Feeding Ecology and Mating System in the Arctic Fox (*Vulpes lagopus*)

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Abstract

The arctic fox is a polar species adapted to one of the harshest environments on earth. It is a canid which lives in extremely different conditions compared to other members of its family. Generally it is assumed that each species adapts to a particular ecological niche showing variable behaviours, strategies and tactics. In this paper few studies on the arctic fox are summarized and put together. Thus, this species behaviour is tackled from an intraspecific comparative approach to determine which ecological conditions lead the arctic fox to behave as it does. This is possible, because of the existence of some isolated populations with different environmental and life constraints. Comparing and contrasting these different conditions, and taking into account different strategies performed in each population, can lead to deeper understanding of the evolutionary forces which have shaped the species. Thereupon, differences in its mating system, reproductive strategies and feeding ecology will be compared.

Content

1 Introduction

The arctic fox (*Vulpes lagopus*) is a small canid living in arctic ecosystems. The different environments which it inhabits are variable. It can live on inland territorires and alpine tundra in the continents (e.g. North America or Eurasia) as well as the inland habitats of some islands (e.g. Iceland, Svalbard or Greenland). But it also occupies coastal, maritime and submaritime habitats in several islands (e.g. Iceland, Bering islands or Mednyi Island) (Angerbjörn, 2004).

The species belongs to the genus *Vulpes* (sometimes it is put into the genus *Alopex*) of the dog family, Canidae. Therefore, the species is either called *Vulpes lagopus* or *Alopex lagopus*. Genetic data appear to contradict the distinction of *Alopex* from other foxes, and DNA hybridization data suggest that the Arctic fox (*Vulpes lagopus*) is as similar to species of *Vulpes* as such species are to each other (Geffen et al. 1992). The genus *Alopex* is commonly considered as a subgenus of *Vulpes* (Angerbjörn, 2004). The term "Vulpes" comes from latin, it means literally fox as well as the word "Alopex" which means fox in greek. The specific epithet, "lagopus", comes from the ancient greek. It is a compound word - λαγως (lagos, namely hair) and πους (pous, which significance is foot) – in reference to the hairy feet of this small fox (Audet et al., 2002).

Four subspecies of this species have been defined (Angerbjörn, 2004).

— A. l. lagopus (most of the range).

— A. l. semenovi (Mednyi Island, Commander Islands, Russia).

— A. l. beringensis (Bering Island, Commander Islands, Russia).

— A.l. pribilofensis (Pribilof Islands, Alaska).

The arctic fox has a relatively compact body in comparison with other foxes. Its legs are short and its snout is oblate. Thick fur covers all of his body during the winter months, with a majority of this fur being fine underfur. The highly insulating fur protects the fox against the critical low temperature of - 40 º C (Prestrud, 1990). It is the only fox changing the pelage seasonally showing a short and much thinner fur in summer months. There are two colour morphs, the "white morph" and the "blue morph", each of which is controlled by an unique locus with two alleles already identified. The white morph allele is recessive against the blue one although its frequency in the total population is way higher (Angerbjörn, 2004).

The species is the smallest mammal living in arctic and subarctic ecosystems. Beside the fur, it has several other adaptations to maintain its thermoregulation during the harsh winters. With respect to thermoregulation, being small is a critical disadvantage since the relationship between body surface and volume increases while body size decreases. It has a powerful and insulating system facilitated not only by its thick winter fur but also by lowering the skin temperature. This is achieved through vasoconstriction of the peripheral regions which minimizes the temperature gradient with the environment (Prestrud, 1991).

2 Feeding ecology

Foxes in general are essentially opportunistic predators and the arctic fox will follow this generalistic strategy as well. Usually we would expect predators to evolve as ‘specialist’ in a reliable environment with a stable availability of food - usually considered the main ecological factor influencing reproduction in mammals (Bronson, 1989) - while unpredictable environmental conditions or external variation would lead to an opportunistic or generalist strategy (Elmhagen, 1999).

Arctic foxes can feed on a broad range of prey including rodents (subfamily *Arvicolinae*, mostly lemmings both *Lemmus* spp. and *Dicrostonyx* spp.), birds (Passeriformes, Galliformes like the ptarmigan, *Lagoppus spp* etc.), reindeer (*Rangifer tarandus*) or some “maritime resources”. Because of the importance of lemmings on the ecology of arctic foxe, two ecotypes have been defined; ‘lemming ecotype’ foxes whose main prey are the lemmings, constituting up to the 85 % of the whole diet and ‘coastal ecotype’ foxes living in ice-free shore areas having a more generalist diet. In this sense, foxes living in coastal areas will be likely to feed on more variable prey since they have access to sea cliffs holding big sea-bird colonies, seal carcasses, several invertebrates linked to the marine environment and other inland preys as well (Prestrud, 1992; Angerbjörn, Tanner- feldt, Bjärvall et al., 1995; Hersteinsson & Macdonald, 1996). A generalist strategy needs obviously a high level of adaptability to the local and present environmental conditions. The feeding ecology and the differences in food abundance or prey dependency would influence several other aspects of the general biology or ecology.

