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Original Contribution

Fatal Pneumonia Epizootic in Musk Ox *(Ovibos moschatus)* in a Period of Extraordinary Weather Conditions

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Abstract: The musk ox is adapted to extreme cold and regarded as vulnerable to the impacts of climate change. Population decline is proposed to occur due to changes in forage availability, insect harassment, parasite load, and habitat availability, while the possible role of infectious diseases has not been emphasized. The goal of the present article is to describe an outbreak of fatal pasteurellosis that occurred in the introduced musk ox population of Dovrefjell, Norway in 2006, causing the death of a large proportion of the animals. The epizootic coincided with extraordinary warm and humid weather, conditions that often are associated with outbreaks of pasteurellosis. The description is based on long series of data from the surveillance of the musk ox population, weather data from a closely located meteorological station, and pathoanatomical investigation of the diseased animals. It is concluded that the weather conditions likely were the decisive factors for the outbreak. It is suggested that such epizootics may occur increasingly among cold-adapted animals if global warming results in increased occurrence of heat waves and associated extreme weather events, thereby causing population declines and possibly extinctions.

Keywords: musk ox, Arctic, climate change, global warming, pasteurellosis, disease

INTRODUCTION

The musk ox (*Ovibos moschatus*) is a large ungulate, adapted to extreme cold, and has its present native distribution in the Arctic Canada and Greenland (Fig. 1A) (Lent, 1999; Blix, 2005). During the late Pleistocene, however, this ruminant had a holarctic distribution (MacPhee et al., 2005). Recent studies have shown that the species was more genetically diverse at that time, indicating that the population at some point of time, presumably after the Last Glacial Maximum and prior to the Pleistocene/Holocene transition, was almost brought to extinction (MacPhee et al., 2005).

According to the Intergovernmental Panel on Climate Change, global warming is unequivocal (Alley et al., 2007). As a part of this, hot extremes, heat waves, and heavy rainfall have become more frequent and atmospheric water vapor has increased. These trends are expected to continue. The warming is expected to be greatest over land and in the high northern latitudes. Additionally, an increase in precipitation is very likely in high latitudes (Alley et al., 2007).

The musk ox was reintroduced to Dovrefjell in Southern Norway in 1932–1953 (Lønø, 1960; Bretten, 1990; Lent, 1999). Dovrefjell is, together with Nunivak Island in

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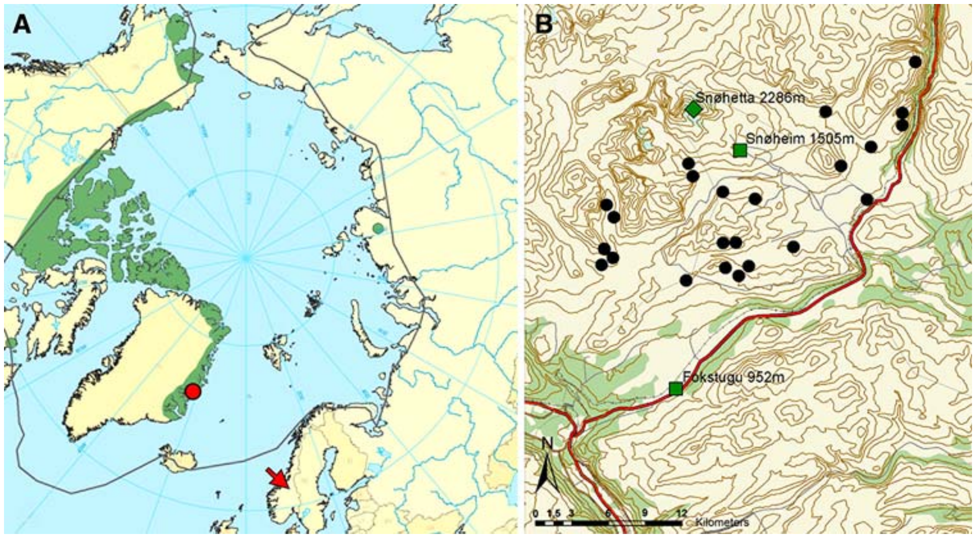

Figure 1. The worldwide distribution of musk oxen and the distribution of diseased animals on Dovrefjell. (**A**) The musk ox has its present native distribution in the Arctic areas of Canada and Greenland and has been successfully introduced to Alaska, Quebec, and the Taimyr Peninsula of Russia (green areas and dots). It was introduced to Dovrefjell (red arrow) from Myggbukta on Greenland (red dot). Dovrefjell is, together with Nunivak Island in Alaska and the Ungava region of Quebec, one of the southernmost locations for successful musk ox introduction, but unlike the other locations, Dovrefjell is far from the Arctic climate zone (the gray line indicates the 10°C isotherm in July) (after Lent, 1999, and Blix, 2005). (**B**) The dead musk oxen were found widely dispersed over their home range, indicating that the outbreak was not restricted to a specific herd. Each of the 24 investigated animals with signs of disease is indicated with a black dot. The weather stations Snøheim and Fokstugu are indicated by green squares and the summit Snøhetta by a green diamond.

