ARCTIC FOX WINTER MOVEMENT AND DIET IN RELATION TO INDUSTRIAL DEVELOPMENT ON ALASKA'S NORTH SLOPE

A

THESIS

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Abstract

I examined winter movement and diet of arctic foxes (*Vulpes lagopus*) in the Prudhoe Bay oilfields and an adjacent undeveloped area (National Petroleum Reserve-Alaska (NPR-A)). Movement metrics were compared between these areas using data from satellite collars. Daily travel rate was approximately 5 times greater in the undeveloped area than in Prudhoe Bay. Four adult foxes collared in NPR-A used the sea ice for extensive time periods. One of these foxes traveled 338 km in three days while another traveled to Banks Island (Northwest Territories, Canada), over 1050 km from its capture location. Prudhoe Bay foxes did not make these long distance movements and remained near their summer capture location throughout winter. I used stable isotope analysis and a mixing model (SIAR) to estimate the contribution of marine, terrestrial, and anthropogenic foods to fox diet. Based on muscle tissue, the average contribution of anthropogenic foods to Prudhoe Bay fox diet was more that 50%. Marine foods were utilized in NPR-A, but not in Prudhoe Bay. Results demonstrate that anthropogenic foods are heavily utilized by foxes that overwinter in the oilfields and this food source is likely responsible for reduced winter movements of Prudhoe Bay foxes. Therefore, industrial development strongly affects winter movement and diet of foxes.

Table of Contents

Page

List of Figures

Page

Chapter 1

Chapter 2

List of Tables

Page

Chapter 1

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General Introduction

Implementation or expansion of human (or industrial) development and associated supplemental resources in the form of anthropogenic foods can have diverse effects on wildlife species, including increased populations or densities (Fedriani et al. 2001; Dip et al. 2003; Beckmann and Berger 2003; Prange et al. 2003; Contesse et al. 2004). Home range, foraging patterns, and movements of animals have been observed to be reduced in more developed areas (Beckmann and Berger 2003; Bozek et al. 2007; Pamperin 2008). There is ample evidence that availability of anthropogenic foods may alter the feeding ecology of wildlife. For example, Newsome et al. (2010) found that San Joaquin kit foxes (*Vulpes macrotis mutica*) in urban areas extensively utilized anthropogenic foods, but did not observe this behavior for nonurban foxes. Urban red foxes (*Vulpes vulpes*) have also been shown to heavily utilize anthropogenic foods (Contesse et al. 2004). Thus, human presence associated with development is often associated with increased food resources, which in turn may affect a suite of ecological conditions for wildlife

One species that appears to have been particularly affected by development of oil and gas resources on Alaska's North Slope is the arctic fox (*Vulpes lagopus*). Since the 1960s the Prudhoe Bay oilfield has been the most developed region on the North Slope and encompasses many types of infrastructure. As generalists, arctic foxes have the ability to utilize anthropogenic foods associated with developed areas on the North Slope (Burgess 2000). When unharmed, the arctic fox is a species that tolerates human presence and activity (Burgess 2000) and has been shown to be attracted to inhabited areas to forage (Fine 1980; Eberhardt et al. 1982, 1983b).

Arctic fox travel more widely during winter when food becomes more limited (Chesemore 1967). However, if no seasonal shift in food resource availability occurs, movements during winter may not increase. A recent study on winter movement of arctic foxes in Prudhoe Bay and in the undeveloped National Petroleum Reserve Alaska (NPR-A) found that movement and utilization area were greatly reduced for Prudhoe Bay foxes (Pamperin 2008). Previous research in Prudhoe Bay has used scat analysis to assess the use of anthropogenic foods and the effects of development on arctic fox diet. The percent occurrence of garbage in scats ranged from 6% to 26%, which the authors suggested likely underestimated anthropogenic contributions due to the lack of indigestible parts (Eberhardt 1977; Fine 1980; Garrott et al. 1983). Research on winter diet of arctic foxes in undeveloped areas near Teshekpuk Lake, Alaska, indicated that diet consisted primarily of small mammals with birds and eggs, marine mammals, caribou (*Rangifer tarandus*), and non-food items being consumed in small amounts (Chesemore 1968). Due to the limitations of these types of diet analyses, the relative contribution of the main winter food sources (marine, terrestrial, anthropogenic) to arctic fox winter diet is relatively unknown and the degree to which arctic foxes rely on anthropogenic foods during the winter remains unclear. A more recent method of diet analysis, stable isotope analysis, allows for examination of assimilated diet over different time frames (Peterson and Fry 1987) and is not biased towards foods with more indigestible parts.

Evidence suggests that the consumption of artificial foods in the oilfield is likely a key factor responsible for a number of changes to local arctic fox populations including increased den densities (Eberhardt et al. 1983a), increased fox density (Fine 1980; Eberhardt et al. 1982; Burgess et al. 1993), increased reproduction and survival (Eberhardt et al. 1982, 1983a), decreased population fluctuations (Eberhardt et al. 1982,1983a; Burgess et al. 1993), and reduced winter movement (Pamperin 2008) in the oilfield compared to adjacent undeveloped areas. These benefits to the arctic fox population may contribute to increased predation on natural prey species and increased disease transmission in developed areas. The NPR-A is currently an undeveloped 95,000 km^2 region on the North Slope and it is anticipated that oil and gas development will soon begin in the northeast portion of the NPR-A because areas around Teshekpuk Lake have high potential oil and gas reserves (BLM 1998, 2008, USGS 2010). Therefore, assessing the impacts of development on arctic fox winter movement and diet is important and should be considered when planning for future oil and gas development on the North Slope.

Chapter 1 examines winter movements of arctic foxes in the developed portions of the Prudhoe Bay oilfields and in the northeast portion of the NPR-A around Teshekpuk Lake using satellite telemetry. I estimated daily travel rates, mean maximum distance from capture location, and utilization area to determine if industrial development affected movement behavior and space use of arctic foxes. This data will also serve as a baseline assessment of arctic fox winter movements in the NPR-A prior to its development for oil and gas resources.

Chapter 2 examines late winter diet of arctic foxes from both study areas using stable isotope analysis to determine if industrial development affects fox diet. Using $\delta^{13}C$ and $\delta^{15}N$ values from arctic fox tissues and three potential winter food sources, I compared the contributions of terrestrial, marine, and anthropogenic foods (determined using the recent Bayesian mixing model SIAR (Parnell et al. 2010)) to diet of arctic foxes in the developed portions of the Prudhoe Bay oilfields and in NPR-A. My goal was to compare late winter diet between both areas and to determine the extent to which arctic foxes in Prudhoe Bay utilized anthropogenic foods compared to fox inhabiting the NPR-A. I also assessed dietary differences in both areas integrated over the arctic foxes' lifetime using bone collagen isotope values from adult foxes. The data presented in this chapter will serve as a baseline measurement of arctic fox winter feeding ecology (SIA) in Prudhoe Bay and NPR-A.

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Chapter 1

Winter Movements of Arctic Foxes in Relation to Industrial Development on Alaska's North Slope[1]

Abstract

I examined winter movements of arctic foxes (*Vulpes lagopus*) in the Prudhoe Bay oilfields and an adjacent undeveloped area (National Petroleum Reserve-Alaska) in northern Alaska. Winter movements of arctic foxes were compared between these two areas using data from satellite collars. Daily travel rate was approximately 5 times greater in the undeveloped area than in Prudhoe Bay. I also obtained baseline data on arctic fox winter movements offshore on the pack ice. Four out of seven adult foxes collared in NPR-A used the sea ice for extensive time periods during the winter. One of these foxes traveled 338 km in three days. This is the highest travel rate recorded for this species to date. Another of these foxes traveled to Banks Island (Northwest Territories, Canada), over 1050 km from its initial capture location. These results demonstrate that industrial development can strongly affect winter movements of arctic fox. Moreover, these results demonstrate the ability of arctic foxes to travel long distances over short time periods and suggest they may use sea ice extensively during the winter.

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Introduction

Implementation or expansion of human development may have diverse effects on wildlife species. Development can increase abundance and/or density of some species in response to supplemental resources associated with human presence (Beckmann and Berger 2003, Fedriani et al. 2001). Reductions in intraspecific competition resulting from anthropogenic food subsidies, sheltered areas, and artificial breeding sites may be responsible for population increases. Increased densities in relation to increased levels of development have been observed for raccoons (*Procyon lotor*) (Prange et al. 2003; Riley et al. 1998) and coyotes (*Canis latrans*) (Fedriani et al. 2001). Higher arctic fox (*Vulpes lagopus*) den density has been reported in developed areas compared to adjacent undeveloped areas (Ballard et al. 2000) and the availability of anthropogenic foods sustains higher fox population densities (Dip et al. 2003; Contesse et al. 2004). Animal movements are also affected by development and the associated availability of anthropogenic food resources. Home range and movements of animals have been observed to be reduced in more developed areas (Bozek et al. 2007; Beckmann and Berger 2003; Pamperin 2008). Thus, human presence associated with development greatly affects a suite of ecological conditions for wildlife.

The arctic fox is a species that has been exposed to oil and gas development on Alaska’s North Slope, (hereafter North Slope) beginning in the 1960s and will likely be exposed to industrial development in other areas on the North Slope in the near future. Arctic fox primarily prey on rodents (Chesemore 1968; Macpherson 1969; Fay and Stephenson 1989; Angerbjörn et al. 1999; Strand et al. 1999; Elmhagen et al. 2000), but are also opportunistic scavengers (Macpherson 1969; Hersteinsson and Macdonald 1996; Bantle and Alisauskas 1998). Arctic fox have been found to switch prey species and become active predators on birds and their eggs once migratory birds arrive (Stickney 1991; Liebezeit and Zack 2008). Arctic fox also scavenge carcasses of large terrestrial mammals such as caribou (*Rangifer tarandus*) (Chesemore 1968). Arctic fox also consume marine mammals (Chesemore 1968; Hersteinsson and Macdonald 1996), scavenging on seals killed by polar bears (*Ursus maritimus*) (Roth 2002, Andriashek et al. 1985) or directly preying on ringed seal (*Phoca hispida*) pups (Smith 1976). As generalists, arctic foxes have the ability to utilize anthropogenic foods associated with developed areas on the North Slope (Burgess 2000). Arctic fox tolerate human activity (Burgess 2000) and are often attracted to developed areas to feed (Fine 1980; Eberhardt et al. 1982, 1983b). For example, Garrott et al. (1983b) found that arctic foxes in the Prudhoe Bay area consumed garbage in small amounts in summer in addition to natural foods.

The impact of anthropogenic food resources on the Prudhoe Bay arctic fox population is likely to be highest in the winter. Food resources for arctic foxes on the North Slope are more abundant during the summer months when pups are being reared. Territories are defended in summer and availability of den sites determine where territories are established and delineate arctic fox distribution (Garrott et al. 1983a). During late fall and throughout the winter, territories are reduced (Eberhardt et al. 1982, 1983b) or may be abandoned, resulting in increased home ranges because arctic foxes must travel greater distances to find food (Chesemore 1967). During this period, Arctic foxes can travel long distances (Northcott 1975, Eberhardt and Hanson 1978, Garrott and Eberhardt 1987, Pamperin 2008, Tarroux et al. 2010), often using the sea ice for extensive time periods (Pamperin et al. 2008, Tarroux et al. 2010). Winter travel rates measured by satellite telemetry have been reported up to 90 km d^{-1} in Canada (Tarroux et al. 2010) and 61 km d^{-1} in northern Alaska (Pamperin 2008). The winter movement patterns of arctic foxes appear to be linked to food availability (Burgess 2000), and because foxes in developed areas may access supplemental foods during the lean winter months, both dietary and movement patterns are likely affected. Although oil and gas development of the North Slope began in the 1960s, the effect on arctic fox winter diets and movement patterns have yet to be fully documented.

