

PERSPECTIVE

The muskox (*Ovibos moschatus*) in Sweden: update on a small wild population with an uncertain fate

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Abstract

Once widespread across the Holarctic region, the iconic and pre-historic muskox (*Ovibos moschatus*) has seen a significant range reduction, with endemic populations now restricted to North America and scattered populations introduced throughout Eurasia. In 1971, five individuals from the introduced Norwegian population migrated across the border into Sweden and re-established a natural Swedish muskox population in Härjedalen. While the size of this population has since fluctuated, up-to-date knowledge on the population size and status has been missing. In the summer of 2024, we therefore conducted a population survey and estimated the current population size to eight individuals. Although the population remains small and despite the absence of a formal wildlife management plan, the presence of a sub-adult and calf still shows an ongoing reproduction and suggests a viability and long-term local continuity of muskoxen in the area. Compared to the well-studied populations in North America and Greenland, little is known about the foraging ecology, habitat selection and ecological role of muskoxen in Scandinavia. Synthesizing published research from other regions, we explore the potential ecological services of the Swedish muskoxen, such as mitigating climate-induced changes like shrubification. We also report the results of our count of the population—eight individuals, including a calf and a sub-adult—and discuss its future prospects in Sweden, arguing that the environmental conditions in Scandinavia are indeed capable of supporting muskox populations.

Introduction

Muskoxen (*Ovibos moschatus*) are among the few large-bodied herbivores to survive the climatic change of the Pleistocene–Holocene transition. Once found with a Holarctic distribution, their populations are today largely concentrated in North America and Greenland, although smaller muskox populations can still be found elsewhere, such as in Scandinavia. Following the translocation of wild muskox herds from Greenland to Norway in the mid-20th century, five individuals later crossed the border into Sweden in 1971 and re-established themselves in the southern parts of Härjedalsfjällen, creating what is now considered the Swedish muskox population (Alendal 1974). Initially, this small group grew, and the population reached its maximum count—about 35 individuals—in the mid-1980s (Lundh 1999). The population declined in the

following decades and the last reported counts in 2010 estimated a total of seven animals (Thulin et al. 2011 and references therein), after which no official inventory has been made. There is an urgent need for a new inventory to be done to provide an updated population estimate and firmly establish the current status of the Swedish muskox population.

Previous studies in, for example, Greenland and Canada have shown that large mammalian herbivores, such as muskoxen, serve key functions in their ecosystems and have important impacts on local biodiversity (Post & Pedersen 2008; Falk et al. 2015; Mosbacher, Kristensen et al. 2016). Through a combination of grazing, fertilization and trampling, muskoxen promote higher species diversity and graminoid-dominated habitats by altering crucial plant and nutrient dynamics (Post & Pedersen 2008; Post 2013; Falk et al. 2015; Mosbacher, Kristensen et al. 2016; Mosbacher et al. 2019). In turn,

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these changes can affect the carbon balance and the phenology of the area (Falk et al. 2015; Mosbacher et al. 2019). It has therefore been shown that the presence of herbivores, including muskoxen, may buffer climate change-induced effects on vegetation and increase the overall resilience and stability of plant communities (Post 2013; Kaarlejärvi et al. 2015). Much of the research on muskoxen has been based on the predominantly endemic populations in Canada, Greenland and Alaska, which together hold about 90% of the global muskoxen population (Cuyler et al. 2020), while little is known about the Scandinavian muskox populations. Over 50 years after the (re-)establishment of muskoxen in the Swedish fauna, no conservation or population management plans are in place, and the role of muskoxen as a potential key species within the sensitive Swedish mountain ecosystem is still unknown.

To help fill this knowledge gap, we here present a compilation of what is currently known about the Swedish muskox population and what we can infer in terms of the ecosystem services they may provide, on the basis of studies of muskox populations in Greenland, Alaska, Canada and Russia. We also report an updated population size estimate, following the 2024 summer population inventory. Some of the questions we aim to answer are: What is the current status of the Swedish muskox population? What is the ideal habitat for muskoxen and what is their preferred diet? Which ecosystem services can the Swedish muskoxen provide and is there a risk for interspecies competition for habitat and trophic resources with, for example, reindeer (*Rangifer tarandus fennicus*)? Our overarching aim is to predict the future of the Swedish muskox population and to assess whether potential conservation and population management actions can be justified.

