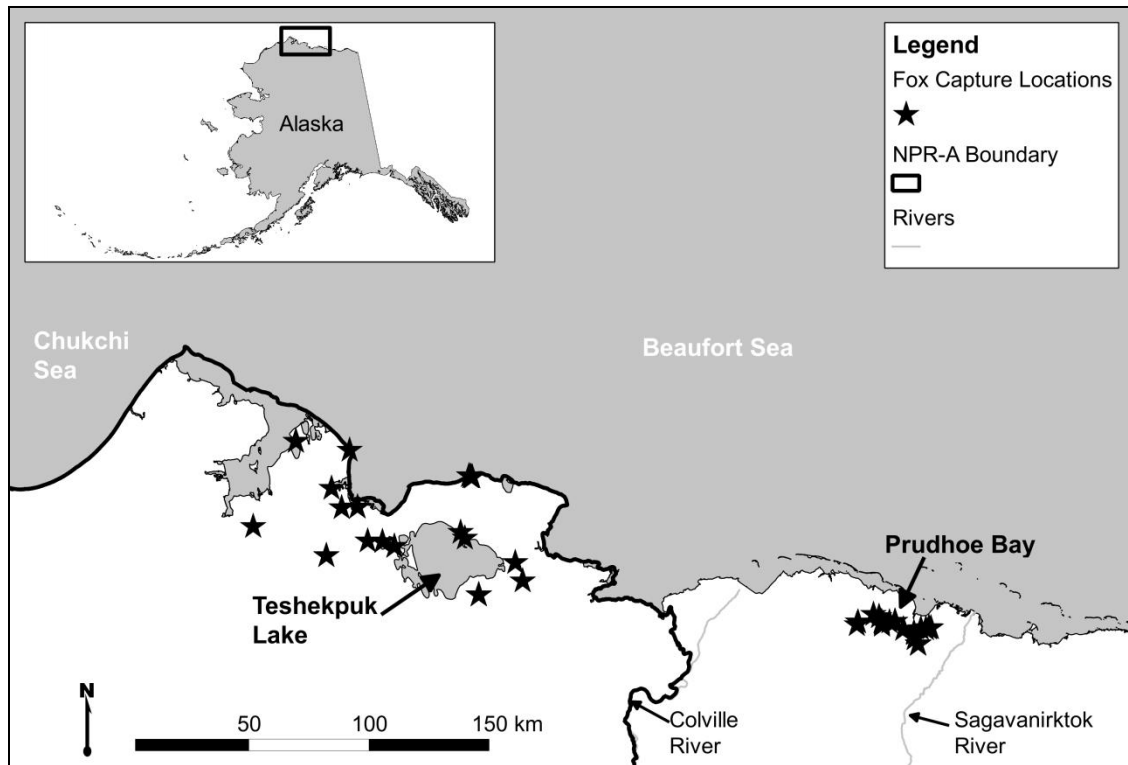
Figure 1 Location of the Prudhoe Bay (developed site) and National Petroleum Reserve-Alaska (NPR-A: undeveloped site) arctic fox capture sites on the Arctic Coastal Plain of Alaska.
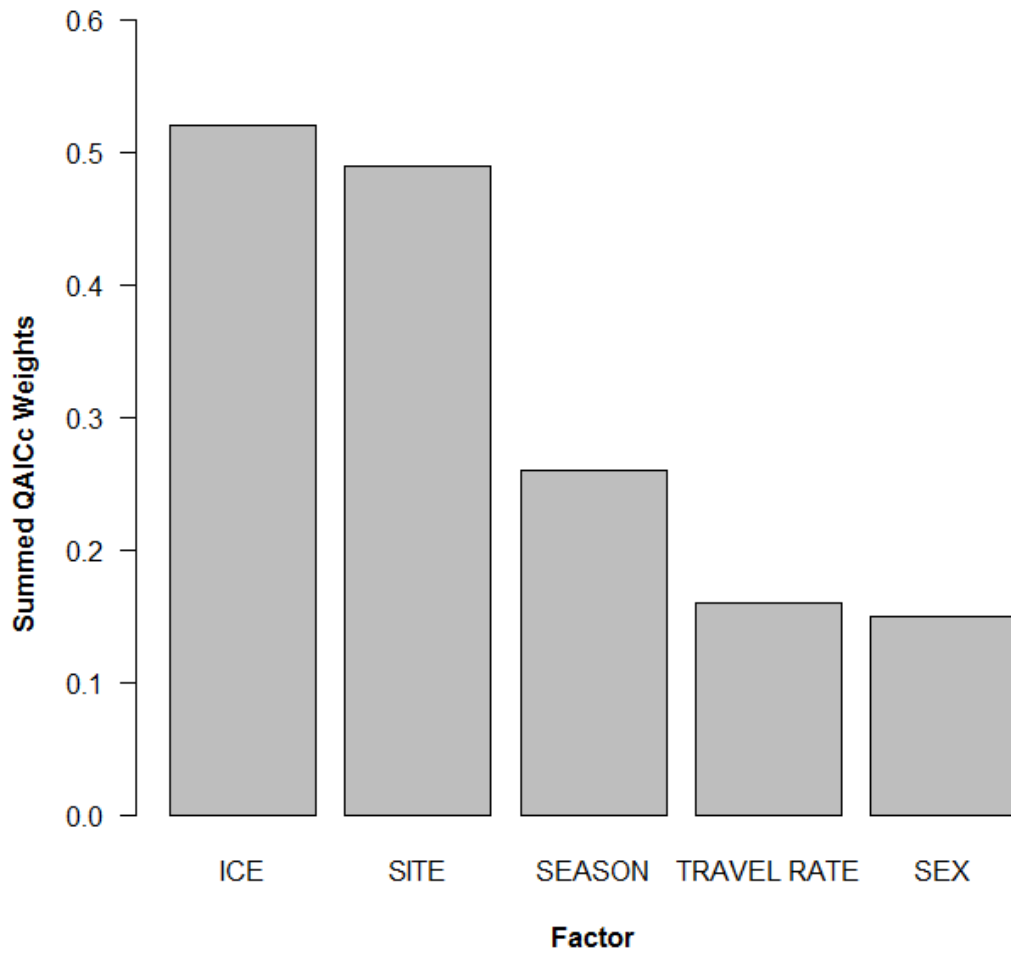
Figure 2 Summed QAICc weights from all models including each factor evaluated in the estimation of arctic fox survival rates on the Arctic Coastal Plain, 2004, 2005, and 2009.
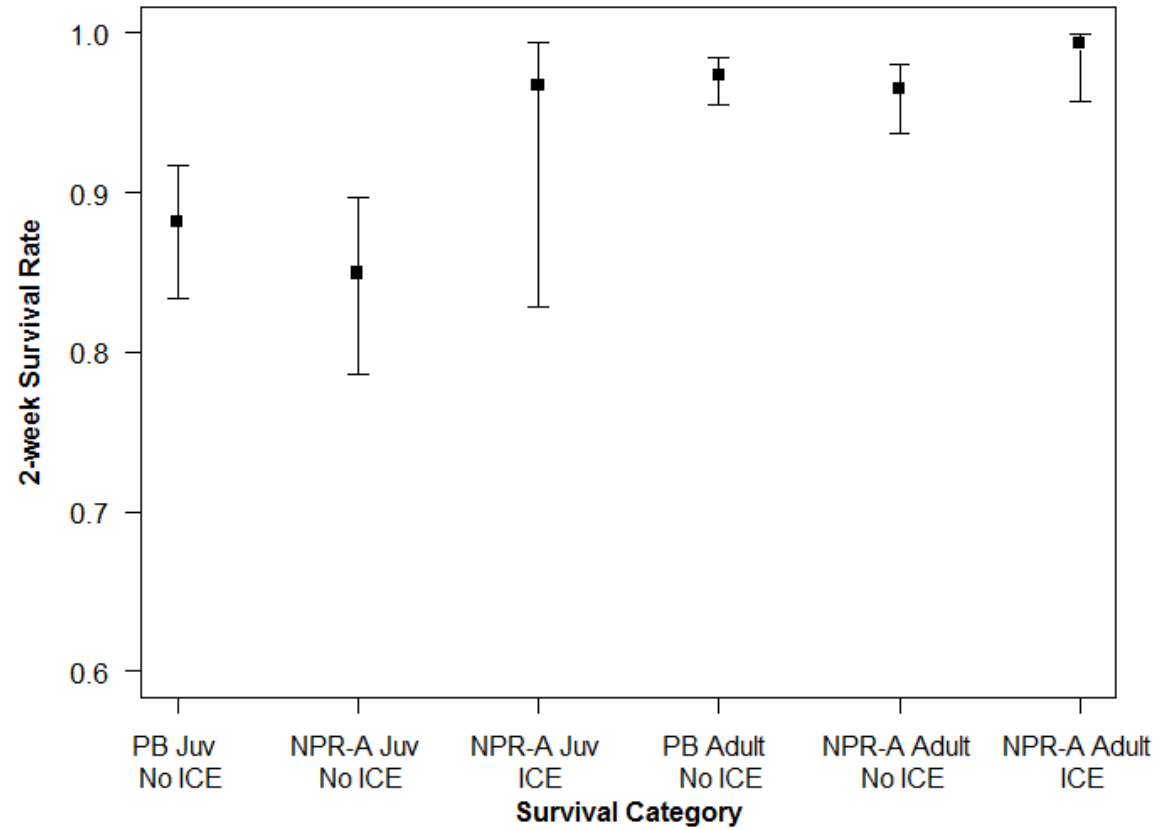