Here I present and compare results on movements of arctic foxes from the undeveloped National Petroleum Reserve Alaska (NPR-A) and developed portions of the Prudhoe Bay oilfield during the winter of 2009-2010, as measured by satellite telemetry. My goal was to quantify differences in winter movement rates, distance moved, and area utilized between these two areas and examine if movement was reduced in the developed area. Although large regions of the North Slope are undeveloped, there is interest in the future development of these lands. By characterizing movement patterns in the NPR-A, this study provides additional baseline data on arctic fox winter movements initially reported by Pamperin (2008), prior to future development for oil and gas resources. I hypothesized that winter movements of arctic foxes in the developed Prudhoe Bay oilfield would be reduced compared to arctic foxes in undeveloped areas in northern Alaska.

Methods

The two study areas were an undeveloped region near Teshekpuk Lake within the NPR-A and the developed region of the Prudhoe Bay oilfields (Figure 1). Vegetation, topography, elevation, climate, and landscape are very similar between these two sites (Raynolds et al. 2006, CAVM 2003). Average precipitation in coastal areas of the North Slope is approximately 200 mm with about 50% falling as snow (Zhang et al. 1996). Snow cover persists from October through May (Wendler et al. 2010, Zhang et al. 1996). Snow cover is usually thin and wind redistributes the snow throughout winter (Liston and Sturm 2002). Wind in the region causes the surface of the snow pack (sastrugi) to become very dense, forming a crust over layers of lower-density snow (Hall et al. 1986). The North Slope is bordered to the north by the Beaufort Sea and to the west by the Chukchi Sea (Figure 1). Sea ice is typically present from October through late June (Wendler et al. 2002, Wendler et al. 2010).

The Prudhoe Bay oilfields have undergone extensive development beginning in the late 1960s whereas the NPR-A is currently an undeveloped 95,000 km^2 region on the North Slope. The NPR-A is roadless and human activity is largely limited to subsistence activities (hunting, fishing, or trapping) and some seasonal oil and gas exploration. It is anticipated that oil and gas development will soon begin in the northeast portion of the NPR-A because areas around Teshekpuk Lake have high potential oil and gas reserves (BLM 1998, 2008, USGS 2010).

Foxes were captured between 11-16 August 2009 in the Prudhoe Bay oilfields (70º 15’ N, 148º 20’ W; n = 20) and between 25-31 August 2009 in NPR-A near

Teshekpuk Lake (70º 34’ N, 153º 30’ W; n = 15) (Figure 1). Cage live traps (Model 208, Tomahawk Live Trap, Tomahawk, WI, USA) baited with fish were used for capture. In the Prudhoe Bay oilfields, road access allowed traps to be set and checked 3 times daily. Traps were set near active dens, kitchen facilities, dumpsters, and locations where foxes were observed. Foxes were captured within the NPR-A using an R-44 helicopter to set and check traps (once daily) due to the remoteness of the study area and the absence of a road system. Traps were set at active den sites, along lake shores and rivers, and near locations where foxes were observed. Trapped foxes were transferred from live traps to a restraint cage (Tru-Catch Traps, Bell Fourche, SD, USA) to facilitate anesthetization. Foxes were injected with a 7:3.5 mg/kg dose of ketamine hydrochloride:xylazine hydrochloride. I placed collars with satellite transmitters on the animals once they were fully anesthetized. While anesthetized, foxes were weighed, sex and age class were determined, and blood and hair samples were collected for a companion study. Foxes were aged as either juveniles or adults based on canine appearance and eruption (Macpherson 1969, Frafjord and Prestrud 1992). All fox handling and capture procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (Assurance No. 149496-4) and by the Alaska Department of Fish and Game (Permit No. 09-140).

Twenty Model A-3110, 185 g satellite collars were deployed on foxes captured in Prudhoe Bay and 15 Model ST-20 TAW-4110, 185 g satellite collars were deployed on foxes captured in the NPR-A (all collars by Telonics, Inc., Mesa, AZ, USA). I utilized two models of collars because I had 20 Model A-3110 collars that were retrieved from a previous study. Collars placed on Prudhoe Bay foxes were scheduled to acquire locations for 4 hours every 4 days and the battery life was predicted to be adequate for the entire winter season. Technological improvements in the Model ST-20 TAW-4110 collars enabled these collars to be programmed to transmit for 4 hours every 3 days. Both collar models contained mortality, temperature, and activity sensors.

Data were collected by CLS America, Inc. (Largo, MD, USA) and retrieved through their website. All location data were processed using the Douglas Argos-Filter Algorithm (Version 7.03, David Douglas, USGS/ASC) (Douglas 2007) in SAS (V 9.2, SAS Institute Inc., Cary, NC, USA) to eliminate redundant locations that were simultaneously obtained by multiple satellites, and to retain only probable locations, based on parameters supplied to the filter. The filter resulted in one location per duty cycle for each individual, provided that at least one location passed all filter criteria (Douglas Argos-Filter Algorithm, Argos User's Manual, CLS 2010). The winter season was defined as October through May and only locations for this period were used for the analyses. If more than 12 days had passed between locations being obtained, data for that period were not included in the analyses. This resulted in only seven intervals being eliminated (all from Prudhoe Bay foxes).

I characterized winter movement by reporting a) the mean ± one standard error (SE) and b) the highest value of daily distance traveled (hereafter travel rate, km d^{-1}) and the maximum distance from initial capture location. I report these values for the two study areas for adults, juveniles, and all foxes combined. The study design did not allow traditional statistical testing because I was unable to replicate the two study areas that I compare. Therefore, I compared movement metrics between study areas by calculating the standard error of the difference between means and constructing 95% confidence intervals. Confidence intervals that did not contain zero indicated means that were significantly different. Travel rate (km d^{-1}) was calculated by dividing the straight-line distance (km) between consecutive locations by the number of days between the dates of those locations. Mean travel rate (km d^{-1}) was calculated as the average of the daily distances for all foxes over the entire winter season. The maximum travel rate (km d^{-1}) was the greatest daily distance traveled. The maximum distance from capture location (km) was calculated as the straight-line distance between initial capture location and the furthest location from that point recorded for that individual. The mean maximum distance from capture location (km) was calculated as the average of the maximum distance from capture location for all foxes. A subset of foxes (n = 4) collared within the NPR-A traveled on the sea ice for extensive periods over the winter. For this subset of foxes two additional movement metrics were calculated: the total distance traveled while on the sea ice and the number of days spent on the sea ice. Total distance traveled while on sea ice was calculated as the sum of all distances between consecutive locations on sea ice for each individual. This represented the minimum distance traveled by an individual fox while on the sea ice. ArcMap 9.3 (ESRI, Redlands, California, USA) was used to plot, inspect, and analyze all location data.

I pooled all locations from each area to estimate the area used by foxes from each study area. Fixed kernel distributions with 90% and 50% probability contour intervals were constructed using the Home Range Tools extension (Rodgers et al. 2007; (Version 1.1, Thunder Bay, Ontario, Canada) in ArcMap 9.3. The 50% probability contour defined the core area used by foxes and the 90% probability contour defined an overall home range for foxes from each study area. The 90% utilization distribution is recommended over the 95% probability contour (Borger et al. 2006) because it reduces overestimation of home range caused by outliers. For the smoothing parameter, I chose the reference bandwidth multiplied by 0.7 (Bertrand et al. 1996) to decrease the effects of over-smoothing (Kie et al. 2010).

Results

The final data set contained 944 locations, with 95% of locations determined with error < 1.5 km and 89% of locations with error < 0.5 km (Table 1). Of the 944 locations, 895 (95%) were from consecutive duty cycles.

NPR-A foxes had a mean travel rate over 5 times greater than Prudhoe Bay foxes, and they traveled more than 6 times farther from their initial capture location than Prudhoe Bay foxes (Table 2A). The mean travel rate was 7.2 ± 0.6 km d^{-1} and 1.3 ± 0.1 km d^{-1} for NPR-A and Prudhoe Bay foxes, respectively. These means were significantly different based on the 95% confidence intervals. The maximum travel rate in NPR-A was approximately 3-fold greater than the maximum travel rate in Prudhoe Bay (Table 2A). NPR-A foxes did not remain near their initial capture locations, with two exceptions. The maximum distance for these foxes was only 5.6 and 12.3 km. One adult female remained near her initial capture location throughout winter and another remained near her initial capture location until she died prior to 25 February.

For adults, the mean travel rate was 7.5 ± 0.7 km d^{-1} and 1.2 ± 0.1 km d^{-1} in NPR-A and Prudhoe Bay, respectively. On average, the maximum distance from capture location was 310 ± 148 km and 24 ± 8 km for NPR-A and Prudhoe Bay adult foxes, respectively (Table 2B). However, the maximum distance from capture location means did not differ significantly between Prudhoe Bay and NPR-A adults (Table 2B).

Due to high juvenile mortality in NPR-A, only data from the first 3 months of the winter period (Oct-Dec) were used in calculating movement statistics for juvenile foxes. NPR-A juveniles traveled both farther per day and farther from their capture location than Prudhoe Bay juveniles (Table 2C). As with adults, mean travel rates of juveniles were significantly different between Prudhoe Bay and NPR-A; the mean travel rate was 5.8 ± 1.1 km d^{-1} and 1.6 ± 0.4 km d^{-1} in NPR-A and Prudhoe Bay, respectively.

Foxes collared in NPR-A never moved into the Prudhoe Bay or Kuparuk oilfields during winter. The majority of Prudhoe Bay collared foxes never left the immediate oilfield area for extended time periods during winter with the exception of two juveniles; one that had traveled approximately 100 km west of Prudhoe Bay and then returned in mid-November and another that had traveled approximately 215 km northwest of its capture location in the oilfield in mid-November and died shortly afterwards.

The area used by NPR-A foxes was much larger than that of Prudhoe Bay foxes and encompassed a large proportion of the North Slope (Figure 2, Figure 3). In the NPR-A, the 90% and 50% probability contours for fixed kernel distributions comprised an area greater than 176,000 km^2 and of 17,250 km^2, respectively. In Prudhoe Bay, the 90% and 50% probability contours comprised areas of only 530 km^2 and 151 km^2, respectively.

Four adult foxes collared in NPR-A traveled on the sea ice for a total of 71 to 118 days and covered distances of 515 to 2878 km (Figure 4, Table 3). Variability in travel rate increased for each of these foxes once they began traveling on the sea ice (Table 3, Figure 5). The earliest use of sea ice occurred in mid-November for AF28, in late December for AF30, and in early January for AF29 and AF34 (Table 3, Figure 5). AF29 spent a total of 87 days on the sea ice and traveled 1051 km from his initial capture location near Teshekpuk Lake to Banks Island, Northwest Territories, Canada (Figure 4). AF28 spent a total of 71 days on the sea ice during 8 different time periods throughout the winter (Table 3). While these four foxes were on the sea ice the mean travel rate was 18.4 ± 1.7 km d^{-1}, the mean maximum travel rate was 63.3 ± 18.4 km d^{-1}, and the mean maximum distance from capture location was 527 ± 199 km.

The maximum travel rate observed during this study was 112 km d^{-1} (AF30, NPR-A) and occurred while the individual was on the sea ice. The next highest travel rate was 69 km d^{-1}; this fox had multiple travel rates of 50-60 km d^{-1}. A travel rate of at least 40 km d^{-1} was observed for 5 foxes (both juvenile and adult). These high travel rates occurred throughout the winter (October-April), with most occurring between January and April (Figure 5).

Discussion

The primary objective was to compare winter movements of foxes collared in Prudhoe Bay and NPR-A and to examine whether movement was reduced near the Prudhoe Bay oilfield. My results suggest that the Prudhoe Bay oilfields have a strong effect on arctic fox winter movements. Furthermore, I observed more variation in NPR-A fox movement behavior than for foxes collared in the developed Prudhoe Bay region suggesting differences in food availability (Burgess 2000) or distribution of prey (Anthony 1997) between study areas and within NPR-A. Some arctic foxes collared in NPR-A traveled long distances (over 1000 km from capture location), attained very high travel rates (up to 112 km d^{-1}), and used the sea ice for extensive periods of time (118 days), while others did not. Foxes in Prudhoe Bay had reduced travel rates, used smaller areas, did not use the sea ice, and remained in the same area throughout winter. The differences observed in winter movement implies that Prudhoe Bay and NPR-A foxes have very different wintering strategies.

