ARCTIC

VOL. 67, NO. 2 (JUNE 2014) P. 196–202 http://dx.doi.org/10.14430/arctic4386

Shifts in Fox Den Occupancy in the Greater Prudhoe Bay Area, Alaska ALICE A. STICKNEY,^{1,2} TIM OBRITSCHKEWITSCH¹ and ROBERT M. BURGESS¹

(Received 3 July 2013; accepted in revised form 6 December 2013)

ABSTRACT. Although shifts in the distribution of red foxes into areas previously dominated by Arctic foxes have been documented over wide areas of the circumpolar North, no such documentation exists yet for the Alaskan Arctic. Fox research in the greater Prudhoe Bay area from the 1970s through the early 1990s focused primarily on Arctic foxes in relation to oil development because red foxes were uncommon. A monitoring program in 2005–12 included annual surveys of 31–48 fox dens within 2 km of the road system. In 2005, 2006, and 2008, Arctic fox dens outnumbered those of red foxes, but from 2010 onward, the reverse was true. There is greater distance between natal dens of Arctic foxes and those of red foxes than between natal dens within each species, suggesting that Arctic foxes avoid red fox denning territories. Of dens in our study that were used by Arctic foxes prior to 2005, 50% have since been occupied by red foxes. Red foxes displaced Arctic foxes from dens closest to oil field camps, pads, and other facilities, and preved on their pups. Access to anthropogenic food sources probably supports red foxes in the area. Predictions from climate change studies indicate the displacement of Arctic foxes by red foxes will continue in the Alaskan Arctic, although the change may be slower away from areas of human occupation and anthropogenic foods.

Key words: Arctic fox, red fox, den occupancy, interference competition, anthropogenic food sources, climate change

RÉSUMÉ. Malgré que des changements sur le plan de la répartition du renard roux dans des régions qui étaient auparavant dominées par le renard arctique aient été répertoriés dans une grande partie du Nord circumpolaire, ce n'est pas encore le cas de l'Arctique alaskien. L'étude des renards de la grande région de la baie Prudhoe, des années 1970 jusqu'au début des années 1990, portait principalement sur le renard arctique dans le cadre de la mise en valeur du pétrole, car le renard roux n'était pas courant à ce moment-là. Un programme de surveillance mené à bien de 2005 à 2012 a notamment pris la forme de dénombrements annuels de 31 à 48 tanières de renards dans un rayon de deux kilomètres du réseau routier. En 2005, en 2006 et en 2008, le nombre de tanières de renards arctiques dépassait le nombre de tanières de renards roux, mais à partir de 2010, c'était l'inverse. La distance qui sépare les tanières de mise bas des renards arctiques de celles des renards roux est plus grande que la distance qui sépare les tanières de mise bas au sein de chacune des espèces, ce qui laisse entendre que le renard arctique évite les territoires de mise bas du renard roux. Parmi les tanières visées par notre étude qui étaient utilisées par les renards arctiques avant 2005, 50 % d'entre elles sont depuis occupées par des renards roux. Les renards roux ont supplanté les renards arctiques qui occupaient les tanières situées plus près des campements de champs pétrolifères, des zones tampons et d'autres installations, et ils ont attaqué leurs petits. L'accès aux sources alimentaires anthropiques permet probablement au renard roux de survivre dans cette région. Les prévisions émanant des études du changement climatique laissent présager que la supplantation du renard arctique par le renard roux s'étendra à l'Arctique alaskien, bien que le changement puisse se produire plus lentement en raison de l'éloignement de l'occupation humaine et de la nourriture anthropique.

Mots clés : renard arctique, renard roux, occupation de la tanière, compétition par interférence, sources alimentaires anthropiques, changement climatique

Traduit pour la revue Arctic par Nicole Giguère.