Figure 3 Model averaged 2-week survival estimates for juvenile (Juv) and adult arctic foxes in Prudhoe Bay (PB) and the National Petroleum Reserve-Alaska (NPR-A) that were (ICE) or were not (NO ICE) observed at locations on the sea ice for ≥ 7 days during the 2-week interval. Error bars are 90% confidence intervals.
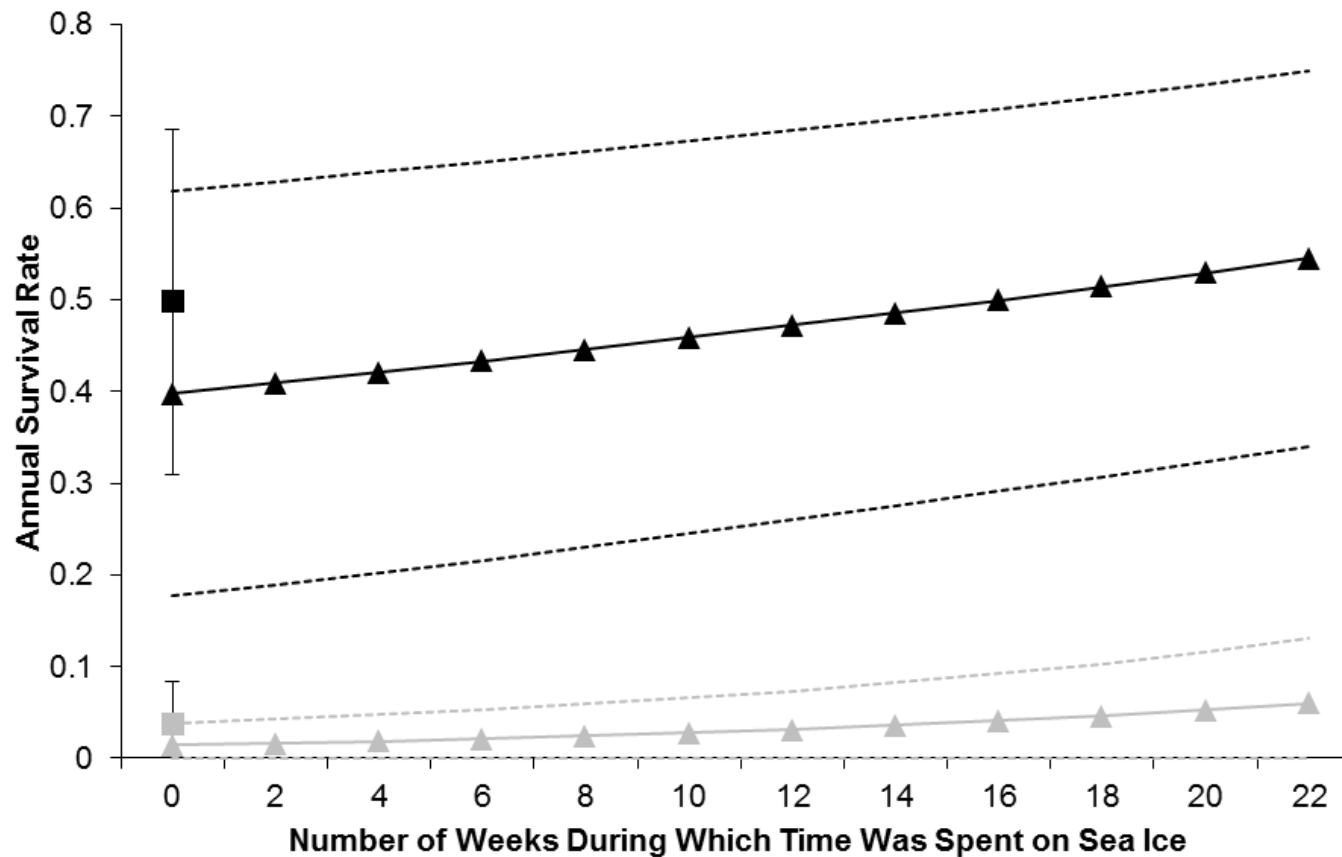
Figure 4 Annual survival estimates calculated from model averaged 2-week survival estimates for juvenile and adult arctic foxes in Prudhoe Bay and the National Petroleum Reserve-Alaska (NPR-A) on the Arctic Coastal Plain as a function of the number of 2-week periods during which arctic foxes were located on the sea ice. Black triangle/solid black line is adult survival in NPR-A. Black square is adult survival in Prudhoe Bay. Grey triangle/solid grey line is juvenile survival in NPR-A. Grey square is juvenile survival in Prudhoe Bay. Dashed lines and error bars are 90% confidence intervals. Note that Prudhoe Bay foxes did not use the sea ice so survival rate as a function of sea ice use is not shown.