Differences in winter strategies based on travel rates have been previously observed for Prudhoe Bay and NPR-A foxes. Pamperin (2008), using a 4-day duty cycle, reported that NPR-A adults had a mean duty cycle travel rate of 15.3 ± 2.7 km and Prudhoe Bay adults had a mean duty cycle travel rate of 4.7 ± 0.3 km. Standardizing their travel rates to the equivalent of the mean daily travel rate in this study gives a mean travel rate of 3.8 km d^{-1} for NPR-A adults and 1.2 km d^{-1} for Prudhoe Bay adults. The mean travel rate for NPR-A adults (7.5 ± 0.7 km d^{-1}) was nearly double that of NPR-A adults reported in Pamperin (2008). I had a shorter duty cycle which in part contributed to higher travel rates in my study. However, the data also suggests that the winter movement of NPR-A foxes may be variable over time. For Prudhoe Bay adults, mean travel rate was 1.2 ± 0.1 km d^{-1}, which was essentially the same as the standardized daily travel rate of 1.2 km d^{-1} for Prudhoe Bay adults reported by Pamperin (2008).

This study documented extensive use of sea ice by individuals in NPR-A. The maximum travel rate that was recorded during this study (112 km d^{-1}; AF30, adult male) was for a fox traveling on sea ice, and was substantially greater than the previously published maximum travel rate of 90 km d^{-1} documented by Tarroux et al. (2010). It is unlikely that ice movement had a large effect on this travel rate. Sea ice data obtained from the National Snow and Ice Data Center International Arctic Buoy Programme (2011) revealed that daily ice movement rates obtained from the two buoys nearest to AF30's path (when it's maximum travel rate was observed) did not exceed more than 4.0 km d^{-1}. Other high travel rates documented in this study were similar to previous observations in NPR-A (Pamperin et al. 2008) and were observed for multiple foxes (Table 3). The use of sea ice by foxes in Northern Alaska has previously been documented (Pamperin et al. 2008; Eberhardt and Hanson 1978) and was observed for NPR-A foxes but not for foxes in Prudhoe Bay. The amount of time four NPR-A foxes spent on sea ice ranged from 71 to 118 days suggesting that sea ice is an important platform for arctic foxes during winter. I documented a fox that traveled on the Beaufort Sea over 1050 km from its initial capture location and ultimately ended up on Banks Island (NT, Canada) (Figure 4). Foxes in Prudhoe Bay did not make long distance movements on the sea ice with the exception of one juvenile, which traveled over 200 km from its initial capture location and died on the sea ice shortly after it had left the oilfield.

The extreme difference in the size of the area used by foxes in Prudhoe Bay compared to NPR-A (Figure 2, Figure 3) emphasizes the fact that differences exist in winter strategies. The majority of Prudhoe Bay foxes remained in a small area throughout winter. Conversely, NPR-A foxes traveled over large areas but despite ranging widely, did not move into the Prudhoe Bay or Kuparuk oilfields although this has been documented for juvenile foxes (Eberhardt and Hanson 1978; Pamperin 2008). I might not have observed movement into the oilfield in this study because few juveniles survived the winter.

The most probable cause for these different patterns of winter movement by arctic foxes is food availability. Food availability has an effect on arctic fox home range and movement (Chesemore 1967). Anthony (1997) reported home range of arctic foxes near Kokechik Bay, AK, to be reduced compared to other regions and suggested this was due to abundant prey in the area. Anthony (1997) did not document any long distance movements and most of the foxes in his study remained near their summer home range throughout the year. Seasonal movement toward the coast by some foxes in northern Alaska occurs in early winter and has been attributed to food scarcity (Chesemore 1967). Small rodents, primarily lemmings, are important to foxes on the North Slope (Chesemore 1968; Fine 1980; Garrott et al. 1983b). In northern Alaska lemming populations are cyclic, with peaks typically occurring every 3-4 years (Pitelka and Batzli 2007). During years of low rodent abundance the use of marine foods by arctic foxes increases (Roth 2002). Although I did not record small rodent abundance during this study, foxes in both study areas had access to the same natural prey and I do not consider differences in natural prey availability a likely explanation for the different movement patterns. Consistent food sources can result in wintering foxes remaining near summer home ranges (Burgess 2000). I did not observe this for NPR-A foxes, which suggests that high rodent abundance was not responsible for reduced winter movements of foxes in Prudhoe Bay. Also, the extensive use of sea ice by NPR-A foxes suggests that rodent abundance was not high.

The presence of anthropogenic food in the Prudhoe Bay oilfield likely explains the difference in winter movement strategies. Predictability of food resources has been shown to affect home range size (Eide et al. 2004) and anthropogenic food resources can have a particularly large effect on animal distribution and movement (Beckmann and Berger 2003; Prange et al. 2004; Bozek et al. 2007). Arctic foxes are attracted to areas associated with anthropogenic foods and utilize this food source when it is available (Eberhardt et al. 1982, Garrot et al. 1983b). Reduction in winter movement of Prudhoe Bay foxes, as well as the lack of sea ice use, suggests that fox behavior is strongly dictated by the presence of anthropogenic food sources in the oilfield. The amount of anthropogenic food available to foxes in Prudhoe Bay is unknown but observations at dumpsters and the landfill as well as the begging behavior of foxes in the oilfield suggest that anthropogenic food resources are readily available.

The different winter strategies observed for foxes in Prudhoe Bay and NPR-A likely have impacts on abundance, reproduction, and survival of foxes. In this study, I did not examine whether fox abundance was greater in the Prudhoe Bay oilfield. However, previous work has found den density to be higher in Prudhoe Bay compared to undeveloped areas outside of the oilfield (Eberhardt et al. 1983a; Ballard et al. 2000). Eberhardt et al. (1983a) also documented reduced fluctuations in fox populations in Prudhoe Bay. Anecdotal evidence suggests that fox density is higher in the oilfields simply because it took a greater effort to capture foxes in NPR-A. Also, higher fox densities may be maintained through access to anthropogenic foods associated with human activity (Fine 1980; Eberhardt et al. 1982, Garrott et al. 1983b). Fox survival and reproduction may also be affected by the availability of anthropogenic foods (Eberhardt et al. 1982).

Energy requirements are positively correlated with movement rates (Underwood 1971). Underwood (1971) found that captive arctic foxes, fed *ad libitum*, had constant fat reserves whereas wild foxes had reduced carcass mass and fat reserves during winter and suggested that fat reserves were used during food shortages. Access to consistent food resources in Prudhoe Bay combined with reduced movement requirements, likely allow foxes to preserve fat reserves and enter the breeding season in better body condition. Under these conditions, arctic fox reproduction may be increased because female reproduction is regulated by winter and spring food availability (Angerbjörn et al. 1991) and lipid reserves (Hall 1989). In contrast, reproduction of NPR-A foxes is related to the abundance of small rodents (MacPherson 1969, Angerbjörn et al. 1999) and other natural prey. In NPR-A, the high travel rates and long distances traveled during winter may result in lower reproductive output due to increased energy expenditure and associated reductions in energy reserves. Survival may also be higher for Prudhoe Bay foxes because of the reliable food resources and reduced energy demands. In addition, remaining near their capture location reduces exposure to the risks associated with traveling long distances (Angerbjörn et al. 2004) or to new areas. In Prudhoe Bay, seven of 20 foxes survived until the end of the study, whereas in NPR-A, only two of 15 foxes survived until the end of the study.

In summary, I found that winter movement of foxes in Prudhoe Bay was greatly reduced and foxes remained in a small area throughout winter. This reduced movement pattern was unlike that of foxes in NPR-A, suggesting that the presence of industrial development in northern Alaska has a strong impact on arctic fox wintering behavior. Availability and distribution of food resources is closely linked to winter movement patterns of the arctic fox. Therefore, differences in food availability between the study areas, such as the presence of anthropogenic foods in Prudhoe Bay, may be a likely factor contributing to reduced winter movements by arctic foxes near Prudhoe Bay.

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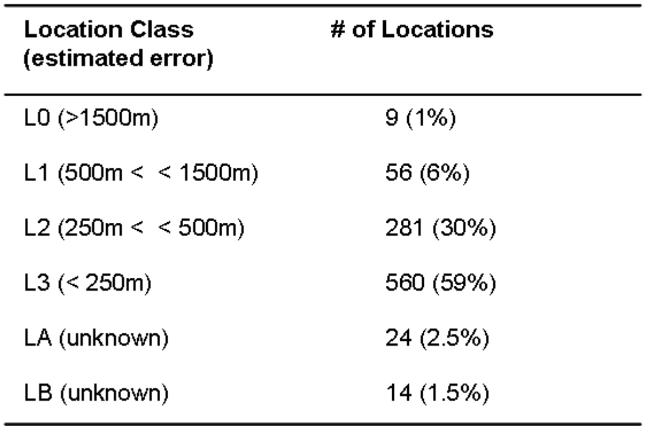
Table 1. Summary of quality classes of locations received from Argos satellite transmitters placed on arctic foxes in NPR-A and Prudhoe Bay (CLS 2010, Argos User's Manual).



Location Class (estimated error)	**# of Locations**
L0 (>1500m)	9 (1%)
L1 (500m < < 1500m)	56 (6%)
L2 (250m < < 500m)	281 (30%)
L3 (< 250m)	560 (59%)
LA (unknown)	24 (2.5%)
LB (unknown)	14 (1.5%)

Table 2. Comparison of fox winter (October- May) movements between NPR-A and Prudhoe Bay foxes for (A) adults and juvenile foxes combined, (B) adult foxes and (C) juvenile foxes (October-December only) for 2009-2010. Distances are calculated as straight line measurements between successive locations. Units for travel rates are km d^{-1} and units for maximum distance are km.

	Groups Compared	**# of Foxes**	**Daily Travel Rate Mean ± SE, (range)**	**Difference in the Mean Daily Travel Rate (SE)**	**Maximum Distance [a] Mean ± SE, (range)**	**Difference in the Maximum Distance [a] (SE)**
A	NPR-A	13	7.2 ± 0.6 (0.01, 112.6)	5.9 (0.6)*	259 ± 82 (0.06, 1055.3)	220 (83)*
	PB	13	1.3 ± 0.1 (0.03, 33.2)		38 ± 16 (0.15, 212.1)	
B	NPR-A Adults	7	7.5 ± 0.7 (0.01, 112.6)	6.3 (0.7)*	310 ± 148 (0.06, 1055.3)	286 (149)
	PB Adults	6	1.2 ± 0.1 (0.03, 11.1)		24 ± 8 (0.40, 60.52)	
C	NPR-A Juveniles	6	5.8 ± 1.1 (0.1, 48.5)	4.2 (1.2)*	198 ± 51 (0.69, 325.5)	151 (59)*
	PB Juveniles	7	1.6 ± 0.4 (0.03, 33.2)		47 ± 29 (0.15, 212.1)	

[a] Measured from capture location

*95% confidence interval of the difference does not contain zero

Table 3. Summary of movement data for the four arctic foxes collared in NPR-A that traveled extensively on the sea ice during winter 2009-2010. Distances are calculated as straight line measurements between successive locations.