INTRODUCTION

The Arctic fox (*Vulpes lagopus*) is the dominant fox species in the circumpolar Arctic tundra region. Within the last century, the range of the Arctic fox has contracted while that of the red fox (*Vulpes vulpes*) has expanded northward (Gallant et al., 2012). There is limited information about when the contraction began in different regions, although MacPherson (1964) reported red foxes on Baffin Island in Canada in 1918. However, within the last 30 years, the contraction of the Arctic fox's range has been extensive enough in the subarctic alpine tundra in Fennoscandia to prompt concern (Hersteinsson et al., 1989; Tannerfeldt et al., 2002; Frafjord, 2003; Herfindal et al., 2010) and to instigate an analysis of the geographical changes across Arctic Canada (Hersteinsson and Macdonald, 1992; Gallant et al., 2012). In both regions, the shifts in distribution of the two fox species have since been considered as part of a suite of physical and biological alterations related to both climate change and increased human activity (Hersteinsson

¹ ABR, Inc. – Environmental Research and Services, PO Box 80410, Fairbanks, Alaska 99708, USA

² Corresponding author: astickney@abrinc.com

[©] The Arctic Institute of North America

and Macdonald, 1992; Walther et al., 2002; Fuglei and Ims, 2008; Post et al., 2009).

In the Alaskan Arctic, unlike Arctic Canada and Fennoscandia, no shift in the distribution of red and Arctic foxes has yet been documented, although there have been published reports of direct interactions between the two species (Schamel and Tracy, 1986; Pamperin et al., 2006). Research on foxes in Arctic Alaska has focused primarily on Arctic foxes in relation to oilfield development (Eberhardt, 1977; Fine, 1980; Garrott, 1980; Eberhardt et al., 1982, 1983; Garrott et al., 1984; Ballard et al., 2000; Pamperin et al., 2006). While Eberhardt (1977) included both species in his research on the biology of foxes on the North Slope of the Brooks Range, red foxes were confined almost entirely to the foothills at that time, and he reported only one record of a red fox seen on the Arctic Coastal Plain.

In the early 1990s, motivated by the increased abundance of Arctic foxes in the Prudhoe Bay region (Burgess, 2000; Ballard et al., 2000) and concern about their potential effects as predators on migratory birds, BP Exploration (Alaska) Inc. (BP) instituted surveys of fox dens in the Prudhoe Bay oilfield and adjacent undeveloped tundra. As part of these surveys, a Geographical Information System (GIS) database of fox den sites was created, incorporating all known records of fox dens prior to the 1990s as well as dens located in the course of three years of surveys in 1991–93 (ABR, unpubl. data). The surveys recorded species occupancy and productivity data for each den, as well as geographical coordinates. Between 1991 and 1993, 119 Arctic fox dens and one red fox den were identified in both developed and remote, undeveloped areas. The single red fox den was recorded on the Sagavanirktok River delta in 1992; previously, this den had been occupied by Arctic foxes. In 2005, BP initiated a long-term monitoring program that included annual surveys for occupancy and productivity of fox dens in the greater Prudhoe Bay area (consisting of Prudhoe Bay and smaller, adjacent oilfields). Between 2005 and 2012, we observed a rapid shift in den occupancy as red foxes displaced Arctic foxes from den sites and breeding territories and became the primary and dominant species in the study area.

MATERIALS AND METHODS

The greater Prudhoe Bay area, a region of relatively dense industrial activity related to oil development, encompasses a portion of the Arctic Coastal Plain ~70 km across, from the Sagavanirktok River delta in the east to Milne Point in the west (~15 km west of the Kuparuk River), and extends inland as much as 20 km from the Beaufort Sea in the north. The climate is characterized by extremes in both daylight and temperature, with minimal daylight and average monthly temperatures colder than -20° C in the winter months and continuous daylight and average monthly temperatures warmer than 0°C in the summer (Truett, 2000). The landscape is frozen for eight to nine months of the year, and soil biological activity is restricted to a thaw layer up to 100 cm deep and underlain by continuous permafrost (Walker, 1985). The landscape is mostly flat and dominated by thaw lakes and drained thaw-lake basins (Carson and Hussey, 1962). The habitat types are primarily wet and moist tundra (Walker and Acevedo, 1987).

Our study area (792 km²) encompassed all tundra within 2 km of the entire road system within the greater Prudhoe Bay area on the Arctic Coastal Plain of Alaska (Fig. 1). Except for the addition of a few new drill sites, this older core oilfield industrial area has remained largely similar in the density of roads and type of development activity since the early 1990s. Our den information came from the GIS database created in the early 1990s, which included all dens recorded by researchers between the 1970s and 1993. This database included both "natural" dens (constructed in natural features such as pingos, mounds, and river banks) and a small number of "artificial" dens (associated with manmade structures such as culverts, road banks, and trailers). Artificial dens were predominantly used as secondary dens; unlike natural dens, they were rarely used for more than a single year.

