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Foreword to Supplement 1: research on a polar species—the Arctic fox

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ABSTRACT

The Arctic fox has a circumpolar distribution and is intensively studied because it is adapted to extreme environments and influences the ecology of many other species. We introduce here a collection of 12 articles on Arctic fox biology and management. After summarizing the main biological features of the species, we explore the peer-reviewed literature dealing with the Arctic fox through a bibliometric network analysis which identifies clusters of papers sharing a high similarity of cited literature. We visualize with a word cloud analysis 10 clusters comprising 97% of 755 articles published by 1742 authors from 1996–2015. Behavioural and ecological questions, including conservation science, dominate this recent literature. The collection of papers published in the supplement offers an excellent representation of current research dealing with Arctic fox biology and management.

KEYWORDS

Biodiversity; mammal; predator; tundra; *Vulpes lagopus*; wildlife

This collection of papers was prepared in parallel with the 5th International Conference in Arctic Fox Biology, in Rimouski, Canada, 12–15 October 2017. The common goal of the conference and this supplement in *Polar Research* was to stimulate circumpolar collaborations among researchers interested in Arctic fox biology and management. More generally, they drew together a large number of people interested in Arctic ecosystems and their rapid evolution. Usually, journal special issues continue the momentum that was generated by a conference session. We did exactly the opposite; the papers published in this supplementary issue prepared the discussions held during the 5th International Conference in Arctic Fox Biology.

The Arctic fox (*Vulpes lagopus*, syn. *Alopex lagopus*) is endemic to the Arctic and the only mammalian predator that is exclusive to the tundra biome. It is the most widespread mammal species in the Arctic, where it has a circumpolar distribution and inhabits most Arctic islands and even—in Fennoscandia—some mountain ranges that extend to the south (Fig. 1). The species is found in a variety of ecological and bioclimatic contexts, from polar deserts at the northern tip of Greenland to oceanic islands in the Bering Strait and lush shrub tundra in Canada at 50° N. This extremely mobile animal is even met far beyond its terrestrial Arctic breeding grounds, on sea ice all the way to the North Pole and sometimes far south into the boreal forest (Audet et al. 2002).

One of the earliest mentions of the Arctic fox in the literature is by the Roman Jordanes, who, writing his *De origine actibusque Getarum* (*The origin and deeds of the*

Goths) in about 551 (Jordanes 2007), described the hunting of black foxes in northern Europe. Later, the Swedish ecclesiastic Olaus Magnus (1555) described white, blue and black foxes and indicated that the fur from black foxes was most valued in the trade with Russia. He also described how lemmings rained down from the sky every third year. Linnaeus described the Arctic fox as *Canis lagopus* 1758. He also described the life of Arctic foxes in his travels in Lapland (Linnaeus 1811, pp. 82–83): “The white, or mountain, fox (*Canis lagopus*) lives among the alps, feeding on the lemming rat or red mouse (*Mus lemmus*) as well as on the ptarmigan (*Tetrao lagopus*). This white Fox is smaller than the common kind. [...] The wolves indeed kill the foxes.” In a more modern biological context, strong cyclic variations in population size of Arctic foxes and their prey fascinated Collett (1912) and Elton (1924).

The Arctic fox has sparked interest for many reasons. Its beauty and fascinating lifestyle have given rise to myths and fairy tales among Arctic peoples (Fuglei 2006). Because it was a valuable furbearer, trapping attained industrial proportions a century ago and farming of the species was developed. More recently, its decline in some parts of its range prompted conservation interest. The Arctic fox has also been intensely used as a study model by scientists interested by its adaptations to the extreme Arctic environments and its ecological dynamics and role in various Arctic ecosystems.