Alaska, and Ungava in Quebec, one of the southernmost locations for successful musk ox introduction (Fig. 1A) (Lent, 1999). Unlike the other locations, however, Dovrefjell is far from the Arctic climate zone and represents an outpost for the musk ox and an exposed position for the effects of climate change.

The musk ox is regarded to be vulnerable to the impacts of climate change (McCarthy et al., 2001; Weller, 2005). Population decline or extinction of the large Arctic ungulates is proposed to occur due to changes in the timing and abundance of forage availability, insect harassment, parasite infestations, and reduced habitat availability (McCarthy et al., 2001; Weller, 2005). Infectious disease has received less attention, though theoretical and historical evidence suggests that infectious disease can drive populations temporarily or permanently to low numbers or densities, predisposing them to extinction by other forces (Smith et al., 2006).

Several researchers have hypothesized that global warming will affect host–pathogen interactions by: (1) increasing pathogen development rates, transmission, and the number of generations per year; (2) relaxing overwintering restrictions on pathogen life cycles; and (3) modifying host susceptibility to infection in such a way that disease will increase the severity of threats associated with climate change (Hoberg et al., 2001; Harvell et al., 2002). Associations between hot, humid weather and increased development of parasites have, for example, been described in outbreaks of cerebrospinal elaphostrongylosis in semi-domesticated reindeer in Northern Norway (Handeland and Slettbakk, 1994), and climate warming is suspected to be the driving force behind increased incidence of verminous pneumonia due to *Umingmakstrongylus pallikuukensis* in musk ox in North America (Kutz et al., 2005).

Furthermore, it is predicted that this increase in disease can contribute to population or species declines, especially for generalist pathogens infecting multiple host species (Harvell et al., 2002), as recently exemplified by the widespread population declines of amphibians caused by *Batrachochytrium dendrobatidis* (Blaustein and Dobson, 2006; Pounds et al., 2006; Alford et al., 2007; Di Rosa et al., 2007).

The following report describes an outbreak of fatal pneumonia caused by a generalist pathogen in musk ox in a period of extreme weather conditions. As such events may become increasingly more common as global warming ensues, it is suggested that such disease episodes pose a serious threat for species adapted to cold climate, like the musk ox.

Materials and Methods

Animal Population

The musk ox was reintroduced from Eastern Greenland to Dovrefjell in 1932 and 1938, but the small population was devastated by avalanches and poachers, until no animals remained by 1945 (Bretten, 1990). In the period from 1947 to 1953, a total of 21 new musk ox calves were released into the mountains and, in 1957, the population consisted of 13 animals. Due to high mortality (from railroad accidents, killing of stray animals to prevent attacks on humans or livestock, lightning strikes, falling from cliffs, phosphorus poisoning, etc.), the population grew slowly during the first 40 years, but has experienced a rapid increase during the last few decades, from 103 animals in 1998 to at least 213 animals (54 calves, 17 yearlings, 100 cows, 42 oxen) in March–April 2006 [unpublished data: Bretten, 2007]. The population seems to be in good condition, having a growth rate comparable to that of other introduced musk ox populations (Asbjørnsen et al., 2005). This is illustrated by the occasional observations of twin births, occasional early reproduction (2-year-old cows giving birth) (Hagen et al., 2006), and a high birth rate (63 [53–69] calves per 100 cows, 3 years or older, counted 10 months after calving) [unpublished data: Bretten, 2007]. Pasture resources do not seem to be a limiting factor for the musk ox population (Hagen et al., 2006) and there is no evidence of density-dependent regulation (Asbjørnsen et al., 2005), although one study indicates that late-winter grazing habitat may be a limiting factor (Nellemann, 1998). The main reasons for mortality seem to be railroad accidents and killing of stray animals (Asbjørnsen et al., 2005). Average mortality between censuses (based on the population difference between the censuses adjusted for known calf mortalities) for the period 1993–2006 was 8.8% (range 6%–14%) [unpublished data: Bretten, 2007]. Apart from an epizootic of orf in 2004 (Vikøren et al., 2008), there have not been any registered major die-offs related to infectious disease or parasites.