It has been observed in many arctic environments that lemmings (and other arvicoline rodents) show highly fluctuating population dynamics with relatively regular cycles of 3 to 5 years (Framstad et al., 1997). Arctic fox’s lemming dependance can vary between populations as they may generally feed on alternative prey both from marine or terrestrial habitats, buffering its population from the fluctuating lemming densities (Schmidt et al., 2012). Hence, ‘lemming ecotype’ foxes which focus their diet on this rodents and have no other important subsides in alternative food resources will suffer in unpredictable environmental conditions within a short time scale. Under these conditions, the population of ‘lemming foxes’ will also fluctuate following that cycles of its main prey. On the opposite, ‘coastal ecotype’ foxes live within a more stable and predictable environment with a continuos and constant food supply from different sources already mentioned. In these cases, when the rodent’s population crashes, foxes are able to substitute them by other prey item and thus present a stable population dynamics independently from that of the lemmings. The reproductive strategy and social complexity is also influenced by its feeding diet and general ecology (Angerbjörn, 1998 and Norén, 2012). Lemming foxes, for example, will rear very large litters during and after lemming population peaks, some times having up to 18 cubs. But, during years when the lemming population crashes they can avoid reproducing. Also, even though the monogamous pair with biparental care is the most common mating system among arctic foxes, higher social organization can be described during lemming peaks in the lemming ecotype. This is not the case for those foxes living in coastal habitats experiencing a much more stable sources of food. Coastal foxes do have intermediate litter sizes and usually show a more aggressive territorial behavior than lemming foxes (Angerbjörn et al., 2004).

The arctic fox is an interesting case where the concepts of generalist and specialist strategies mix together. Arctic foxes in inland habitats of Sweden are specialists on lemmings, which always conform the main prey in its diet at anytime. But at the same time they are usually considered generalist predators because they do suffer much less decrease in reproduction success when lemmings numbers retreat to minimum. Arctic foxes would then be specialist-generalist predators suffering around a 30% decrease in reproduction succes in contrast to the real lemming specialists like the snowy owl (*Bubo scandiacus*) which would almost avoid breeding suffering a decrease of the 98% percent in the production of chicks (Schmidt, 2012). A generalist predator is less dependent on the availability of a specific prey giving up hunting a declining prey type earlier (Elmhagen, 1999). Form this viewpoint, lemming ecotype foxes will show a high specialization on lemming prey unlike coastal ecotype foxes which could be considered truly opportunistic.

3 Mating system on Arctic foxes

3.1 Comment on the article "From monogamy to complexity: social organization of arctic foxes (Vulpes lagopus) in contrasting ecosystems", by Norén et al., 2012.

Canids present an interesting case where a fairly high intraspecific variation in mating systems is observed. It is considered that the basic unit of mating system in canids is the breeding pair of a male and a female rearing the cubs of the season (Baker, 2004). But other systems have been described with higher social complexity such as cooperative breeding, additional non-reproducing adults, plural breeding females or other formations (Baker, 2004). Arctic foxes can form social groups with different levels of complexity as described for the dog family but generally they are considered monogamous. In the research that is explained in the following section, "From monogamy to complexity: social organization of arctic foxes (*Vulpes lagopus*) in contrasting ecosystems" carried out by Norén et al., 54 breeding groups of arctic foxes in a variety of contrasting ecosystems were studied. The data collected was used to compare and model the ecological factors influencing group formation in arctic fox (*Vulpes lagopus*).