Table 1 Factors evaluated in relation to arctic fox survival rates on the Arctic Coastal Plain of Alaska 2004, 2005, and 2009.

Factor	Description
AGE	Juvenile (<1 year old) or adult (≥ 1 year old). AGE was included in all models to account for known differences in survival between adult and juvenile arctic foxes.
SITE	Initial capture location: Prudhoe Bay (developed site) or the National Petroleum Reserve-Alaska (NPR-A; undeveloped site). Arctic foxes in Prudhoe Bay are expected to have higher winter survival than foxes in NPR-A because of access to anthropogenically sourced foods when natural food abundance is low.
ICE	A time varying individual covariate indicating whether or not a fox was located on the sea ice for ≥7 days during a 2-week estimation period. Fox satellite telemetry locations were considered to be on the sea ice if ≥ 5 km seaward of the shore.
TRAVEL RATE	A time varying individual covariate equal to the sum of the straight line distance (km) traveled between all consecutive locations in a 2-week period.
SEASON	Summer (June-October) or winter (November-May). Survival is expected to be higher in summer because of greater food availability.
SEX	Female or male.

Table 2 Number of arctic fox encounter histories used to estimate survival rates of adults and juveniles in Prudhoe Bay and the National Petroleum Reserve Alaska (NPR-A) on the Arctic Coastal Plain; 2004, 2005, and 2009.

		Number of Foxes			
		Female		Male	
Area	**Age Class**	Summer[1]	Winter	Summer[1]	Winter
Prudhoe Bay	Juvenile	13	10	14	9
Prudhoe Bay	Adult	10	7	9	8
NPR-A	Juvenile	12	5	11	8
NPR-A	Adult	7	6	5	4

[1] The number of summer fox encounter histories equals the number of fox encounter histories when SEASON is not included in a model.

Table 3 Arctic fox survival estimation models with ΔQAICc < 4. Model factors defined in Table 1. A ĉ of 1.18 was used to correct for overdispersion.

Survival Estimation Model	K^1	QAICc	ΔQAICc	w_i^2
$S_{AGE+SITE+ICE}$	4	311.21	0	0.13
$S_{AGE+ICE}$	3	311.65	0.44	0.10
$S_{AGE + SEASON + ICE}$	4	312.37	1.17	0.07
S_{AGE}	2	312.53	1.32	0.07
$S_{AGE+SITE*TRAVEL RATE}$	5	312.55	1.34	0.07
$S_{AGE*SITE+ICE}$	5	312.62	1.42	0.06
$S_{AGE + SITE + ICE + SITE * ICE}$	5	313.23	2.03	0.05
$S_{AGE + SITE}$	3	313.41	2.20	0.04
$S_{AGE + SEX + ICE}$	4	313.65	2.44	0.04
$S_{AGE + SEASON}$	3	314.07	2.86	0.03
$S_{AGE + SEASON + ICE + AGE * SEASON}$	5	314.40	3.19	0.03
$S_{AGE + SEASON + ICE + SEASON * ICE}$	5	314.40	3.19	0.03
$S_{AGE + TRAVEL RATE}$	3	314.45	3.24	0.03
$S_{AGE + SEX}$	3	314.50	3.29	0.03
$S_{AGE + SITE + AGE * SITE}$	4	314.77	3.56	0.02
$S_{AGE + SITE+ TRAVEL RATE}$	4	314.86	3.65	0.02
$S_{AGE + SITE + SEASON}$	4	314.88	3.68	0.02

