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In the eye of the reindeer

Infectious eye diseases, impact on animal welfare, and herders' perceptions

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In the eye of the reindeer: Infectious eye diseases, impact on animal welfare, and herders' perceptions

Abstract

Semi-domesticated reindeer (*Rangifer tarandus tarandus*) are central to Sámi reindeer husbandry in Fennoscandia. Infectious keratoconjunctivitis (IKC) is a painful and multifactorial eye disease in reindeer, associated with reduced welfare and practical challenges for herders. Knowledge is limited regarding the occurrence of IKC, associated pathogens, risk factors, and how ocular disease is perceived and managed in reindeer husbandry. This thesis aimed to investigate microorganisms and risk factors associated with IKC in reindeer, as well as herders' perceptions and management of the disease. It is based on four studies: a questionnaire survey, a field study of conjunctival swab samples from reindeer with and without clinical signs, a virological study of parapoxvirus red deer, and an interview study exploring herders' experiences of ocular disease. The results showed that IKC was commonly observed at herd level in Norway and Sweden, particularly during autumn and winter. Feeding in enclosures, especially during the challenging herding year 2019/2020, was associated with outbreaks, and calves were most frequently affected. Multiple pathogens were detected, including cervid herpesvirus 2 (CvHV2), *Chlamydia* spp., *Mycoplasma* spp., *Moraxella bovoculi*, poxviruses, and several opportunistic bacteria. *Staphylococcus aureus* and *Pseudomonas aeruginosa* were associated with clinical signs of IKC. *Chlamydia* spp. was associated with conjunctivitis and cervidpoxvirus with periocular lesions. Parapoxvirus red deer was detected for the first time in reindeer, showing evidence of host adaptation and cross-species transmission. Ocular disease was primarily perceived as a herd-level threat, and management was strongly influenced by contextual factors such as labour, logistics, and access to veterinary support. Disease management was described as labour-intensive and emotionally demanding, highlighting the need for improved communication, preparedness, and trust between herders, veterinarians, and other stakeholders.

Keywords: alphaherpesvirus, CvHV2, IKC, infectious keratoconjunctivitis, *Rangifer*, RDPV, reindeer husbandry, supplementary feeding, ocular disease

I renens öga: ögoninfektioner, påverkan på djurvälfärd samt renägares erfarenheter

Sammanfattning

Renen (*Rangifer tarandus tarandus*) utgör en central- och kulturbärande del av renskötseln och de samiska samhällena i Norge, Sverige och Finland. Infektiös keratit och konjuntivit (IKC) är en smärtsam och multifaktoriellt orsakad ögoninfektion hos ren som är förknippad med nedsatt djurvälfärd och praktiska utmaningar för renskötarna. Kunskapen är begränsad avseende sjukdomens förekomst, associerade mikrober, riskfaktorer samt hur sjukdomen uppfattas och hanteras inom renskötseln. Syftet med denna avhandling var att undersöka mikroorganismer och riskfaktorer kopplade till IKC hos ren, samt renskötares uppfattningar och hantering av ögonsjukdom. Avhandlingen baseras på fyra studier: en enkätundersökning bland renskötare i Norge och Sverige, provtagning med konjunktivalsvabbar från renar med och utan kliniska symtom, en studie av kronhjortens parapoxvirus, samt en intervjustudie om renskötares erfarenheter av ögonsjukdom. Resultaten visade att IKC är vanligt förekommande på hjordnivå i Norge och Sverige, särskilt under höst och vinter. Utfodring i hägn, särskilt under det utmanande renskötselåret 2019/2020, var associerad med utbrott av IKC, och kalvar var den mest drabbade åldersgruppen. Flera patogener påvisades i ögonprover, inklusive cervint herpesvirus 2, *Chlamydia* spp., *Mycoplasma* spp., *Moraxella bovoculi*, poxvirus samt opportunistiska bakterier. *Staphylococcus aureus* och *Pseudomonas aeruginosa* var associerade med kliniska symtom på IKC, medan *Chlamydia* spp. kopplades till konjunktivit och renkoppsvirus till periokulära lesioner. Kronhjortens parapoxvirus påvisades för första gången hos ren och visade tecken på värdanpassning och smittspridning mellan djurarter. Ögoninfektioner såsom IKC uppfattades främst som ett problem på hjordnivå, där förebyggande åtgärder för att skydda hjorden var centrala. Hanteringen påverkades i hög grad av kontextuella faktorer såsom arbetsbelastning, logistik och tillgång till veterinär. Sjukdomshanteringen beskrevs som arbetskrävande och emotionellt belastande, vilket understryker behovet av förbättrad kommunikation, beredskap och tillit mellan renskötare, veterinärer och andra aktörer.

Nyckelord: alfaherpesvirus, infektiös keratokonjunktivit, kronhjortens parapoxvirus, *Rangifer*, renens herpesvirus, renskötsel, stödutfodring, ögonsjukdom

Preface

This PhD thesis presents the outcome of a PhD project funded by Formas - the Swedish Research Council for Sustainable Development (Grant No. 2019-02090). The project was a collaboration between the Swedish University of Agricultural Sciences (SLU) and the Swedish Veterinary Agency (SVA). Other important collaborators along the way have been Sámiid Riikkasearvi (Sámi Reindeer Association, SSR), The Arctic University of Norway (UiT), and the Swedish advisory organisation Farm and Animal Health.

The initial aim of the project was to analyse the prevalence, risk factors, aetiology, and herders' perceptions of infectious diseases affecting the eye and mouth in reindeer. Initial investigations at abattoirs revealed that lesions associated with infectious diseases of the mouth were uncommon, and there were no reports of disease outbreaks involving the oral cavity from the field. In contrast, clinical signs of keratoconjunctivitis were reported annually in several reindeer herds, with notable impacts on animal health and welfare, antibiotic use, and herders' livelihoods. The aim of the project was therefore refined to include only ocular diseases, particularly infectious keratoconjunctivitis (IKC), in reindeer. Furthermore, two poxviruses were discovered in reindeer in Norway and Sweden for the first time during the course of the project. These findings resulted in further investigations of these newly identified viral conditions. Overall, the project followed a mixed-methods approach to strengthen the scientific foundation for understanding the impact of IKC in reindeer husbandry, combining epidemiological and microbiological analyses with participatory research involving herders.

The work presented in this thesis was conducted between April 2020 and April 2026, a period encompassing the COVID-19 pandemic, and was undertaken primarily at SVA and at the Faculty of Veterinary Medicine and Animal Science, SLU. The work was interrupted by a period of maternity leave (from April 2023 to March 2024) and by institutional project-related duties at the Department of Animal Health and Antimicrobial Strategies, Section of Farm Animals, SVA, corresponding to 20% of my time during the project. In addition, from February to May 2025, I worked full-time as a ruminant veterinarian at the same department.

Uppsala, 16 April 2026

Karin Wallin Philippot

RENÖGA

Dedication

Till min familj,

Joëlle, Julie, Émile & Gaëtan

Att göra ingenting är aldrig bortkastad tid

- James Norbury

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. **K. Wallin Philippot**, J. Baron, J. Sánchez Romano, H. Rautiainen, J. Frössling, I. H. Nymo, Y. Persson, A. Omazic & M. Tryland (2023). Infectious keratoconjunctivitis in semi-domesticated reindeer (*Rangifer tarandus tarandus*): a questionnaire-based study among reindeer herders in Norway and Sweden. Acta Veterinaria Scandinavica 2023 Vol. 65 (Issue 1), pp.34 DOI: 10.1186/s13028-023-00694.

II. **K. Wallin Philippot**, J. Frössling, C. Berg, M. Hakhverdyan, M. Leijon, U. Rockström, J. Johansson Wensman, & Y. Persson. Pathogens associated with infectious keratoconjunctivitis in reindeer (*Rangifer tarandus tarandus*) in Sweden. (Manuscript).

III. **K. Wallin Philippot**[a], M. Leijon[a], Y. Lindgren, F. Banihashem, T. Jinnerot, V. Lengquist, F. Suhel, C. Arnason Bøe, B. Spilsberg, I. H. Nymo, U. Rockström & J. Johansson Wensman (2025). First report of a parapoxvirus red deer infection in reindeer (*Rangifer tarandus tarandus*): clinical presentation and full-genome characterization. Virology Journal (2025) Vol. 23 (Issue 1), pp.87 DOI: 10.1186/s12985-025-03046-5.

IV. **K. Wallin Philippot**, H. Rautiainen, A. Omazic, N. Lind, & C. Berg Reindeer herders' perceptions of ocular disease in reindeer: a One Welfare perspective based on a qualitative Interview study in Sweden. (Manuscript).

Papers I and III are reproduced with the permission of the publishers.

[a] These authors contributed equally and share first authorship.

The contribution of Karin Wallin Philippot to the papers included in this thesis was as follows:

I. Contributed to the planning and design of the study. Developed the questionnaire in collaboration with the co-authors and the reference group. Was responsible for distributing the survey in Sweden, issuing reminders, and recruiting participants. Analysed the data with support from the supervisors. Drafted the manuscript with continuous input from supervisors and co-authors.

II. Contributed to the planning and design of the study, including continuous dissemination regarding the opportunity to submit samples, development of the referral form, and definition of the data collected. Performed field sampling. Contributed to data analysis and visualisation, including interpretation and discussion of the results. Drafted the manuscript with continuous input from the supervisors and co-authors.

III. Contributed to the study design and wrote the original draft of the manuscript together with M. Leijon, while coordinating the overall work and leading the progression of the study. Contributed to discussions and interpretations of the results and reviewed, edited, and approved the final version of the manuscript together with the co-authors. Corresponded with the journal.

IV. Designed and planned the study together with the supervisors and co-authors. Conducted all the interviews, coding, and initial data analysis. The final analysis and development of themes were conducted in collaboration with the co-authors. Drafted the manuscript with continuous input from supervisors and co-authors.

Other papers that are not included in the thesis:

S. Bull-Aurbakken, E. Malmström, J. Baron, J, Sánchez Romano, **K. Wallin Philippot**, H. Rautiainen, A. Omazic, I H. Nymo & M. Tryland (2026). Reindeer Health and Supplementary Feeding Practices – A Survey of Herders in Norway and Sweden. Acta Veterinaria Scandinavica (Accepted for publication).

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Abbreviations

BPSV	Bovine papular stomatitis virus
C. pecorum	*Chlamydia pecorum*
CvHV2	Cervid herpesvirus 2
CvPV	Cervidpoxvirus
E. coli	*Escherichia coli*
F. necrophorum	*Fusobacterium necrophorum*
IKC	Infectious keratoconjunctivitis
K. pneumoniae	*Klebsiella pneumoniae*
L. monocytogenes	*Listeria monocytogenes*
Mes. bovoculi	*Mesomycoplasma bovoculi*
Mes. conjunctivae	*Mesomycoplasma conjunctivae*
Mes. ovipneumoniae	*Mesomycoplasma ovipneumoniae*
MIC	The minimum inhibitory concentration
Mor. bovoculi	*Moraxella bovoculi*
MRL	Maximum residue limits
NM	Nictitating membrane (third eyelid)
OD	Ocular disease
ORFV	Orf virus
P. aeruginosa	*Pseudomonas aeruginosa*
P. multocida	*Pasteurella multocida*
PCPV	Pseudocowpox virus
PPV	Parapoxvirus
RDPV	Parapoxvirus red deer
RHD	Reindeer herding district
S. aureus	*Staphylococcus aureus*

SEPV	Seal parapoxvirus
T. pyogenes	*Trueperella pyogenes*

AI declaration

This thesis reflects the author’s own scholarly work, and the author takes full responsibility for its content and accuracy.