	Fox ID			
	AF34	**AF30**	**AF29**	**AF28**
Age	Adult	Adult	Adult	Adult
Sex	Male	Male	Male	Female
Total number of days	85	118	87	71
Dates	Jan. 08-Apr. 02	Dec. 27-Apr. 23	Jan. 08-Mar. 21 Mar. 27-Mar. 30 Apr. 08-Apr. 17	Nov. 15-Nov. 27 Dec. 09-Dec. 21 Jan. 02- Jan. 08 Jan. 14-Feb. 04 Feb. 28-Mar. 03 Mar. 21-Mar. 24 Mar. 30-Apr. 02 May 11-May 14
Total distance traveled (km)	1501	2878	1651	515
Mean travel rate (km d^{-1})	17.9 (SE 2.4)	23.6 (SE 3.7)	19.7 (SE 3.9)	8.2 (SE 1.8)
Maximum travel rate (km d^{-1})	41.5	112.6	69.6	29.7
Date of maximum travel rate	Jan. 29-Feb. 01	Jan. 05-Jan. 08	Mar. 15-Mar. 18	Nov. 24-Nov. 27
Maximum distance[a] (km)	355.9	584.6	1051.8	115.7
Mortality Date	Apr. 02	Survived	Apr. 26	Survived

[a] Measured from capture location

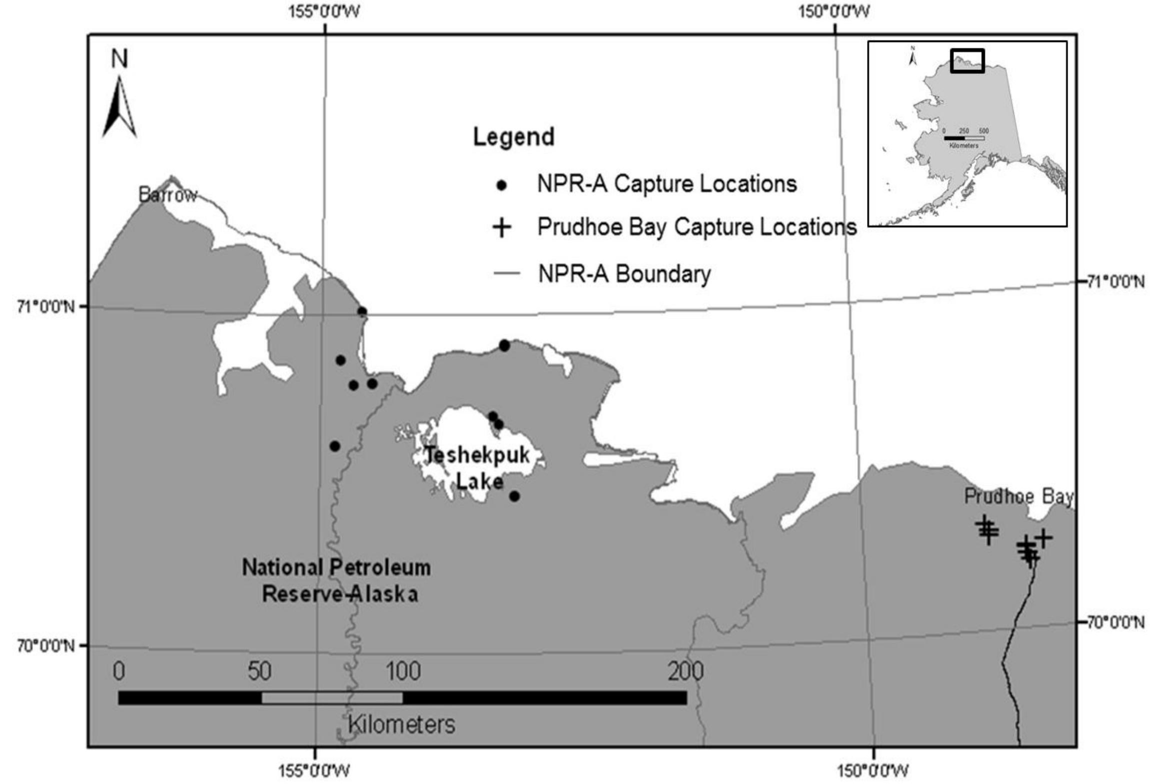


Figure 1. Capture locations of arctic foxes collared in the Prudhoe Bay oilfield and NPR-A in August 2009.

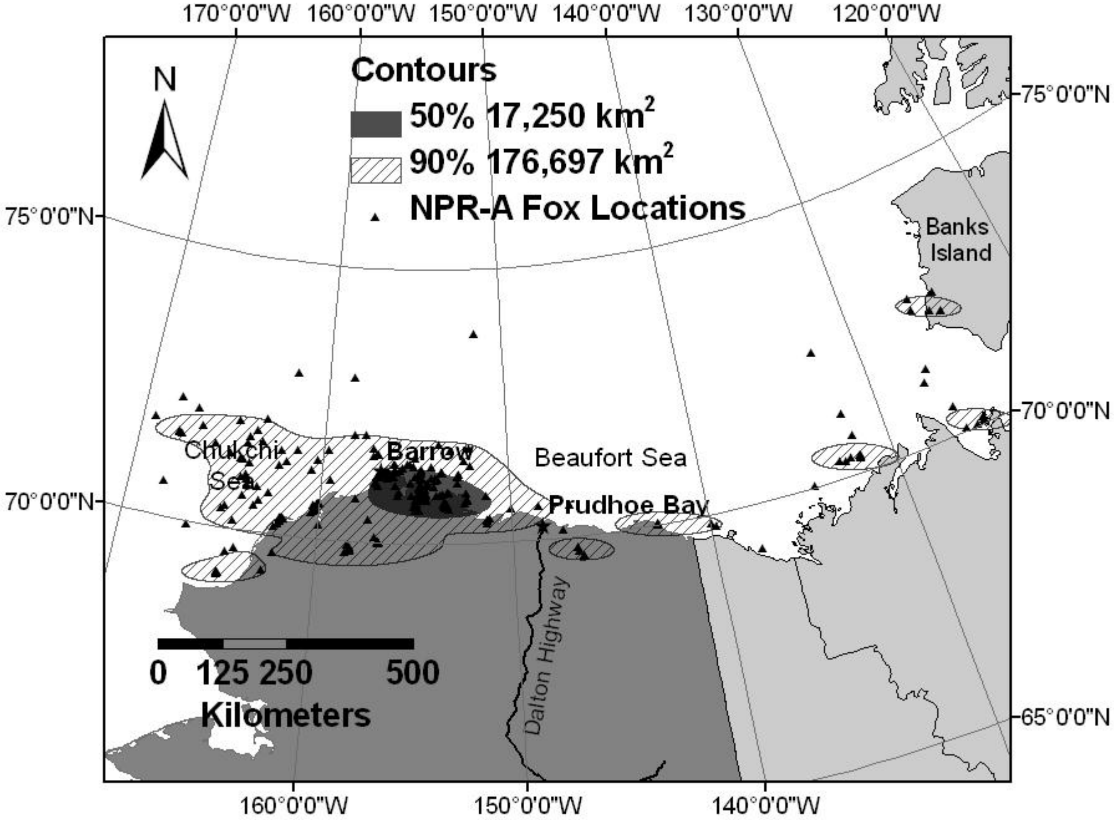


Figure 2. Probability contours for 90% and 50% fixed kernel distributions of area utilized by arctic foxes from NPR-A during the winter of 2009-2010. Map projection is Alaska Albers Conic Equal-Area, N. American Datum 1983.

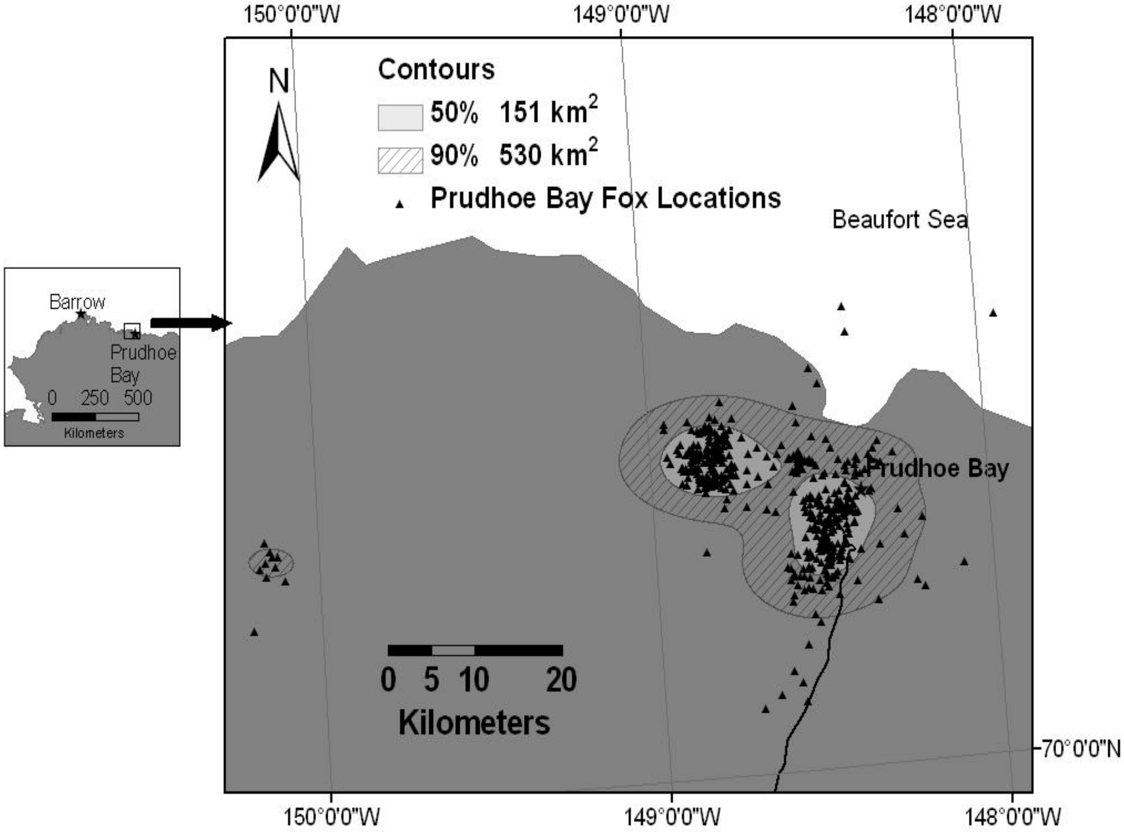


Figure 3. Probability contours for 90% and 50% fixed kernel distributions of area utilized by arctic foxes from Prudhoe Bay during the winter of 2009-2010. Map projection is Alaska Albers Conic Equal-Area, N. American Datum 1983.

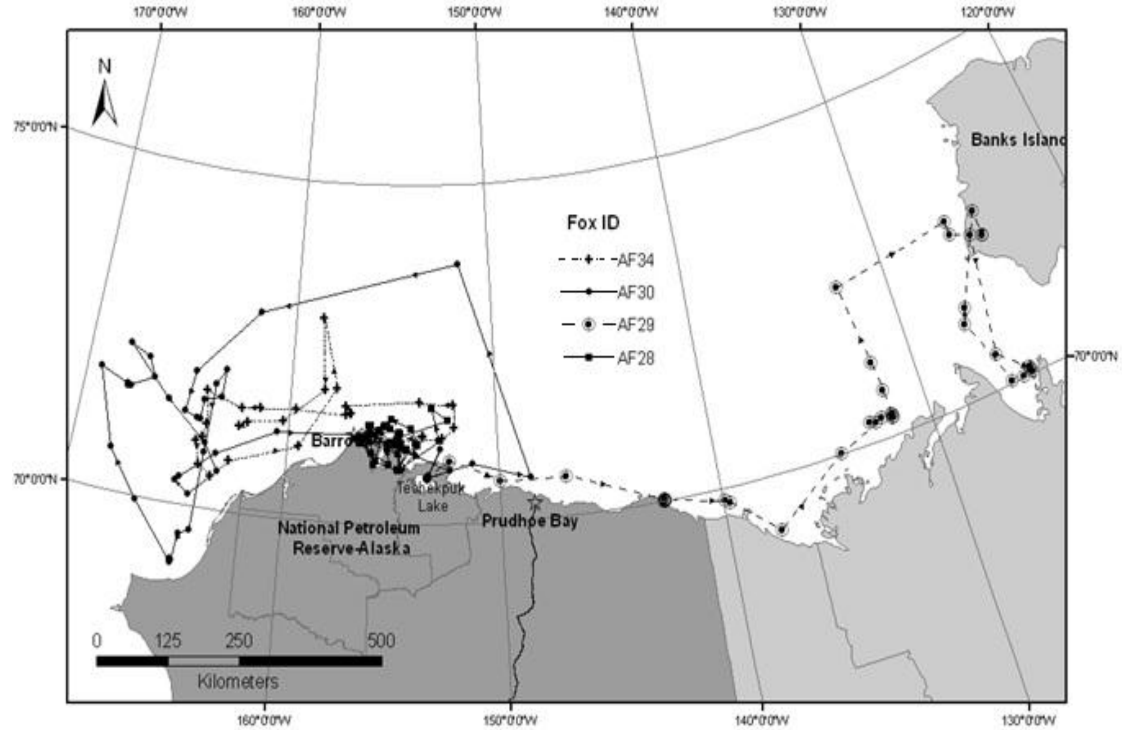


Figure 4. 2009-2010 winter movements of arctic foxes from NPR-A that used the sea ice for extensive time periods. Map projection is Alaska Albers Conic Equal-Area, N. American Datum 1983.

