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Do arctic foxes *Alopex lagopus* depend on kills made by large predators?

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Many hypotheses have been raised to try explaining the failure of Fennoscandian arctic fox *Alopex lagopus* populations to recover following 60-70 years of protection. One of the most appealing hypotheses has been that they depend on scavenging the kills of ungulates made by large carnivores, mainly wolves *Canis lupus*, which have been absent for much of the 20th century. We examine this hypothesis using a variety of data from throughout the holarctic range of arctic foxes and conclude that there is little evidence for the importance of this food source - although it is an issue that needs to be examined in greater detail.

Key words: Alopex lagopus, arctic fox, Canis lupus, diet, interactions, intraguild, scavenging, wolf

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Fennoscandian arctic foxes *Alopex lagopus* were trapped and hunted to very low levels in the first decades of the 20th century (Hersteinsson, Angerbjörn, Frafjord & Kaikusalo 1989). Following protection in 1928, 1930 and 1940 in Sweden, Norway and Finland, respectively, the populations have failed to recover, and in many cases have declined even further (Angerbjörn, Tannerfeldt, Bjärvall, Ericson, From & Norén 1995, Kaikusalo & Angerbjörn 1995, Frafjord & Rofstad 1998, Linnell, Strand, Loison, Solberg & Jordhøy 1999b). While the cause of original decline without doubt was overexploitation, the reasons why they have failed to recover are less clear (Linnell et al. 1999b). Many hypotheses as to why they have not recovered have been raised in the scientific, popular and official literature. One of the most commonly raised hypotheses has been that arctic foxes depend on being able to scavenge on remains of large ungulate kills made by large predators like wolf *Canis lupus*, wolverine *Gulo gulo* and golden eagle *Aquila chrysaetos* (Hersteinsson et al. 1989, Angerbjörn et al. 1995). As large predators were hunted to very low levels during the early 20th century throughout the mountain areas of Scandinavia it has been argued that arctic foxes suffer reduced reproduction and/or survival because of a consequent reduction in food availability. Despite the widespread citation of this hypothesis as a fact, it has never been tested, or even properly examined. In this article we present several lines of argument against the importance of large carnivore-killed ungulate carcasses for the ecology of Scandinavian arctic foxes in general, and especially in the context of population non-recovery.

Ecological and historical context

In Scandinavia, arctic foxes are found exclusively in alpine habitats above the treeline (Landa, Strand, Linnell & Skogland 1998a, Linnell, Strand & Landa 1999a). Therefore, reindeer *Rangifer tarandus* are the only wild ungulate which are, or have ever been, potentially available in significant numbers. In Scandinavia, wild reindeer are only found in the mountains of southern Norway. Reindeer are exclusively of the semi-domestic type throughout the central and northern parts of Norway and Sweden. Domestic sheep are also allowed to graze without supervision in most Norwegian alpine areas during summer. The numbers of domestic sheep and semi-domestic reindeer have generally increased throughout the 20th century, whereas wild reindeer numbers have increased from near extinction around 1900 to peak levels during the 1960s and 1970s. Following a density-dependent crash, they have since been maintained at moderately high numbers.

Of the predator species found in Norway, it is only wolves, wolverines and golden eagles that have ever had any significant ecological presence above the treeline. Wolves were effectively exterminated from alpine areas throughout Scandinavia during the 19th century (Elgmork 1996), and wolverines were exterminated from southern Scandinavian alpine habitats by the 1960s. Wolves have not yet returned to any alpine habitats, although wolverines have now recolonised all but the southernmost areas, albeit occurring at low density (Landa, Tufto, Franzén, Bø, Lindén & Swenson 1998b). Wolves are capable of killing both wild and semi-domestic reindeer, while wolverines regularly kill only semi-domestic reindeer (Landa, Strand, Swenson & Skogland 1997). Wolverines also kill many thousands of sheep each year, primarily above the treeline (Landa, Gudvangen, Swenson & Røskaft 1999). Golden eagles are widespread throughout Scandinavia, and regularly kill both wild and semi-domestic reindeer and domestic sheep (Nybakk, Kjelvik & Kvam 1999). Because there were no ecological studies of wolf ecology in Scandinavian alpine habitats prior to their extermination we have had to draw on some data from the closest available parallel which is the forest/mountain mosaic of central Alaska.

How much meat would be available to scavenge?