History and status of the Swedish muskox population

Muskoxen originated in Asia and spread into Europe about 1 million years ago. Pleistocene ranges for muskoxen included large areas outside of their current distribution (Raufuss & von Koenigswald 1999; Canteri et al. 2022), reaching as far south as the Iberian Peninsula (Escalera 1978). Transitioning into the Holocene, muskoxen ranges contracted and abundance sharply declined, most likely linked to climate-driven environmental changes (Campos et al. 2010). Radiocarbon dates of muskox sub-fossil bones place the species in Scandinavia about 40 000 years ago (Hufthammer et al. 2019), with local extirpation occurring about 12 000 years ago (Canteri et al. 2022).

During construction work in the Dovre region of Norway in the early 20th century, muskoxen fossils were uncovered, and the initial idea of reintroducing the species to the region conceived (Collins 2022). A number of reintroductions were attempted in Norway in the 1920s–1940s, with unsuitable habitat and the consequences of World War II causing most to fail (Andreassen 2017; Collins 2022). Following the end of the Second World War, a renewed effort on behalf of the Norwegian government to bring muskoxen back into Norway was launched (Collins 2022). Between 1947 and 1953, 27 calves and yearlings from eastern Greenland were introduced into the Dovrefjell region of Norway (Lønø 1960; Andreassen 2017), founding today's Norwegian muskox population of about 200–250 animals (Andreassen 2017; Cuyler et al. 2020). It was from this population that five animals—one bull, two cows and their two calves—separated, crossed the Norwegian–Swedish border in 1971 and created what is now considered the Swedish muskox population (Alendal 1974).

While other introduced or re-established muskoxen populations, such as in western Greenland (Post & Pedersen 2008), have quickly grown, the Swedish population has been less successful. Initially, the population grew steadily. After peaking in the mid-1980s, it declined. This decline is largely attributed to low genetic diversity and inbreeding depression (Laikre et al. 1997), although impacts from environmental changes such as temperature, deposition and snow depth may also play an important role, as we consider below (see also Asbjørnsen et al. 2005). In an effort to remedy the concern of genetic diversity, a captive bull originating from Greenland was mated with a cow captured from and then re-introduced to the Swedish muskoxen population, resulting in a calf in 2006 (Thulin et al. 2011). This infusion of new genetic material 19 years ago is believed to explain why the Swedish muskoxen population has greater genetic diversity than its founder population in Norway (Thulin et al. 2011). This highlights the importance and lasting benefit of even a single out-breeding or rewilding effort.

Recent studies have estimated the global muskoxen population size to about 168 700 animals, of which about 109 000 are in Canada, about 39 000 are in Greenland, about 15 000 are in Russia and about 4300 are in Alaska (Cuyler et al. 2020). The Scandinavian populations, estimated to about 250 animals, amount to a mere 0.15% of the total global population (Cuyler et al. 2020 and references therein). Up-to-date estimates of the Swedish population have been lacking (Fig. 1). To fill this knowledge gap, we inventoried the population in the summer of 2024. There were eight animals: three adult bulls, three adult females, one