This cluster of articles on Arctic fox biology and management shows that the Arctic fox still generates intense interest among researchers at the beginning of the 21st century. In this introductory paper, we

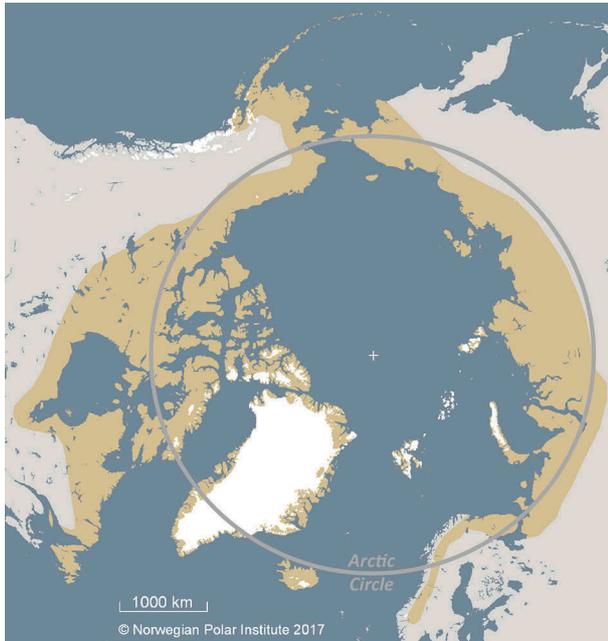


Figure 1. Circumpolar distribution of the Arctic fox (modified from Angerbjörn & Tannerfeldt 2014).

first summarize the main biological features of the Arctic fox, we then explore the recent peer-reviewed literature dealing with the species and, finally, we present the 12 papers comprising the supplement.

Arctic fox biology

The Arctic fox can survive in the extreme cold despite long periods of food shortage, experiencing 100°C temperature differences between its body core and the environment. From a thermoregulatory point of view, being small (3–4 kg) in cold

environments is a disadvantage because of the low volume to surface ratio. However, small, rounded ears and a short muzzle reduce somewhat the body surface of the Arctic fox compared to similarly sized canids. In addition, its thick winter fur is of exceptional quality, trapping a layer of air next to the skin (Underwood & Reynolds 1980). Scholander et al. (1950) measured the insulative property of the fur in a range of Arctic animals and found a linear relationship between fur thickness and insulation up to the size of the Arctic fox. Larger animals all had the same or lower winter fur insulation than the Arctic fox.

Variability in fur colour of the Arctic fox sometimes generates confusion, as it is widely assumed that Arctic foxes are always white. Such confusion is enhanced by the also variable colouration of the red fox (*Vulpes vulpes*), which can share the same habitat as the Arctic fox. Fur colouration is complex in these species and Adalsteinsson et al. (1987) distinguished four colour phenotypes in the Arctic fox and seven in the red fox. Most Arctic foxes, however, appear in one of two distinct colour morphs: white (most individuals) and blue. The proportion of the two morphs varies geographically. In summer, the white morph turns brown-grey and yellowish-white. The blue morph remains dark charcoal all year round, but becomes lighter in winter. Red foxes are usually reddish-brown to yellow (red morph), but sometimes mostly black (silver morph) or a combination of both (cross fox) (Butler 1945). Figure 2 illustrates these various pelage colours. Arctic and red foxes are easy to distinguish as the red fox is bigger and has proportionally longer ears and a pointier nose.



Figure 2. The two most common colour morphs (summer and winter pelage) of the Arctic fox and the three most common colour morphs of the red fox.

The Arctic fox readily stores body fat, which can represent 20–30% of body mass in winter (Prestrud & Nilssen 1992). Subcutaneous fat is rich in unsaturated fatty acids (Shultz & Ferguson 1974), which improves insulation. Abdominal fat is an important energy reserve. A 3.5-kg individual with a 22% fat content can survive 30 days without food at its basal metabolic rate (Prestrud 1991). The legs contain a counter-current vascular heat exchange system (Irving & Krog 1955), so that the temperature of the paws is regulated to within a degree from freezing (Henshaw et al. 1972). The foot pads are hair-covered, which reduces heat loss and potentially also reduces noise when walking on the snow. The species' scientific name *lagopus* means hare-footed, because hares' feet are furry.