Prediction 1: In order for wolf kills to be of importance for arctic foxes, a significant number of kills would need to be available within a given arctic fox territory each year.

Wolves and other large carnivores occur at low densities in alpine and tundra ecosystems (Mech, Adams, Meier, Burch & Dale 1998, Landa et al. 1998a). This low density is in part due to the low productivity of the environments, but is further accentuated by the temporal variability in prey availability caused by the migratory/nomadic habits of reindeer/caribou. Published data on wolf density, kill rates and prey utilisation rates in mountain/tundra - forest habitats similar to those in Scandinavia are available from studies in Alaska (Table 1). Based on these studies it can be estimated that only an average of 0.03-0.08 kills per km^2 per year would be available to scavengers. Given that an arctic fox territory size in Scandinavia usually is in the order of 30 km^2 (Angerbjörn, Ströman & Becker 1997, Landa, Strand, Linnell & Skogland 1998a) this works out as a maximum potential of 1-2 kills per arctic fox territory per year. Given that wolves routinely consume >90% of their kills (Ballard, Ayres, Kaufman, Reed & Fancy 1997, Mech et al. 1998), and that many other effective scavengers will also be attracted to the kill, it does not leave much meat for arctic foxes as potential carrion.

Table 1. Calculated numbers of large ungulate kills that could be expected to be made within an average 30 km^2 arctic fox territory per year, assuming an even distribution of kills within a wolf pack territory.

Study site	Territory size (km^2)	Kills/pack/day [3]	Kills/km^2/year [4]	Kills/fox territory/year
Northwest [1]	1,868	0.4	0.078	2.3
South-central [2]	1,645	0.14	0.031	0.9

[1] Ballard et al. 1997

[2] Ballard et al. 1987

[3] Winter kill rates

[4] Assumes winter kill rate throughout the whole year and wolf territories to be exclusive.

The actual amount of meat available per annum is likely to be even less than estimated above, because many large predators like wolves can be expected to disproportionately utilise the lower altitude portions of their home ranges, especially during winter (Ballard et al. 1997, Ballard, Whitman & Gardner 1987, Landa et al. 1998a). This will reduce the proportions of kills occurring in alpine habitats during winter. Arctic foxes do not move to lower altitudes during winter, and are not able to occupy forested habitats (Landa et al. 1998a).

However, wolves would not only be a provider of carrion; they would also be competing scavengers for reindeer that die from other causes. Although wolves mostly eat what they have killed, Ballard et al. (1997) found that over 10% of carcasses that wolves were observed on were scavenged. Wolverines would also be more of a competitor for carrion than a provider when wild reindeer are considered (Landa et al. 1997).

The above estimates are probably also overestimated with respect to historical wolf density in the Scandinavian mountains. All wild ungulate densities were very low in the last decades of the 19th century and the early decades of the 20th century, indicating that the environment was probably not able to support Alaska densities of wolves. Elgmork (1996) has also shown that at least for southern Norway, wolves were greatly reduced in number through control in the early part of the 19th century, almost 50-100 years before the arctic fox decline, and that they were always far more common in the forested habitats.

Why have arctic foxes not recovered along with wolverines and eagles in northern and central Scandinavia?

Prediction 2: If kills from large predators are important, arctic foxes should have recovered in areas where wolverines and golden eagles have recovered and kill semi-domestic reindeer and domestic sheep.

Although wolves are still not present in alpine ecosystems in Scandinavia, wolverine and golden eagle populations have recovered along the mountain ranges that form the northern and central parts of the border between Norway and Sweden (Gjershaug, Thingstad, Eldoy & Byrkjeland 1994, Bergström, Attergaard, From & Melqvist 1997, Landa et al. 1998b). Together these species kill a large number of semi-domestic reindeer in alpine habitats. Even in winter, when a large part of the reindeer herds are moved into forested areas, there are always some individuals left behind that fall prey to the predators (Bjärvall, Franzén, Nordkvist & Åhlman 1990). However, there is no sign that arctic fox populations have increased in these areas (Angerbjörn et al. 1995, Frafjord & Rofstad 1998).

Wolverines recolonised the Snøhetta region of south-central Norway in the 1980s. Although they are relatively poor predators of wild reindeer, they do kill many hundreds of domestic sheep each summer (Landa et al. 1999). In contrast to the prediction, not only have arctic foxes failed to recover in Snøhetta following wolverine recolonisation (Strand, Landa, Linnell, Zimmerman & Skogland 2000), but they have actually declined to the point of extinction (Linnell et al. 1999b). In addition, only trace amounts of wool has been found in arctic fox diet (Strand, Linnell, Krogstad & Landa 1999), indicating that arctic foxes do not even scavenge the abundant wolverine-killed sheep.