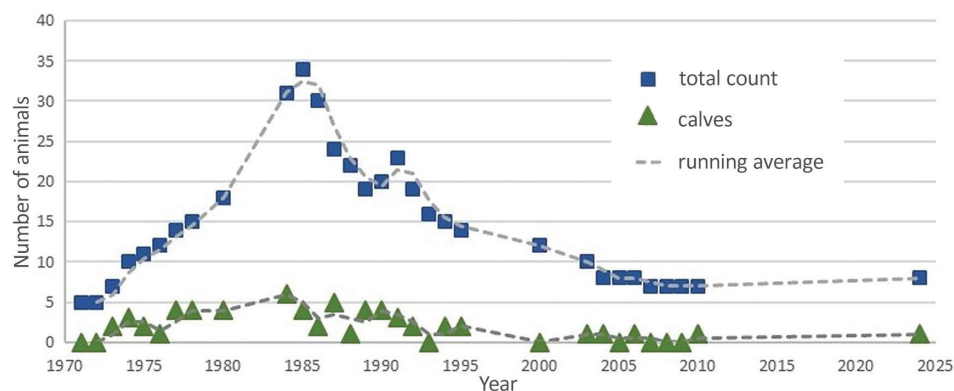


Figure 1 Population development of the Swedish muskoxen from its re-establishment in the Swedish fauna in 1971 to the latest population inventory performed in the summer of 2024. Prior to 2024, the last population count was undertaken in 2010. Redrawn and adapted from Thulin et al. (2011).

sub-adult individual and one calf of the year. Although this number is very small, the calf and the sub-adult indicate that the population is still reproducing and should thus be considered viable.

Climate and habitat selection

While the muskox is considered an Arctic species, there is a wide range of temperatures in its endemic habitat. Average summer maximums range between 21° and 27 °C and average winter minima temperatures are around –34 °C (Tener 1965). For example, Nault et al. (1993) and references therein reported environmental conditions favourable to muskox populations in northern Québec as temperature ranges of –29 to –18 °C in winter and 4 to 15 °C in summer, a growing season lasting 40–60 days and an annual precipitation of 410 mm of which 40–45% fell as snow. In north-eastern Greenland, where the wild Zackenberg muskoxen population resides, average winter temperatures range from –15 °C to –20 °C and summer averages 3–7 °C, with an average of 35 days without frost and an average precipitation of 261 mm (Hansen et al. 2008). Compared to the habitat of endemic populations of muskoxen in Greenland and Canada, the climate of the Scandinavian populations is notably warmer and wetter, particularly in the summer months (Yttrhus et al. 2008). Temperature data from Zackenberg (mean summer temperature: 6 °C, mean winter temperature: –20 °C [van Beest et al. 2023]), Dovrefjell (mean summer temperature: 9.8 °C, mean winter temperature: –8.8 °C [Davidson et al. 2014]) and Härjedalen (mean summer temperature: 11–13 °C, mean winter temperature: between –12 and –9 °C [Bruun et al. 2003]) attest to the Scandinavian muskoxen populations experiencing warmer summers and winters than their Greenlandic counterparts. Paring these differences in temperatures with population trends

suggests that the climatic conditions in Sweden, while tolerable, may not be ideal.

Satellite tracking of collared muskoxen at Zackenberg provides evidence for high site fidelity and small home ranges, with animals venturing only about 40 km from the collaring site (Schmidt et al. 2016). Other studies have shown that muskoxen may seasonally shift their habitat selection to optimize their access to, and quality of, forage (Tener 1960; Gunn & Fournier 2000; Cuyler et al. 2020). For example, during the summer months in Greenland, muskoxen tend to be more concentrated in graminoid-dominated, wetter ecosystems and to move up to more barren and wind-exposed mountain ridges in the winter (Klein & Bay 1991; Larter & Nagy 2004; Kristensen et al. 2011). Similar seasonal movement patterns have also been seen on Wrangel Island, in Russia, where muskoxen are generally found in moist depressions or along river banks and streambeds in the summer, moving to wind-exposed hilltops for winter forage (Rozenfeld et al. 2012).

This switch to higher and more wind-exposed grounds is likely driven by snow cover and forage accessibility as their lower chest height, shorter legs, smaller hoofs and greater foot loading limit muskoxen in their habitat selection compared to, for example, reindeer (Smith 1989; Klein 1992; Ihl & Klein 2001). In fact, snow conditions have been reported as a key driver of muskoxen population dynamics (Schmidt et al. 2015; Mosbacher, Kristensen et al. 2016; Tomassini et al. 2019) and a prolonged snow cover, or harder snow, has been linked to the wintertime mortality of muskoxen because such snow conditions limit the animals' access to food (Parker et al. 1975; Gunn et al. 1989). In addition to snow cover, studies have also shown a link between air temperatures and population dynamics (Asbjørnsen et al. 2005), indicating that winter severity, including snow depth and snow extent, also plays an important role in population fluxes (Beumer et al. 2019; Duncan et al. 2021; van Beest et al. 2023).