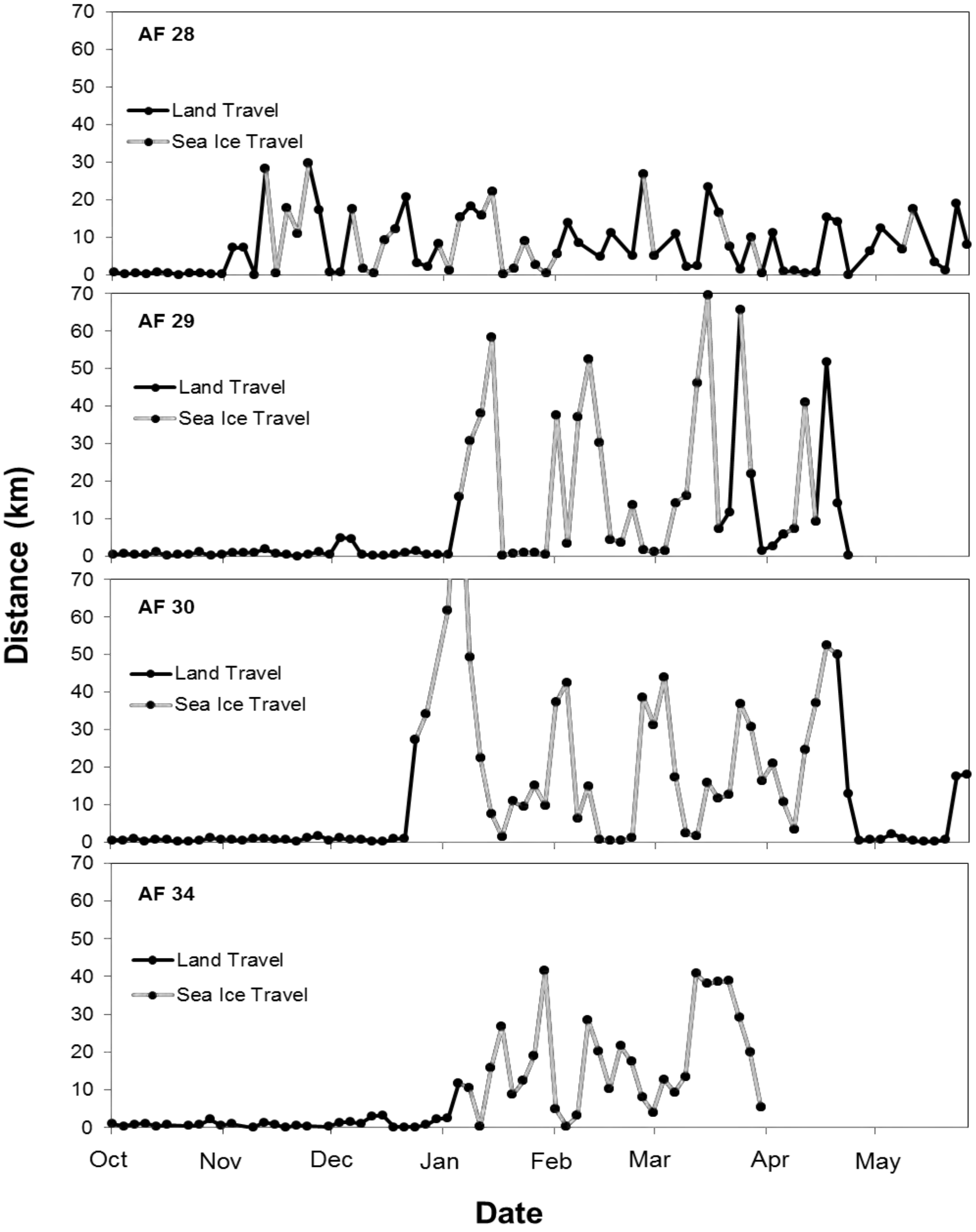


Figure 5. Daily travel rates for the four NPR-A foxes that used the sea ice for extensive time periods. Additional details on individual foxes and movements are in Table 3.

Chapter 2

Winter Diet of Arctic Foxes in Relation to Industrial Development on Alaska's North Slope[1]

Abstract

I examined the winter diet of arctic foxes (*Vulpes lagopus*) in the Prudhoe Bay oilfields and adjacent undeveloped regions of the National Petroleum Reserve-Alaska (NPR-A). Stable isotope analysis was used to assess fox diet over different time frames using muscle, claw, and bone collagen samples. Muscle and claw samples were analyzed to obtain diet information throughout the winter, whereas bone collagen was used to assess lifetime diet. Nitrogen stable isotope ratios from muscle and claw samples had higher marine signatures (higher $\delta^{15}N$ ratio) for NPR-A foxes than Prudhoe Bay foxes. Nitrogen stable isotope ratios obtained from bone collagen samples were similar between the two areas. A two-element, three-source mixing model (SIAR) was used to estimate the contribution of marine, terrestrial, and anthropogenic foods to arctic fox diet. Based on muscle tissue, the contribution of anthropogenic foods to the diet of Prudhoe Bay foxes ranged from 41% -77% with a mean of 59% compared to a mean of 17% (range 0% -38%) for NPR-A foxes. Marine food sources were utilized by NPR-A foxes but not by Prudhoe Bay foxes. My results demonstrate that anthropogenic foods are heavily utilized by arctic foxes that overwinter in the oilfields and therefore, that industrial development strongly affects winter diet of arctic foxes.

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[1] Lehner NS, Person BT, Kielland K, O'Brien DM (2012) Winter diet of arctic foxes in relation to industrial development on Alaska's North Slope. Prepared for submission to Polar Biology.

Introduction

Anthropogenic foods associated with developed or urban areas alter the availability of food resources to wildlife (Prange et al. 2004; Fischer et al. 2012). Small carnivores may be particularly affected; for example, urban red (*Vulpes vulpes*) and San Joaquin kit foxes (*Vulpes macrotis mutica*) have been shown to extensively utilize anthropogenic foods (Contesse et al. 2004, Newsome et al. 2010). Increased anthropogenic food availability to consumers in developed areas is positively correlated with population size, density, productivity, body mass, and survival (Eberhardt et al. 1983a ; Riley et al. 1998; Cypher and Frost 1999; Fedriani et al. 2001; Beckmann and Berger 2003a,b; Dip et al. 2003; Prange et al. 2003; Contesse et al. 2004). Additionally, home range and movements associated with foraging are decreased in developed regions compared to non-developed areas (Chapter 1, this thesis; Prange et al. 2004; Bozek et al. 2007; Pamperin 2008).

The arctic fox (*Vulpes lagopus*) is a species that has been exposed to industrial development on the North Slope of Alaska, (hereafter North Slope) and that occurs in higher densities in these developed regions (Eberhardt et al. 1983a; Burgess et al. 1993; Ballard et al. 2000). It has been suggested that access to anthropogenic foods in the oilfield is the key factor behind increased fox and den densities, increased survival and reproduction, stable population size, and reduced winter movement (Chapter 1, this thesis; Fine 1980; Eberhardt et al. 1982,1983a; Burgess et al. 1993; Pamperin 2008).

The importance of anthropogenic foods to arctic fox diet is likely to vary seasonally. Natural prey is more abundant during the summer months, consisting primarily of brown (*Lemmus trimucronatus)* and collared lemmings (*Dicrostonyx groenlandicus*) (Chesemore 1968; Eberhardt 1977; Fine 1980; Garrott et al. 1983; Burgess 2000), but also including opportunistic use of birds, bird eggs, and caribou carcasses (*Rangifer tarandas*) (Chesemore 1968; Eberhardt 1977; Fine 1980; Garrott et al. 1983; Burgess 2000; Liebezeit and Zack 2008). The winter diet of arctic foxes has been little studied; however, foxes may use anthropogenic foods more heavily as resources become limited. Winter use of anthropogenic foods by arctic foxes could potentially be quite high, as scat analysis of summer diets estimated garbage use ranging from 6 to 26% (Eberhardt 1977; Fine 1980; Garrott et al. 1983), likely an underestimate due to the high digestibility of these foods (Eberhardt 1977; Fine 1980; Garrott et al. 1983). Alternatively, foxes that travel onto sea ice can scavenge marine mammal carcasses from polar bear (*Ursus maritimus*) kills and prey directly on ringed seal (*Phoca hispida*) pups (Smith 1976; Chesemore 1968; Andriashek et al. 1985; Burgess 2000; Roth 2002). Use of these alternative food sources during the winter is likely to cause the large differences in movement patterns observed between arctic fox populations on the North Slope (Chapter 1, this thesis; Pamperin 2008), but winter foraging behavior has been difficult to assess.

A more recent method to examine diet composition uses stable isotope analysis, which allows for an examination of assimilated diet over different time frames (Peterson and Fry 1987, Kielland 2001), due to differential turnover rates of different tissues (Lecomte et al. 2011). Therefore, analyzing tissues assimilated during different periods of winter can be used to assess winter diet.

In northern Alaska, potential food sources to arctic fox diet include anthropogenic, terrestrial, and marine derived foods, which are isotopically distinct (Peterson and Fry 1987; Kelly 2000). Stable isotope ratios are expected to distinguish anthropogenic and arctic terrestrial foods because of a large and well described difference in carbon isotope ratios due to differences in photosynthetic pathways of C_3 and C_4 plants (Smith and Epstein 1971; Vogel and Van Der Merwe 1977; O'Leary 1981,1988; Farquhar et al. 1989). In northern Alaska, the native vegetation is exclusively C_3 (Sage et al. 1999), whereas C_4 plants (corn and sugar cane) are significant components of the North American diet, as sweeteners and feed for domestic animals (Jahren et al. 2006; Jahren and Kraft 2008). Nitrogen stable isotope ratios differ between marine and terrestrial sources (Schoeninger and Deniro 1984; Peterson and Fry 1987; Kelly 2000) and along trophic level (Hobson and Welch 1992). Because of these differences, anthropogenic, arctic terrestrial, and marine inputs to diet can be distinguished by analyzing carbon and nitrogen stable isotopes.

In this study I compared $\delta^{13}C$ and $\delta^{15}N$ values of tissues collected from satellite-collared and non-collared foxes in Prudhoe Bay and the National Petroleum Reserve-Alaska (NPR-A). My goal was to compare late winter diet between both areas and to determine the extent to which foxes in Prudhoe Bay utilized anthropogenic foods compared to foxes within the NPR-A. I hypothesized that anthropogenic foods would be utilized by foxes in Prudhoe Bay but not by foxes in NPR-A. Bone collagen values from adult foxes were also compared to determine if lifetime diet differed between study areas. This study also provides baseline information on arctic fox winter feeding ecology in Prudhoe Bay and in NPR-A prior to the expansion of oil and gas development within the NPR-A.