Importance of slaughter remains following human predation on reindeer

Prediction 3: If predator killed large ungulate carcasses are important, then human-killed reindeer carcasses or other human food sources should substitute for wolf-killed reindeer.

Even though wolves are absent from all wild reindeer areas in south Norway, wild reindeer populations are high and support a large annual harvest; animals are slaughtered on the spot, leaving behind for instance head, skin, intestines and lungs. In addition, wounded animals may die during the following winter. This food source is potentially available for arctic foxes, and other scavengers. Although this food is available only for a 6-week period each autumn, the proportion of meat is large compared to what would be left behind from wolves, and the ability of arctic foxes to cache food for later use (Vander Wall 1990) should allow them to avail of the food for many months afterwards. For example, on the Hardangervidda plateau in southwest Norway 2,000-4,000 reindeer are shot each year within 8,000 km^2 of former arctic fox habitat. This averages 0.25-0.5 reindeer carcasses per km^2, or 7-15 per 30 km^2 arctic fox territory, and is around 5-10 times the potential remains from wolf kills.

In contrast, domestic-reindeer herding in central and northern Scandinavia utilises slaughter-houses in lowland areas, which means that slaughter remains are not available to arctic foxes. Contrary to what would be expected, arctic fox populations have declined further in south Norway, where reindeer remains from hunters are available, than in central and northern Scandinavia where they are not (Angerbjörn et al. 1995, Frafjord & Rofstad 1998, Linnell et al. 1999a).

Even when supplemental food was provided to Swedish and Finnish foxes, the effects of lemming *Lemmus lemmus* cycles were still evident (Angerbjörn et al. 1995, Kaikusalo & Angerbjörn 1995). In the Swedish study, 50-100 kg of meat was placed at each experimental den in each winter in a manner which meant that only arctic foxes could access it (Angerbjörn, ArvidSon, Norén & Strömgren 1991). This level of feeding is far greater than could be expected from large predator kills. As even this level of feeding could not mask the overriding effects of lemming cycles (Angerbjörn et al. 1991), the extent to which large predator kills can modify the survival or reproduction of arctic fox in areas where lemmings occur is probably very limited.

Adult survival, population viability and food availability

Prediction 4: If predator kills are important to arctic fox population dynamics, there should be a clear relationship between food availability and the most sensitive demographic parameters.

Recent population viability analysis has highlighted that the persistence of arctic fox populations is most dependent on adult survival (Loison, Strand & Linnell 2001). While there are abundant data indicating that reproduction and early pup survival are dependent on food availability (Angerbjörn et al. 1991, Tannerfeldt, Angerbjörn & ArvidSon 1994, Strand et al. 1999, Elmhagen, Tannerfeldt, Verucci & Angerbjörn 2000), there is as yet no empirical data showing that adult survival is affected by food availability, and therefore potentially by the availability of large predator kills. Data from ear-tagged (Tannerfeldt & Angerbjörn 1996) and radio-collared individuals indicate that adult survival is still relatively high (Strand et al. 2000, J.D.C. Linnell & O. Strand, unpubl. data) in Scandinavian populations.

Arctic foxes are lemming specialists but can survive without them

Prediction 5: If large predators are important in allowing arctic foxes to exploit reindeer/caribou, we should expect these to be more important in arctic fox diet in locations where large predators exist.

In contradiction to what would be expected if large predators were important in making reindeer accessible to foxes, reindeer have a greater importance in the diet of arctic foxes in areas where large predators do not exist than where they do (Table 2). It would appear from this that wolves are more important as competitors than providers of reindeer carcasses. It must also be born in mind that arctic foxes occur naturally in many environments (Iceland, Svalbard, Kommandor Islands, Islands in the Berring straits, western Greenland) where larger predators do not exist, indicating that arctic fox survival cannot depend on them to provide food supplements. Available data indicate that in many environments arctic foxes are lemming specialists, and able to

Table 2. Frequency of occurrence of reindeer/caribou in the diet of arctic foxes from various parts of their range. Unless otherwise stated information comes from scat analysis (st = stomach contents, pr = prey remains found at den). All values are frequency of occurrence.