In very cold conditions, Arctic foxes shelter in snow lairs or simply “ball up”, creating a microclimate that reduces heat loss (Prestrud 1991). Food caches may be an important supplement to the fox's fat reserves (Prestrud 1991; Careau et al. 2008). An individual can cache more than 1000 goose eggs (Samelius & Alisauskas 2000), representing enough energy to carry a fox through one winter (Careau et al. 2008).

Arctic foxes are generally socially monogamous and raise a litter with biparental care (Audet et al. 2002), but the social structure of the species is flexible. More than 60% of Arctic foxes breeding on Mednyi Island live in complex groups (Kruchenkova et al. 2009). Communal nursing and help from non-breeders also exist in Sweden, where related females can live in “fox towns” consisting of several adults and their litters (Elmhagen et al. 2013). In the Canadian Arctic, extrapair paternity was found in 31% of Arctic fox litters (Cameron et al. 2011) and one case of polyandry was observed (Carmichael et al. 2007).

Being an opportunistic predator and scavenger, the Arctic fox can maintain viable populations in many different food webs. Braestrup (1941) described two lifestyles of the Arctic fox, which he named the lemming ecotype (most widespread) and the coastal ecotype. The former is found in most of the tundra biome, where lemmings exhibit high-amplitude 3–5-yr population density cycles (Stenseth & Ims 1993). The lemming cycle causes a cyclic demography in Arctic foxes, with pulses of recruitment characterized by many large litters at high lemming density and hardly any recruitment at low density.

The coastal lifestyle is geographically much more restricted. It is found on Arctic and sub-Arctic regions without lemmings such as Iceland, Svalbard and west Greenland, as well as on the Commander Islands. These populations rely mostly on subsidies from the marine ecosystem, such as seabirds and marine mammals. They do not face as much

interannual variability in food supply as do foxes relying on lemmings, but seasonal variability can be high. The relatively high and stable food supply during summer results in more stable demography (Angerbjörn et al. 2004; Kruchenkova et al. 2009; Eide et al. 2012). Coastal foxes can breed most years and produce lower litter sizes that are less variable in size (Angerbjörn et al. 2004; Kruchenkova et al. 2009; Eide et al. 2012).

Genetic divergence between the two types is typically low or absent (Norén et al. 2017) and some populations do not fall into the classical dichotomous classification of Braestrup (1941). Where lemming cycles or marine subsidies are weak or absent, Arctic foxes may subsist on medium-sized (geese, ptarmigan, hare) or large (reindeer, muskox) terrestrial herbivores that they hunt or scavenge (Schmidt et al. 2012; Ehrich et al. 2015).

The Arctic fox can have a strong top-down effect on some of its prey (Fuglei & Ims 2008). This is especially true for ground-nesting birds. For example, seabird populations have collapsed on islands where Arctic foxes were introduced, with cascading impacts on vegetation (Croll et al. 2005; Maron et al. 2006). In lemming areas, Arctic foxes can also strongly impact the demography of geese and shorebirds because of increased predation pressure on nests and chicks in years of low lemming abundance (Bêty et al. 2001; Ims & Fuglei 2005).

Being a rather small animal, the Arctic fox may also be limited or regulated by larger predators. In particular, the red fox probably sets the southern range limit of the Arctic fox through interspecific competition. Other significant natural enemies of the Arctic fox are parasites and diseases. The Arctic fox is an important vector of infectious diseases that can be transmitted to humans (zoonoses), such as rabies and *Echinococcus multilocularis*.

The Arctic fox is drawing increased attention among researchers and conservationists because of climate change. The International Union for Conservation of Nature and Natural Resources has selected the Arctic fox as one of 10 flagship species to represent climate change and its consequences on the natural world (IUCN 2009). The species is on the organization's Red List in Europe (Temple & Terry 2007), where it lives on the border of the Arctic and is pushed northwards through competition with the red fox and rarefaction of the lemmings, all indirect impacts of climate change. On a circumpolar scale, the Arctic fox is listed as “Least Concern” (Angerbjörn & Tannerfeldt 2014).