For our study, we selected a subset of natural dens from the GIS database as described below and visited them between mid-June and early July in every year from 2005 to 2012. Any new dens observed during the effort were added to the database. In 2005 and 2006, the dens surveyed were randomly selected from those within 1 km of the road system. Beginning in 2007, all natural dens within 2 km of the road system were surveyed. Artificial dens were checked opportunistically in all years of the study. The status (active, inactive) and species occupancy of each den were assessed on the first visit, and prey remains on the surface of the den were qualitatively categorized. Active dens were revisited to confirm their status and to count pups, if possible. Active dens were often visited several times and were observed from a distance (for 10 to 120 minutes per visit) to record the number of adults and pups, as well as any prey items brought to the den by adults.

Active dens were classified as natal dens if on the first visit we saw or heard pups or observed signs denoting the presence of pups (small scats, pup-sized footprints in burrow entrances, vegetation trampling). Active dens were classified as secondary dens if they were inactive when first visited in June, but casual observations in July revealed subsequent occupation by a fox family (no special effort was made to locate or identify secondary dens). Active dens at which pups were never seen were assigned to species when adult foxes were seen or when shed fur around the entrances could be identified to species.

We examined the patterns of displacement of Arctic foxes and their potential avoidance of red foxes by comparing distances between active natal dens, both within and between species, and between natal dens of each species and facilities where human activities are concentrated (e.g., camps, drill sites, processing facilities). To assess potential avoidance between species, we used our complete sample

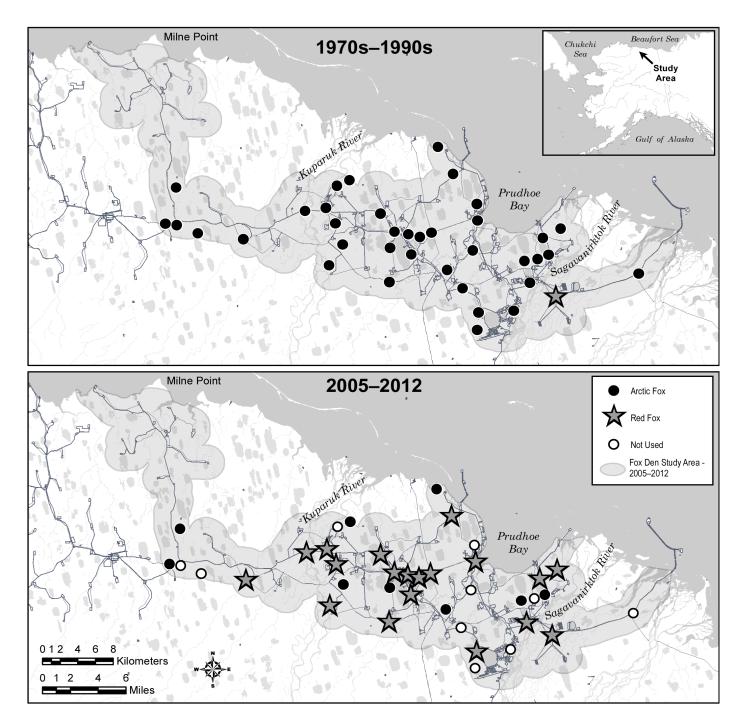


FIG. 1. The Greater Prudhoe Bay area, Alaska, where surveys for fox den occupancy and productivity were conducted from 2005 to 2012. Although the study area (outlined gray area; 792 km²) included all known dens from the 1993 GIS den database that were within 2 km of the road system and any new dens discovered after 2005, the figure shows only the dens common to both survey periods. Den occupancy by Arctic and red foxes is shown for (top) the 1970s to 1993 and (bottom) the current study period (2005–12).

of dens, but to look at whether displacement had occurred in relation to facilities, we used a subset of dens that was common to the surveys done in the 1990s and this study.

RESULTS

In 2005 and 2006, 31 to 33 dens were surveyed. Between 2007 and 2012, when all known dens in the study area were

included, 39 to 48 dens were surveyed annually. Most dens were located within 1 km from the road system; only four or five dens each year were located 1-2 km away. Ten dens had been destroyed (by erosion, collapse, or other process) or abandoned (indicated by extensive vegetation growth that obscured entrances) prior to our study, and these were removed from further consideration. Beginning in 2006, one to four natural dens were added to the database in each year except 2010.