Study site	Season	% reindeer	Source
Wolf present			
Siberia, 17 sites	summer	< 5	Angerbjörn et al. 1999
Northwest Territories	summer	< 4	Bantle & Alisauskas 1998
Northwest Territories	summer	< 1	MacPherson 1969
	winter (st)	25	
	all year (pr)	17	
Prince of Wales Island	summer	28	Kennedy 1980
Alaska	summer	1	Garrott, Eberhardt & Hanson 1983
Alaska	summer	15	Chesemore 1968
	winter	5	
	summer (pr)	15	
Wolf absent			
West Greenland	summer	42.7	Birks & Penford 1990
East Iceland	summer	39.5	Hersteinsson & Macdonald 1996
Sweden	summer	21	Elmhagen et al. 2000
Norway, Sylane	summer	1.1	Frafjord 1995
Norway, Snøhetta	all year	43	Strand et al. 1999
Svalbard	winter (st)	42	Prestrud 1992
	summer (st)	23	
	autumn (pr)	82	
Svalbard	summer	< 1	Frafjord 1993

obtain a high proportion of their diet from lemmings even in the low phases of the cycle (Angerbjörn, Tannerfeldt & Erlinge 1999, Strand et al. 1999, Dalerum & Angerbjörn 2000, Elmhagen et al. 2000). In the absence of lemmings, birds appear to be the second most important dietary component. Therefore, lemmings and birds, and factors affecting their abundance, are by far the most important factors affecting arctic fox productivity.

Large ungulate kills - a double-edged sword

Even if arctic foxes are able to locate a large ungulate kill, it is likely to be a double edged sword. While it may provide a source of meat the equivalent of many tens or hundreds of lemmings, it is also likely to be a very dangerous location for an arctic fox. Intra-guild predation is a widespread phenomena in mammalian carnivores (Palomares & Caro 1999, Linnell & Strand 2000) and has also been documented in arctic foxes (Frafjord, Becker & Angerbjörn 1989, J.D.C. Linnell & O. Strand, unpubl. data). Although there is some debate concerning the importance of the larger red fox *Vulpes vulpes* in preventing arctic fox population recovery (Linnell et al. 1999a), any conflict is likely to be most intense close to a large and defendable food source such as a dead reindeer (Gese, Stotts & Grothe 1996). It is not only red foxes that pose a risk to arctic foxes, as species like wolf, wolverine, golden eagle and even white-tailed sea eagle *Haliaeetus albicilla* which are potential predators of arctic foxes will also scavenge kills (Wille & Kampp 1983, Gjershaug et al. 1994, Landa et al. 1997, Marquard-Petersen 1998). Observations on carcasses have also shown that even corvids can hinder arctic foxes from accessing the kill (Haglund & Nilsson 1977). However, it cannot be ruled out that possible competition from red foxes could be reduced in the event that wolves and wolverines disproportionately killed red foxes rather than arctic foxes. As arctic fox populations are far more sensitive to adult survival rather than reproduction (see above and Loison et al. 2001) it would require a very great reproductive benefit from the additional food source to overcome the risks from scavenging such sites.

Increased food availability may destroy the arctic foxes refuge

Current theory concerning red fox/arctic fox co-existence proposes that alpine and tundra habitats provide a competition refuge (sensu Durant 1998) for arctic foxes from larger, more dominant species like the red fox, primarily because of the low availability of food (Hersteinsson & Macdonald 1992, Linnell et al. 1999a). Therefore, if kills left over from large predators actually make a significant increase in the availability of food, it is likely that this will favour alpine dwelling red fox populations, to the possible detriment of arctic fox populations.

Conclusion

Being opportunistic, arctic foxes would certainly exploit leftovers from larger predator kills if they were available. However, there is very little evidence that this source of food has ever played a pivotal role in their ecology. If the hypothesis of arctic fox dependence on large predator kills is to be further advanced, data in support of it are required. With respect to the non-recovery of arctic foxes in Scandinavia it seems very unlikely that the absence of wolves or other large predators from the alpine habitats is responsible for a significantly reduced food supply for arctic foxes. Therefore, other factors, possibly demographic (Linnell et al. 1999b, Loison et al. 2001) need to be examined to determine why arctic foxes are currently threatened with regional extinction. Identifying the cause of non-recovery is a prerequisite for the establishment of effective recovery plans (Linnell et al. 1999b).

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