Arctic fox research

We examined the peer-reviewed literature to reveal the focus of research conducted on Arctic foxes

during the last two decades. We retrieved from Web of Science all publications published in 1996–2015 containing “polar fox” or “Arctic fox” or “*Vulpes lagopus*” or “*Alopex lagopus*” in their title, abstract, author keywords or Web of Science keywords. We then submitted publications to a bibliometric network analysis to identify clusters of papers sharing a high similarity of cited literature. These clusters were visualized through a word cloud analysis based on word frequency in article titles (see Fig. 3 for methodological details).

Our search yielded 755 articles published by 1742 authors. As shown in Fig. 3, the two most voluminous clusters identified by the analysis comprise together 384 (51%) of the 755 publications, whereas the first 10 comprise 729 (97%). The first two clusters (Fig. 3a, b) are largely dominated by behavioural and ecological questions (including conservation science), ranging from the trophic ecology of Arctic foxes and their effects on bird colonies to the demography and conservation of Arctic fox populations. Research included in these two clusters generally relied on intensive field data collection. The third cluster (Fig. 3c) is dominated by farming and welfare and clearly connects to the fur industry. This cluster is the only one with an indisputable declining trend in terms of research intensity. The fourth cluster (Fig. 3d) is mostly physiological in nature and includes both metabolic ecology and ecotoxicology. The fifth and sixth groups of papers (Fig. 3e, f) are rather homogeneous and concern genetics and nutrition, respectively. The remaining clusters (Fig. 3g–j) each gather less than 5% of published papers. They deal respectively with rabies, parasites, reproduction and chemical immobilization, in decreasing order of importance. The parasitology cluster is the only one with a very clear upward trend. However, we note that the bibliometric network analysis places some papers dealing with Arctic fox parasites within the first cluster, so that a more refined analysis of this research topic would be needed to conclude on temporal trends. Figure 3k shows a general increase through time in the number of publications dealing with Arctic foxes. This is in line with the increase in publication output observed in science in general.

This supplemental issue

Most papers in this group of articles fit the first two clusters identified above. Berteaux et al. (2017) provide the first exhaustive survey of contemporary Arctic fox monitoring programmes. They describe 34 projects located in eight countries and point out large differences between populations in multi-annual fluctuations, diet composition, degree of competition with red fox and human interferences. This situation

provides a great opportunity to address new challenging questions. Berteaux et al. (2017) indicate, however, that harmonization of protocols of data collection and management is needed, and they offer recommendations in that respect.

The Arctic fox lives in a species-poor environment characterized by a low primary and secondary productivity. It can have both strong top-down effects on its prey and suffer strong bottom-up control from its prey. Lots of research addresses these trophic relationships. In North America, lemmings and geese are important parts of the Arctic fox diet. Interestingly, McDonald et al. (2017) and Samelius & Alisauskas (2017), who worked in Hudson Bay (Canada) and Nunavut (Canada) respectively, both found that, although Arctic foxes preyed heavily on geese, their reproduction was highly dependent on lemmings. Arctic foxes therefore seem to depend strongly on lemmings in large parts of Fennoscandia, Siberia and North America, whatever the alternative food sources.

Arctic foxes live in areas devoid of cyclic rodents in parts of Greenland, in Iceland and in many Arctic islands, such as the Commander Islands, the Pribilof Islands and Svalbard. In such cases they compensate with marine resources such as birds, fish and other remains along shorelines. In the Commander Islands, Arctic foxes have long been isolated and their main food is large seabirds and marine mammals, prey that are considerably larger than lemmings. In their original study of cranial features, Nanova & Prôa (2017) showed that Arctic foxes in the Commander Islands have evolved larger mouth openings to use effectively these food resources. These results show very well the importance that distinct foraging strategies can have on the diverging evolution of the Arctic fox in the absence of gene flow. This has direct consequences for conservation plans of different Arctic fox subspecies.