Study Area

Dovrefjell (62°15'N, 9°20'E) is a mountain range with Snøhetta (2286 m a.s.l.) as the highest summit. The mountain range is a typical Alpine tundra environment. The vegetation ranges from snow-bed vegetation to lichen, grass, and heath communities and barren rock. The present tree limit in the actual area is at 1000–1050 m a.s.l. The climate is continental. For the normal period 1961–1990, the mean annual air temperatures (MAAT) at Fokstugu is −0.1°C. July is the warmest month (9.8°C) and January the coldest one (−8.8°C). The highest measured temperature was 28.2°C which occurred in June 1960, and the lowest measured temperature was −36.4°C, which occurred in January 1942. The mean annual precipitation (MAP) at Fokstugu is 435 mm. The average yearly precipitation at Istjørni at the base of the mountain Snøhetta (2286 m a.s.l., (Fig. 1) is 600 mm (Østrem et al., 1988). In general, Dovrefjell is one of the driest mountain areas in Norway, due to the sheltering effect of the high mountains in the west. July has the greatest amount of precipitation (68 mm) and April the smallest (14 mm). The precipitation during summer is connected to heavy, but local showers, often with thunder. Unstable and stormy weather is common in winter and the prevailing winds are from the south and southwest. During winter, strong winds result in a scarce snow cover on exposed sites. Average snow depth in the central area of the musk ox range is 1.0–1.5 m (Isaksen et al., 2002).

Temperature scenarios for Scandinavia show a considerable spread concerning projected warming rates (Benestad, 2002ab, 2004). Projected July warming rates are between 0.05° and 0.35°C per decade (Benestad, 2004), and it is concluded that warming rates will be higher in winter than summer, and inland compared to coastal regions (Benestad, 2002ab, 2004; Hanssen-Bauer et al., 2003). Regional winter warming rates are estimated to be 0.3° to 0.6°C per decade, and summer warming rates estimated to be 0.2° to 0.3°C per decade (Hanssen-Bauer and Førland, 2000). In addition, a tendency for increased large-scale humidity over Scandinavia implies that projections for the 21st Century typically indicate increased annual precipitation (Hanssen-Bauer et al., 2005). Interannual temperature variability is likely to increase in the summer in most areas in Europe (Christensen et al., 2007). Along with the overall warming, and changes in variability, heat waves are likely to increase in frequency, intensity, and duration (Christensen et al., 2007).

Data Collection

The musk oxen on Dovrefjell have been monitored closely. However, from the early 1950s to 1965, no systematic population censuses were performed. With some exceptions, censuses were performed on a yearly basis from 1965 to 1982 and from 1989 to present. Since 1994, the Norwegian Nature Inspectorate has carried out the registration of mortalities and standardized censuses of the total winter population. Since 2004, the musk ox population has been included in National Health Surveillance Program for Cervids, administrated by the National Veterinary Institute (NVI), providing systematic registration of the causes of mortality.

The mortality registration is handled by Oppdal Bygdealmenning (OBA). When carcasses are found, OBA is contacted and registers discovery date, location, gender, age, and other observations. Mountain rangers undertake a field examination of the carcasses and submit samples to NVI. The yearly censuses are mainly executed over 2 days, though stray animals may be counted the day prior to, or subsequent to, the main count. It is performed in March–April by five to six mountain rangers on foot and on snowmobile. Mortality is calculated based on the difference between the censuses plus calves found dead during the year. Comparison of winter population censuses and mortality registration during the last decade has shown that, on average, 90% of the true mortality has been discovered between the censuses.

Climate data and analyses are mainly based on data from the weather station at Fokstugu (972 m a.s.l.), which is 10–20 km south of the area where the musk oxen were found (Fig. 1B). The first station was established in 1923 (Fokstua, 952 m a.s.l.) and was moved ~300 meters to its present position in June 1968. Observations here are therefore not strictly homogenous. Some differences are found in air temperature during October–June. However, during July–September, no significant temperature deviations exist. At Fokstugu, air temperature, wind speed, wind direction, and humidity are registered every 6 hours. In addition normal synoptic observations, precipitation, and snow depth are registered. Temperature and precipitation data and calculations of humidity are used in the present study. In the central area for the musk ox, a permafrost monitoring program was started in autumn 2001 (Sollid et al., 2003). Ground temperatures to 9-m depth and air temperature are registered every 6 hours. The highest monitoring site is located at Snøheim (1505 m a.s.l.)(Fig. 1B). This station is representative for the more elevated parts of the musk ox range. The temperature data from this station indicate that the MAAT is ~2.5°C lower than at Fokstugu.