A seasonal variation in habitat selection has also been observed for the Swedish muskox population, although, unlike their Greenlandic, Canadian and Russian counterparts, the Swedish muskoxen appear to head to higher grounds during the summer and remain in the lowlands during the winter. During the winter, the population can be found towards the eastern areas of their estimated about 260 km² home range, whereas they move westwards—crossing the border into Norway—during the summer (Fig. 2; Lundh 1999). It should be noted that the Swedish population does not intermix with the Norwegian population in Dovrefjell, as the two home ranges are located about 140–150 km apart, and that the potential eastward movement of the Dovre population is hindered by a railway, the E6 highway and the local management and culling programme.

Although studies of the specific habitat selection by the Swedish muskoxen and the suitability of such habitats for them are lacking, some information can be inferred from the Norwegian population in Dovrefjell. For example, the region of Scandinavia where the Dovrefjell and Härjedalen muskoxen live are both on the Fennoscandian Shield, which is composed of gneissic, granite and additional hard siliceous stone (Sjors 1999; Bruun et al. 2003 and references therein). Both areas also possess an abundance of high elevation land and a rich alpine flora with a wealth of shrubs, graminoids and lichens (Bruun et al. 2003; Michelsen et al. 2011), and in

this respect, the region does appear suitable for muskoxen in spite of the somewhat warmer climate. To fully decipher the driving mechanisms behind their habitat selection and movement patterns of the Swedish muskoxen, more detailed studies are needed, especially to determine the full extent of their current home range.

Forage pattern and preferred diet

Muskoxen are categorized as grazers and their diet across the Arctic predominantly comprises graminoids and willows (*Salix* spp.; Ihl & Klein 2001; Kristensen et al. 2011; Mosbacher, Kristensen et al. 2016; Mosbacher, Michelsen et al. 2016; Schmidt et al. 2018). *Dryas* spp., *Vaccinium* spp., *Equisetum* spp., *Saxifraga* spp., lichens, mosses and legumes have also been reported (e.g., Biddlecomb 1992; Larter & Nagy 1997; Larter & Nagy 2004; Rozenfeld et al. 2012; Schmidt et al. 2018). Although graminoids dominate the muskox diet in most studies, the particular preferences for forage appear somewhat influenced by geographic location of the population and may also shift between seasons and years. For example, in a study using stable isotope analysis of muskox guard hairs, Mosbacher, Michelsen et al. (2016) showed that summer diets of muskoxen in Zackenberg were dominated by graminoids and remained relatively consistent between years, whereas the winter diet not only included a broader range of species but also shifted between years, most