Methods

Study Areas

The two study areas sampled, both located on Alaska's northern coastal plain, were an undeveloped region near Teshekpuk Lake (70º 34' N, 153º 30' W) within the NPR-A and the developed region of the Prudhoe Bay oilfields (70º 15' N), (148º 20' W) (Figure 1). Hereafter, these regions are referred to as NPR-A and Prudhoe Bay, respectively. The NPR-A is a roadless, undeveloped 95,000 km^2 region and human activity is limited to subsistence activities and some seasonal oil and gas exploration. In contrast, Prudhoe Bay is a highly developed region of industrial development. Both regions have similar topography, vegetation, elevation, climate, and landscape (Raynolds et al. 2006, CAVM 2003). Winter conditions exist on the North Slope from October through May (Wendler et al. 2010, Zhang et al. 1996). Wind redistributes snow throughout winter (Liston and Sturm 2002) and creates a dense surface (sastrugi) covering layers of lower density snow (Hall et al. 1986). The Beaufort and Chukchi Seas border the coastal plain to the north and west and sea ice begins to form in October and is present until late June (Wendler et al. 2002, Wendler et al. 2010).

Study Design

Foxes were initially fitted with satellite collars (see Chapter 1 for collar information) in Prudhoe Bay (n = 20) and NPR-A (n = 15) in August 2009 as part of a companion study on winter movements and to facilitate recapture of foxes at the end of winter (May) to analyze winter diet from animals with known winter distributions. Five collared foxes were captured between May 19-29, 2010 in the Prudhoe Bay oilfields. A bone sample from a single Prudhoe Bay collared fox that had died during the winter was also collected earlier in the winter, facilitated from satellite collar location data. Foxes that were collected in Prudhoe Bay had spent the entire winter (October-May) in the oilfields as determined by satellite collars (Chapter 1, this thesis). Only 1 collared fox with a known winter distribution was recovered from NPR-A due to the remoteness of NPR-A, and large home ranges used by foxes in NPR-A compared to Prudhoe Bay. This fox was taken by a trapper in early April 2010 who provided the carcass to me. In NPR-A, I also received non-collared foxes from hunters near Teshekpuk Lake in May 2010 (n = 5) during recovery attempts for collared foxes in that region of NPR-A. For these foxes, I assumed that they had spent the winter in NPR-A and did not utilize the Prudhoe Bay oilfields. I believe this assumption is valid because telemetry data has revealed that there is little to no movement by foxes between NPR-A and Prudhoe Bay (Chapter 1, this thesis; Pamperin 2008). Overall, I collected five collared foxes from Prudhoe Bay and six foxes from NPR-A, one of which had been collared.

Sampling/Handling Procedures

Foxes were captured using live traps (Model 208, Tomahawk Live Trap, Tomahawk, WI, USA) baited with fish. Traps were set in areas where telemetry data indicated collared foxes were most recently located and were checked 3 times daily. Trapped collared foxes were transferred from live traps to a restraint cage (Tru-Catch

Traps, Bell Fourche, SD, USA) to facilitate anesthetization. Foxes were injected with a dose of ketamine hydrochloride and xylazine hydrochloride (7.0:3.5 mg/kg) and then euthanized using an injection of sodium pentobarbital. All fox capture, handling, and collection procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (Assurance No. 149496-4) and by the Alaska Department of Fish and Game (Permit No. 09-140, 10-027).

Sample Collection

Muscle and claw samples were obtained from 5 and 6 foxes from Prudhoe Bay and NPR-A, respectively, and bone collagen samples were collected from 6 adult foxes in both Prudhoe Bay and NPR-A.

To provide reference stable isotope values for anthropogenic foods I collected a small hair sample from guests (n = 6) at the Prudhoe Bay Inn, Prudhoe Bay, AK who had been working on the North Slope for at least 2 weeks and presumably were eating cafeteria foods. Hair sample collection was approved by the University of Alaska Fairbanks Institutional Review Board (Assurance No. 201923).

Sample Preparation and Analysis

Hair samples were washed in a 2:1 mixture of choloroform:methanol and rinsed with distilled water to remove surface contaminants. The first 5mm of hair was cut from the root end of each hair sample for analysis of most recent diet. Claw samples were cleaned of surface contaminants using a 2:1 mixture of choloroform:methanol and an ultrasonic bath. A small (1mm) section of claw was taken every 5 mm starting at the base (hair line) of the claw. Bone samples (0.75 g) were cut from the mandible after the flesh had been removed. Bone collagen was extracted from these samples using methods in Matheus (1997). All samples were freeze dried, then 0.1-0.3 mg of tissue was placed into a tin cup for stable isotope analysis. All samples were analyzed for carbon and nitrogen isotope ratios via continuous flow isotope ratio mass spectrometry using a Costech Elemental Analyzer (ESC 4010), Finnigan Delta Plus XP Isotope Ratio Mass Spectrometer, and ThermoFinnigan Conflo III interface at the Alaska Stable Isotope Facility, Fairbanks, Alaska. Isotope ratios are expressed in delta notation (permil (‰)) relative to international standards for carbon (Vienna PeeDee Belemnite) and nitrogen (Atmospheric N). Precision and accuracy were assessed by multiple peptone standards, and were within 0.3 and 0.1‰, respectively

Tissue Turnover and Growth Rates

I estimated diet over different time frames using tissues that differ in growth and/or turnover rates (Tieszen et al. 1983). These rates were estimated for arctic foxes from a captive feeding study by Lecomte et al. (2011). Based on these data, I expect muscle to provide dietary information on late winter diet (April-May). Bone collagen turns over slowly throughout an animal's life; therefore, bone collagen provided information on average lifetime diet (Angerbjörn et al. 1994; Dalerum and Angerbjörn 2005).

In contrast, claws grow at a nearly constant rate. This provides a sequential record of diet at the time each claw section was deposited (Bearhop et al. 2003). Assuming a claw growth rate of approximately 1 cm month^{-1} (Lecomte et al. 2011), successive 5 mm claw sections reflect the diet at 2 week intervals. I assigned the base of the claw a deposition date of mid-May to account for collection of samples in late May and extension of the base of the claw back beyond the hair line. Claws were typically 30 mm long, providing a diet record from March to May.

Statistical Analysis

I used a Bayesian stable isotope mixing model (SIAR; Parnell et al. 2010) to estimate contributions of prey sources to arctic fox diet using posterior probability distributions based on $\delta^{13}C$ and $\delta^{15}N$ isotope values from fox muscle, claw, and potential prey items. One advantage of this model over conventional mixing models is that potential uncertainty and variability of discrimination factors are accounted for (Parnell et al. 2010; Bond and Diamond 2011). Discrimination factors can affect model output and accurate estimates of discrimination factors for the species (and tissues) being studied are required (Bond and Diamond 2011). I used tissue-specific discrimination estimates for arctic fox from Lecomte et al. (2011) in my analysis, as follows: muscle was 0.37 ± 0.76 for $\delta^{13}C$ and 1.79 ± 0.41 for $\delta^{15}N$ and claw was 2.19 ± 0.64 for $\delta^{13}C$ and 3.60 ± 0.73 for $\delta^{15}N$.

I used three prey sources in the mixing models, these represented potential marine-, terrestrial-, and anthropogenic-food inputs. $\delta^{13}C$ and $\delta^{15}N$ isotope ratios for ringed seals (n = 78) from northern Alaska (Dehn et al. 2006) were used to represent marine input because ringed seals are the main prey of polar bears (Bentzen et al. 2007) and foxes scavenge polar bear kills and directly prey on ringed seal pups (Smith 1976; Roth 2002). I excluded other marine mammal species as potential food items because telemetry data from a companion study revealed that foxes traveled on the sea ice long distances from the coast (Chapter 1, this thesis) where access to other marine food items, such as bowhead whale carcasses, would be limited. Although the remains of subsistence harvested bowhead whales are present around some villages, telemetry data showed that foxes did not remain in these areas (Chapter 1, this thesis). Stable isotope values from lemmings (brown and collared) ($n = 7$) collected on the North Slope (Alaska Department of Fish and Game unpublished data) were used to represent the terrestrial source in the model. Hair samples from individuals consuming cafeteria foods on the North Slope ($n = 6$) were corrected for diet-hair discrimination (1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$) (Newsome et al. 2010). The most proximal 5mm of each hair sample was analyzed to determine diet over the previous two weeks, assuming a growth rate of 0.35 mm d^{-1} (Hayashi et al. 1991). I used the mean and standard deviation for each source and diet-tissue discrimination value in the SIAR models.

To examine the contribution of the main prey items to fox diet in the two study areas I ran the mixing model for muscle tissue. The contribution of each food source was compared between study areas using 95% credible intervals. Credible intervals that did not overlap were considered significantly different. I also examined the contribution of the three sources to diet for each claw section for each individual fox using the SiarSolo command in SIAR. Estimated proportions are presented as means and ranges based on 95% credible intervals (Parnell et al. 2010).

Because collagen reflects both winter and summer diets, and summer diets include numerous dietary items not well sampled in this study, I did not apply mixing models to collagen data. I restricted my analysis of bone collagen to adults only, so that all samples reflected diet integrated across all seasons. I compared carbon and nitrogen stable isotope ratios for bone collagen between study areas using two sample *t*-tests. All tests were performed in JMP version 9.0.2 (SAS Institute Inc., Cary, North Carolina), and significance was set at $\alpha \leq 0.05$.

Results

Stable Isotope Ratios

In Prudhoe Bay $\delta^{13}C$ muscle values ranged from -23.1‰ to -20.0‰ (mean ± SD) (-21.2 ± 1.3) and $\delta^{15}N$ ranged from 6.5‰ to 7.9‰ (7.2 ± 0.5). In NPR-A $\delta^{13}C$ ranged from -24.8‰ to -19.3‰ (-22.1 ± 1.8) and $\delta^{15}N$ ranged from 7.9‰ to 17.1‰ (13.0 ± 3.1) (Figure 2A).

Claw sections were highly variable in $\delta^{13}C$ both within and among individuals (Figure 2B). In Prudhoe Bay $\delta^{13}C$ ranged from -23.5‰ to -17.0‰ (mean ± SD) (-20.1 ± 1.8) and $\delta^{15}N$ ranged from 7.1‰ to 9.1‰ (8.1 ± 0.5). In NPR-A $\delta^{13}C$ ranged from -24.0‰ to -16.2‰ (-21.8 ± 2.6) and $\delta^{15}N$ ranged from 7.5‰ to 19.9‰ (10.9 ± 4.5).

Bone collagen $\delta^{13}C$ values were significantly higher in Prudhoe Bay foxes compared to NPR-A ($t = 3.57$, df = 10, $p = 0.005$). NPR-A $\delta^{13}C$ collagen values ranged from -23.1‰ to -21.9‰ (-22.5‰ ± 0.4‰, mean ± SD) whereas Prudhoe Bay $\delta^{13}C$ collagen values ranged from –22.1‰ to –19.8‰ (-20.9‰ ± 0.9‰). Values of $\delta^{15}N$ from bone collagen were similar for NPR-A and Prudhoe Bay foxes ($t = 0.81$, df = 10, *p*

= 0.439). Mean $\delta^{15}N$ values for NPR-A and Prudhoe Bay foxes were 8.0 ± 0.6‰ and 7.6 ± 0.9‰, respectively.

Mixing Models

Winter Diet in Prudhoe Bay and NPR-A

Based on muscle analyses, the average input of anthropogenic foods to arctic fox winter diets in Prudhoe Bay was high (59%, range 41%-77%), especially compared to those in NPR-A (17%, range 0%-38%). Mean marine input to winter diet in Prudhoe Bay was minimal (6%, range 0%-13%), whereas in NPR-A it comprised nearly half of fox winter diet (46%, range 25%-65%). Inputs of anthropogenic and marine-derived foods differed significantly for foxes between the study areas. Mean terrestrial input to diet was similar for Prudhoe Bay and NPR-A foxes (35% and 37%), respectively (Figure 3).