Generative artificial intelligence (AI) tools (ChatGPT and OpenAI) were used during the preparation of this thesis for language editing and stylistic refinement of the text. In addition, AI-based tools (ChatGPT, Claude by Anthropic, and Gemini by Google) were used to assist in refining and preparing selected figures.

All AI-assisted outputs were carefully reviewed and, where necessary, modified by the author. No AI tools were used in the generation, analysis, or interpretation of scientific data.

1. Background

1.1 The reindeer

Rangifer tarandus, commonly referred to as reindeer in Eurasia and caribou in North America, is a circumpolar migratory ungulate adapted to Arctic and sub-Arctic environments surrounding the Arctic Circle. The species occupies a wide range of tundra and boreal ecosystems across Eurasia and North America and is grouped into three major ecotypes: the tundra/barren ground, the forest/woodland, and the high arctic type. Most herds of *Rangifer* migrate between seasonal ranges (Åhman & White 2019). In recent decades, many wild populations have experienced substantial declines, with the majority of monitored populations showing negative trends (Vors & Boyce 2009). The global population of wild *Rangifer* is currently estimated at approximately 2.4 million (Gunn & Russell 2022).

The genus *Rangifer,* species *Rangifer tarandus*, is further divided into at least eight recognized subspecies, and several more are suggested depending on classification (Harding 2022). *Rangifer* are classified as intermediate foragers, and the diet is varied during the summer, leading to rapid body growth and accumulation of body reserves. In contrast, terrestrial lichens dominate the diet during the winter and support survival (Hofmann 1989; Åhman & White 2019). The *Rangifer*-lichen interaction is essential to understanding the ecology of the species and its population dynamics, fluctuation, and management (Skogland 1990; Åhman & White 2019). In Fennoscandia, wild reindeer were originally an important resource for hunting, before humans gradually began domesticating them by herding and managing them. The Eurasian tundra reindeer subspecies *Rangifer tarandus tarandus* is the form managed within reindeer husbandry systems and the basis of Sámi reindeer husbandry across Fennoscandia: Norway, Sweden, and Finland, as well as in parts of Russia, including the Kola Peninsula and Karelia. It is commonly described as semi-domesticated, reflecting its relatively low degree of domestication compared to many other livestock species (Holand *et al.* 2022a). Most of the 3–4 million wild and semi-domesticated reindeer in Eurasia belong to this subspecies (Røed *et al.* 2019). There are populations of wild reindeer in Finland and Norway, but not in Sweden.

1.2 Reindeer husbandry in Fennoscandia

In Fennoscandia, reindeer husbandry represents an important component of the traditional Sámi livelihood and constitutes a central element of Sámi indigenous culture (Holand *et al.* 2022b). Around the seventeenth century, different forms of reindeer pastoralism had emerged, ranging from small-scale and relatively stationary systems in the boreal forest to highly mobile systems involving long-distance seasonal migrations between mountain summer pastures and winter pastures in the boreal landscape. Traditionally, reindeer herding was organised within Sámi herding communities (siida), consisting of several households with shared responsibility for the herds (Bjørklund 2013). Historical, political, and socio-economic processes have since shaped the development of reindeer husbandry. Until the nineteenth century, reindeer herding was relatively intensive, with small herd sizes (around 100 animals per household) and practices such as milking. Since then, reindeer husbandry has gradually shifted towards a more extensive management system, characterized by larger herds and a primary focus on meat production. Hides, antlers, handicrafts (*duodji*), as well as tourism, fishing, and hunting, remain integral to contemporary reindeer pastoralism, not only as sources of income, but as key elements of Sámi culture. (Riseth *et al.* 2016; Holand *et al.* 2022a; Holand *et al.* 2022b).

In reindeer husbandry, each reindeer is individually owned and marked. Although these animals are not wildlife, their degree of tameness varies considerably, and they are rarely considered fully tame (Skarin & Åhman 2014). Today, there are different types of reindeer herding districts (RHD) in Norway, Sweden, and Finland, based on migration patterns and geography (Figure 1a-b). In Sweden, there are 51 RHDs ("Sameby"), of which 33 are mountain, 10 are forest, and 8 are concession herding districts. The Swedish Sámi concession herding districts resemble the forest herding districts, with seasonal migration confined to the boreal forest throughout the year. All districts are further divided into year-round lands and winter lands, the latter being available for grazing between 1 October and 30 April. In contrast, mountain districts are characterized by migration between summer pastures in the mountain areas (year-round lands), typically used from April until late autumn, and winter pastures located in the forest (Figure 1b). According to the Swedish reindeer mark register ("renmärkesregister"), there are approximately 5,000 registered reindeer owners in Sweden, with around 1,000 people working as professional herders. Although one person typically works full-time with reindeer herding, family members and relatives frequently assist with labour-intensive tasks such as calf marking, round-ups, and slaughter (Sametinget 2025).

In both Sweden and Norway, the right to practice reindeer husbandry is an exclusive right of the Sámi people. However, in concession areas, special legislation allows non-Sámi to own reindeer. In Finland, reindeer husbandry is practiced by both Sámi and non-Sámi, although within the Sámi Homeland most reindeer owners are Sámi (Figure 1a). The population, following slaughter and prior to calving, is approximately 240,000 reindeer in Sweden, around 215,000 in Norway, and about 185,000 in Finland (Sametinget 2023; Landbruksdirektoratet 2025; Paliskuntain yhdistys 2025).

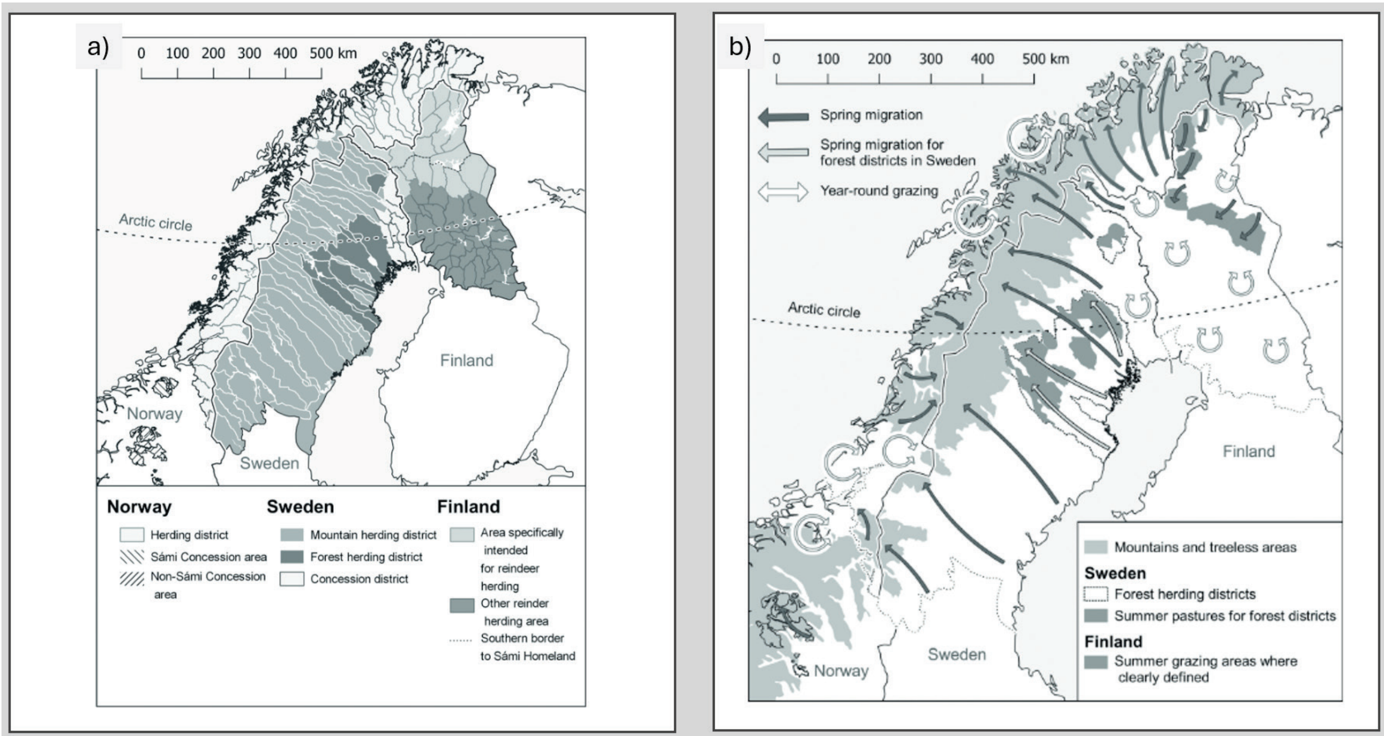

Figure 1. Reindeer herding districts and seasonal pasture use in Fennoscandia. a) Reindeer herding districts in Fennoscandia. Reproduced from Holand et al. (2022a, p. 36). b) The three main forms of seasonal pasture use in Fennoscandia. Reproduced from Holand et al. (2022a, p. 17).

1.3 Climate change and environmental pressures

Reindeer husbandry is an extensive pastoral system in which the herders adapt their herding strategies (e.g., land use) and management according to the reindeer's seasonal movements, behaviours, and needs throughout the year (Skarin *et al.* 2022). This can be reflected in the eight seasons of a herding year, where the reindeer are gathered regularly for calf marking and slaughter (Figure 2).

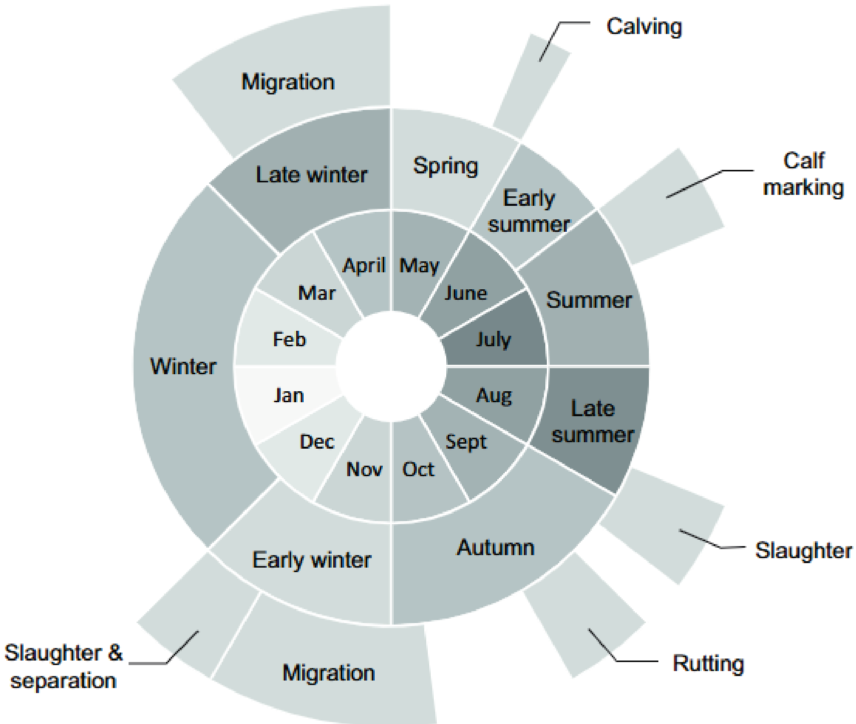

Figure 2. The reindeer herding year has eight seasons, starting with calving in May. The operations marked out may vary between years and districts in Fennoscandia, mainly due to weather. Adapted from Holand et al. (2022, p.18).