The total number of natal dens (both species combined) varied from 11 to 18 in all years except 2007, when no dens were active and no pups were produced. The lack of breeding in foxes in 2007 may be related to a rabies/distemper epizootic that occurred across the Arctic Coastal Plain of Alaska in the winter of 2006-07.

At the beginning of our study in 2005, 85% of natal dens (11 of 13 total) were inhabited by Arctic foxes (Fig. 2). One of the red fox natal dens in 2005 was the same den known to have harbored a red fox family in 1992, and one was a completely new den. In 2006, Arctic foxes inhabited eight of a total 11 natal dens, but red foxes inhabited the other three (comprising 27% of total natal dens in the study area), including the earliest occupied den. The number of Arctic fox natal dens was stable at eight in 2006, 2008, and 2009 but dropped to two or three each year in 2010, 2011, and 2012. The number of dens inhabited by red foxes grew to six (43%) in 2008 and continued to increase each year to a high of 15 (83%) in 2011, before declining slightly in 2012. The dens that have been inhabited by red foxes include six new dens and eight that were occupied by Arctic foxes sometime between 2005 and 2008, but were taken over, as well as some dens from the database that were not occupied by Arctic foxes during this study. No den taken over by red foxes was subsequently inhabited by Arctic foxes. Despite the small sample sizes, there is a significant negative correlation between the number of Arctic fox natal dens and the number of red fox dens over the short time span of the study (Pearson r = -0.83, p = 0.02).

In addition to physically displacing Arctic foxes from den sites, red foxes may displace them from larger foraging territories, perhaps with an additional avoidance effect due to direct aggression by red foxes, as documented by observations of predatory attacks on Arctic fox adults (Frafjord et al., 1989; Pamperin et al., 2006). Because dens were a potentially limiting commodity with variable numbers occupied by each species in each year, we used the mean distance between natal dens of Arctic foxes in 2005 (when Arctic fox dens were most abundant and red foxes uncommon) to represent mean distance between natal dens of Arctic foxes when relatively unaffected by red foxes. Similarly, we used the mean distance between natal dens of red foxes in 2011 (when red fox dens were most abundant) to represent the mean distance between natal dens of red foxes at the peak of abundance observed so far. Somewhat surprisingly, the average distance between Arctic fox natal dens when red fox den occupancy was low (2005: n = 11) was 6.2 km (minimum distance 2.4 km), while that between red fox natal dens at their peak (2011: n = 15) was only 3.7 km (minimum 1.6 km). The smaller inter-den distance of red foxes suggests that they may have inhabited the most productive foraging territories or that they somehow exploit their territories differently, perhaps more effectively, than Arctic foxes had previously done. To further assess potential avoidance of red fox breeding and foraging territories by Arctic foxes, we computed the average distance from

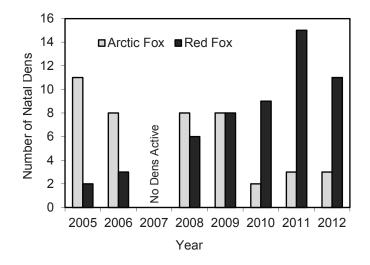


FIG. 2. Numbers of natal dens recorded for Arctic and red foxes in the Greater Prudhoe Bay area, Alaska, from 2005 to 2012.

each Arctic fox natal den to the nearest red fox natal den in 2009, when they were equally abundant (eight natal dens of each species). The average distance between red and Arctic fox natal dens in 2009 was 8.8 km (minimum 2.6 km), suggesting that avoidance further displaced Arctic foxes from parts of the study area that were inhabited by red foxes. This analysis is somewhat flawed because dens (and other resources) are not uniformly distributed across the land-scape, our sample sizes are small, and our study area was defined by proximity to roads.

To represent the extent of displacement of Arctic foxes from dens more precisely and to explore the likelihood that red foxes were more closely associated with human activities or with anthropogenic foods, we identified a subsample of 38 dens within our current study area that were part of the original GIS database (i.e., recorded as natal dens at some time between the 1970s and 1993) and were also surveyed in each year of our study (Fig. 1). As previously mentioned, there was a single red fox den from 1992 in the original database, and all other dens were occupied by Arctic foxes. During our study, an additional 18 dens were taken over by red foxes (making 19 of 38, an increase from 3% to 50% red fox dens), 10 (26%) were not used by foxes of either species, and only nine (24%) were occupied exclusively by Arctic foxes. However, three of these latter dens have not been used since 2005, making the current level of occupancy by Arctic foxes between 16% and 24%.