[1] K= number of parameters

[2] w_i = QAICc weights

General Conclusions

This thesis examined how resource development is potentially impacting red and arctic foxes on the Coastal Plain. The results from Chapter 1 showed both red and arctic foxes fed extensively on anthropogenic foods in Prudhoe Bay. Although use of anthropogenic foods in summer was only about 10 % for both species, mixing models estimated that approximately half of late winter diet and integrated lifetime diet of red fox came from anthropogenic food. Similarly, nearly 40% of arctic fox late winter diet came from anthropogenic foods. The level of anthropogenic food use by red foxes may explain red fox persistence in Prudhoe Bay; however, we could not test whether red foxes are simply using anthropogenic foods opportunistically or if they require this supplemental food source for survival and reproduction. Testing this would require estimating survival and reproduction at Prudhoe Bay with access to anthropogenic foods removed or severely reduced. This kind of experiment has been done at two villages in Israel, where native foxes had been exposed to anthropogenic food waste for many years. There, elimination of access to anthropogenic food waste caused severe declines in red fox survival (Bino et al. 2010). Any study investigating the degree to which red foxes on the Coastal Plain require anthropogenic foods for survival and reproductive output would need to be conducted over different levels of lemming abundance because red foxes were highly specialized on lemmings (Chapter 1) and the availability of this prey will influence the foxes' requirement for anthropogenic foods. If anthropogenic foods are a key factor permitting red foxes to persist on the Coastal Plain, then limiting fox access to sites where anthropogenic foods are available could be an effective management tool for controlling or eliminating local red fox populations. Both fox species used similar amounts of abundant foods (anthropogenic foods and lemmings) but differed enough in their use of other, less common, foods that their foraging niches were moderately distinct. It is unknown if arctic foxes exhibited a moderately different niche from red foxes because they were excluded from prime foraging habitat, or if red foxes were unable to fully use the dietary niche occupied by arctic foxes because they lacked the adaptations required to exploit a greater array of diet items.

In Chapter 2, we found that both location and sea ice use affected arctic fox survival. Foxes captured in NPR-A, an undeveloped site, had lower annual survival rates (adult: 0.40, 90% CI 0.18-0.62; juvenile: 0.01, 90% CI 0.0-0.04) than foxes in Prudhoe Bay (adult: 0.50, 90% CI 0.31-0.69; juvenile: 0.04, 90% CI 0.0-0.08) unless they spent extended time periods on the sea ice. The differences in survival rates for arctic foxes in NPR-A and Prudhoe Bay correspond to differences in area used (Pamperin 2008, Lehner 2012) and amount of anthropogenic food in the diet (Lehner 2012; Chapter 1 of this thesis). We identified three groups of foxes that used different foraging strategies based on capture location and use of sea ice, that had different survival rates: Prudhoe Bay foxes, NPR-A foxes that did not use sea ice, and NPR-A foxes that traveled extensively on sea ice. Foxes resident in Prudhoe Bay had modestly higher survival than NPR-A foxes that did not use sea ice, presumably due to the predictable anthropogenic food subsidy and a low need for travel associated with feeding. NPR-A foxes that used the sea ice had modestly higher survival than NPR-A foxes that did not use sea ice. This third group likely had high energetic costs with a high risk of not locating food on the sea ice. However, this group was likely rewarded with high-calorie foods such as seal carcasses when they located food. The balance of cost-risk-reward for these strategies would depend on lemming abundance. Future studies of arctic fox survival and development should investigate how lemming cycles affect survival of arctic foxes in undeveloped areas, compared to arctic foxes that forage on anthropogenic foods at developed sites or marine mammals on the sea ice.

Changes to the Arctic, including increased development, increased ice-free periods in the Arctic Ocean, and disruptions to lemming cycles, could significantly impact both red and arctic fox populations. The anthropogenic food subsidies accompanying development may allow red fox to survive year-round on the Coastal Plain and establish viable breeding populations, while arctic fox populations may decline due to increased red fox predation and competition for denning sites. Increased ice-free periods in the Arctic may also result in reduced opportunities for arctic foxes to scavenge on marine mammal carcasses on sea ice, a foraging strategy associated with relatively higher survival. Natural food subsidies such as marine mammal carcasses are likely to be particularly important to arctic foxes during periods of low lemming abundance. Changes in both fox populations have the potential to affect the populations of other species, including

lemmings and nesting birds, and disease dynamics, in the long term. Thus, food subsidies may have far-reaching effects on Arctic wildlife, as observed in the red and arctic fox populations on the Coastal Plain.

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