In recent decades, reindeer husbandry in Fennoscandia has increasingly been affected by climate change and other environmental pressures. Warmer winters, increased precipitation, and rapid changes in snow conditions have led to more frequent rain-on-snow and freeze–thaw events, resulting in ice-locked pastures that prevent reindeer from accessing their natural forage (Post *et al.* 2019; Moen *et al.* 2022). At the same time, land-use changes such as forestry, infrastructure development, mining, windmill parks, and tourism, together with predation by large carnivores, have reduced the availability of grazing resources (Skarin *et al.* 2018; Hovelsrud 2021; Landauer *et al.* 2021). These combined pressures reduce the flexibility in the use of pasture areas and have contributed to an increased need for supplementary feeding during winter in many reindeer herding regions (Brännlund & Axelsson 2011; Turunen *et al.* 2016; Persson 2018).

1.3.1 Supplementary feeding

Supplementary feeding or winter feeding is practiced when natural pastures are unavailable or grazing conditions are particularly challenging (Figure 3). Feeding may occur directly on natural pastures or by keeping reindeer in enclosures where full feed rations are provided over several weeks or months during winter. Here, supplementary feeding refers to providing additional feed when natural grazing is insufficient; however, it does not constitute a full ration, as the animals still have access to natural pasture. In contrast, winter feeding involves providing the animals with their entire feed ration, typically in enclosures, where access to natural grazing is minimal or absent. Feeding practices vary between countries and regions in Fennoscandia. Emergency feeding to prevent starvation, usually during particularly harsh weather conditions, is practiced in all countries. Prolonged winter feeding is most common in the southern parts of the Finnish reindeer herding area, where it has been practiced since the 1980s, and occurs more sporadically, when needed, in Norway and Sweden. Temporary feeding is widely practiced, particularly during gathering and migration periods, and has been used for decades across all countries. In Norway and Sweden, it has also been applied in affected regions since the Chernobyl disaster in 1986 (Åhman 1999; Wiklund *et al.* 2019). Common feed types include grass silage, hay, lichen, and grain-based compound feed (Turunen *et al.* 2014; Uboni *et al.* 2020; Åhman *et al.* 2022).

Although feeding can be crucial for preventing starvation during difficult winters, as well as increasing early calf survival and calf weight (Rognmo *et al.* 1983), it also presents several challenges. Gathering animals for feeding may induce stress (Rehbinder 1990; Forristal *et al.* 2012; Vetter-Lang *et al.* 2025) and increase animal density, leading to unfavourable hygienic conditions and increased risk for pathogen transmission and development of infectious diseases (Tryland 2012; Tryland *et al.* 2019a; Tryland *et al.* 2019b), as well as feeding-related and metabolic disorders (Åhman *et al.* 2019). This will negatively affect animal health and welfare. Supplementary feeding and winter feeding can also alter reindeer behaviour, influencing tameness, habitat selection, grazing behaviour, and migration patterns. It also represents a considerable financial cost and workload for reindeer herders (Horstkotte *et al.* 2020; Åhman *et al.* 2022; Skarin *et al.* 2024). The influence of multiple actors, including state legislation, in reindeer herding areas must be considered to avoid driving herders towards systemic winter feeding. However, climate-related challenges will persist, and emergency feeding will remain a necessary response during limited or inaccessible grazing (Åhman *et al.* 2022).

Figure 3. Supplementary feeding of reindeer. Photograph by Lotta Berg.

1.3.2 Infectious diseases

Several large disease outbreaks in reindeer populations have been described in historical records. In the eighteenth and nineteenth centuries, severe disease outbreaks affecting large numbers of reindeer in Sweden and Norway were often referred to as "reindeer pest". *Clostridium septicum* and anthrax have been suggested as causes, but these events likely involved different infectious agents, and the specific pathogens responsible remain unknown (Josefsen *et al.* 2019).

Today, reindeer husbandry faces several challenges as described above. Although the overall health status of reindeer is generally regarded as good, the combined effects of stressors may compromise animal health and welfare, because of an increased risk of infectious disease transmission (Tryland 2012; Tryland *et al.* 2019b; Tryland *et al.* 2022). Some of the most important infectious diseases are those affecting the mouth and eyes, including necrobacillosis, contagious ecthyma, and IKC, as described below. These can cause outbreaks affecting large numbers of animals and have severe consequences for animal welfare, result in economic losses, and impact herders' livelihoods.

In addition to these infections, parasites, insect harassments, vector-borne diseases, and feeding-related disorders, among others, are recognised as increasing threats in reindeer husbandry due to climatic and environmental changes and reduced flexibility of natural pastures (Tryland *et al.* 2022).

Necrobacillosis

The same infectious agent may give rise to different clinical manifestations, one example being the bacterium *Fusobacterium (F.) necrophorum*, an obligate anaerobic rod that forms parts of the normal ruminal microbiota of reindeer and is commonly found in the alimentary tract of ruminant species (Aagnes *et al.* 1995). *Fusobacterium necrophorum* is an opportunistic pathogen that can cause digital, oral, and alimentary forms of disease. The digital form is primarily reported in wild reindeer in Norway, whereas the oral form predominates in reindeer husbandry and is associated with feeding. It is also described as one of the most common diseases in corralled reindeer in Finland (Wikström 2014; Laaksonen 2019; Tryland *et al.* 2019b). Necrobacillosis is considered a severe infection in reindeer, and the prognosis is often poor if treatment is not initiated at an early stage, leading to difficulties eating, pain, starvation, and ultimately, death.

Contagious ecthyma and lesions induced by poxviruses

The genus *Parapoxvirus* (PPV), within the family *Poxviridae* and subfamily *Chordopoxvirinae*, causes contagious pustular dermatitis and stomatitis in various host species. This genus currently comprises five recognised species:

Parapoxvirus orf (ORFV), *Parapoxvirus bovinestomatitis* (BPSV), *Parapoxvirus pseudocowpox* (PCPV), *Parapoxvirus sealpox* (SEPV), and *Parapoxvirus reddeerpox* (RDPV) (McInnes *et al.* 2023). In addition, a related, unclassified parapoxvirus has been identified in horses with dermatitis in Finland (Virtanen *et al.* 2023) and recently in horses in Sweden (unpublished data). All PPVs are known or suspected to be zoonotic, although their host ranges vary. ORFV has a broad host range and is distributed worldwide, causing contagious ecthyma (syn. contagious pustular dermatitis, scabby mouth) in sheep and goats and has also been detected in other domestic and wild ruminants, including reindeer, caribou, muskoxen, Alaskan mountain goats, and camelids (Tryland *et al.* 2001; Vikøren *et al.* 2008; Tryland *et al.* 2018; Rziha & Büttner 2021). Bovine papular stomatitis virus and PCPV primarily infect cattle, whereas RDPV has mainly been detected in red deer (*Cervus elaphus*) in New Zealand, Italy, and Germany (Robinson & Mercer 1995; Friederichs *et al.* 2015; Rziha & Büttner 2021).

Sporadic cases in reindeer have been reported in Norway and Sweden since the 1970s and are primarily attributed to ORFV, with sheep and goats considered the likely source of infection, either through direct or indirect contact (e.g. shared pastures, transport, feed troughs, etc.). (Nordkvist 1973; Kummeneje & Krogsrud 1979; Tryland *et al.* 2001).

In Finland, a large outbreak caused by ORFV occurred during the winter of 1992–1993, in which approximately 400 reindeer died, and around 2,800 were affected (Palatsi *et al.* 1993; Büttner *et al.* 1995). Since then, sporadic outbreaks, some more severe than others, have been reported (Hautaniemi *et al.* 2011). More recently, PCPV has also been identified as a causative agent of outbreaks in Finland, with reindeer displaying mild inflammatory lesions and ulcers in the oral cavity (Tikkanen *et al.* 2004; Hautaniemi *et al.* 2010; Hautaniemi *et al.* 2011). Both ORFV and PCPV are zoonotic (Palatsi *et al.* 1993; Büttner *et al.* 1995; Rziha & Büttner 2021).

Clinical signs caused by ORFV include severe crusty, proliferative and cauliflower-like lesions, particularly on the muzzle, lips, and in the oral mucosa. These lesions may predispose affected animals to secondary bacterial infections, such as those caused by *F. necrophorum*, which can impair feed intake and consequently lead to starvation and increased mortality (Kummeneje & Krogsrud 1979; Palatsi *et al.* 1993; Büttner *et al.* 1995; Tryland *et al.* 2001; Tikkanen *et al.* 2004; Tryland *et al.* 2013; Tryland *et al.* 2019b). Supportive therapy and antibiotic treatment of secondary bacterial infections are possible. However, the short-lived humoral immune response observed in sheep is thought to be similar in reindeer, limiting the efficacy of commercial ORFV vaccines, which are not used under natural herding conditions (Tryland *et al.* 2013).

In addition, a cervidpoxvirus (CvPV) was first described in reindeer from Norway and Sweden in September 2023 (Nymo *et al.* 2025). However, similar clinical signs had been reported since at least 2018 from reindeer herders, suggesting that the virus has circulated in the reindeer population for several years. The infection causes clinical signs somewhat resembling those of PPV infections, but with additional manifestations including periocular lesions and crusty lesions on the genitals, nostrils, and ears, often accompanied by lethargy in affected reindeer (Nymo *et al.* 2025). This virus is previously described in various species of *Capreolinae* in USA and Canada, including reindeer from a zoo population originating from Finland (Barker *et al.* 1981; Moerdyk-Schauwecker *et al.* 2009). As for PPV, there are no specific treatments other than supportive care and control of secondary infections.

2. Infectious keratoconjunctivitis

A disease affecting the eyes, known in North Sámi as Čalbmevikke, meaning "eye disease", refers to infectious keratoconjunctivitis (IKC), which has been described in reindeer for more than a century.

The first scientific investigations of keratitis in reindeer were conducted in 1912, where severe outbreaks occurred in Västerbotten and Norrbotten during the autumn of 1909, primarily affecting calves, and again in the spring and autumn of 1910, this time also affecting adults, were described (Bergman 1912). The disease could affect one or both eyes, and initially presented with increased lacrimation (epiphora), leading to discoloration of the fur beneath the eyes, followed by mucopurulent discharge from the medial canthus. As the condition progressed, corneal oedema developed and the cornea acquired a whitish appearance, which could progress to corneal ulceration and panophthalmitis. In response to the outbreaks, herders dispersed the herds and slaughtered the most severely affected animals. According to the herders, the animals clearly suffered from the disease and often had difficulty keeping up with the herd, even when only one eye was affected (Bergman 1912).