On average, the 19 dens that have been taken over by red foxes were significantly closer ($p \le 0.01$) to facilities (mean = 0.54 km, range 0.00-1.53 km) than the six dens that were still used by Arctic foxes (mean = 1.12 km, range 0.83-1.47 km). These data suggest that red foxes are particularly attracted to den sites where anthropogenic resources are available and that, through interference competition or direct aggression, red foxes are displacing Arctic foxes to den sites that are farther away from those resources.

DISCUSSION

Hersteinsson and MacDonald (1992) suggested that the northern limit of the red fox's geographic range was determined by food availability, while the southern limit of the Arctic fox's range was determined by the distribution and abundance of red foxes. Burgess (2000) noted that the range of red foxes was limited by the generally low primary and secondary productivity of the wet coastal tundra around the oilfields; but he also noted that in more productive riparian habitats along the Colville and Sagavanirktok Rivers, red foxes could be found as far north as the Beaufort Sea coast.

In addition to the data we have collected in the oilfields, additional anecdotal information on the shift in predominance from Arctic foxes to red foxes is available from long-term oilfield personnel. Many of these field operators have told us that in the past they rarely saw red foxes in the field, whereas now they see many red foxes and very few Arctic foxes. Because many fox dens are near drilling pads and processing facilities, operators typically are well aware of active dens and fox activity near their work areas. The apparent dominance of red foxes in recent years may be exaggerated by their tendency to den closer to facilities, compared to Arctic foxes.

The presence of red foxes on the both the Colville and Sagavanirktok river deltas in the early 1990s (ABR, unpubl. data) suggests that the recent dispersal of red foxes may have occurred from these habitats into the adjacent coastal plain tundra in the oilfield industrial area. The ability of red foxes to remain in the less productive habitat suggests that additional resources are available to support them. There is no evidence to suggest, however, that natural fox foods (small mammals, nesting birds, and carrion) have increased in abundance. Anecdotal evidence (Wildlife Conservation Society, unpubl. data) confirms that lemming populations have completed some cycles of abundance during the study, and fox breeding appears to be correlated with lemming abundance to some degree, but no quantitative data are available on small mammal populations. Two studies in the Alaskan Arctic prior to the 1980s indicated some differences in fox diets depending on proximity to human activity (Eberhardt, 1977; Garrott, 1980). While both studies found that small mammal and birds (including eggs) were the primary foods for foxes, Eberhardt's work within the oilfields and near pipeline camps found that garbage was used by both species of foxes. Garrott's study included only Arctic foxes on the Colville River delta, which was then remote from industrial development. He did not find any garbage in his diet analysis.

More recent information suggests that access to anthropogenic food sources affects the density of foxes in the oilfield industrial area in all seasons, but especially through the critical winter months. Arctic foxes are known to be attracted to and tolerant of human activity, particularly in the oilfields, where they are rarely harassed (Burgess, 2000). Habituated Arctic foxes readily consume refuse and handouts and use artificial structures as dens. Although efforts since the early years of the oilfield have reduced access to anthropogenic food somewhat, it is still available. Telemetry studies done in 2004-06 and 2009 demonstrated very low winter movement rates and high densities of habituated Arctic foxes in the oilfields (Pamperin, 2008; Lehner, 2012). Discussions with oilfield personnel suggest that red foxes are similarly tolerant and readily habituated. Research recently completed through the University of Alaska Fairbanks, which used stable isotopes to look at the diet of both Arctic and red foxes in the oilfields, should contribute more information on the use of anthropogenic food sources in the winter, but the study confirmed that red foxes, as well as Arctic foxes, remained in the oilfields in the winter and spring months (G. Savory, pers. comm. 2013). In Fennoscandia, a study indicated that red foxes inland from the coast relied on reindeer carcasses (considered a human-induced subsidy) during the low phase in the lemming cycle, which helped maintain the red fox presence in the area (Killengreen et al., 2011).

