Annotated Bibliographies

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**Avoidance Behavior Articles**

These articles are ultimate influences on arctic fox behavior in relation to red fox intrusion on their territory. Arctic foxes are avoidant of red foxes. This is likely due to lower food availability in tundra areas, which has caused arctic foxes to evolve a smaller body size that require lower energy input. By leaving productive areas during summer breeding months to avoid red foxes, arctic foxes lose dens they have been using for hundreds of years and live in less productive areas.

**Dalén, L., Elmhagen, B., & Angerbjörn, A. (2004). Dna analysis on fox faeces and competition induced niche shifts: Competition and niche shifts in the arctic fox. *Molecular Ecology*, *13*(8), 2389–2392.** [**https://doi.org/10.1111/j.1365-294X.2004.02249.x**](https://doi.org/10.1111/j.1365-294X.2004.02249.x)

Summary

Interference competition occurs between the red and arctic fox in the mountain tundra of Sweden. During summer breeding season the cost of competitive interactions are as red foxes are predators of arctic fox cubs. The hypothesis of this research states that if the red fox is the dominant competitor, then the arctic fox would move higher into the mountains and away from the red fox, into less optimal habitat during breeding season.

To test this hypothesis the researchers used fox fecal samples to compare a change in range overlap during winter and summer months. DNA was extracted and analyzed from 119 fecal samples. The results did not show a change in altitude or distance from tree-lines of either fox species during winter months. Red foxes did not change their range during summer months; however, the arctic fox species did move higher in altitude and further from the tree-line during their summer breeding season.

Availability of rodents limits the arctic and red fox population in northern Sweden, however arctic foxes are willing to move to less productive tundra grounds during the summer breeding season. Moving away from this limited resource is likely due to the risk red foxes pose to their cubs. During the winter arctic foxes outwait red foxes at carcasses and can run to escape red fox predation. Both tactics are not possible with vulnerable cubs. Protection of offspring may be the reason red and arctic fox territory overlaps only during winter months.

Contribution

This article was included in my review as it confirms that an ultimate influence, like the ability to evolve independent of arctic foxes in a colder and more barren climate, has given the arctic foxes avoidant behavior strategies. During a vulnerable time, like breeding season, when confronted with a predator species in a resource limited environment arctic foxes will leave, even though the consequences are being displaced from well-established breeding dens.

**Elmhagen, B., Tannerfeldt, M., & Angerbjörn, A. (2002). Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology*, *80*(7), 1274–1285.** [**https://doi.org/10.1139/z02-108**](https://doi.org/10.1139/z02-108)

Summary

In Fennoscandia as the red fox has spread northward over the last century the arctic fox has also changed its range to one of higher altitude, particularly during summer months. One variable may be that arctic foxes have different prey preferences than the red fox, redistributing its range according to a change in prey location. If so, this should be reflected by a difference in food niches between the two species. If the two species food niches overlap to a significant degree it could be hypothesized that red foxes, as a stronger competitor, are pushing arctic foxes out of previously occupied territory. The objective of this study is to determine whether there is competition occurring between the two species of fox, as related to whether there exists a difference in food niche.

Scat was collected, stored and dried from inhabited red and arctic fox dens over the course of 4 summers in the 1990’s. Individual fox scats were broken apart and examined under microscope to categorize approximate percentage of mammal, fur, bone, feather, eggshell, and vegetation. Food niche overlap was calculated from average volume of different types of prey remains in scats per year. Unsurprisingly, lemmings occurred more often in the arctic fox diet and field voles and birds in the red fox diet. Field voles have a natural habitat at lower altitudes than that of lemmings. Despite this altitudinal prey difference the percentage overlap in food niche was about 75-80 % in 3 out of the 4 years.

This significant food niche overlap suggests that the relatively recent altitudinal range change of arctic foxes is due to interference competition. Arctic foxes have likely moved to higher altitudes to avoid red foxes, rather than relocating due to a difference in food niche and change in their prey location.

Contribution

The arctic fox has employed range reduction, moving to higher altitudes in order to avoid the red fox avoidance, despite having both species having a very similar diet. It is important to examine alternate theories, like a difference in food niche and change in prey location, when trying to discover causal factors in animal behavior. This study adds weight to the conclusion that interspecific competition with the red fox is what has displaced arctic foxes from productive areas and dens.