Methods

The animals included as suspected disease cases, in this report, were either found with clinical disease or were recently dead, without any signs of trauma, during August and September 2006. Early autumn is normally a period characterized by virtually no mortality in this musk ox population [unpublished data: Bretten, 2007]. Of the 24 animals classified as suspected disease cases in this report, 21 were examined by mountain rangers. Standard procedure included age determination based on morphology, external examination, and opening and inspection of thorax and abdomen. Samples of feces, blood, lung, heart, liver, spleen, kidney, skeletal muscle, and brain were routinely taken and submitted by post to NVI. In cases where the carcass was severely decomposed (11 of 21), no samples were taken. Upon arrival at NVI, the samples from the remaining 10 animals were inspected by veterinary pathologists and tissue samples sent for bacteriological and histological examination. Due to the warm weather and the unalterable time delay between the death of the animal and the investigation, the tissue samples showed varying degrees of autolytic changes. A full field necropsy by veterinary pathologist was performed on the remaining 3 of 24 animals. One of these was euthanized immediately before the necropsy. From two of these, blood agar was inoculated directly from lung, liver, and spleen. From all three, samples from lung, heart, liver, kidney, and brain were taken for histology, while lung, liver, and spleen were taken for bacteriological examination. Histology samples were fixed in 4% phosphate buffered formaldehyde, dehydrated in alcohol, embedded in paraffin, cut in 4–5 lm sections, stained with hematoxylin-eosin (HE) and martius-scarlet-blue (MSB), and examined with a light-microscope. The bacteriological samples were inoculated on two 5% bovine blood agar plates and one bromthymol blue lactose sucrose agar (blue agar plate). One of the blood agar plates was streaked with a ß-toxic *Staphylococcus aureus* (ATTC 25923) and incubated in a 5% CO_2 atmosphere. The other blood agar plate and the blue agar plate were incubated in an anaerobic atmosphere and an aerobic atmosphere, respectively. All plates were incubated at 37°C ± 1°C overnight. Single bacterial colonies were subcultured on blood agar and identified by microscopy and biochemical tests. One isolate was analyzed by 16S rDNA sequencing.

A single cow euthanized because of apparent blindness was necropsied at NVI's regional laboratory in Trondheim. This animal was, in addition to severe ophthalmic lesions, found to have chronic pneumonia with presence of the nematode *Dictocaulus* sp. and *Pasteurella* sp. As the pathological findings were much more complex and this case

Figure 2. Eight of the animals, among them this adult cow that was found dead the 26th of August, but not inspected by rangers until the 2nd of September, were so decomposed that the examination did not reveal the cause of death. However, as these animals were found in locations where accidents (traffic accidents, falling from cliffs, drowning, etc.) were unlikely to occur, had no obvious signs of trauma, and mortality at this time of year is a rare event [unpublished data: Bretten, 2007], disease was the suspected cause of death in these cases.

was found months after the original outbreak, it is not reckoned among the primary cases.

Results

Clinical and Pathological Findings

The index case of the outbreak was reported on the 14th of August 2006. In the following 6 weeks, 24 animals were found recently dead (21) or dying (3). The carcasses were geographically dispersed within the home range of the musk ox population (which is approximately 340 km^2) (Fig. 1B). Among them were 3calves, 3 yearlings, 10 adult cows, and 8 adult oxen. Eight of the animals were so decomposed that the examination not revealed the cause of death, but were found in a location where accidents (traffic accidents, falling from cliffs, drowning, etc.) where unlikely to occur and had no obvious signs of trauma (fractures or other major structural damage) (Fig. 2). Notably, mortality at this time of year is a rare event in this musk ox population and has, if present, been due to trauma [unpublished data: Bretten, 2007]. The 16 intact animals seemed to be in good condition with a thick layer of subcutaneous fat. The three animals observed while still alive were found lying in sternal recumbency. They were able to rise, but were drowsy and showed severe ataxia and diarrhea. The surroundings of all the animals found dead did not show major signs of struggle, like torn up grass or soil, or long-term recumbency, like clear-grazed vegetation (Fig. 3A). The perineum and tail of the animals were, however, smeared with feces. Postmortem investigation of the 16 intact carcasses and samples from 13 of these showed marked consolidation of the ventral parts of the cranial, middle, accessory, and caudal lung lobes, clearly demarcated from the rest of the tissue (Fig. 3B). The affected parts were dark red and firm. On cut surface, these areas were edematous and hemorrhagic, and showed an irregular pattern of variegated bright red, dark red, and grayish tissue. In the animals necropsied by a veterinary pathologist, moderate amounts of blood-tinged fluid were found in the pericardium. Petecchial and ecchymotic hemorrhages were found in the pericardium and on the pleura, and fibrinous pleuritis was found in some of the calves (Fig. 3C). The rumen was well filled, while the intestines only contained small amounts of liquid content, and the rectum was empty. Lymph node hyperplasia was not observed. Histological examination of 13 cases showed a consistent picture where the lung alveoli were atelectatic and/or filled with exudate consisting of macrophages, neutrophil granulocytes, protein-rich fluid, bacteria, and debris (Fig. 3D). Small amounts of fibrin were present in the exudate in some of the cases. Bacteriological examination revealed growth of a hemolytic *Pasteurellaceae or Mannheimia sp.*, as classified by 16S rDNA sequencing, in samples from the lungs of two animals found dead (among them the index case), whereas *Pasteurella multocida subsp. multocida* was found in lungs, spleen, liver, and blood from an animal euthanized right before the necropsy. In the remaining 10 examined animals, bacterial examination did not reveal any pathogens.