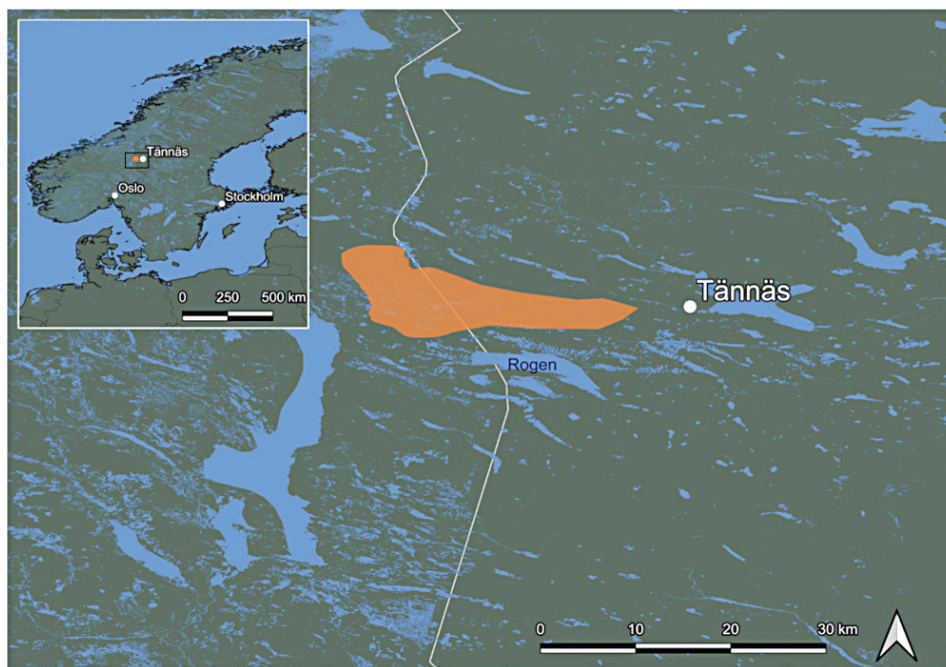


Figure 2 Geographical extent of the year-round core area of the Swedish muskox population, with the Norwegian–Sweden border noted in white. The map was made using the software QGIS 3.34.11 based on, and updated from, Nilsson (2014).

likely because of differences in snow depth and snow coverage, which limited the animals' access to their preferred foods and to forage in general (Mosbacher, Kristensen et al. 2016; Mosbacher, Michelsen et al. 2016). There were occasional prolonged periods of starvation, when the muskoxen relied heavily on their body reserves (Mosbacher, Michelsen et al. 2016). Fatty acid analysis of muskoxen tissues confirms that they are well adapted to periods of restricted forage in the winter (Alves et al. 2015).

Although new techniques, such as stable isotope analysis and DNA meta-barcoding, can provide great taxonomic resolution of the constituents of muskoxen diet and seasonal variations of forage (e.g., Schmidt et al. 2018; Brodeur et al. 2023), studies applying these methods to investigating the muskox diet of Scandinavian muskoxen are scarce to non-existent and much therefore remains unknown in terms of their diet and specific forage patterns.

Ecosystem services and potential interspecies competition with reindeer

Muskoxen offer a host of benefits to their local ecosystems, including after their demise. Their efforts to break through snow to access vegetation in the winter provide access to forage for other herbivores (Schmidt et al. 2018). More generally, muskoxen foraging has been shown to have positive impacts on plant nutrient content and cycling, phenology, community composition and above-ground biomass (Mosbacher et al. 2019). After death, decomposing large-bodied herbivores, such as muskoxen, create 'green islands' of nutrients that benefit local plant communities and render essential elements bioavailable (Wenting et al. 2023). A key consequence of global warming for Arctic ecosystems is the ongoing phenomenon of shrubification, in which the tundra shifts from being graminoid dominated to shrub dominated (Mekonnen et al. 2021). Although not as urgently as in the High Arctic, this is also affecting the vegetation composition of the Swedish mountain ecosystem. A multi-species ecosystem composition, such as a combination of herbivores, like reindeer, moose (*Alces alces*) and muskoxen, has been shown to mitigate this change (Post et al. 2023). More muskoxen in the Swedish alpine ecosystem could therefore help impede this climate-induced change.

Interest in the interspecies competition for ecological niches between muskoxen and caribou/reindeer (*Rangifer tarandus*) in North America and the Eurasian Arctic has remained at the forefront of Arctic tundra research (McKendrick 1981; Klein 1992; Kutz et al. 2017;

Brodeur et al. 2023). Generally, reindeer/caribou and muskoxen only minimally—and not to either species' detriment—overlap in requirements for foraging resources, so they can successfully coexist (Klein 1992; Ihl & Klein 2001). Morphological and physiological differences, notably muzzle dynamics and digestive efficiency, have led these two species to have differing foraging strategies (Klein 1992). For example, muskoxen are considered grazers, whereas caribou are intermediate feeders (Bliss et al. 1973; Hofmann 1989; Hofmann 2000). This is primarily attributed to physiological differences in digestive systems: muskoxen have larger rumens and slower digestion compared to *Rangifer* (Klein 1992).