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

Summary

Global warming has caused a change in the ecosystem of the tundra over the last century. Red foxes (*Vulpes vulpes*) are establishing new territory at increasingly higher latitudes. Arctic foxes (*Vulpes lagopus*) are leaving established breeding dens and moving northward due to interspecific competition with the red fox. Two previous similar studies done give conflicting data regarding den abandonment. This research explores interactions newly occurring in this area between the two species, particularly now that they’re living within the same area and competing for resources.

Observations during field work were conducted along the Erkutayakha River, Yamal Peninsula, Russia during July 15–August 10, 2007. One of the two red foxes seen in the area during this time was observed to interact with an arctic fox mother and her pups.

Eight arctic fox pups and their mother were photographed living in a sandy den July 19, 2007. Three days later a red fox was photographed entering the arctic fox territory, causing the pups to bark a warning call before the red fox entered their den. The mother arctic fox returned to the area, sensed an intruder, and barked at the den from a distance without entering. The red fox was observed to stay in the den. These arctic foxes, as well as any remains of them, were never seen for the remainder of the observational study. Lack of remains and observation suggests no physical aggression occurred to expel the arctic fox family; however, they still abandoned their den.

Direct competition for breeding dens has contributed to expulsion of the arctic fox from territory they previously held in the southern tundra. Red foxes are larger, may outcompete for resources, and have been known to attack the subordinate arctic fox species.

Contribution

This study contains observational data about den abandonment, and the type of direct interaction occurring between red and arctic foxes in southern tundra lands. It demonstrates physical dominance of the red fox as it pushes the arctic fox out of den and territory. Not many studies of this type have been done, as interactions between the species are infrequent. As I am studying red fox aggression towards and intrusion on arctic fox territory, this observation of red fox takeover behaviour, and arctic fox retreat response was significant.

**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.** [**https://doi.org/1.1016/S0006-3207(02)00314-2**](https://doi.org/1.1016/S0006-3207%2802%2900314-2)

Summary

Arctic fox dens have been used for hundreds, or even thousands of years, by their kind and are distinct; being surrounded by vegetation, dug out of a sandy mounds, and having multiple entrances. Red fox dens are less traditional, with less surrounding vegetation and having scattered fewer entrances. Red foxes are seen as the greatest threat to the arctic fox population in Scandinavia as arctic fox generational dens are being taken over by red foxes.

Recorded in 8 regions across north Norway, and one region in south Norway, multiple den characteristics were recorded and analyzed in order to determine what factors influenced arctic fox den use. Position of arctic fox dens by sea level, altitude, distance from nearest tree-line, distance from red fox den or arctic fox den, human activity and main roads were all recorded. The past and present use of the arctic fox den by either red or arctic fox, and whether there had been litters born from these dens was also recorded and studied between the years 1980-2001.

The most important factors for arctic fox den use were distance from red fox dens and distance above the tree-line. Of the 9 areas studied there was a range of 13.3 to 63.6 % of previous arctic fox dens that were now being used by red foxes. Although the height above the tree-line leaves arctic foxes in a barren land, with fewer food options, it appears to be more important to arctic foxes to leave established dens in more habitable areas to have their pups away from red foxes. It seems unlikely that two mid-level predator species of this type can cohabitate in a resource limited area.

Contribution

Previous findings that red foxes force arctic foxes to relocate to areas with less resource availability are supported by this article. Arctic fox generational dens are being abandoned as red foxes intrude on their territory, which may be affecting the population numbers of the arctic fox. This article uses den analysis to give reason for abandonment behavior of the arctic fox by linking it to red fox den proximity, and low arctic fox numbers to a decrease in habitable range. An interesting experiment would be to determine why red foxes do not keep generational dens like arctic foxes do.

**Hersteinsson, P., & MacDonald, D. W. (1992). Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*, *64*(3), 505.** [**https://doi.org/10.2307/3545168**](https://doi.org/10.2307/3545168)

Summary

In 1992, Hersteinsson and Macdonald hypothesized that the northern limit of the red fox would be determined by food availability and climate, while the southern distribution of the Arctic fox would be determined by interspecific competition with the red fox. Analyzing 25 years of research and 33 field-based papers written on red fox interactions with the arctic fox, over three major geographical regions this hypothesis has been tested. Researchers studied demographic changes, reproduction, and population trends of each species since 1992. Each group focused on their study area, namely, Fennoscandia, Russia (Southern Yamal), and North America.