Temporal Variation in Winter Diets

Sequential analyses of claws allowed me to evaluate changes in anthropogenic, marine, and terrestrial food use across the winter period, for both Prudhoe Bay and NPR-A foxes. In Prudhoe Bay, individuals utilized moderate to high proportions of anthropogenic foods in almost all time periods (Figure 4A), although use of those foods varied both temporally and intraindividually (Figure 4A). In contrast, anthropogenic input during all time periods was consistently low among NPR-A foxes, with estimates close to zero (Figure 4B). For Prudhoe Bay foxes, marine input in fox diet was minimal and showed no temporal pattern (Figure 4A). In contrast, NPR-A foxes utilized marine foods extensively during the late winter but not during other periods, with the exception of one fox who utilized marine foods throughout winter (Figure 4B). Terrestrial foods were utilized by foxes in both Prudhoe Bay and NPR-A throughout winter.

Discussion

In Prudhoe Bay, arctic foxes heavily utilized anthropogenic foods during the winter, and did not appear to use marine food sources. In contrast, NPR-A foxes utilized marine food sources heavily during the winter, but consumed little food of anthropogenic origin. Terrestrial food sources (lemmings) were important components of the winter diet for both NPR-A and Prudhoe Bay foxes. Telemetry data from a companion study revealed that arctic foxes in Prudhoe Bay remained in the oilfield throughout winter and did not travel on the sea ice, which supports the finding of little reliance on marine foods and the heavy reliance on anthropogenic foods by these foxes. Foxes in NPR-A traveled over large areas, including the sea ice, which supports the finding that these foxes are utilizing marine foods. These results reveal that different winter foraging strategies exist between fox populations in Prudhoe Bay and the NPR-A, and point to the availability of anthropogenic foods as a key factor in the reduced movement patterns of Prudhoe Bay foxes (Chapter 1, this thesis; Pamperin 2008).

Anthropogenic foods made up 59% of the winter diet of Prudhoe Bay foxes. This estimate of anthropogenic input to Prudhoe Bay fox diet is much higher than previously published estimates (Eberhardt 1977; Fine 1980; Garrott et al. 1983). However, these previous studies assessed diet using scat analysis, which likely underestimated anthropogenic input (Fine 1980; Garrott et al. 1983; Newsome et al.

2010) and focused primarily on summer diet when natural prey is abundant. Anthropogenic foods are likely utilized more in the winter than in the summer (Fine 1980; Garrott et al. 1983; Burgess 2000) and this could, in part, contribute to the higher use of anthropogenic foods observed in this study. Also, territorial behavior is stronger during spring and summer (Eberhardt et al. 1982, 1983b) which may limit access to anthropogenic foods. The high proportion of anthropogenic foods and lack of marine foods in Prudhoe Bay fox diet demonstrates that development has a strong effect on the winter feeding ecology of foxes. Heavy anthropogenic food use has also been observed for arctic foxes caught near air bases in Greenland, compared to foxes in more remote regions (Kapel 1999). Newsome et al. (2010) found that urban kit foxes had isotope values similar to humans and heavily utilized anthropogenic foods compared to rural foxes. Telemetry data showed that Prudhoe Bay foxes remained near their late summer capture locations throughout winter and had reduced travel rates (Chapter 1, this thesis; Pamperin 2008). The high proportions of anthropogenic foods in winter diet demonstrated by this study suggest that the presence of this food source enabled foxes to remain in a relatively small area throughout winter. Bone collagen isotope values suggest that anthropogenic foods are being utilized by Prudhoe Bay foxes throughout their lifetime.

NPR-A foxes consumed little food of anthropogenic origin and relied on marine and terrestrial food resources. However, the use of marine foods varied among individuals and throughout different periods of winter. In NPR-A, analysis of only muscle tissue would have indicated that marine foods made up 46% of fox diet.

However, sequential analysis of claw sections revealed that marine input to NPR-A fox diet fluctuates among individuals and over time periods, with most foxes using marine resources only in late winter when foxes directly prey on ringed seal pups (Smith 1976). Only one fox used marine foods consistently over time. Variation in the use of marine foods also suggests that NPR-A foxes do not have a consistent food source throughout late winter. It is also of interest that bone collagen values indicated that marine foods were of less importance when assessing lifetime diet of NPR-A foxes despite their use of this resource in late winter.

Bone collagen results appear to contrast with those of muscle and claw tissue results from NPR-A foxes, in that δ^{15}N values were not elevated. The lower δ^{15}N ratio suggests that marine food use, while important during late winter in this study, only comprises a small part of total lifetime diet. Telemetry data for NPR-A foxes indicated that the majority of foxes that used the sea ice only used the sea ice for 4 months (Chapter 1, this thesis). Whereas bone collagen values represent lifetime diet history, seasonal inputs to diet, inferred from stable isotopes, become diluted. Additionally, foxes in NPR-A may only heavily utilize marine foods during a year of extreme low lemming abundance because the use of marine food sources increases when small rodents are scarce (Roth 2002).

The high use of anthropogenic foods by arctic foxes in Prudhoe Bay likely affects home range size, population density, den density, survival, and reproduction. Use of anthropogenic foods likely increases foraging efficiency, which is supported by smaller core areas and reduced travel rates by foxes in Prudhoe Bay compared to NPR-

A (Chapter 1, this thesis; Pamperin 2008). Although I did not examine density, survival, and reproductive success of foxes in this study, previous work has documented differences in these parameters between foxes in Prudhoe Bay and adjacent undeveloped areas (Eberhardt et al. 1983a; Burgess et al. 1993; Ballard et al. 2000) and many researchers have suggested that anthropogenic foods were likely responsible for these differences (Fine 1980; Eberhardt et al. 1983a; Burgess et al. 1993). Eberhardt et al. (1983a) also found that fox populations were more stable in Prudhoe Bay compared to an undeveloped area when small rodent abundance was low in both areas. The foxes in Prudhoe Bay that successfully reared pups during that study were located near developed areas and the authors concluded that anthropogenic foods were likely responsible for the differences between the two fox populations (Eberhardt et al. 1983a). The presence and utilization of anthropogenic foods by arctic foxes during winter likely impacts reproduction because female arctic fox reproduction is regulated by winter and spring food availability (Angerbjörn et al. 1991) and lipid reserves (Hall 1989). I acknowledge that other factors besides the presence of anthropogenic foods may contribute to the population differences observed between fox populations in previous studies, including regional differences in natural prey abundance and small rodent cycles as well as the availability of artificial dens and cover (shelter) available to Prudhoe Bay foxes. However, pre-development data on arctic fox ecology is not available for the Prudhoe Bay oilfield.

Although telemetry data from a companion study indicated that foxes in NPR-A used the sea ice throughout winter (Chapter 1, this thesis), diet analysis revealed that only one fox in NPR-A consumed marine foods throughout the winter whereas others only utilized marine foods at the end of winter, based on sequential analysis of claw sections. This difference could be related to individual variation in the use of marine foods, given the small sample sizes in both studies. It could also be related to differences in claw growth rates between wild foxes and captive foxes, upon which the temporal chronology was based. If the claw growth rate that I used differed for wild foxes, the date that each claw section represented could be skewed.

The mean contribution of anthropogenic foods to NPR-A fox diet was higher than expected for all tissues analyzed, given the limited occurrence of this resource in this area. Importantly, both carbon and nitrogen residual error was large in the model outputs for NPR-A foxes for all analyses, which was likely due to the higher variation in feeding ecology among individuals in NPR-A. Further, NPR-A foxes travel long distances (Chapter 1, this thesis; Pamperin 2008) and could potentially come into contact with anthropogenic food sources, but their use would be limited. Also, the consumption of caribou by NPR-A foxes would shift $\delta^{13}C$ slightly towards those of anthropogenic values because caribou isotope values are slightly enriched in $\delta^{13}C$ compared to lemmings. I did not include caribou in the diet analysis because caribou is not a main winter food item for the arctic fox (Chesemore 1968). Additionally, access to this food source would be different for Prudhoe Bay and NPR-A foxes based on the winter distribution of caribou (Cronin et al. 2000; Person et al. 2007) and differences in ranging behavior of foxes in Prudhoe Bay and NPR-A (Chapter 1, this thesis; Pamperin 2008).

This diet analysis demonstrated that differences exist in the winter feeding ecology of arctic foxes from Prudhoe Bay and NPR-A. Prudhoe Bay foxes heavily utilized anthropogenic foods in combination with terrestrial foods and did not rely on marine foods. By contrast, NPR-A foxes consumed little food of anthropogenic origin and relied on marine and terrestrial food sources. Telemetry data from a companion study showed that Prudhoe Bay foxes remained near their late summer capture locations throughout winter (Chapter 1, this thesis). The high proportion of anthropogenic foods in their diet suggests that the presence of this food source enabled these foxes to remain in a relatively small area throughout winter. In contrast, NPR-A foxes traveled great distances and several foxes used the sea ice for extensive time periods (Chapter 1, this thesis). The amount of anthropogenic foods available to wildlife in the oilfield has decreased in recent years due to state laws and changes in oilfield policies aimed at reducing access to these food sources through better waste management practices and by prohibiting the intentional feeding of wildlife (Burgess 2000). However, these results clearly demonstrate that anthropogenic foods are still available and heavily utilized by foxes in the oilfields. Based on my analysis of winter diet, it appears that Prudhoe Bay foxes have adapted a winter foraging strategy that is different than that of foxes in undeveloped areas. From my results of the high use of anthropogenic foods by Prudhoe Bay foxes, I conclude that the utilization of this food source is likely the key factor responsible for differences in winter feeding ecology between Prudhoe Bay and NPR-A foxes.

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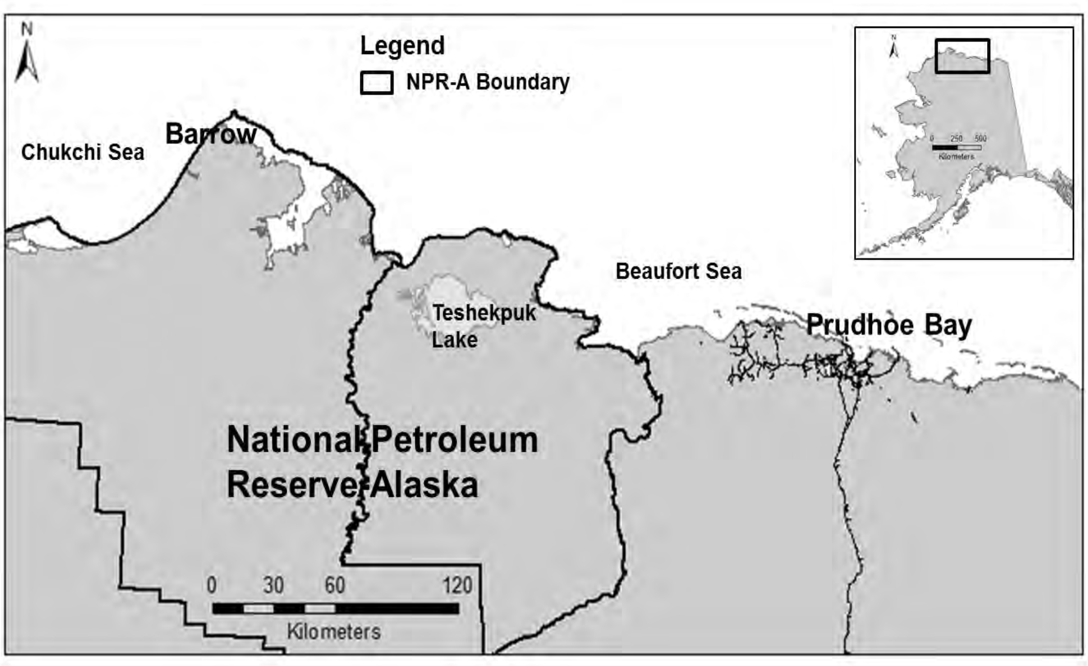

Figure 1. Map of the North Slope of Alaska showing the study areas where fox diet was examined.