Later investigations by Rehbinder with colleagues in the 1970s described IKC in reindeer as a multifactorial disease in which mechanical irritation, environmental conditions, and secondary bacterial infections contribute to the development of keratitis and conjunctivitis (Rehbinder 1977; Rehbinder *et al.* 1978). He further reported that outbreaks were often observed in forest reindeer during summer. Mechanical irritation of the eye was suggested to be associated with factors such as ultraviolet radiation (UV) and dust during herd gatherings for calf marking, while larvae of the nasal bot fly (*Cephenemyia trompe*) may also act as a predisposing factor. Several bacterial species were identified in affected eyes, including *Moraxella* spp., *Neisseria* spp., and *Staphylococcus* spp. in Norway and Sweden from that time (Kummeneje 1976a; Rehbinder & Glatthard 1977; Rehbinder *et al.* 1978). In addition, a severe outbreak occurred among reindeer calves during the winter of 1993–1994 following supplementary feeding and stressful handling in corrals. Mechanical irritation by feed particles and opportunistic bacteria, exacerbated by stress and poor nutritional status, likely contributed to the disease development (Rehbinder & Nilsson 1995). Also in Finland, an outbreak of IKC in a corralled herd during the winter of 1993 was reported, in which *Moraxella ovis* was detected (Oksanen *et al.* 1996).

Recent studies have confirmed that IKC in reindeer remains a multifactorial disease influenced by environmental conditions, management practices, such as gatherings and transport, and infectious microbes. In addition, several more microorganisms have been identified in the eyes of affected reindeer, including the alphaherpesvirus cervid herpesvirus 2 (CvHV2), *Chlamydia* spp., and *Moraxella* spp. (Rockborn *et al.* 1990; Tryland *et al.* 2009; Tryland *et al.* 2016; Tryland *et al.* 2017; Sánchez Romano *et al.* 2018; Sánchez Romano *et al.* 2019). The disease may affect single animals within a herd, but large outbreaks can occur, sometimes involving tens or hundreds of animals, primarily calves and yearlings, as described in previous studies. Such outbreaks are often associated with supplementary feeding and stress, which, in turn, may have increased the prevalence of IKC (Rehbinder & Nilsson 1995; Aschfalk *et al.* 2003; Tryland *et al.* 2009b; Sánchez Romano *et al.* 2019; Tryland *et al.* 2019b).

One or both eyes may be affected, and the disease often begins with epiphora, discoloration of the fur beneath the eyes, commonly referred to as "wet chin", and photophobia. Clinical signs may then rapidly progress to purulent discharge, conjunctivitis, corneal and periorbital oedema, and keratitis. In severe cases, corneal ulceration and rupture, with permanent visual impairment, may occur (Tryland *et al.* 2009; Tryland *et al.* 2017). The disease is painful and poses both an animal welfare concern and an economic burden for herders. Treatment usually consists of cleaning the affected eye and surrounding area with sterile saline, followed by topical antibiotic eye ointment or systemic antibiotics against bacterial infections (Rehbinder & Nilsson 1995; Tryland *et al.* 2009; Tryland *et al.* 2016). More benign outbreaks of IKC have also been reported, characterized by high morbidity but with a large proportion of cases healing spontaneously (Skjenneberg & Slagsvold 1968).

2.1 The eye of the reindeer

2.1.1 Anatomy of the eye

The conjunctiva is a mucous membrane that lines the inner surface of the eyelids, the anterior and posterior aspects of the nictitating membrane (NM), also known as the third eyelid, and the exposed sclera. The bulbar conjunctiva transitions at the limbus into the corneal epithelium, whereas the junction between the palpebral and bulbar conjunctiva forms the conjunctival fornix. Together with the NM, this structure forms the conjunctival sac (Figure 4) (Cook 2021).

The conjunctiva contains lymphatic tissue, glands, nerves, and blood vessels, primarily supplied by branches of ciliary arteries, reflecting its important role in ocular immune defence. It has recently been demonstrated that cattle possess conjunctiva-associated lymphoid tissue (CALT), which forms part of the mucosal immune system and contributes to local immune surveillance by detecting and responding to pathogens at the ocular surface (Kosenda *et al.* 2023).

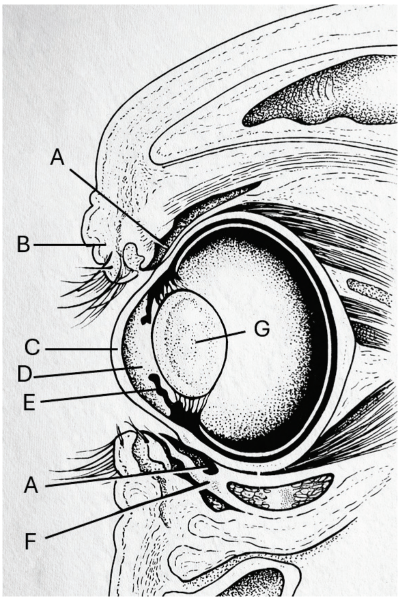

Figure 4. Orbit in cross-section with anterior segment structures indicated; A: conjunctival sac; B: eyelid; C: cornea; D: aqueous chambers containing aqueous humour, E: iris; F: nictitating membrane (third eyelid); G: lens. Adapted from Dyce, Sack, and Wensing (2002, p. 642) and modified using AI.

Openings of the lacrimal gland ducts are located dorsolateral in reindeer, in the conjunctival fornix. In cattle and bison, dorsal lacrimal glands and superior- and deep (Harderian) glands of the NM have been described (Pinard *et al.* 2003). However, some variation has been reported among cervids, with comparative studies indicating that the presence, morphology, and type of glandular tissue of accessory ocular glands may differ between cervid species (Klećkowska-Nawrot *et al.* 2020).

Functionally, the tear film produced by the lacrimal glands contributes to the maintenance of corneal function, whereas the conjunctivae provide both a physical and a physiological barrier against microorganisms and foreign bodies. The conjunctival sac also harbours a resident microbial flora, including potential pathogens (Figure 4) (Cook 2021).

The cornea is a transparent and avascular component of the fibrous tunic of the globe. Its nourishment depends primarily on diffusion from the aqueous humour and the tear film. Corneal thickness varies between species and with age. The cornea is richly innervated with sensory nerves, particularly nociceptors, which contribute to its high sensitivity and play an important protective role. Histologically, the reindeer cornea consists of five layers: a non-keratinized epithelium, Bowman's layer, the stroma, Descemet's membrane, and the endothelium (Winqvist & Rehbinder 1973; Cook 2021). Examinations of the reindeer eye in young calves showed that the corneal epithelium measured approximately 80–100 µm in thickness and consisted of 15–20 cell layers, similar to what has been described in other ungulates (Winqvist & Rehbinder 1973). The stroma constitutes the largest proportion of the corneal thickness (up to 90%). The cornea, together with the tear film, acts as a physical barrier (Cook 2021).

The sclera constitutes the remaining portion of the fibrous tunic of the globe. At the limbus, the cornea merges with the sclera and the bulbar conjunctiva. The sclera is composed primarily of dense connective tissue and contains numerous blood vessels, providing structural support and protection to the globe. The uvea consists of the iris, ciliary body, and choroid. The iris and ciliary body together form the anterior uvea, whereas the choroid constitutes the posterior uvea (Figure 4) (Cook 2021).

2.1.2 Ocular responses to external infectious agents

During IKC, the anterior of the eye is affected, particularly the conjunctiva and/or cornea, as the causative agents are typically pathogens of exogenous origin. In an acute infection, the host immune system, predominantly the innate immune response, plays a central role in controlling and clearing the pathogens. The ability of bacteria to adhere to epithelial cells, interact with host cell receptors, and express specific virulence factors are key determinants of whether infection and subsequent inflammation of the ocular tissues will occur (Gould *et al.* 2021). Alphaherpesviruses such as CvHV2, bovine herpesvirus-1 (BHV-1), and feline herpesvirus-1 (FHV-1) infect and destroy ocular epithelial cells during replication, resulting in keratoconjunctivitis and, in severe cases, corneal ulceration, among other clinical manifestations (Tryland *et al.* 2009; Tryland *et al.* 2017; Gould *et al.* 2021).

Only a limited number of pathogens are capable of causing primary keratitis. In addition to the previously mentioned alphaherpesviruses, piliated, haemolytic strains of *Moraxella bovis* have been shown to induce infectious bovine keratoconjunctivitis (IBK) in cattle as a primary pathogen (Hughes *et al.* 1968; Pedersen *et al.* 1973). In addition, many opportunistic bacteria are capable of establishing infection once the integrity of the corneal epithelium has been compromised (Gould *et al.* 2021). In response to infection or injury, the cornea may exhibit several pathological changes, including oedema, resulting in a characteristic bluish corneal opacity, and vascularization, characterized by the ingrowth of blood vessels from the limbus into the normally avascular cornea. In addition, fibrosis (scar formation) resulting from stromal repair processes and stromal infiltration by inflammatory cells, and stromal malacia ("melting") of the cornea might appear. Melanosis, involving deposition of melanin within corneal tissues, and finally, accumulation of abnormal substances, such as lipid or mineral deposits within the cornea, can also appear. Furthermore, if the inflammation proceeds, corneal ulceration, uveitis, and panophthalmitis can occur, with corneal rupture and further damage to the interior structures of the eye, causing pain and visual impairment (Figure 4) (Maggs 2007; Martins 2021).

In addition to the mechanical protection provided by the outer layers of the eye, the tear film plays a key role in ocular defence. It is a complex fluid containing proteins, lipids, mucins, and electrolytes, as well as antimicrobial factors such as immunoglobulins, mainly IgA, lactoferrin, and enzymes like lysozyme. Together, these components help maintain ocular surface integrity and protect against microbial invasion.

In domestic ruminants, antimicrobial components of the tear film include lactoferrin, which has been detected in cattle and bison, and lysozyme, which has been identified in sheep and goats. The composition of the tear film in cervids, however, remains poorly characterised (Plummer *et al.* 2022).

2.2 Ocular microbial pathogens in reindeer

2.2.1 Cervid herpesvirus 2

Herpesviruses are large enveloped, and linear double-stranded, DNA viruses (genome 125-241 kb), surrounded by an icosahedral nucleocapsid, a protein layer known as tegument, and a typical host lipid membrane envelope with inserted virus-encoded glycoproteins (Gatherer *et al.* 2021). Herpesviruses are widely distributed in nature, and most animal species studied, including humans, harbour one or more herpesvirus species that are generally highly adapted to their host. The herpesvirus family *Orthoherpesviridae* is further divided into three subfamilies: *Alpha*-, *Beta*-, and *Gammaherpesvirinae*. *Alphaherpesvirinae* contains the genus *Varicellovirus*, which includes bovine herpesvirus 1, human herpesvirus 3, and CvHV2, among others. Most alphaherpesviruses are usually restricted to their natural host, replicate rapidly, and lyse infected cells during replication (MacLachlan & Dubovi 2017; Gatherer *et al.* 2021).

In *Rangifer*, herpesviruses from all three subfamilies have been detected, but CvHV2 and *Gammaherpesvirinae* (tentatively named *Rangiferine gammaherpesvirus 1* detected in Norway recently) have been described as important pathogens (Tryland *et al.* 2019a; das Neves *et al.* 2020). Malignant catarrhal fever has been described in one reindeer with signs of IKC in Norway, caused by ovine herpesvirus (Tryland *et al.* 2019a). However, CvHV2 is the primary agent associated with IKC in semi-domesticated reindeer.