Experiments done by Rudzinski et al. (1982) demonstrated that when they shared a pen, red foxes displaced Arctic foxes from denning sites and preferred foraging areas. Extensive studies in Fennoscandia, where the Arctic fox population is now considered to be at critically low levels (IUCN, 2013), have identified interference competition with red foxes as a primary mechanism preventing population recovery (Dalerum et al., 2002; Elmhagen et al., 2002; Tannerfeldt et al., 2002; Frafjord, 2003; Selås and Vik, 2006; Killengreen et al., 2007; Shirley et al., 2009; Herfindal et al., 2010; Angerbjörn et al., 2013; Hamel et al., 2013). Responses of Arctic foxes to red foxes include avoidance (Rudzinski et al., 1982; Schamel and Tracy, 1986; Frafjord et al., 1989; Selås et al., 2010) and den abandonment (Rodnikova et al., 2011). Frafjord et al. (1989) reported red foxes killing an Arctic fox at a caribou carcass site, and Pamperin et al. (2006) reported an instance of red fox predation on an Arctic fox adult within the oilfields. In our study, it was not uncommon to find dead Arctic fox pups as prey remains at red fox dens (as seen at five dens), or to see red fox adults bringing dead Arctic fox pups back to the den (Fig. 3). The threat to pup survival, along with interference competition, may be influencing the increasing distances of Arctic foxoccupied dens from oilfield infrastructure, where red foxes now are dominant.

Hersteinsson and MacDonald (1992), as well as Fuglei and Ims (2008), predicted that over time, global warming and associated increases in primary and secondary productivity throughout the Arctic would negatively affect Arctic foxes. First, these changes would decrease the lemming prey base on which mainland Arctic foxes depend. Second, they would allow the intrusion of more dominant predators such as the red fox, which has greater food requirements and would benefit from higher plant productivity and the resultant, more diverse herbivore prey base. As this prey base could potentially include animals that are less preferred by Arctic foxes or larger than they can easily capture, the red fox would gain a competitive advantage.



FIG. 3. A female red fox carrying an Arctic fox pup to her den as prey.

However, the review by Gallant et al. (2012) of 40 years of fox surveys, in a northern Yukon region with few anthropogenic sources of food, found that although red foxes were present, they had not been able to exclude the still dominant Arctic fox. The authors suggested that climate change had not yet overcome the effect of food limitation on foxes in their study area.

Our study was limited to a small segment of the Arctic Coastal Plain of Alaska, within 2 km of the road system within the oilfields. It is unknown whether or not red foxes are increasing in abundance in other areas of the Arctic Coastal Plain, where roads and industrial development are lacking and where anthropogenic food sources are much less available. However, within our area, it is clear that red foxes are increasing their distribution into areas where they did not exist 20 to 30 years ago and are displacing Arctic foxes around facilities. It is likely that this trend will continue elsewhere on the Arctic Coastal Plain, although the shift may be slower in areas farther away from human activity and infrastructure.

ACKNOWLEDEGMENTS

We would like to thank Dr. Bill Streever, BP Senior Environmental Studies Advisor, for instituting the long-term monitoring studies of which this fox study is part and for his continued support, and Dr. Diane Sanzone, formerly with BP Environmental Studies, for overseeing the early years of the project. BP provided both funding and logistic support. Nathan Jones and James Smith of ABR and Kerry Tope, Kiel White, and Chris Tijerina from the NMS (part of NANA Regional Corporation) summer hire program helped with the fox den surveys. Alex Prichard assisted with statistics, Dorte Dissing created figures, and Sue Bishop reviewed the earliest draft. We would also like to thank the three reviewers who made useful suggestions on the first draft of the paper.