Based on the pathological findings and the epidemiology of the outbreak, supported by the bacteriological findings from three of the animals, a diagnosis of pasteurellosis was made.

Figure 3. The diseased musk oxen showed consistent pathological findings. (**A**) Musk ox carcass—the ox is in good condition and the surroundings of the carcass do not show any major signs of a struggle, like torn up grass or soil, or of long-term recumbence, like clear-grazed vegetation. This indicates an acute course of disease. (**B**) Typical lung lesions in the right lung of a musk ox calf—there is a marked consolidation of the anteroventral third of all the lung lobes (below the arrows), clearly demarcated from the rest of the tissue. The affected parts are dark red and firm. The changes are most prominent in the cranial lobe (to the right), and affect only a minor portion of the caudal lobe (to the left). This image is typical for pneumonic pasteurellosis, and a hemolytic *Pasteurellaceae or Mannheimia sp.* was isolated from the affected parts of the lungs of this animal. (**C**) The thoracal cavity of the same musk ox calf as in (B), showing petecchial and ecchymotic hemorrhages and fibrinous exudate on the pleura and pericardial sack (asterisks). Note the large amounts of fat in the pericardial sack (arrow), illustrating the good condition of the animal. (**D**) Histological image of the lung lesions—the alveoli are atelectatic and/or filled with exudates (asterisks) consisting of macrophages, neutrophil granulocytes, protein-rich fluid, bacteria (arrows), and debris. The alveoli walls were hyperemic and edematous. Stained with hematoxylin-eosin, 20×; bar equals 100 lm.

Estimation of Mortality

The census performed at the end of March 2007 revealed only 191 animals (42 calves, 37 yearlings, 74 cows, 37 oxen, and 1 unknown) compared to 213 the year before. During the year since the previous census, 44 mortalities (9 calves, 4 yearlings, 15 adult cows, and 16 adult oxen) had been registered. In addition to the 24 animals already mentioned, 2 were found as newborn calves, 6 (3 calves, 1 yearling, 1 cow, and 1 ox) were killed in railroad accidents, 5 (2 cows and 3 oxen) were stray animals that were shot, and 1 cow was euthanized due to blindness. Six animals (one calf, one cow, and four oxen) were found as decomposed carcasses during the census in March 2007, on which no diagnosis could be made. Based on the census performed in 2006, the average calving rate and the known mortalities, it can be estimated that the population should have counted about 232 animals (54 calves, 50 yearlings, and 128 adults) in March 2007. An unregistered mortality of about 41 animals (about 12 calves, 13 yearlings, and 16 adults) occurred, in addition to the 44 discovered animals. In sum, this represents a loss of about 85 of 276 animals (30.8%) . As the total mortality is more than threefold higher than that of previous years, the disease outbreak must be regarded as the main cause of the unregistered mortalities and the death of the animals found as decomposed carcasses in autumn/winter 2006–2007 (14 animals), in addition to the 16 cases with pathological findings, rendering an outbreak mortality of up to 71 animals (25.7%), conservatively estimated to around 20%.

Weather Conditions

During the instrumental record of air temperature in the 20th Century, there have been significant decadal and multi-decadal August–September mean temperature variations on Dovrefjell. A rather cold period in the beginning of the series was followed by "the early 20th Century warming" (Hanssen-Bauer and Førland, 2000), which culminated in the 1930s. A period of cooling followed before the recent period of strong warming, which has dominated Dovrefjell since the mid-1980s (Fig. 4A). Since 1985, the linear trend at Fokstugu weather station (Fig. 1B) is +0.16°C yr^{-1}. A significant increase in air humidity has also been observed during the series (Fig. 4B) in close association with the higher temperatures. Since 1973, the linear trend is +0.03 gr kg^{-1} yr^{-1}.

An extreme weather event affected the region during late summer and autumn 2006 and produced record-breaking air temperatures and humidity. The extreme anomalies were associated with an unusual synoptic situation with long periods of warm and humid southerlies that dominated the late summer and early autumn. The mean air temperature on Dovrefjell in August–September 2006 was as high as 10.1°C, which is 3.2°C above the 1961–1990 average (Fig. 4A). This is the warmest since records began in 1923, equaling the previous record from 2002, and amounting to an offset of 3.3 standard deviations from the mean (1961–1990). Maximum temperatures in August and September were 20.4 and 17.6°C, respectively. The average minimum temperature was ~2–3°C higher than normal in August and ~3–4°C higher in September. There were no days with temperatures (T_{min}) below freezing in August and September. This has only happened once before: in 1988. The mean humidity (mixing ratio) in August–September 2006 was as high as 6.9 gr/kg, which is the highest since records began in 1973 and 26% higher than the previous 30-year average. Especially the mid- and late-September values were extreme. In addition, large thunderstorms were recorded on several days in mid- and late-August.