As with other herpesviruses, CvHV2 establishes life-long latency in nervous tissue, where it has been detected in the *ganglion trigeminale* in reindeer (das Neves *et al.* 2009c). Serological screenings have revealed that the virus is enzootic in caribou and in the Fennoscandian reindeer herds (das Neves *et al.* 2010; Evans *et al.* 2012; Kautto *et al.* 2012). In addition, previous studies have shown that the virus can cause systemic infection and be transferred across the placenta to the foetus. Experimental studies have shown that CvHV2 can be reactivated upon immunosuppressive corticosteroid treatment, giving rise to lesions in the mucocutaneous junction of the lips and nostrils, and may contribute to abortion and weak-born calves (Rockborn *et al.* 1990; das Neves *et al.* 2009a; das Neves *et al.* 2009c). The virus has also been detected in the lungs of reindeer associated with pneumonia and may possibly pave the way for secondary bacterial infections, such as pasteurellosis (*Mannheimia haemolytica* and *Pasteurella multocida*) in reindeer (Kummeneje 1976b; das Neves *et al.* 2009b).

Pathogenesis of CvHV2 in the eye

Transmission occurs presumably via direct contact with secretions or through aerosols, as described for other ruminant herpesvirus infections (Engels & Ackermann 1996; MacLachlan & Dubovi 2017). During primary infection, the virus infects cells of the mucosal membranes and replicates in the cell lining of the cornea and conjunctiva, causing mucosal and epithelial lesions. Replication and virus shedding take place within hours, followed by lysis of the infected cell. Experimental studies have shown that the disease progression is rapid, with severe clinical signs of periorbital oedema, conjunctivitis, and purulent discharge after 3-5 days post-inoculation. Upon inspection on day 5, corneal oedema was also present (das Neves *et al.* 2009b; Tryland *et al.* 2017).

Histopathological investigations revealed similar severe pathological findings in the cornea, conjunctiva, and lacrimal glands, such as oedema, loss of epithelial cells, infiltration of neutrophils and mononuclear cells, hyperemia, focal necrosis, and loss of epithelium (Rockborn *et al.* 1990; Rehbinder & Nilsson 1995; Tryland *et al.* 2009; Sánchez Romano *et al.* 2020).

Antibodies typically seem to develop around 6-10 days p.i., thus too late in order to protect against disease (das Neves *et al.* 2009a; Tryland *et al.* 2017). Serological studies also show a typical high seroprevalence in adults compared to calves (das Neves *et al.* 2009d; Kautto *et al.* 2012). This is in line with reports that IKC outbreaks primarily affect naïve calves and young reindeer under stressful events, such as gatherings, transportation, or being placed in a new environment (das Neves *et al.* 2009a; Tryland *et al.* 2009). The mucosal lesions, initially caused by CvHV2, may rapidly be colonised by pathogenic or opportunistic bacteria. Bacteriological investigations have revealed a variety of bacteria, such as *Moraxella* (*Mor.*) *bovoculi* and *Chlamydia* (*C.*) *pecorum* in affected eyes of reindeer. However, no firm conclusion about their role in the development of IKC has been established (Sánchez Romano *et al.* 2018; Sánchez Romano *et al.* 2019).

2.2.2 Bacteria associated with IKC

Given the multifactorial nature of IKC in reindeer and the frequent detection of multiple microorganisms in affected eyes, particular attention has been directed towards the role of bacterial agents. Several bacterial species have been isolated in association with IKC in reindeer, although their relative importance in disease pathogenesis remains incompletely understood. The latest bacterial discovery associated with IKC in reindeer is *Chlamydia* spp., also detected in various ruminants and wild cervids, such as sheep, goat, and red deer. Microorganisms associated with IKC in ruminants are summarized in Table 1.

Table 1. Microorganisms identified from domestic and wild ruminants with clinical signs of infectious keratoconjunctivitis.

Species	**Pathogen involved**	**Reference**
Cattle (*Bos taurus*)	*Moraxella bovis*	(Postma *et al.* 2008; Angelos 2015; Loy *et al.* 2021b)
	Moraxella bovoculi	(Angelos 2010; Galvão & Angelos 2010; Loy *et al.* 2021b)
	Mesomycoplasma bovoculi[1]	(Loy *et al.* 2021a; Schnee *et al.* 2015)
	Listeria monocytogenes	(Erdogan 2010; Läkemedelsverket, 2025)
Riverine buffalo (*Bubalus bubali*)	*Chlamydia psittaci*	(Osman *et al.* 2013)
Alpine ibex (*Capra ibex*)	*Mesomycoplasma conjunctivae*[1]	(Giacometti *et al.* 2002; Gelormini *et al.* 2017)
Bighorn sheep (*Ovis canadensis*)	*Chlamydia* spp.	(Meagher *et al.* 1992)
	Mesomycoplasma conjunctivae	(Jansen *et al.* 2006)
Chamois (*Rupicapra rupicapra*)	*Mesomycoplasma conjunctivae*[1]	(Marco *et al.* 2009; Giacometti *et al.* 2002)
Domestic goat (*Capra aegagrus hircus*)	*Chlamydia* spp.	(Osman *et al.* 2013; Gupta *et al.* 2015)
	Mesomycoplasma conjunctivae[1]	(Hsu *et al.* 2017)

Species	Pathogen involved	Reference
Domestic sheep (*Ovis aries*)	*Chlamydia* spp.	(Egwu *et al.* 1989; Gupta *et al.* 2015; Osman *et al.* 2013)
	Mesomycoplasma conjunctivae[1]	(Åkerstedt and Hofshagen, 2004; Janovsky *et al.* 2001)
	Moraxella ovis	(Åkerstedt and Hofshagen, 2004)
	Listeria monocytogenes	(Erdogan 2010; Läkemedelsverkat 2025)
European mouflon (*Ovis gmelini musimon*)	*Mesomycoplasma conjunctivae*[1]	(Terrier 1998)
Iberian ibex (*Capra pyrenaica*)	*Mesomycoplasma conjunctivae*[1]	(Fernández-Aguilar *et al.* 2017a)
Mountain goat (*Oreamnos americanus*)	*Mesomycoplasma conjunctivae*[1]	(Jansen *et al.* 2006)
Moose (*Alces alces*)	*Moraxella bovis*	(Kuiken *et al.* 1997)
	Moraxella ovis	(Dubay *et al.* 2000)
Mule deer (*Odocoileus hemionys*)	*Moraxella ovis*	(Dubay *et al.* 2000)
	Chlamydia spp.	(Taylor *et al.* 1996)
	Yersinia pestis	(Edmunds *et al.* 2008)
	Alphaherpesvirus	(Muñoz Gutiérrez *et al.* 2018)
Red deer (*Cervus elaphus*)	Cervid herpesvirus 1	(Squires *et al.* 2012)
	Chlamydia psittaci	(Zaragoza *et al.* 1998)
Reindeer (*Rangifer tarandus*)	Cervid herpesvirus 2	(Sánchez Romano *et al.* 2018; Tryland *et al.* 2009)
	Chlamydia pecorum	(Sánchez Romano *et al.*2019)
	Moraxella spp.	(Oksanen *et al.* 1996; Sánchez Romano *et al.* 2018)

Adapted from Sánchez Romano (2018, p.23). [1]Species names follow current taxonomy.

Chlamydia spp.

Chlamydiae are Gram-negative obligate intracellular bacteria that infect both humans and animals. The family *Chlamydiaceae* currently comprises a single genus, *Chlamydia*, which includes several species (Borel & Greub 2025). The primary habitat is the gastrointestinal tract, and chlamydia can establish prolonged, persistent infections, which are typically asymptomatic. Despite this, chlamydial infections are associated with a wide range of diseases across different host species, including conjunctivitis, arthritis, abortion, enteritis, pneumonia, urethritis, and encephalomyelitis (Quinn 2011; Sachse & Borel 2020).

Chlamydial species are typically linked to specific clinical manifestations depending on the host. For example, *Chlamydia felis* is a well-known cause of conjunctivitis in cats and is one of several chlamydial species with zoonotic potential (Quinn 2011; Sachse & Borel 2020). Overall, infections caused by *Chlamydia* spp. can result in clinical syndromes of varying severity, suggesting that both strain-specific characteristics and host-related factors play important roles in determining disease outcome. This has been demonstrated for *C. pecorum* in cattle (Jelocnik *et al.* 2014; Hagenbuch *et al.* 2024).

Chlamydia pecorum has a broad host range, including livestock and wild ruminants, with clinical presentation varying between host species (Sachse & Borel 2020). In koalas, *C. pecorum* has been described as a cause of keratoconjunctivitis as well as genital infections (Kayesh *et al.* 2024). Furthermore, *Chlamydia* spp. have been reported as a primary cause of IKC outbreaks in bighorn sheep (*Ovis canadensis*) in North America (Table 1) (Meagher *et al.* 1992).

In semi-domesticated reindeer, chlamydia exposure has previously been demonstrated through serological screenings in Sweden and Finland (Neuvonen 1976; Rehbinder *et al.* 1986). More recently, chlamydial DNA has been detected in ocular swabs, although without any significant association with clinical signs of IKC (Sánchez Romano *et al.* 2018). However, during an IKC outbreak in semi-domesticated reindeer in Sweden, *C. pecorum* was identified as a likely causative pathogen (Table 1) (Sánchez Romano *et al.* 2019). Clinical findings included epiphora, follicular conjunctivitis, purulent ocular discharge, and corneal oedema. Notably, the outbreak coincided with herding activities during the winter months of 2016/2017 (Sánchez Romano *et al.* 2019).

These findings suggest that *C. pecorum* may be widespread in reindeer populations across Fennoscandia and could play a role in the development of IKC. However, its pathogenic potential and genetic characteristics remain poorly understood and warrant further investigations. *Chlamydia suis*, a pathogen of pigs, is the only known chlamydial species that can maintain stable tetracycline resistance at present (Sachse & Borel 2020).

Mycoplasma spp.

Mycoplasma species are small bacteria that lack a cell wall. Several species are described as pathogens, and others exist as commensals or opportunists. Several *Mycoplasma* species are important pathogens in cattle, including *Mycoplasmopsis bovis*. In sheep and goat, *Mes. ovipneumoniae* is described as a respiratory pathogen (Quinn 2011). Furthermore, *Mes. ovipneumoniae* seems to be emerging in wild *Caprinae* in North America and has also been detected in caribou. The bacterium has also been reported during outbreaks of severe pneumonia in muskoxen in Norway, where contact with domestic sheep flocks was considered a likely source of infection. (Handeland *et al.* 2014; Highland *et al.* 2018; Maksimović *et al.* 2022).

Mesomycoplasma (*Mes.*) *conjunctivae*, are an important pathogen of the eye, causing IKC in sheep and goats as well as in wild cervids (Table 1) (Giacometti *et al.* 2002; Åkerstedt & Hofshagen 2004; Boileau & Gilmour 2012; Gupta *et al.* 2015). In reindeer, *Mes. conjunctivae* was detected in 2 out of 197 reindeer in a recent study based on conjunctival samples collected from reindeer in Sweden, Norway, and Finland (Sánchez Romano *et al.* 2018). Also, *Mes. bovoculi* is associated with IKC in cattle (Schnee 2015; Loy *et al.* 2021a). Ocular co-occurrence of *Mycoplasma* species with other pathogens has been reported in several host species. For example, co-detections with *Chlamydia* spp. have been described in chamois, sheep, and goats (Holzwarth *et al.* 2011; Boileau & Gilmour 2012; Arnal *et al.* 2013; Fernández-Aguilar *et al.* 2017b). *Mesomycoplasma bovoculi* has been described as highly prevalent in clinically normal eyes in calves, suggesting it can establish asymptomatic infections (Barber *et al.* 1986). However, later studies have indicated that, in association with *Moraxella* spp., *Mes. bovoculi* may act as a potentiating factor in the development of IBK (Schnee 2015; Loy *et al.* 2021b; Maartens *et al.* 2025). These findings suggest that *Mycoplasma* spp. may act synergistically or opportunistically with other pathogens in the development of IKC.