Numerous investigations into the overlap in trophic resources and habitats suggest minimal competition between the two species. Baseline dietary isotopic data from pre-Dorset (Bocherens et al. 2016) and Thule (Coltrain et al. 2004) contexts in the Canadian Arctic indicate limited overlap in trophic resources between muskox and *Rangifer tarandus caribou*. An analysis (with small sample sizes for some parts of the year) of faeces from reindeer and muskoxen on Wrangel Island revealed that the two species ate the same proportion of particular plants, but their consumption of these flora was at different times of the year (Rozenfeld et al. 2012). Muskoxen on the island consumed a notably higher diversity of plants over the year than reindeer in all ecosystem types considered, and reindeer had fewer species that they exclusively consumed (Sheremetev et al. 2014). In northern Québec, tracking satellite-collared caribou and muskoxen, combined with DNA metabarcoding of faecal samples, found minimal evidence for overlap between the two species' ranges (Brodeur et al. 2023). In 450 hours of observation on Banks Island, in the Canadian Arctic Archipelago, muskoxen and caribou encountered each other only three times, and none of these encounters led to any interactions between the two species (Wilkinson et al. 1976). All these findings suggest that a continued presence of muskox in Sweden does not pose a significant risk to already established fauna.

Predicted future, conservation efforts and population management

Among the pantheon of Arctic fauna, muskoxen are among the species that are highly susceptible to range contraction resulting from climate change (van Beest et al. 2021), with shifts in their ranges already being noted in Greenland (van Beest et al. 2023). Ongoing or predicted changes include warmer summers, more parasite occurrences, more precipitation (and more of it falling as rain),

more variable snow depth and more icing events (Beumer et al. 2019; Kaffle et al. 2020; Duncan et al. 2021; McCrystall et al. 2021; van Beest et al. 2023). These are key factors to bear in mind when considering the longevity and continuity of muskoxen in Sweden, especially since the possibility to move to higher grounds—to counter the effects of warmer summer temperatures (potentially including heat stress)—remains limited within their current estimated home range (Fig. 2). Also to be taken into consideration is the knock-on effect of climate change and rewilding efforts that are changing the ranges of potential predators—grizzly bears (*Ursus arctos horribilis*) in North America (Arthur & Del Vecchio 2017), brown bears (*U. arctos*) in Eurasia (Niedziakowska et al. 2019) and wolves (*Canis lupus*) on both continents (Marquard-Petersen 1998; Bonin et al. 2023).

While competition with other herbivores for resources is apparently minimal, proximity to other ungulate species has the potential for introducing pathogens and disease into muskoxen populations. For example, the spillover of parasites (Ytrehus et al. 2008; Davidson et al. 2014) and viruses (Vikøren et al. 2008) from sheep and reindeer into the Norwegian muskoxen population has already been documented. As the Swedish muskoxen are not in close proximity to any animal husbandry activities, this spillover risk is likely low, which is a positive factor for their future continuity. There appears to be little evidence for the transmission of disease in the other direction—from muskoxen—posing any significant threat to other ungulates (Alendal & Helle 1983; Davidson et al. 2014).

One of the principal and often-cited concerns for the persistence of muskoxen populations is their remarkably low genetic diversity, the consequence of numerous founder events and genetic bottlenecks since the late Pleistocene (Hansen et al. 2018). A more granular approach to muskoxen genetics, which confirms their overall low genetic diversity, has also highlighted that the portion of their genome responsible for innate and acquired immunity has sufficient diversity and is comparable to other Arctic ruminants (Lok et al. 2024). This indicates that the functional genetic diversity of muskoxen may not be the main causative threat to the survival of the population, a notion supported by the lack of genetic diversity documented in both the Swedish population and its ancestral population in Dovrefjell (Thulin et al. 2011). Enforcing a comprehensive population management plan, which also entails genetic enrichment efforts, would reinforce the viability of the Swedish muskox population.

The neighbouring Norwegian muskox population in Dovrefjell benefits from a well-established population management plan that dates back to 1996, with revisions

in 2006 and 2017 (Andreassen 2017 and references therein). The main goal of this plan is to ensure a continued existence of muskoxen in Norway by allowing the muskoxen to naturally develop within the core area of 340 km² that has been allocated to it. It ensures that the population does not exceed 200 (winter) individuals, that the authorities have up-to-date knowledge of the population size and that the risk of pathogens and diseases is reduced.