Conservation of the Arctic fox can be challenging where humans strongly interfere with its habitat, such as in many parts of Fennoscandia. Ims et al. (2017) show that in north-eastern Norway, irregular lemming peaks (the result of milder winters) and abundant red foxes (subsidized by carrion from increasingly plentiful ungulates) have caused the present critically small size of the Arctic fox population. They use this knowledge to discuss options for future research and management of the regional Arctic fox population.

The causes and effects of the competitive interactions between the Arctic and red foxes have a strong theoretical context. This is treated by Elmhagen et al. (2017), who present the classical hypothesis according to which the northern distribution limit of the red fox is determined by resource availability (and therefore ultimately climate), whereas the southern

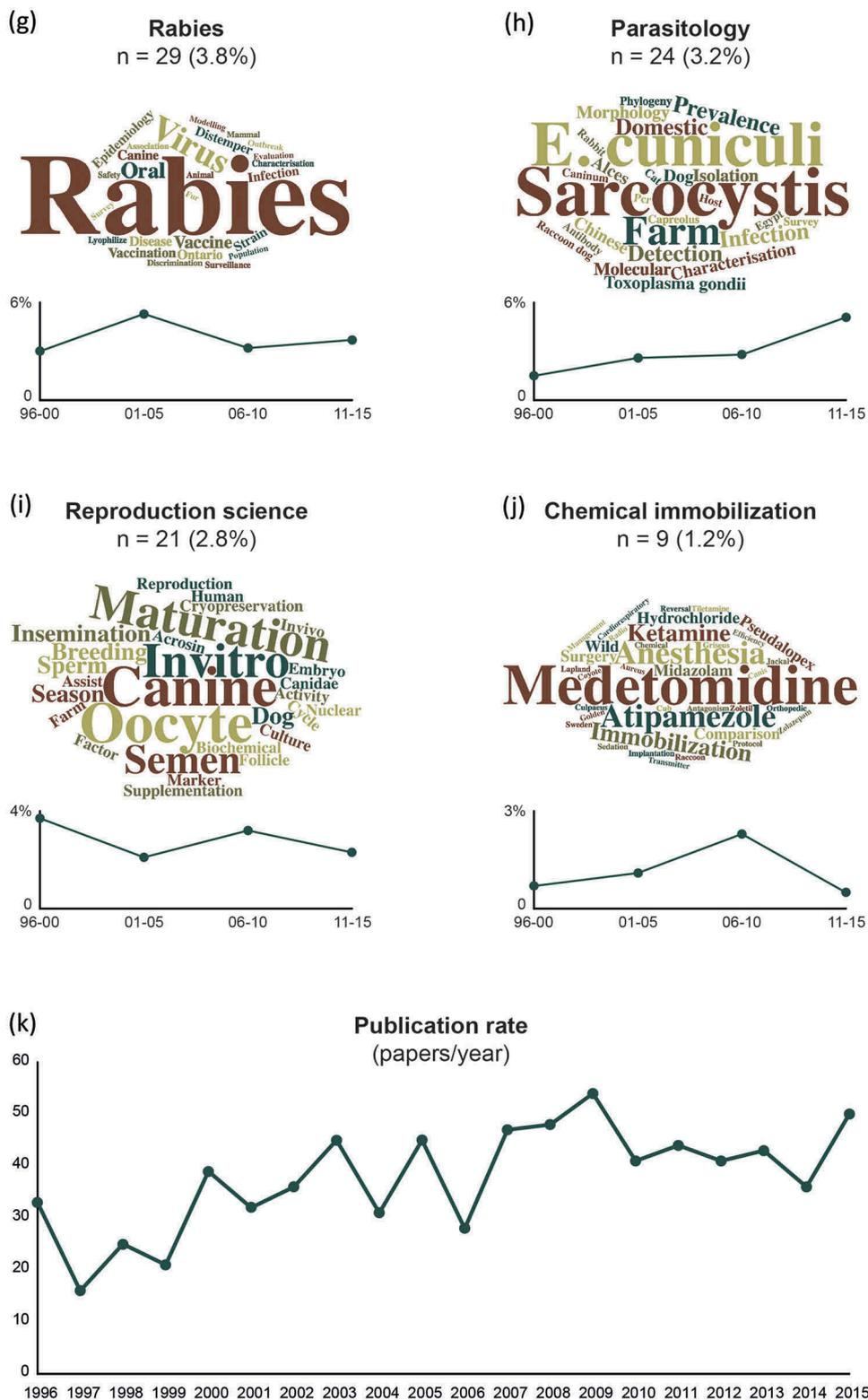


Figure 3. (continued).

distribution limit of the Arctic fox is determined by competition with the red fox (Hersteinsson & MacDonald 1992). Elmhagen et al. (2017) review research carried out since the hypothesis was published and provide a useful discussion in the context of climate warming, anthropogenic resource subsidies and changing species interactions.

One tool in the conservation of the Arctic fox is to breed wild animals in captivity and later release their offspring in suitable habitats. Landa et al. (2017) launched such a programme with several enclosures in the Arctic fox habitat. The programme has been running for 10 years and they have released about 370 animals in mainland Norway. Many released

foxes produced several litters in the wild. Since the Arctic fox habitat in this study is in the mountains along the Norwegian and Swedish border, many of the animals have also settled down in Sweden. The programme has been most successful and contributed to the recovery of the Fennoscandian Arctic fox population.

Another aspect of human activity that can affect Arctic foxes is tourism. In Svalbard, many tourists travel using snowmobiles. Fuglei et al. (2017) showed that snowmobile traffic impacted the diurnal activity of Arctic foxes. This could influence what prey Arctic foxes feed on, and thereby also their management.

For logistic reasons, the Arctic fox has mostly been studied during the summer time. Electronic devices, however, now offer the opportunity to study elusive wildlife in the most extreme conditions of cold and darkness. A study with a winter perspective was the analysis of spatial movements by Arctic foxes around Bylot Island (Canada) by Rioux et al. (2017). Using satellite telemetry, they found that pairs of foxes remain in or close to their home range during winter. Their few excursions outside the territory were short and not synchronized among pair members. Clearly, technology will allow many more fascinating studies of Arctic fox behaviour.