Moraxella spp. and *Listeria monocytogenes*

Moraxella are gram-negative rods or cocci and are common in the upper respiratory and ocular microbiome in cattle (Quinn 2011; Cullen *et al.* 2017). Three species within the genus *Moraxella* have been studied in relation to

IBK: *Moraxella bovis, Mor. bovoculi*, and *Mor. ovis*. However, overlap between *Mor. bovoculi* and *Mor. ovis* has been reported, since *Mor. bovoculi* was recognized as a separate species in 2007 (Angelos *et al.* 2007; Angelos 2010). In cattle, extensive research has been conducted, with current studies focusing on different strains of *Mor. bovoculi* and *Mor. bovis* and their virulence factors, as both species appear to play important roles in the development of IBK (Loy *et al.* 2021b).

Moraxella spp. has previously been detected in semi-domesticated reindeer with clinical signs of IKC in Fennoscandia and has more recently been characterized as *Mor. bovoculi*. (Tryland *et al.* 2009; Sánchez Romano *et al.* 2018; Laaksonen 2019). However, in a challenge study conducted in Norway, the bacterium alone failed to induce clinical signs of IKC (Tryland *et al.* 2017). Since strains of *Mor. bovoculi* appear to exhibit pathogenic properties in cattle (Loy *et al.* 2021b), further investigations are needed to determine whether pathogenic strains of *Mor. bovoculi* also occur in reindeer populations.

Based on aerobic cultures performed at SVA in Uppsala, a recent compilation identified *Moraxella* spp. and *L. monocytogenes* as the most commonly detected bacteria in samples from cattle and sheep in Sweden (Läkemedelsverket 2025). Keratoconjunctivitis caused by *L. monocytogenes* has been associated with silage feeding and is commonly referred to as "silage eye" in cattle and sheep (Erdogan 2010). It has also been reported as a cause of IKC in reindeer in Finland, particularly in association with feeding of poor-quality silage (Laaksonen 2016).

Normal ocular flora, other bacteria, and commensals

The normal ocular surface usually consists of a wide range of both commensals and transient bacterial and fungal species from the environment. Bacteria can be cultured from the conjunctiva in approximately 87% of clinically normal cows and 40% of normal sheep (Gould *et al.* 2021), reflecting the presence of a normal conjunctival microbiota. Examples of bacteria isolated from normal eyes in cattle and sheep include *Staphylococcus* spp., *Streptococcus* spp., *Corynebacterium* spp., *Moraxella* spp., *Mycoplasma* spp., and *Escherichia (E.) coli*, among others (Gould, 2021). The compositions of the ocular flora vary depending on host species, age, geography, climate, season, local environment, and the sampling, culture, and diagnostic methods applied. The normal flora also plays an important role in maintaining ocular health by competing with pathogenic species for colonization of the ocular surface. However, immunosuppression, epithelial damage to the ocular surface, or co-infection with other pathogens may allow otherwise non-pathogenic bacteria to become opportunistic pathogens and cause disease. In these situations, pathogens may act cumulatively or synergistically, contributing to the development of disease (Gould *et al.* 2021).

2.3 Diagnostics and treatment of keratoconjunctivitis

The semi-domesticated nature of reindeer, combined with extensive husbandry practices, makes thorough clinical examinations challenging, and detailed ophthalmological assessments are often not feasible. In addition, the use of fluorescein staining is restricted due to maximum residue level (MRL) regulations, further complicating the evaluation of ocular lesions.

Conjunctival sampling can be performed in ruminants with signs of IKC for both bacteriological culture and PCR-based diagnostics to establish the pathogens involved. PCR is particularly valuable for detecting viral pathogens and bacteria that are difficult to culture, such as *Mycoplasma* spp. and *Chlamydia* spp. Furthermore, real-time PCR (qPCR) enables estimation of the pathogen load in the sample. However, antimicrobial susceptibility testing *in vitro* can only be performed following bacteriological culture, for example, by determining the minimum inhibitory concentration (MIC) (Gould *et al.* 2021). Furthermore, specific PCR assays, for example, targeting toxin genes in *Mor. bovoculi* and *Mor. bovis*, appear to increase co-detection compared with culture alone. Culture results may thus be false negatives, for instance, due to contamination or the presence of multiple pathogens (Loy *et al.* 2021b).

Serology, for example through the detection of antibodies against CvHV2 in the context of IKC outbreaks, may also be applied. However, neither PCR nor serology alone confirms causality to clinical signs or treatment failure, as positive results may reflect prior exposure, subclinical infection, or asymptomatic carriage rather than the cause of active disease (Gould *et al.* 2021). Cytological examination of the conjunctiva or cornea can also be performed in field laboratories, allowing Gram staining and characterisation of cellular infiltrates (Gould *et al.* 2021).

More advanced molecular techniques, such as sequencing and metagenomics, may also be applied and are increasingly contributing to research in the field, although they are rarely used in clinical practice.

2.3.1 Treatment strategies

The management of IKC in a reindeer herd depends on several factors, including the severity of the disease, the number of affected animals, and the herder's ability and willingness to invest time and resources in treatment and care.

In a survey of 57 reindeer herders conducted in Norway and Sweden in 2010, slaughter was the measure most commonly initiated when IKC was observed, but none of the herders reported isolating affected animals from the rest of the herd. In addition, veterinarians were rarely consulted for medical treatment of IKC. When treatment was administered, local therapy with ophthalmic ointment with antibiotics was the most commonly used approach (Tryland *et al.* 2016). However, as IKC often is a contagious disease, it is recommended that affected animals are separated and isolated from the rest of the herd. In addition, local treatment can only be performed using off-label drugs, as no ophthalmic preparations with antibiotics are currently licensed for use in reindeer in Sweden. In fact, reindeer health presents a challenge for today's veterinarians in Fennoscandia. There are only a few drugs registered for reindeer, and the species represents only a small part of veterinary practice; clinical experience may therefore take years to acquire. In addition, veterinary education contains limited coverage of reindeer health and diseases. This leads to new generations of veterinarians with limited knowledge and understanding of reindeer health, herding systems, population dynamics, and welfare needs (Baker *et al.* 2022; Tryland 2022).

When selecting antimicrobial treatment, the choice of antibiotic should not only be based on the susceptibility of the causative bacterium but also on factors such as the availability of approved preparations, the suitability of the route of administration, and appropriate pharmacokinetic and pharmacodynamic properties. For example, systemically administered penicillin has limited ocular penetration and might only reach therapeutic concentrations if corneal neovascularisation has occurred or the ocular inflammation has affected the blood-ocular barriers (Punch *et al.* 1985; Gelatt & Plummer 2017). In addition, compliance with MRLs must be ensured, as these must be established for drugs used in food-producing animals such as reindeer.

In addition to antibiotics, administration of non-steroidal anti-inflammatory drugs (NSAIDs) may be beneficial, as IKC is a painful disease and uveitis may be present. Topical treatment with atropine may also be used. However, local treatment is only feasible in a limited number of relatively tame animals with mild clinical signs, as repeated administration requires handling without causing excessive stress (Rehbinder 1990; Vetter-Lang *et al.* 2025). The feasibility of such treatment depends on several factors, including season, age, and access to enclosures or other handling facilities.

Preventive measures are therefore important for disease control. These include quarantine of new animals before entry into established enclosures, strict isolation or slaughter of animals showing clinical signs, and maintaining animals in good body condition. Furthermore, stress associated with herding, gathering, handling, and transport should be minimised, as these factors may act as stressors that can trigger disease outbreaks, such as IKC (Tryland *et. al.* 2019). Currently, no vaccine is available against alphaherpesvirus in reindeer.

2.4 Reindeer welfare

Animal welfare can be defined in several ways depending on the conceptual framework applied. According to the World Organisation for Animal Health (WOAH), animal welfare means ‘the physical and mental state of an animal in relation to the conditions in which it lives and dies (WOAH, 2023). Good welfare implies that the animal is healthy, comfortable, well nourished, safe, and able to express natural behaviour, without experiencing pain, fear, or distress, referred to as the “Five Freedoms” (FAWC 2009). More recently, the Five Domains model has been developed to further incorporate the animal’s mental state and both negative and positive welfare experiences (Mellor 2016).

In Sweden, reindeer welfare is regulated by the Swedish Animal Welfare Act (SFS 2018:1192) and the Animal Welfare Ordinance (SFS 2019:66). The Act stipulates that animals must be treated well and protected from unnecessary suffering. Furthermore, there are specific rules related to reindeer during transport (SJVFS 2019:7, L5) and at slaughter (SJVFS

2019:8, L22), as well as national guidelines on helicopter herding (SJVFS 2008:68, L 9).

Reindeer, being production animals, are also covered by the animal welfare regulations in the EU related to transport and slaughter, respectively. Animal welfare regulations largely focus on the measures taken by humans to promote good animal welfare and to minimize the risk of animal welfare problems. These are often assessed through resource- or environment-based (i.e., input-based) indicators (Scientific Council for Animal Welfare (SLU) 2020). The aim of the legislation is therefore not to ensure an optimal level of welfare, but to provide animals with conditions that enable at least a minimum acceptable level of welfare.

Assessing legislative compliance based on a rather limited set of input-based parameters can still be done, but in addition to this, there is also a need for outcome-based (often animal-based) indicators. However, there is very little scientific work on animal-based assessment of reindeer welfare, and there are currently no developed species-specific guidelines for assessing reindeer welfare, although general indicators such as cleanliness and body condition can nevertheless be used.

Assessing welfare in semi-domesticated reindeer can be challenging due to the unique characteristics of reindeer husbandry systems, and therefore, specific "reindeer-based" indicators and checklists or manuals for how to assess reindeer welfare would be useful (Svensson 2021), both for official animal welfare inspectors and official veterinarians at slaughterhouses, as well as for potential future voluntary animal welfare certification schemes for reindeer owners.

2.4.1 Challenges in reindeer welfare

Understanding the significance of stress is important for safeguarding the welfare and health of reindeer. Reindeer are highly sensitive to stress, and various measures associated with herding and handling may induce both physiological and behavioural stress responses (Rehbinder 1990; Lian *et al.* 2019; Trondrud *et al.* 2022; Vetter-Lang *et al.* 2025). For example, stress-related conditions such as abomasal haemorrhages and muscular degeneration have been described in reindeer (Rehbinder 1990). Repeated handling and gathering of animals that are relatively unused to human presence may therefore represent a considerable challenge in reindeer husbandry (Rehbinder 1990; Trondrud *et al.* 2022; Vetter-Lang *et al.* 2025).