Traditionally, the benefits of group hunting or communal defense have been used to explain the success of social complex groups from an evolutionary perspective (MacDonald, 1983). Some species display a elaborated foraging behavior with the coordination and cooperation of more than one individual which allows such predators to kill larger preys which would be impossible to hunt by the only effort of a single individual. This has been studied and evidenced in several species, particularly in lyons, *Panthera leo*, (Stander, 1992). But the same argument is not suitable to explain social complexity in species like the arctic fox (*Vulpes lagopus*) which normally forage singly, probably the most efficient way of hunting being that the main prey are small rodents or birds (Angerbjörn, 2004b). The model or the pattern used to explain social complexity in arctic fox mating system is the "resource dispersion hypothesis" (MacDonald, 1983). This theory states that food abundance or resource availability constraints the formation of complex social groups. An increase in group size will decrease food availability creating resource depletion thus making group living unprofitable (MacDonald, 1983). In general, a marginal or nonexisting cost from resource depletion is required for this complexity to appear. Thus, a stable, predictable and resource-rich habitat is needed for social complexity to appear and be evolutionary successful. Once these conditions are achieved, other benefits such as territorial group defense, cubs guarding or kin selection may facilitate the process, without being decisive (Hamilton, 1984). But, furthermore, the cost and benefits of group living will be likely to differ in its relevance under the pressure of contrasting ecological conditions like food abundance or predation pressure (Norén et al., 2012).

In the investigations, groups of arctic foxes in Svalbard, Iceland, Canada and Scandinavia have been studied. A social group would take into consideration "all foxes (both adults and cubs) present at the same den site during the post-weaning part of cub rearing" (Norén et al., 2012). 'Coastal ecotype' foxes were studied in the populations of the islands (Iceland and Svalbard) and 'lemming ecotype' foxes were followed in the continents (Canada and Scandinavia). Population of foxes in both Iceland and Svalbard were considered as temporally and spatially stable. Their diet was very similar being based on ptarmigan, reindeer carcasses, migratory birds and marine subsides. The only difference was found in the egg catching carried out by Svalbard foxes from goose colonies. In Iceland, resource abundance is high and relatively equally distributed along the territory. Territoriality is consequently common, especially among the shore line (Hersteinsson and Macdonald 1982). On the other hand, resources are much more variable along the island in Svalbard with very rich habitats nearby sea bird breeding colonies and very poor habitats within the inland valleys. Population size varies temporarly more than it does in Iceland but much less than what happens in the 'lemming ecotype'. In both populations, predator pressure is null with arctic fox being top predator in Iceland and with no real threat of predation in Svalbard.

This scene changes dramatically in the two continental populations in Canada and Scandinavia. Both countries support the 'lemming ecotype' with relatively regular population cycles. Those cycles in Scandinavia are more regular and have a broader amplitude than the ones occurring in canadian foxes (Norén et al., 2012). This could be in relation to differences in the dynamics of local rodents population but also because the Canadian samples were taken mainly around a geese colony and egg catches could conform a kind of buffer when lemmings are at their low. The other main factor is guarding against predators. In Canada no red fox was observed but other larger predators were detected within the study area. Conditions were slightly different in Scandinavia where red fox and golden eagle, potential predators and competitors of the arctic fox, do coexist sympatrically (Norén et al., 2012).

Hence, because of these variations in environmental conditions, social complex groups of arctic foxes are expected in areas were food abundance is high and therefore the cost of resource depletion is low. This will be the case of the coastal-line of Iceland and Svalbard as well as the surroundings of the goose colony in Canada. Arctic foxes in Scandinavia can be "pushed" to group living formations since the guarding the cubs from predators brings high benefits outweighing resource depletion. In contrast, monogamous breeding pairs will be expected in resource poor habitats with low predation pressure such as inland territories of Svalbard, Iceland and outside the goose colony in Canada.

In conclusion, mating system in Iceland was the basic unit of a monogamous pair rearing mutual cubs. This is explained because the absence of competition and predation turns communal defense and cub guarding not to be beneficial compared with resource depletion caused by increasing group size. Social groups were more complex in those resource-rich territories of Svalbard along the shore line with non-reproducing yearlings staying at the den. It was not the case in some inland habitats where costs from resource depletion were higher. Conditions in Canada seem to resemble those in Iceland with a relatively stable food supply (within and close to the goose colony) and low predation pressure (Norén et al., 2012).

Scandinavia showed the higher variation in social systems. This may be explained because of the superabundant food source in lemming peaks of the cycles as well as the supplementary feeding launched out by conservation plans. The article argues that difference between Canada and Scandinavia are due to both the stability of food sources and the predation pressure or predator body size (Norén et al., 2012). In Scandinavia, the red fox (*Vulpes vulpes*) lives within the same habitats as the arctic fox and its body sizes are nearly similar. This makes it capable of entering the arctic fox dens and have a more significant predation effect than do other larger predators (Frafjord et al. 1989). Perhaps the influence of the red fox on the arctic fox has an overstated effect, both in predation or competition, due to the low numbers of arctic foxes left (Frafjord et al. 1989).