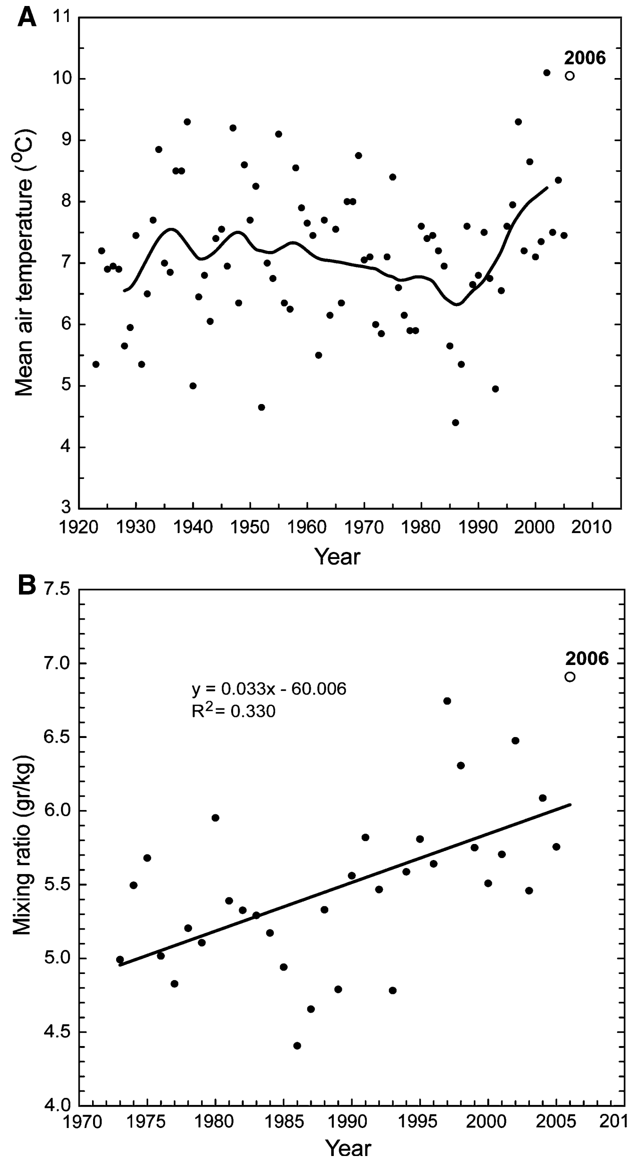

Figure 4. The outbreak of fatal pasteurellosis coincided with extraordinary weather conditions. (**A**) Series of mean air temperature for August–September for the period 1923–2006 from Fokstugu weather station. The year 2006 is highlighted (open circle). To identify variations on decadal time scales, a low-pass Gaussian filter (thick line), with a standard deviation of 3 years in the Gaussian distribution, was applied. (**B**) Series of mean humidity of the air for August–September for the period 1973–2006 at Fokstugu (972 m a.s.l.), expressed as the mixing ratio (*r*), e.g., the ratio of the mass of water vapor to the mass of dry air with which the water vapor is associated. The linear regression coefficient and coefficient of determination (R^2) for the fitted regression line (thick line) in the series are shown.

Discussion and Conclusions

The present article is, to our knowledge, the first to describe pasteurellosis in musk ox. Pasteurellosis is the nomination for a wide range of infections caused by bacteria in the genera *Pasteurella* and *Mannheimia*. These bacteria are mainly regarded as opportunistic pathogens, prevalent in the pharynx of healthy animals (Miller, 2001). Pasteurellosis is seen both in domesticated, captive, and free-ranging animal populations worldwide, and disease has been reported in a remarkable variety of terrestrial, aquatic, and marine mammals and birds (Miller, 2001), including Arctic and Alpine species like reindeer *(Rangifer tarandus)* (Kummeneje, 1976) and bighorn sheep *(Ovis canadensis)* (Spraker et al., 1984). Both pneumonia and sepsis are common manifestations (Miller, 2001). In the present cases, pneumonia was a consistent finding, while the finding of *Pasteurella multocida multocida* in multiple organs from one of the cases, indicated that this animal also experienced a septicemia.

Knowledge of diseases in musk oxen on East Greenland is very limited (Clausen and Hjort, 1986), but there are, to our knowledge, no reports of large outbreaks of disease. However, as it has been proposed that musk oxen easily are infected with pathogens occurring in other ruminants (Alendal and Helle, 1983), it may be assumed that the introduced musk oxen of Dovrefjell, in any case, have received *Pasteurella* spp. from indigenous reindeer, sheep, or cattle. Typically, systemic pasteurellosis is associated with predisposing factors such as intercurrent disease or environmental stress, like severe weather events or overcrowding. Stress-induced suppression of host immunity is believed to be the underlying mechanism triggering these cases (Miller, 2001).