REFERENCES

- Angerbjörn, A., Eide, N.E., Dalén, L., Elmhagen, B., Hallström, P., Ims, R.A., Killengreen, S.T., et al. 2013. Carnivore conservation in practice: Replicated management actions on a large spatial scale. Journal of Applied Ecology 50(1):59–67. http://dx.doi.org/10.1111/1365-2664.12033
- Ballard, W., Cronin, M.A, Rodrigues, R., Skoog, R.O., and Pollard, R.H. 2000. Arctic fox, *Alopex lagopus*, den densities in the Prudhoe Bay oil field, Alaska. Canadian Field-Naturalist 114:453–456.
- Burgess, R.M. 2000. Arctic fox. In: Truett, J.C., and Johnson, S.R., eds. The natural history of an Arctic oil field: Development and biota. New York: Academic Press. 159–178.
- Carson, C.E., and Hussey, K.M. 1962. The oriented lakes of Arctic Alaska. Journal of Geology 70(4):417–439. http://dx.doi.org/10.1086/626834
- Dalerum, F., Tannerfeldt, M., Elmhagen, B., Becker, D., and Angerbjörn, A. 2002. Distribution, morphology and use of Arctic fox *Alopex lagopus* dens in Sweden. Wildlife Biology 8(3):185–192.
- Eberhardt, L.E., Hanson, W.C., Bengston, J.L., Garrott, R.A., and Hanson, E.E. 1982. Arctic fox home range characteristics in an oil-development area. Journal of Wildlife Management 46(1):183–190.

http://dx.doi.org/10.2307/3808421

Eberhardt, L.E., Garrott, R.A., and Hanson, W.C. 1983. Den use by Arctic foxes in northern Alaska. Journal of Mammalogy 64(1):97–102.

http://dx.doi.org/10.2307/1380754

- Eberhardt, W.L. 1977. The biology of Arctic and red foxes on the North Slope. MS thesis, University of Alaska, Fairbanks.
- Elmhagen, B., Tannerfeldt, M., and Angerbjörn, A. 2002. Foodniche overlap between Arctic and red foxes. Canadian Journal of Zoology 80(7):1274–1285. http://dx.doi.org/10.1139/z02-108
- Fine, H. 1980. Ecology of Arctic foxes at Prudhoe Bay, Alaska. MS thesis, University of Alaska, Fairbanks.
- Frafjord, K. 2003. Ecology and use of Arctic fox (*Alopex lagopus*) dens in Norway: Tradition overtaken by interspecific competition? Biological Conservation 111(3):445–453. http://dx.doi.org/10.1016/S0006-3207(02)00314-2
- Frafjord, K., Becker, D., and Angerbjörn, A. 1989. Interactions between Arctic and red foxes in Scandinavia – predation and aggression. Arctic 42(4):354–356. http://dx.doi.org/10.14430/arctic1677
- Fuglei, E., and Ims, R.A. 2008. Global warming and effects on the Arctic fox. Science Progress 91(2):175–191. http://dx.doi.org/10.3184/003685008X327468
- Gallant, D., Slough, B.G., Reid, D.G., and Berteaux, D. 2012. Arctic fox versus red fox in the warming Arctic: Four decades of den surveys in north Yukon. Polar Biology 35(9):1421–1431. http://dx.doi.org/10.1007/s00300-012-1181-8
- Garrott, R.A. 1980. Den characteristics, productivity, food habits, and behavior of Arctic foxes in northern Alaska. MS thesis, Pennsylvania State University, University Park.

- Garrott, R.A., Eberhardt, L.E., and Hanson, W.C. 1984. Arctic fox denning behavior in northern Alaska. Canadian Journal of Zoology 62(8):1636–1640. http://dx.doi.org/10.1139/z84-237
- Hamel, S., Killengreen, S.T., Henden, J.-A., Yoccoz, N.G., and Ims, R.A. 2013. Disentangling the importance of interspecific competition, food availability, and habitat in species occupancy: Recolonization of the endangered Fennoscandian Arctic fox. Biological Conservation 160:114–120. http://dx.doi.org/10.1016/j.biocon.2013.01.011
- Herfindal, I., Linnell, J.D.C., Elmhagen, B., Andersen, R., Eide, N.E., Frafjord, K., Henttonen, H., et al. 2010. Population persistence in a landscape context: The case of endangered Arctic fox populations in Fennoscandia. Ecography 33(5): 932–941.