3.1.1 Spatial variation in food availability predicts extrapair paternity

Extra-pair paternity may be higher in resource-rich ecosystems or in ecosystems without predation because the cost suffered by the female of losing male investment in the cubs care should be lower under such conditions (Norén, 2012). The distribution of food can promote extrapair copulations in two ways: first of all, if the food is patchily distributed population density can be locally high favouring females to be involved in extrapair paternities. The second term influencing polyandry comes from the fact that higher food abundance can decrease the cost of losing male parental investment if it gets aware of the cuckoldry (Cameron, 2011). Extrapair copulations appear to be more usual in close relative canids of the arctic fox such as the swift fox (*Vulpes velox*) or the red fox (*Vulpes vulpes*). This other species live on milder climate conditions and higher food abundance. One plausible explanation is that due to the tough and hard arctic conditions linked with scarce food resources, parental care requirements may change. If this is so, it would be reasonable to think that losing parental offspring investment is more costly for arctic foxes than other canids (Cameron, 2011).

3.2 Comment on the article; "Effects of food availability on dispersal and cub sex ratio in the Mednyi Arctic fox", by Goltsman et al., 2005.

Arctic foxes in the Mednyi islands have been isolated since the Pleistocene. They are

considered an endemic subspecies named as *Vulpes lagopus semenovi.* The arctic fox is top predator in the islands and within these particular terms we find a relatively simple and special system (Goltsman et al., 2005). Field conditions in Mednyi island are quite similar to those in Svalbard where the spatial and temporal availability of food resources was proved to be the most significant factor to influence arctic fox distribution (Eide et al., 2004). While the research was carried out, 48% of the social groups followed had more than three adult individuals at the den (one male, several females and one or two non-reproducing adults) (Goltsman et al., 2005).

The aim of this paper is to see the effect of the environmental variation measured as 'habitat quality heterogenity' on the reproductive strategy, in particular the effect on the sex ratio deviation. Julliard's model is the one that fits better with the results of this study (Goltsman et al., 2005). Julliard proposed that the sex ratio should be biased (assuming a sex-specific dispersal) if the breeding adults live in a rare habitat. For this model to be applied, environmental heterogenity is required, defined as the "spatial variability of reproductive success" (Julliard, 2000). Hence, there will be expected an "unique evolutionarily stable habitat-dependent sex ratio reaction norm" (Julliard, 2000). If the occupied territory is rare (there are few territories with the same quality) and presents low food abundance (low quality, low reproductive success), the sex ratio should be biased towards the most dispersing sex to reach higher probabilities for the cubs to take over a better quality habitat. If the proportion of offspring from the sex which is more likely to disperse to a better patch is higher, the reproductive success will also increase (Julliard, 2000). The opposite should occur in high quality habitats when they are rare, in which case it would be expected for the breeding pair to rear more offsprings of the most philopatric sex raising the opportunities of their offspring of finding (staying in) a high quality habitat (Julliard, 2000).

To truly asses the adaptability of this model to the case of Mednyi island arctic foxes, four premises must be tested successfully. Firstly, food resources must be spatially variable leading to environmental heterogeneity. Secondly, this unequal share of quality between territories must be reflected on a distinct reproductive success. Thirdly, it is necessary to test if dispersal is sex dependent and finally prove that sex ratio is different in rare habitats, either good or poor, than in common habitats (Goltsman et al., 2005). Every of the four hypothesis were tested. Food is actually patchily distributed by different concentration of sea bird colonies. This means there were evidence for reproductive success to be higher in some habitats (those with a good access to big sea bird colonies). Also, male and female cubs were observed to disperse differentially independently from the quality or commonness of the habitat where they were grown. And, to finish, sex ratio were significantly deviated from parity in rare habitats. It is necessary to mention it was not the same biased when the habitat was resource-rich than when it was resource-poor, being higher biased towards the dispersing sex in the latter (compared to how it is biased towards the non dispersing sex in those rare food rich territories). Overall, the sex ratio, defined as proportion of males produced, was notably lower in den sites located at high quality habitats (54 females in contras to 24 males). On the other hand, sex ratio in low quality dens was close to parity with 51 females and 56 males (Goltsman et al., 2005).

4 Conclusion

As always, results don't perfectly fit with mathematical models. Usually because biological and environmental conditions are very complex and variably it is difficult to take all of them into account when making predictions. But even though, I think there are some consistent conclusions which are possible to draw from explained the studies discussed above. The artic fox is mainly monogamous and will just form complex social groups under specific conditions. Such groups are more liklely to be formed under conditions of high and stable abundances of food resources as well as a high predtaion pressure (demanding cubs guarding). It has also been shown how arctic foxes in simple environmentes like the Mednyi islands can deviate the sex ration of the offspring from parity to obtain a higher reproductive succes. It will be interesting to do a more extensive interspecific comparative approach between close relatives such as the swift fox or the red fox.