No such management plan exists in Sweden. The Swedish Environmental Protection Agency does not classify muskoxen as an endangered or threatened species, on the grounds that it has not naturally established itself in the country for a substantial amount of time. That is, according to Swedish legislation (Jørgensen 2015; Ericsson 2023), a species must have been present in Swedish territory since 1800 to be formally recognized as native to Sweden. From the Swedish authorities' point of view, the muskoxen are considered to have been introduced in Norway and then to have spontaneously migrated into Swedish territory, making them ineligible to be classified as part of the Swedish fauna. Paradoxically, paragraph 33 of the hunting regulations (Jaktförordning 1987:905 33 §) classifies muskoxen as state-owned wildlife (Government of Sweden 1987) and becomes property of the state when they die, a classification with the purpose of protecting endangered, rare or particularly valuable species. Although the muskox is listed as a globally significant species under the Bern Convention on the Conservation of European Wildlife and Natural Habitats, which, in theory, grants muskoxen protection under the Swedish Species Protection Ordinance, the convention does not require any specific conservation actions or management plans to be in place. Consequently, the Swedish muskoxen population is not prioritized in any national species protection efforts. From a conservation perspective, these bureaucratic hurdles have left the Swedish muskoxen in a wildlife management limbo.

Consisting of eight animals today and peaking at 34 in the 1980s, muskoxen are among the least abundant of Sweden's wildlife species. Varying densities of muskoxen reported throughout the world provide some insight into the optimal density for a viable population. The Dovrefjell population has a density of 0.59 animals/km² (Andreassen 2017), whereas a density of 1 animal/km² has been reported for Greenland (Thing et al. 1987) and for the Canadian Arctic Archipelago (Thomas et al. 1981); the density in northern Québec is slightly higher at 1.2 animals/km² (Nault et al. 1993). Higher densities are less common but still support viable, healthy populations with densities of 1.65 animals/

km² noted as being a high density in the Canadian Arctic (Larter & Nagy 2001). Given the result of our population count reported here, and that the current observed home range spans an area of about 260 km² (Nilsson 2014), the estimated density of muskoxen in Sweden would be 0.03 animals/km²—far lower than densities observed elsewhere. It therefore seems unlikely that they would exceed the carrying capacity of their current range even if rewilding efforts and conservation management were implemented to assist in increasing the population. It should be noted that knowledge of the exact span of their home range is lacking. The current estimation is based merely on observational data, rather than GPS/location trackers. Also, there is no assessment of forage availability in this area; this is a key factor in understanding resource availability and also carrying capacity. Future research should aim to fill these two knowledge gaps.

Conclusions and future directions

Over 50 years after five muskoxen ventured across the Norwegian–Swedish border and re-established a population in Härjedalen, there are eight animals that arguably demonstrate a long-term local continuity for the species in this location. While the size of the population has fluctuated in that half century, it has remained relatively stable over the past decade, in spite of the lack of a management plan and legislative protections. Many of the today's muskox populations exist in colder and drier climates, but the sustained Norwegian population in neighbouring Dovrefjell, combined with palaeo-ecological evidence, demonstrates that the environmental conditions in Scandinavia can also support muskox populations. A review of the literature also shows that these large-bodied herbivores offer a plethora of ecosystem services and that it appears unlikely that there are any negative interactions between muskox and other wild ungulates. Yet factors such as potential predation, climate change and low genetic diversity makes the future of the Swedish muskox population uncertain.

Predictions regarding the future Swedish muskoxen response to climate change are scarce to non-existent as they will rely on more detailed information about home range, movement patterns and other information. Bringing in genetic input from other muskox populations would strengthen the Swedish gene pool, but such outbreeding events would require the support (financial and/or authorization) from the relevant governing agencies. The future survival of the Swedish muskox population depends heavily upon having a management plan and clear legislation in place.

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Disclosure statement

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