http://dx.doi.org/10.1111/j.1600-0587.2009.05971.x

- Hersteinsson, P., and Macdonald, D.W. 1992. Interspecific competition and the geographical distribution of red and Arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos 64(3):505–515. http://dx.doi.org/10.2307/3545168
- Hersteinsson, P., Angerbjörn, A., Frafjord, K., and Kaikusalo, A. 1989. The Arctic fox in Fennoscandia and Iceland: Management problems. Biological Conservation 49(1):67–81. http://dx.doi.org/10.1016/0006-3207(89)90113-4
- IUCN (International Union for the Conservation of Nature). 2013. The IUCN Red List of Threatened Species: *Alopex lagopus*. http://www.iucnredlist.org/details/899/0
- Killengreen, S.T., Ims, R.A., Yoccoz, N.G., Bråthen, K.A., Henden, J.-A., and Schott, T. 2007. Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. Biological Conservation 135(4):459–472. http://dx.doi.org/10.1016/j.biocon.2006.10.039
- Killengreen, S.T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N.G., and Ims, R.A. 2011. The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the Arctic tundra. Journal of Animal Ecology 80(5):1049–1060.

http://dx.doi.org/10.1111/j.1365-2656.2011.01840.x

- Lehner, N.S. 2012. Arctic fox winter movement and diet in relation to industrial development on Alaska's North Slope. MS thesis, University of Alaska Fairbanks, Fairbanks.
- MacPherson, A.H. 1964. A northward range extension of the red fox in the eastern Canadian Arctic. Journal of Mammalogy 45(1):138–140.

http://dx.doi.org/10.2307/1377304

- Pamperin, N.J. 2008. Winter movements of Arctic foxes in northern Alaska measured by satellite telemetry. MS thesis, University of Alaska Fairbanks, Fairbanks.
- Pamperin, N.J., Follmann, E.H., and Petersen, B. 2006. Interspecific killing of an Arctic fox by a red fox at Prudhoe Bay, Alaska. Arctic 59(4):361–364. http://dx.doi.org/10.14430/arctic284

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325(5946):1355–1358. http://dx.doi.org/10.1126/science.1173113

Rodnikova, A., Ims, R.A., Sokolov, A., Skogstad, G., Sokolov, V., Shtro, V., and Fuglei, E. 2011. Red fox takeover of Arctic fox breeding den: An observation from Yamal Peninsula, Russia. Polar Biology 34(10):1609–1614. http://dx.doi.org/10.1007/s00300-011-0987-0

- Rudzinski, D.R., Graves, H.B., Sargeant, A.B., and Storm, G.L. 1982. Behavioral interactions of penned red and Arctic foxes. Journal of Wildlife Management 46(4):877–884. http://dx.doi.org/10.2307/3808220
- Schamel, D., and Tracy, D.M. 1986. Encounters between Arctic foxes, *Alopex lagopus*, and red foxes, *Vulpes vulpes*. Canadian Field-Naturalist 100(4):562–563.
- Selås, V., and Vik, J.O. 2006. The Arctic fox Alopex lagopus in Fennoscandia: A victim of human-induced changes in interspecific competition and predation? Biodiversity and Conservation 16(12):3575–3583. http://dx.doi.org/10.1007/s10531-006-9118-6
- Selås, V., Johnsen, B.S., and Eide, N.E. 2010. Arctic fox *Vulpes lagopus* den use in relation to altitude and human infrastructure. Wildlife Biology 16(1):107–112. http://dx.doi.org/10.2981/09-023
- Shirley, M.D.F., Elmhagen, B., Lurz, P.W.W., Rushton, S.P., and Angerbjörn, A. 2009. Modelling the spatial population dynamics of Arctic foxes: The effects of red foxes and microtine cycles. Canadian Journal of Zoology 87(12):1170–1183. http://dx.doi.org/10.1139/Z09-104
- Tannerfeldt, M., Elmhagen, B., and Angerbjörn, A. 2002. Exclusion by interference competition? The relationship between red and Arctic foxes. Oecologia 132(2):213–220. http://dx.doi.org/10.1007/s00442-002-0967-8
- Truett, J.C. 2000. Introduction. In: Truett, J.C., and Johnson, S.R., eds. The natural history of an Arctic oil field: Development and biota. New York: Academic Press. 3–13.
- Walker, D.A. 1985. Vegetation and environmental gradients of the Prudhoe Bay region, Alaska. Report 85-14. Hanover, New Hampshire: Cold Regions Research and Engineering Laboratory.
- Walker, D.A., and Acevedo, W. 1987. Vegetation and a Landsatderived land cover map of the Beechey Point Quadrangle, Arctic Coastal Plain, Alaska. Report 87-5. Hanover, New Hampshire: Cold Regions Research and Engineering Laboratory.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature 416:389–395.

http://dx.doi.org/10.1038/416389a