Recent range overlap, with red fox expansion north, has allowed red foxes to outcompete arctic foxes for resources and breeding dens. Almost half of the 38 arctic fox dens counted in the early 90’s have been taken by red foxes. An unforeseen factor was the effect anthropogenic influence would have. Arctic foxes will not have breeding dens close to human infrastructure, nor do they take advantage of human subsidies like red foxes do, exacerbating arctic fox range contraction and decreasing their competitive ability.

In all areas red foxes have been documented excluding arctic foxes from dens, possibly reducing their reproductive success. First noted in Yamal was den abandonment by an arctic fox, caused by a red fox. Results show that red fox abundance in North America correlates with access to anthropogenic food sources (garbage and livestock) and expands north as new area is colonized. Arctic foxes appear to be restricted to higher altitudes within their previous range in Fennoscandia, as they avoid building dens around human infrastructure and interactions with red foxes during breeding season. With increased productive habitat available, and subsidized by human activity, red fox culling has been implemented in Fennoscandia due to their overwhelming success in this area.

Significance

Red fox northern distribution is influenced by resource availability and climate change, while the southern distribution of the arctic fox is limited by its interaction with the red fox. This research is important when trying to understand aggression towards and intrusion on arctic fox territory by the red fox. It would be interesting to know why an increase in human activity in arctic regions has influenced range expansion of the red fox and contraction of the arctic fox territory. Why is the red fox more likely to take advantage of human food sources when arctic foxes are avoidant?

**Rudzinski, D. R., Graves, H. B., Sargeant, A. B., & Storm, G. L. (1982). Behavioral interactions of penned red and arctic foxes. *The Journal of Wildlife Management*, *46*(4), 877.** [**https://doi.org/10.2307/3808220**](https://doi.org/10.2307/3808220)

Summary

 Human extension into arctic regions may have facilitated the red fox expansion into arctic fox occupied areas as artificial food sources, roads for travel, and denning sites in man-made structures have increased the density of red foxes in northern Alaska. It is known that arctic fox dens are being increasingly inhabited by red foxes, and that denning sites are limited in the frozen tundra of northern Alaska. In order to study the potential consequences of competition and ongoing interactions between the two species in a resource limited situation this experiment of penned arctic and red fox behavior was conducted.

 In 1978-1979 seven pairs of arctic fox pups from Alaska were used in a penned enclosure experiment, after being raised in male-female pairs for a year in enclosures in North Dakota. Five pairs of red fox pups were used in the same experiment after having eight months bonding time. The arctic foxes were first released to an enclosure to establish themselves for one week, followed by the addition of a female red fox for approximately a week, and then a male red fox for the same amount of time. After attaching a rabbit carcass to one fence, data from observations at once every 5-minutes was collected. In 8 of 9 trials red foxes dominated arctic foxes. Provided food was only used by one species at a time, red foxes displaced arctic foxes from denning and resting sites, species active cycles did not coincide, and red foxes dominated in agonistic (threats and chases) encounters.

 This study suggests that if red foxes extend their range so that direct competition occurred, they would outcompete the arctic fox by taking over limited resources, like dens. The possibility remains that if food became limited even this resource could become dominated by the red fox.

Contribution

This study was one of the first times data gathering was done about the interactions between red and arctic foxes. It suggests that tension between the two species could be negative for the smaller arctic fox as red foxes encroach on their territory. Behavior exhibited by the two species, like den abandonment and avoidance by the arctic fox, as well as dominance of the red fox was directly observed. This experiment confirmed what has been observed in wild encounters and foreshadows continued expulsion of arctic foxes from their dens as red foxes continue northward range expansion.

**Tannerfeldt, M., Elmhagen, B., & Angerbjörn, A. (2002). Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, *132*(2), 213–220.** [**https://doi.org/10.1007/s00442-002-0967-8**](https://doi.org/10.1007/s00442-002-0967-8)

Summary

 A predator’s range can be constrained by their interaction with a larger predator species. The red and arctic fox coexist in mainland Europe, as red foxes venture further north into arctic fox territory however, if the red fox is the larger more dominant predator species, then arctic fox territory would be constrained by their interaction, particularly during breeding season.