Stress factors associated with the present outbreak were: (i) rutting season, involving aggressive behavior of the males, running and chasing; (ii) reindeer hunting season with hunters dispersed throughout the range of the musk oxen; and (iii) unusual weather conditions with unusually high temperatures and high humidity in a period when the musk oxen already have fairly well-developed winter fur.

The challenge for an homeothermic animal, that survives in the extreme climate of the Arctic, is to balance heat loss against the rate of metabolic heat production (Blix, 2005). This is mainly achieved by control of heat loss. The musk ox avoid heat loss over the body surface by having a stout body shape with short extremities, thus reducing the surface area, and by wearing a massive pelage with a thick layer of underwool, the qiviut, covered by very long and coarse protective hairs (Fig. 5) (Bretten, 1990; Lent, 1999). In addition, a musk ox on good summer pastures will have a thick layer of subcutaneous fat, giving even more insulation. The qiviut is shed during the spring, but already fully replenished by the beginning of October (Bretten, 1990). When animals breathe, cold air is inhaled into the lungs, where it is warmed to body core temperature and saturated by water vapor. Heat and water may then be lost upon expiration, representing a significant loss of energy, not only because of the heat loss, but also because lost water has to be replaced and this is often only available as snow (Blix, 2005). In the reindeer, the blood-rich mucosa of the scrolled nasal conchae constitutes a counter-current heat exchange system that heats the inhaled air and supplies it with moisture. When the animal exhales, the warm air is cooled and the water vapor condensed in the same conchae. This allows the animals to breathe cold dry air without losing unacceptable amounts of energy. A similar such adaptation mechanism may be present in the musk ox.

Figure 5. A musk ox (left) and cow (right) in Dovrefjell, Norway: The species is adapted to extreme cold, having a stout body shape with short extremities, and a massive coat with a thick layer of very insulative underwool, the qiviut (visible on the neck of the cow), covered by very long and coarse protective hairs, which even covers the ears and the tail. This is suitable in the native areas of the species, but may become an hindrance when the animal is exposed to high temperatures and high humidity (Image courtesy of Line Aukrust).

All this energy-saving is beneficial when the musk ox stands in gale force wind and −40°C. However when the sun shines and warms up the dark animal and the air is between 15° and 20°C and almost saturated with water vapor, one should anticipate that the capacity of the temperature regulatory system of the musk ox is overcome. There were, however, no findings that indicated that the animals could have died from heat stroke, indicating that over-heating itself was not the cause of death. However, experimental exposure of bovine calves to a temperature of 35°C for 4 hours, seemed to favor colonization of their lungs by *Pasteurella multocida* and *Mannheimia haemolytica* (Reinhold and Elmer, 2002). This was suggested to be caused by heat-induced immunosuppression and by the increased respiration rate and volume, exposing the lungs for larger number of pathogens per time unit and disturbing the laminar flow of the inhaled air such that more bacteria were deposited in the lungs (Reinhold and Elmer, 2002).

The stress associated with the reindeer hunting and rutting season has, to our knowledge, never been associated with fatal infectious disease in musk ox. These factors may, however, have aggravated the situation. During warm periods in summer, one can often observe the musk oxen resting on glaciers or standing with their feet in cold streams (Bretten, 1990), probably to get cooler. This behavior would be hampered by both frequent contact with hunters and the rutting behavior, both of which force the animals to assemble in groups in open landscape.

Apart from a few cases, introduction of musk ox to non-polar areas has been met with failure (Lent, 1999). Climate has often been proposed as the limiting factor (Lønø, 1960). The exposure to new species of pathogens and increased levels of parasites has also been proposed to be important (Alendal and Helle, 1983). Compared to the areas of origin for the musk oxen, Dovrefjell is characterized by a relatively warmer and more humid climate (Fig. 6). It may thus be speculated that even small perturbations in an unfavorable direction may reach a critical threshold where the conditions become more or less unacceptable for this species.

In conclusion, extraordinary weather conditions, characterized by high temperatures and humidity, modifying musk ox susceptibility to infection, were the likely decisive factors of this disease outbreak. The disease may, of course, be seen merely as the result of an accidental coincidence of harmful conditions, each of them within the limits of natural variation. However, heat waves are predicted to increase in frequency, intensity, and duration as global warming ensues (Christensen et al., 2007). Therefore, this outbreak may not be a single incident, but something that may be expected to occur regularly in the near future. If so, increased incidence of heat-stress–related infectious disease may, together with other predicted changes, be a driving force in the decline, and perhaps extinction, of a cold-adapted species like the musk ox.