At the same time, reindeer are exposed to a range of environmental and anthropogenic stressors in their habitat. These include climate change and extreme weather events affecting grazing conditions, reduced pasture availability due to competing land use, such as disturbances from infrastructure development, mining, wind power, tourism, dogs, and other human activities, as well as risks related to predation and traffic accidents. (Horstkotte *et al.* 2022; Moen *et al.* 2022). Additional welfare concerns may arise from infectious diseases, parasites, insect harassment, and the limited possibility for daily supervision and follow-up on individual animals. Other challenges are pain management during castration of males (Nurmi *et al.* 2022; Nurmi *et al.* 2025), and issues associated with transport and slaughter (Rockström *et al.* 2026). Altogether, this illustrates that reindeer health and welfare are influenced by the cumulative effects of multiple factors acting at different spatial and temporal scales (Berg 2026).

However, semi-domesticated reindeer also benefit from several positive welfare aspects associated with extensive husbandry systems. Reindeer generally roam freely over large areas, allowing them to express natural behaviours such as migration, grazing, and social herd dynamics. They typically have access to natural forage, experience low stocking densities, and often live in relatively stable social groups. These conditions may reduce infection pressure and the risk of injuries that are sometimes associated with more intensive livestock systems (Berg 2026).

Consequently, the health and welfare of reindeer reflect a complex balance between natural living conditions and the various environmental, management-related, and societal pressures affecting the modern reindeer husbandry. Nevertheless, stress and management-related factors still play an important role in the occurrence and severity of infectious diseases, in particular the infectious eye diseases, in reindeer. Diseases that will, in turn, affect the welfare of the reindeer negatively.

2.4.2 The concept of One Welfare

The concept of One Welfare, within the broader One Health framework, recognises the interconnections between animal health and welfare, human wellbeing, and the environment, and aims to improve both human and animal wellbeing (Pinillos *et al.* 2016; Tarazona *et al.* 2019). The dynamics of reindeer health and welfare illustrate how challenges to animal health are embedded within broader socio-ecological systems, where animal welfare, management practices, and human well-being are closely interconnected (Figure 5).

Since IKC causes pain, suffering, and functional impairment in individual animals and may lead to outbreaks affecting many reindeer, which are often free-ranging and unattended, it constitutes a significant animal welfare concern. The disease also affects herders' working conditions, economy, practices, and well-being (Rehbinder & Nilsson 1995; Furberg *et al.* 2011; Tryland *et al.* 2016; Ocobock *et al.* 2023; Horstkotte *et al.* 2024). Therefore, the One Welfare approach could be a way to integrate reindeer health and welfare into a broader socio-ecological context, recognising the links between animal health and welfare, human well-being, and the environment (Pinillos *et al.* 2016; Tarazona *et al.* 2019). Consequently, improving animal health and welfare through preventive management strategies and herding practices adapted to changing environmental conditions is central to maintaining a sustainable reindeer husbandry system.

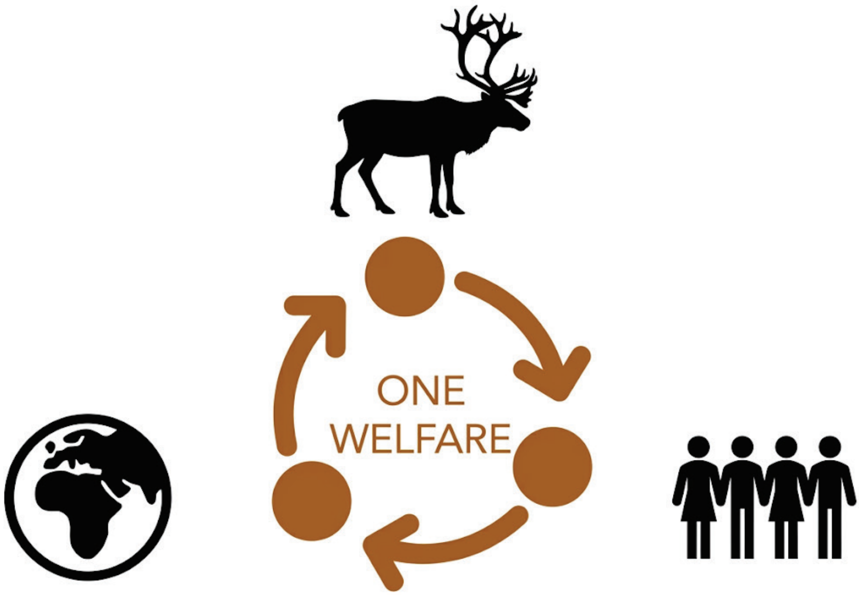

Figure 5. The concept of One Welfare describes the interrelationships between animal health and welfare, human well-being, and the environment.

3. Aims

The overall aim of this thesis was to investigate the microorganisms and risk factors associated with infectious keratoconjunctivitis (IKC) in reindeer, as well as the herders' perceptions of the disease. The specific objectives were to:

- Obtain an overview of the current presence of IKC in semi-domesticated reindeer in Norway and Sweden, and the potential association between IKC and feeding. We hypothesized that the occurrence of IKC is associated with feeding practices (Paper I).

- Investigate the occurrence of pathogens associated with IKC in conjunctival swabs from reindeer with and without clinical signs, and to evaluate associations between pathogen detection, clinical signs, and potential covariates, including age, region, and season (Paper II).

- Document the clinical signs associated with RDPV and to genetically characterize the virus at the full-genome level to enhance the understanding of its origin and potential implications for reindeer health (Paper III).

- Explore reindeer herders' experiences and perceptions of ocular disease (OD), including IKC, and its impacts on both reindeer and herders within a One Welfare perspective. Particular attention was given to how OD is understood, managed, and experienced in practice to identify needs for improved preparedness and prevention of disease spread (Paper IV).

4. Materials and methods

This section gives a brief overview of the study designs and main analytical approaches used in the papers included in the thesis. Detailed descriptions of the methodologies applied in this thesis are provided in the respective papers (I–IV).

4.1 Study populations

All RHDs in the Swedish part of Sápmi (n = 51) were invited to participate in Papers I and II. In Paper I, all RHDs in Norway (n = 82) were also invited. In Paper III, five reindeer from one RHD in Norrbotten County were included, and in Paper IV, eight herders from different RHDs were included. An overview of the sampling process and the number of RHDs included in each paper is presented in Figure 6.

4.2 Sampling of reindeer

For Paper II, conjunctival swab samples, primarily consisting of eSwab™ (Copan Diagnostics, Italy), were collected from semi-domesticated reindeer in Sweden between December 2019 and April 2025. Sampling was conducted mainly in herds displaying clinical signs of IKC, as well as from clinically unaffected animals within the same herds.

Samples were collected by veterinarians and reindeer herders using a standardised referral form to record data on animal characteristics, clinical signs, herd conditions, and recent management events.

The transport time from sampling to laboratory analysis was relatively long (commonly 2–5 days), which may have permitted overgrowth of mixed flora or reduced the viability of certain bacteria before cultivation. In addition, samples were not transported under chilled conditions and were at risk of freezing. These factors may have influenced the results of primary bacterial culture and, potentially, PCR analyses.

For Paper III, animals with clinical signs consistent with poxvirus infection were investigated through targeted sampling of skin, periocular, and oral lesions, including tissue samples from the spleen and a submandibular lymph node of one euthanized reindeer.

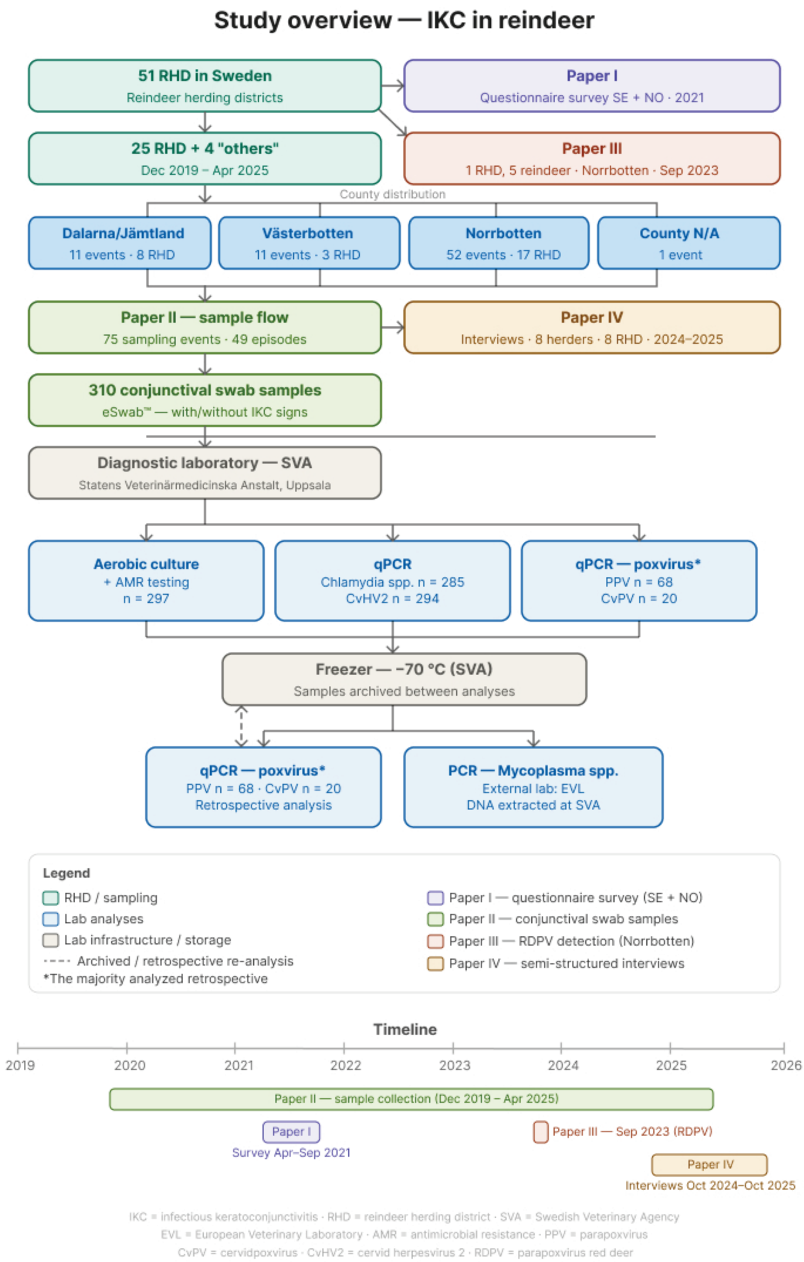

Figure 6. Flowchart of conjunctival swab sampling and analysis, integrated with an overview of the scientific papers and the number of reindeer herding districts (RHDs), including four “other owners”, sampling events, and episodes (i.e., aggregated events from the same time period within an RHD/owner) represented in each paper.

4.3 Laboratory diagnostic methods

In the study presented in Paper II, conjunctival samples were analysed at SVA using qPCR for the detection of alphaherpesviruses. The assay was originally developed to detect bovine herpesvirus 1 (BHV-1) (Wang *et al.* 2007). To confirm the identity of the detected virus, two positive samples were subjected to sequencing, verifying the presence of CvHV2. Given the host specificity of herpesviruses, the remaining positive samples were therefore assumed to represent CvHV2.

Detection of *Chlamydia* spp. was performed using qPCR (Everett *et al.* 1999). Ten positive samples were subsequently analysed by 16S rRNA gene sequencing, of which four were confirmed and identified as *C. pecorum*.

In parallel, routine bacteriological culture and antimicrobial susceptibility testing were performed as part of a standard diagnostic panel for ocular samples from reindeer (‘paket renöga’). In addition, a subset of samples was analysed for the detection of PPV and CvPV using different qPCR assays (Nitsche *et al.* 2006; Nymo *et al.* 2025) primarily retrospectively during 2024–2025, although a smaller number of samples were analysed upon specific request (Figure 6).