 To test this theory, den occupancy and arctic fox breeding success was analyzed in Sweden from 1986 – 2000 using data from the Swedish Arctic Fox Project to discover if the arctic fox did avoid the red fox during breeding season. Three predictions were made; arctic foxes would avoid having breeding dens close to red fox dens, arctic fox dens would be found in higher altitudinal and less productive regions than previously, and if red foxes were removed from the area arctic foxes would use quality denning areas once again.

 Results were that arctic foxes were less likely to reproduce successfully as number of red fox reproductions increased. Quality dens were less likely to be used by arctic foxes when red foxes were found in the area, and their dens were found at a significantly higher altitude than red fox dens. Out of 3 instances where arctic fox litters were born within 8 km of red fox dens 2 kits were killed by a red fox. Red foxes were removed at 1.8/year, by hunting, which had no significant impact on arctic foxes returning to quality denning areas.

 It is likely that due to using a less suitable competition refuge during breeding season European arctic fox population numbers have not significantly increased, regardless of over 70 years of protected species status. This demonstrates the dependence of arctic foxes on their high-quality denning sites, which red fox competition excludes them from.

Contribution

 By analyzing European arctic fox dynamics, the potential long-term repercussions of what red fox exclusion of arctic foxes from high quality denning sites could mean for other arctic fox populations. This research supports other work done about red fox behavior towards the arctic fox and the competitive exclusion occurring in limited resources areas. As one of the behaviors I am studying is red fox exclusion of arctic foxes from their dens the research showing this pattern of behavior and its results are important.

**Aggressive Behavior Articles**

Red foxes are acting out against arctic foxes in aggressive behavior, both violent and threatening, as they move northward and vie for limited resources with arctic foxes. Observation of injury and death of arctic foxes by red foxes have been made. The stress response is a proximate behavior in arctic foxes that make them less likely to successfully breed and whelp when in proximity of red foxes.

**Pamperin, N. J., Follmann, E. H., & Petersen, B. (2006). Interspecific killing of an arctic fox by a red fox at Prudhoe Bay, Alaska. *Arctic*, *59*(4), 361–364.**

Summary

Winter means scarcity for both red and arctic foxes in northern Alaska. Intraguild competition is different from traditional competition as the killing and eating of competitors, a similar species who also use limited resources. Interspecific killing between carnivores occurs more commonly when body size difference is between 41 and 88 %, which is the category that wild red and arctic foxes fit into. With contact increasing between these species intraguild competition could be harmful to northern Alaska’s arctic fox population. The objective of this article is to report rarely witnessed observations in the wild of interspecies interactions as red foxes move into arctic fox territory.

Video clips recorded a fight between a red and arctic fox in Prudhoe Bay, Alaska, during the winter of 2004 that ended in the demise, and at least partial eating of an arctic fox. The red fox in these clips repeatedly tried to roll the arctic fox on its back and bite its neck, maintaining a superior position. The arctic fox struggled beneath the red fox, biting and kicking unsuccessfully. The arctic fox’s neck was bitten, and the violent shake that followed paralyzed or killed it. Afterward, the red fox bit around the back of the arctic fox’s neck to break open the skin for consumption, and the next night was recorded carrying the leg of the arctic fox.

In areas, like Norway and Sweden, where red foxes have recently advanced upon arctic fox territory to vie for resources, arctic foxes have adjusted their range to an altitudinal height that lowers risk of red fox predation. Regions of coastal plain in northern Alaska do not allow the same altitudinal retreat, and competition may become frequent and aggressive between these species, especially outside the oilfield where anthropogenic food sources are not available to the red fox.

Contribution

This article demonstrates the type of behavior that can occur when the arctic fox is unable to relocate to a safe distance from the red fox. If red and arctic fox have ranges continually overlap, and they coexist in resource limited circumstances, it seems likely that intraguild competition will occur. As observed, the larger red fox will likely predate upon the arctic fox. As the arctic fox is known to harbour rabies in northern Alaska it would be fascinating to use rabies transmission as a marker of increased contact between these species over the coming years.