References

Angerbjörn, A., Hersteinsson, P., and Tannerfeldt, M. 2004*a*. *Europe and North and*

Central Asia (Palearctic): Arctic fox, Alopex lagopus. In *Canids: foxes, wolves, jackals and dogs. Status Survey and Conservation Action Plan*. C. Sillero-Zubiri, M. Hoffman, and D.W. Macdonald. International Union for the Conservation of Nature/Species Survival Commission (IUCN/ SSC) Canid Specialist Group, Gland, Switzerland. pp. 117–123.

Angerbjörn, A., Hersteinsson, P., and Tannerfeldt, M. 2004*b*. *Consequences of resourcepredictability in the Arctic fox: two life history strategies.* In *The biology and conservation of wild canids*. Oxford University Press, Oxford, U.K. pp. 163–172.

Audet, A.M., Robbins, B. and Lariviere, S. 2002. Alopex lagopus. *Mammalian species* No.713, pp. 1–10, 3 figs.

Baker, P.J., Funk, S.M., Bruford, M.W., and Harris, S. 2004. Polygynandry in a red foxpopulation: implications for the evolution of group living in canids? *Behav. Ecol*. 15: 766–778.

Cameron, C., Berteaux, D., and Dufresne, F. 2011. Spatial variation in food availability predicts extra-pair paternity in the arctic fox. *Behav. Ecol.* 22(6): 1364–1373.

Eide, N.E., Jepsen, J.U., and Prestrud, P. 2004. Spatial organization of reproductive Arctic foxes Alopex lagopus: response to changes in spatial and temporal availability of prey. *J. Anim. Ecol.* 73(6): 1056–1068.

Elmhagen, B., Tannerfeldt, M., Verucci, P. and Angerbjörn, A. 2000. The arctic fox (Alopex lagopus): an opportunistic specialist. *J. Zool.*, Lond. 251, 139-149

Frafjord, K., Becker, D., and Angerbjörn, A. 1989. Interactions between Arctic and red foxes in Scandinavia: predation and aggression. *Arctic*, 42(4): 354–356.

Framstad, E., Stenseth, N., Bjørnstad, O. and Falck, W. 1997. *Limit cycles in Norwegian lemmings: tensions between phase− dependence and density-dependence*. Proc. R. Soc. Lond. B 264.

Goltsman, M., Kruchenkova, E.P., Sergeev, S., Johnson, P.J., and Macdonald, D.W. 2005. Effects of food availability on dispersal and cub sex ratio in the Mednyi Arctic fox. *Behav. Ecol. Sociobiol.* 59(2): 198–206.

Hamilton, W.D. 1964. The genetical evolution of social behaviour I. *J. Theor. Biol*. 7(1): 1–16.

Hersteinsson, P., and Macdonald, D.W. 1982. Some comparisons between red and Arctic foxes, *Vulpes vulpes* and *Alopex lagopus*, as revealed by radio-tracking. *Symp. Zool. Soc. Lond*. 49 (3): 259-289.

Julliard, R. 2000. Sex-specific dispersal in spatially varying environments leads to habitatdependent evolutionarily stable offspring sex ratios. *Behav. Ecol.* 11:421–428

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature*, 301 (5899):379–384

Norén, K., Hersteinsson, P., Samelius, G., Eide, N.E., Fuglei, E., Elmhagen, B., Dalén, L.,

Meijer, T., and Angerbjörn, A. 2012. From monogamy to complexity: social organization of arctic foxes (Vulpes lagopus) in contrasting ecosystems. *Can. J. Zool*. 90: 1102–1116.

Prestrud, P. 1991. Adaptations by the Arctic Fox (Alopex lagopus) to the Polar Winter. *Arctic* Vol. 44, No. 2. P. 132-138

Prestrud, P. 1992. *Arctic foxes on Svalbard: population ecology and rabies*. Ph.D. thesis, University of Oslo, Oslo, Norway.

Schmidt, N., Ims, R., Høye, T., Gilg, O., Hansen, L., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M. and Sittler, B. 2012. *Response of an arctic predator guild to collapsing lemming cycles*. Proc. R. Soc. B. Published on-line.

Stander, P. E. 1992. Cooperative hunting in lions: the role of the individua. *Behavioral Ecology and Sociobiology*, 29, 445-454.