Other research topics identified in our bibliographic analysis are also represented in this supplemental issue. First, Bolton et al. (2017) analyse organic pollutants and stable isotopes of Arctic foxes from the Pribilof Islands, where individuals feed along marine shorelines as well as from human food resources. Bolton et al. (2017) found several persistent organic pollutants in the fat tissue of the Arctic fox. They also found that foxes with access to anthropogenic food resources had lower levels of persistent organic pollutants compared to foxes that had a more marine diet. This is important new knowledge for the conservation of the Arctic fox in the Pribilof Islands.

Genetics has allowed considerable progress in our understanding of Arctic fox biology and management. Norén et al. (2017) review genetic processes in the Arctic fox at the level of species, populations and individuals. They show how dispersal across sea ice creates a highly homogeneous genetic structure across the circumpolar distribution of the species, with populations isolated because of lack of sea ice being genetically divergent. Small populations generally show genetic drift, inbreeding, inbreeding depression and sometimes hybridization with domestic fox breeds, which raise conservation concerns.

Finally, one paper addresses the important topic of parasites. Andreassen et al. (2017) report several species of parasites in the Arctic fox from Greenland, and suggest that some of these parasites can be connected to the prey species. Such findings constitute

the required baseline data for further parasitological monitoring.

In conclusion, this collection of articles offers an excellent representation of current research dealing with the biology and management of the Arctic fox. We hope that the 12 papers presented here will collectively demonstrate the richness of scientific enquiries currently devoted to the Arctic fox. Perhaps more importantly, we hope that they will demonstrate how this remarkable species can help to generate and test scientific hypotheses valuable to a much wider community of researchers, whether they work in polar areas or beyond.

Disclosure statement

No potential conflict of interest was reported by the authors.

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