**Korhonen, H., Alasuutari, S., Mäkinen, A.** [**Niemelä**](https://link.springer.com/article/10.1007/PL00013374#auth-Paavo-Niemel_)**, P. ( 1997) Inter- and intraspecific competition between the fox species Alopex lagopus and Vulpes vulpes: an evaluation trial under penned conditions. *Polar Biol* 17, 330–336 https://doi.org/10.1007/PL00013374**

Summary

Over the last few decades, the red fox range has expanded into northern arctic tundra habitat, overlapping with arctic fox range. Through competition for the same resources arctic foxes are being displaced from their most productive territory. Penned trials of these species were used to test whether competition between red and arctic foxes could be an explanation for low population numbers of the wild Scandinavian arctic fox.

Reproductive success and dominance in both species were compared during a trial conducted from 1994-1995 of farm-born foxes in Finland. Human bred arctic foxes are opposite to wild arctic foxes in respect to their weight being significantly greater than red foxes. This factor may lead to the dominant behavior shown by arctic foxes during the initial non-breeding months. During breeding months, and as the foxes began to mature, dominance increased in red foxes. Red foxes came into heat before arctic foxes, as measured by vulval swelling. Observation of three enclosures of fox groups showed that in one enclosure both red foxes mated, however no whelpings were successful. The arctic fox in enclosure 1 did not breed. In the other enclosure both red fox females mated, but only one arctic fox female did. The second enclosure had successful whelpings from the matings and all lost their kits after birth, however the red fox had kits that survived the longest.

Adult farm-bred red foxes display dominant behavior and greater reproductive success in comparison to adult farm-bred arctic foxes. This supports the idea that one factor enabling red foxes to be more successful at breeding and whelping than arctic foxes is greater dominance, in penned and wild situations.

Contribution

It is interesting that although arctic foxes outweigh red foxes in farm-bred conditions, red foxes will eventually display greater dominant behavior, and breed and whelp more successfully than arctic foxes. This teases out the factor of dominance increasing reproductive success in the red fox, as opposed to size of animal alone increasing competitive ability of either fox species. This article is helpful as it explores reasons for population dynamics in areas where red and arctic fox ranges overlap, which is why it’s included in my selection as a significant causal factor of red fox expansion limiting the arctic fox.

**Frafjord, K., Becker, D., & Angerbjörn, A. (1989). Interactions between arctic and red foxes in Scandinavia — predation and aggression. *Arctic*, *42*(4), 354–356.** [**http://www.jstor.org/stable/40510856**](http://www.jstor.org/stable/40510856)

Summary

The red and arctic fox compete for resources where their range overlaps. It seems likely that the upper range of the red fox is limited by productivity of the land and the lower range of the arctic fox is limited by competition with the red fox. Possibly due to the larger size of the red fox, in aggressive confrontations the red fox can prey on the arctic fox. Dens in habitat with more available prey are taken over by red foxes and the arctic fox is displaced to unproductive range. The northward expansion and aggressive behavior of the red fox may be limiting the arctic fox population. The objective of this study was to observe the type of interactions happening between red and arctic fox populations, as territory overlap is a new phenomenon and red fox competition may restrict the recovery of the diminished arctic fox population numbers in this region.

953 hours, split between Norway and Sweden, were spent observing den sites where interactions between red and arctic foxes could occur. Multiple, separate observations were made. In a unique instance one large arctic fox male chased a red fox female, however in three other incidences arctic foxes were chased by red foxes. Twice red foxes killed arctic foxes. In one of those events a red fox female killed arctic fox pups, and another time two red foxes killed an arctic fox. In one other observation a red fox was seen following an arctic fox into its den.

The inability of the arctic fox population to recover from its low numbers in the European tundra, even with protected species status, may be due to the predation and aggression of red foxes, and the avoidance tactic it uses with the red fox that puts it in a resource limited area.

Contribution

There are multiple examples of den takeover and violent aggression of the red fox against the arctic fox in this article, which supports previous findings of red fox aggression and is specifically the behavior of interest I am studying. Interesting to note, is the one incident where the arctic fox did not flee, which may be due to its unusually large size. Future research could be conducted using large arctic foxes and smaller red foxes in penned situations to see if size, sex, or species, plays the greatest role in dominance.