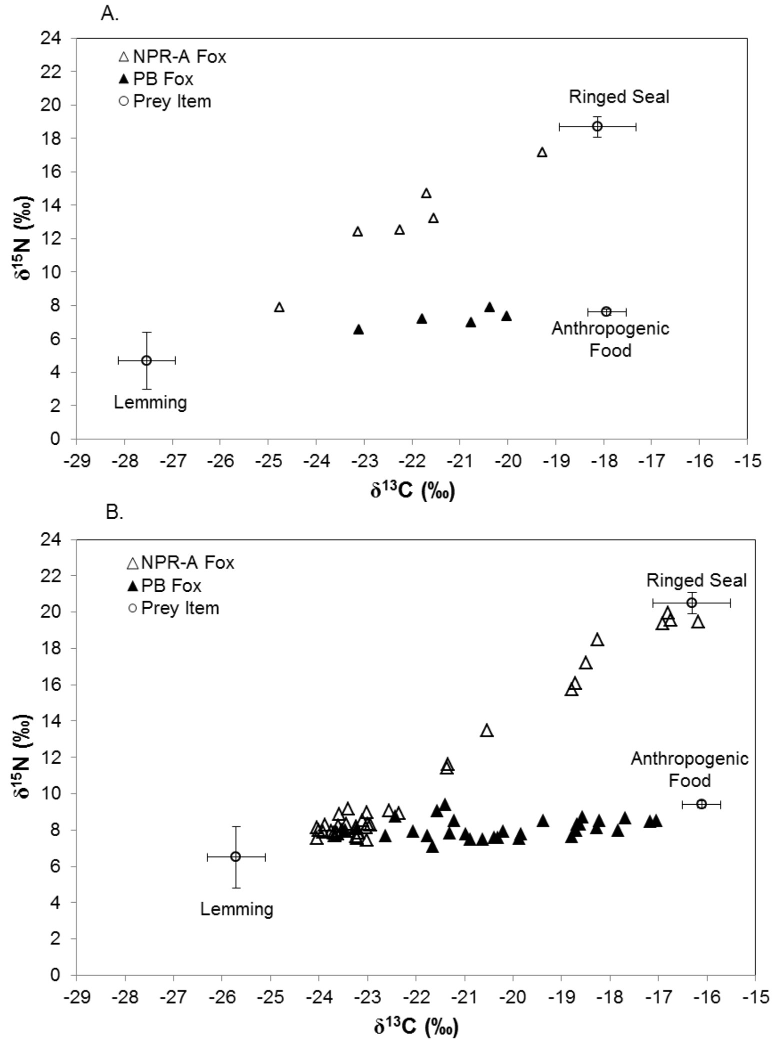

Figure 2. Carbon and nitrogen stable isotope ratios for (A) muscle tissue from NPR-A (n = 6) and Prudhoe Bay (n = 5) arctic foxes; and (B) claw sections for NPR-A (n = 33) and Prudhoe Bay (n = 30) arctic foxes. Mean (SD) stable isotope ratios for potential prey items were taken from the following sources: (Dehn et al. 2006) for ringed seals (n = 78) and (Alaska Department of Fish and Game, unpublished data) for lemmings (collared and brown; n = 7). The stable isotope ratios for anthropogenic foods were represented by human hair collected at Prudhoe Bay (n = 6, this study), corrected for human diet-tissue isotopic discrimination (1‰ for δ^{13}C and 3‰ for δ^{15}N). Potential food sources, including calculated values of anthropogenic foods, have been adjusted one trophic level using diet-fox tissue isotopic discrimination estimates from Lecomte et al. (2011).

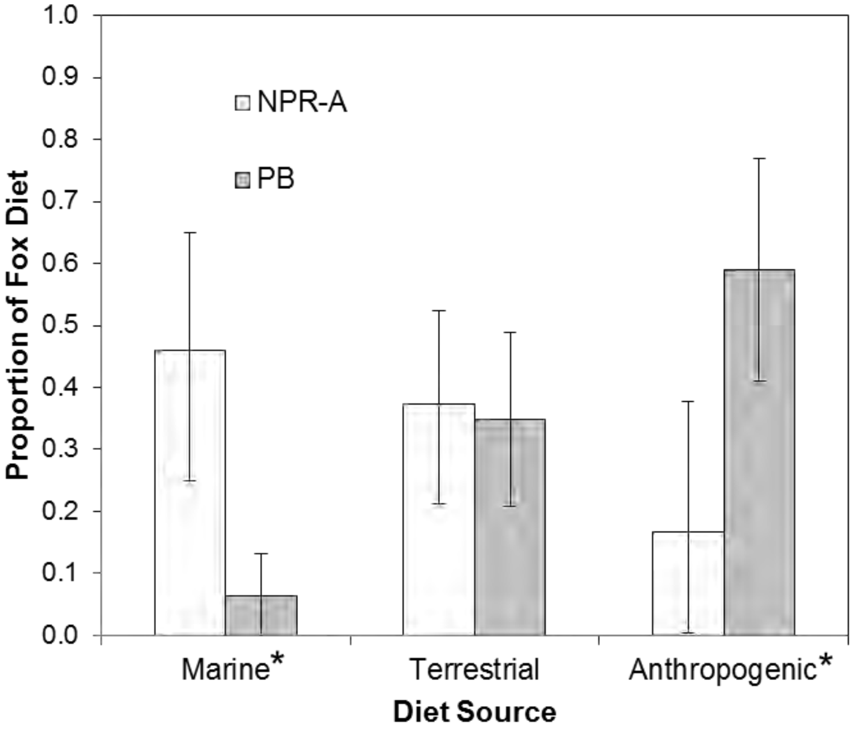

Figure 3. Proportion of marine, terrestrial, and anthropogenic food sources in arctic fox diet in NPRA and Prudhoe Bay estimated from muscle tissue stable isotope ratios. Bars represent mean proportion and error bars represent upper and lower 95% credible intervals. An asterisk next to the column name indicates food sources that differ between study areas based on non-overlapping 95% credible intervals.

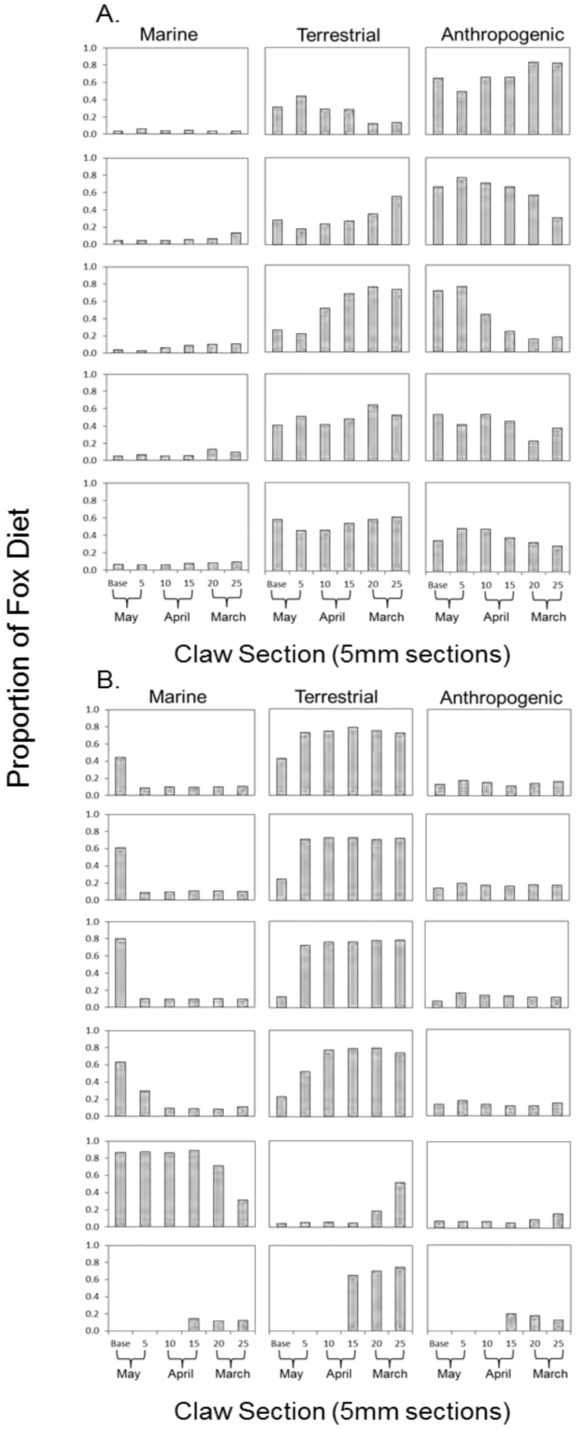

Figure 4. Proportion of marine, terrestrial, and anthropogenic food sources in (A) Prudhoe Bay (n = 5) and (B) NPR-A (n = 6) individual arctic fox diet estimated from sequential claw samples taken 5 mm apart. Bars represent the mean proportion of each food source.

General Conclusions

Telemetry data on fox winter movements suggest that industrial development has altered movements of arctic foxes in developed areas of the Prudhoe Bay oilfields. Prudhoe Bay foxes remained near summer capture locations throughout the winter and had reduced travel rates compared to NPR-A foxes. The mean daily travel rate for NPR-A foxes was over 5 times higher than for Prudhoe Bay foxes. Further, Prudhoe Bay foxes did not use the sea ice, whereas some NPR-A foxes appeared to rely on this habitat extensively during winter. There was a 330-fold difference in the area used by NPR-A foxes in winter compared to Prudhoe Bay foxes. NPR-A foxes used an area that included a large proportion of the North Slope of Alaska including the offshore sea ice of the Beaufort and Chukchi Seas. The capacity for arctic fox to travel long distances during the winter was illustrated by a fox collared in NPR-A that traveled to Banks Island, Northwest Territories, Canada and observation of a maximum travel rate of 112 km d^{-1}. It has been suggested that foxes may be attracted to developed areas during the winter but I did not observe NPR-A foxes moving into the oilfield during winter. Different winter strategies between the two populations were apparent based on the large differences observed in area used, travel rates, and maximum distance traveled from capture location.

Analysis of late winter diet suggests that the presence of anthropogenic foods associated with industrial development has altered the winter foraging ecology of arctic foxes in developed areas of the Prudhoe Bay oilfields. Prudhoe Bay foxes heavily utilized anthropogenic foods throughout late winter with over half of their diet consisting of anthropogenic foods. Marine foods were unimportant to Prudhoe Bay foxes. In contrast, marine foods were an important food source for NPR-A foxes but not during all periods of late winter. Terrestrial foods sources were important for foxes in both areas during late winter.

My results from winter diet and movement analysis indicate that arctic foxes in Prudhoe Bay and NPR-A have different winter strategies, which is likely due to the presence of anthropogenic foods in the oilfield. Utilization of this resource by Prudhoe Bay foxes enabled them to remain in the oilfield throughout the winter instead of traveling great distances to find food when natural prey becomes scarce. NPR-A foxes do not have access to this consistent reliable winter food source, resulting in the use of larger areas and the utilization of marine foods during some periods of late winter. The high consumption of anthropogenic foods and reduced winter movement of foxes in Prudhoe Bay may also result in increased reproduction, survival, and density of foxes in this area. This in turn could increase predation on natural prey, as well as increase the number of human-fox interactions, a human health concern. Analysis of summer and early winter diet using stable isotope analysis would help further resolve the degree to which Prudhoe Bay foxes utilize anthropogenic foods during different seasons, although results from adult bone collagen analysis suggest that anthropogenic foods are utilized by foxes in the oilfield throughout their life. Because future oil and gas development is likely to occur in currently undeveloped areas of northern Alaska, efforts to further minimize the availability of anthropogenic foods to foxes should be taken.