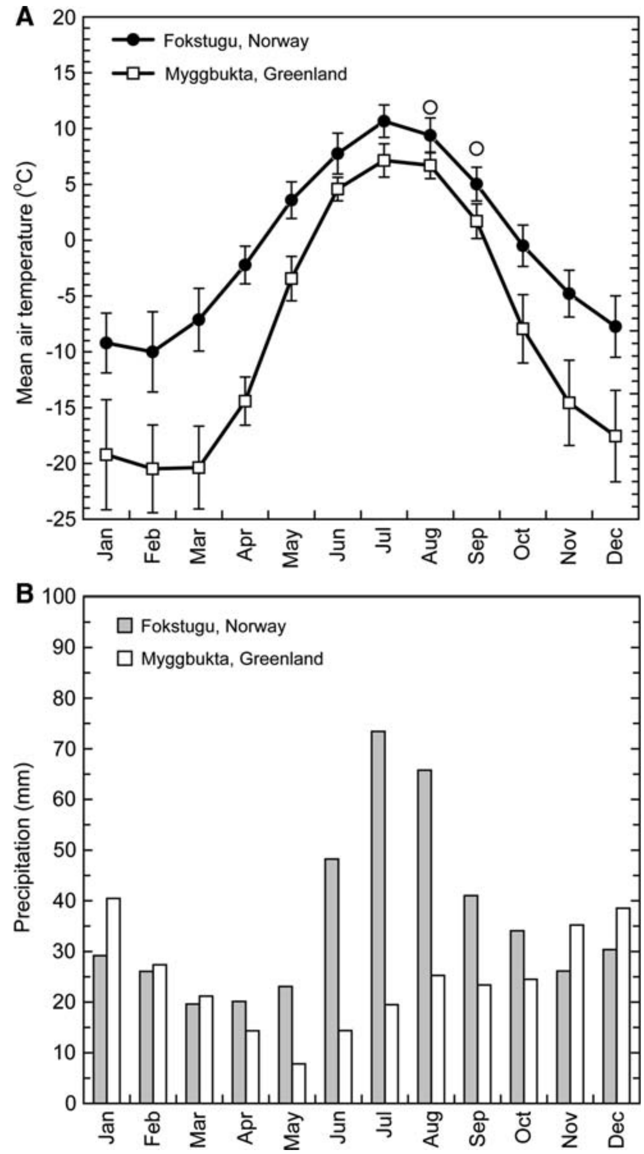

Figure 6. Monthly mean values of air temperature and precipitation registered at Dovrefjell (Fokstugu) in Norway (952 m a.s.l.) and Myggbukta in Greenland (3 m a.s.l.), the origin of Dovrefjell's musk ox population, for the period 1924–1958. At Myggbukta, there are missing values during the Second World War (1941–1945). Thus, the period covers 30 years (e.g., a normal period) of data, corresponding to the period the musk ox were reintroduced from Greenland to Dovrefjell. To be comparable, the data during the Second World War was taken out of the series from Fokstugu. (**A**) Monthly mean air temperature. The error bars display the 30-year standard deviations. The open circles show the 2006 mean temperature for August and September at Fokstugu. (**B**) Monthly precipitations sums.

As stated by Kutz and co-workers (2005): Arctic species have evolved under severe seasonal and environmental constraints and the life history patterns of these species can be dramatically altered by even minor climatic perturbations. Thus, the Arctic serves as a sentinel region, where studies to detect, understand, and predict the responses of high-latitude host–parasite systems to changing temperature can provide considerable insight into the biotic implications of warming on a global scale. Epstein (2002) suggests that the effects of extreme and anomalous weather that accompanies global warming, may have more profound health effects (in humans) than the mere increase in temperature, and that the volatility of infectious diseases may be one of the earliest biological expressions of climate instability.

To recognize alterations in the association between hosts and pathogens that may result from anthropogenic and/or climatological global change, adequate knowledge of baseline disease and pathogen occurrence is critical. The lack of long-term monitoring programs for the prevalence and severity of wildlife diseases is, hence, an inherent challenge in the study of the impacts of environmental change on animal health (Harvell et al., 2002; Hoberg et al., 2003; Kutz et al., 2004; Kuiken et al., 2005). In this context, the musk ox population of Dovrefjell, that has a limited size, lives in a geographically limited area, and has been under close syndromic surveillance for a long period, constitute an exception, and we can, with conviction, assert that an incidence as the described above, has not occurred before on Dovrefjell.

In this respect, the described disease outbreak may represent a canary bird in the coal mine scenario, teaching us the lesson that climate change may encourage disease outbreaks of opportunistic pathogens, and that such outbreaks may have large impacts on population health and survival. For the small musk ox population on Dovrefjell, repeated outbreaks with such high mortality would be devastating.

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