Detection of *Mycoplasma* spp. was performed in retrospect (October 2025) using conventional PCR at the European Veterinary Laboratory (EVL), followed by species-specific PCR assays for further characterisation of detected *Mycoplasma* species.

For Paper III, samples were analysed using qPCR for PPV and CvPV, and one selected sample was subjected to next-generation sequencing and phylogenetic analysis to characterise viral genomes and assess genetic relationships. Histopathological examination was performed on tissues from one severely affected reindeer.

4.4 Questionnaire, interviews, and analysis

The study presented in Paper I was conducted as a questionnaire survey among reindeer herders in Norway and Sweden during April-September 2021. A digital questionnaire was distributed via herding district representatives, Sámi organisations, and online platforms. The questionnaire collected information on herd characteristics, occurrence and clinical signs of IKC, management practices, and feeding strategies. However, the relatively small number of respondents and the low response rate may limit the geographical representativeness of the findings. In addition, participation was voluntary, which may have introduced selection bias, as herders with a particular interest in feeding practices and/or reindeer health may have been more likely to respond. The retrospective nature of the questionnaire, covering a period of 5–10 years, also introduces a risk of recall bias. These factors should be considered when interpreting the findings.

In Paper IV, semi-structured, in-depth interviews were conducted with reindeer herders experienced with ocular disease, including IKC, to explore their experiences and management of such outbreaks. Ocular disease is used here broadly to reflect the herders' perspective, where any ocular or periocular signs may be perceived as indicative of infectious eye disease, and is not restricted to IKC as a single diagnosis. Three of the eight informants participating in the interview study were recognised by their local communities as key persons in reindeer health, frequently consulted for advice on sick reindeer, thereby strengthening the study through the inclusion of experienced and information-rich participants.

Interviews were carried out digitally in Swedish, audio-recorded, and transcribed verbatim. Data were analysed using thematic analysis following Braun and Clarke (2021). An inductive coding approach was initially applied to identify patterns emerging from the data. These codes were then systematically grouped into subthemes and organised into broader overarching themes. The analysis was iterative, involving repeated reading and refinement of both codes and themes. During this process, it became evident that herders frequently expressed emotional engagement and reflected on how experiences of treatment and management shape future decisions and practices, as well as potential needs for improvement. The One Welfare concept (Pinillos *et al.* 2016) was therefore adopted as an analytical lens. It was used to examine how herders describe and experience OD outbreaks, and how it impacts on animal health and welfare, together with physical and social conditions, relate to their well-being during and after such events. Particular attention was given to perceived consequences, management responses, and needs for improved preparedness and prevention. Qualitative data management software (NVivo) was used to support the organisation and analysis of the data, and illustrative quotations were selected to represent key aspects of the context and identified themes. The aim was not to obtain a representative sample of perceptions, but rather to explore the diversity of perceptions within this group of herders.

Therefore, the findings are specific to the participating herders, the researchers, and the analytical process. However, similar concepts, meanings, and experiences may also be recognisable in other contexts within reindeer husbandry.

4.5 Statistical analysis

In Papers I and II, data were summarised descriptively and analysed using standard statistical methods, including chi-square and Fisher's exact tests. In Paper II, sampling events were grouped into episodes based on time and herd origin to better reflect disease occurrence within herds. However, population dynamics within and between RHDs were unknown, which may have influenced the results. In Paper I, associations between IKC outbreaks and feeding practices were further assessed using mixed-effects logistic regression models, accounting for repeated observations within herds over time.

4.6 Animal ethics approval and consent to participate

Ethical approval for animal use was not required, as all samples (Papers II and III) were collected during routine veterinary diagnostics and treatment, with no additional handling of animals. Sampling was conducted with prior informed consent from animal owners

For studies involving human participants, approval for Paper I was obtained from the Norwegian Social Science Data Services (No. 457339). In Sweden, no formal approval was required, as the survey did not involve sensitive personal data. Paper IV was approved by the Swedish Ethical Review Authority (Dnr 2024-04033-01); participants provided written informed consent, were informed about the study aims, and were assured pseudonymisation.

4.7 Outreach and communication activities

Throughout the project, a participatory approach was applied, with planning and study design developed in collaboration with stakeholders, including the Sámiid Riikkasearvi (Sámi Reindeer Association, SSR) and professionals in reindeer health, such as Farm and Animal Health, as well as with colleagues in Norway.

The project was continuously communicated and discussed through a range of activities, including webinars, stakeholder meetings, and seminars organised in collaboration with SSR, Farm and Animal Health, and the Swedish Board of Agriculture's District Veterinary Organisation. Additional dissemination channels included blog posts on the SVA website (e.g., 'Renögabloggen'), engagement in the Nordic TARANDUS research network, and outreach through media appearances.

These activities facilitated ongoing knowledge exchange between researchers, reindeer herders, veterinarians, and other stakeholders, and contributed to building trust in both the research and the institutions involved. They also supported the participatory approach throughout the data collection process by increasing project visibility, enabling dialogue around ongoing work, thereby strengthening the relevance and reliability of the research, and facilitating the collection of biological samples, questionnaire responses, and recruitment of interview participants.

5. Results and discussion

This chapter provides an overview and a general discussion of the results, as well as comments on the methods used. More detailed discussions are presented in the individual papers.

5.1 Occurrence of infectious keratoconjunctivitis and associated clinical signs

The questionnaire study (Paper I) revealed that IKC was commonly observed by herders in both Norway and Sweden, reported by 51 (67%) of the respondents, consistent with findings from a similar survey conducted ten years earlier (Tryland *et al.* 2016). The most frequently reported clinical sign was epiphora, described as "wet cheeks", followed by keratitis and conjunctivitis, whereas more severe manifestations, such as chemosis and purulent discharge, were reported less frequently (Paper I). Similar patterns were observed in the referral forms submitted with conjunctival swab samples (Paper II). However, purulent discharge was reported as frequently as conjunctivitis and epiphora in Paper II. This discrepancy is likely explained by differences in data collection methods: In the questionnaire study, participants selected clinical signs based on images, whereas in the referral forms, clinical signs were indicated by ticking predefined options. However, this indicates that most clinical signs observed by the herders are mild to moderate, as more severe clinical signs were reported less frequently.

In addition, Paper II identified associations between pathogen presence and specific clinical signs, including conjunctival hyperaemia with *Chlamydia* spp., and eyelid lesions with CvPV (Figure 7). This is in agreement with previous studies identifying *Chlamydia* spp. as important causes of conjunctivitis and keratoconjunctivitis in reindeer and other species (Sánchez Romano *et al.* 2019; Sachse & Borel 2020), and with recent observations of characteristic eyelid lesions in reindeer infected with CvPV (Nymo *et al.* 2025).

Figure 7. Reindeer exhibiting clinical signs of infectious ocular disease, sampled during the study period. (A) Calf positive for parapoxvirus red deer. (B) Calf positive for cervidpoxvirus (episode six in Paper II). (C) Adult female positive for cervid herpesvirus 2 and bacterial infection (episode 40 in Paper II). (D) Calf positive for *Chlamydia* spp. and bacteria (episode 34 in Paper II).

Furthermore, most observations of clinical signs were reported during autumn and winter across all age groups, including calves, juveniles, and adults (Papers I–II). This is consistent with previous studies reporting IKC outbreaks predominantly during these seasons, when animals are handled more frequently, exposed to stress, and kept at higher densities (Tryland *et al.* 2009; Tryland *et al.* 2016; Sánchez Romano *et al.* 2019; Tryland *et al.* 2019b).

However, a slight shift towards late winter, particularly February–March, was observed in the distribution of herd samplings over a 12-month period (Paper II). This may reflect the increasing prevalence of winter-feeding practices, driven by loss of pastureland and harsh weather due to climate change in both countries (Horstkotte *et al.* 2020; Åhman *et al.* 2022). In addition, reindeer condition may be compromised towards the end of winter, potentially impairing immune function and increasing susceptibility to infectious diseases (Stubsjøen & Moe 2014; Macbeth & Kutz 2019). Management-related factors may also contribute to stress and impaired immune function, including feeding practices such as feeding calves separately in enclosures. Notably, feeding in enclosures was associated with the reporting of IKC outbreaks (Paper I), suggesting a potential increase in outbreaks linked to such practices over the past decade. As most herd sampling events were conducted during 2020–2021 (Paper II), and the herding year 2019/2020 was associated with both reported IKC outbreaks and the highest use of feeding (Paper I), outbreak frequency appears to vary between herding years. This is consistent with reports indicating that 2019/2020 was a particularly challenging year (Åhman *et al.* 2022). Such variation may reflect regional and temporal differences in feeding practices influenced by pasture availability. In addition, winter feeding in enclosures, harsh weather conditions, and round-ups were frequently reported as preceding events prior to the observation of clinical signs of IKC (Paper II and IV).

Furthermore, calves were more frequently fed in enclosures than the herd as a whole (Paper I), which may further contribute to the occurrence of IKC. In Paper II, a higher proportion of conjunctival samples originated from calves with clinical signs compared to adults, reflecting sampling patterns rather than necessarily a higher true prevalence. Nevertheless, this is consistent with previous studies showing that IKC primarily seems to affect calves and yearlings. This pattern may partly be explained by the biology of CvHV2, where reactivation of latent infection enables viral transmission and disease development in susceptible animals. Calves may be particularly at risk as maternal antibodies decline (Tryland *et al.* 2009; Sánchez Romano *et al.* 2019; Tryland *et al.* 2019b). However, it has been suggested that CvHV2 can spread through leukocytes to other sites and has been detected in several tissues after primary infection. Furthermore, reactivation is not restricted to the site of primary infection (das Neves *et al.* 2009a; das Neves *et al.* 2009b; Tryland *et al.* 2017; Sánchez Romano *et al.* 2020).

In contrast, free-range feeding appeared to be protective against IKC outbreaks (Paper I), likely reflecting lower animal density, group-wide feeding without separation of calves, and improved hygiene. Taken together, these findings suggest that increased stress and closer contact between infected and immunologically naïve young animals may have a greater impact on IKC occurrence than feeding itself.

5.2 Pathogens associated with eye infection

A range of pathogens was detected in conjunctival swabs from reindeer, primarily originating from herds with clinically observed transmissible eye infections. These included CvHV2, *Chlamydia* spp., *Mes. bovoculi*, *Mes. ovipneumoniae*, *Mor. bovoculi*, poxviruses, and several opportunistic bacteria. CvHV2 was detected in 23.1% of analysed samples (68/294), while 28.4% (81/285) tested positive for *Chlamydia* spp. and 50.6% (91/180) for *Mycoplasma* spp., of which 90.1% (83/91) were identified as *Mes. bovoculi.* Several additional bacterial species were isolated, although most occurred sporadically. Overall, these findings support a multifactorial aetiology of IKC (Paper II).

Mesomycoplasma bovoculi was the most frequently detected *Mycoplasma* species in the eye, although neither of the species have been previously reported in semidomesticated reindeer in Sweden. Its frequent detection in the study of Paper II suggests that *Mes. bovoculi* may be involved in the development of IKC in reindeer. The observed trend of co-occurrence of *Mes. bovoculi* with *Moraxella* spp. further supports a potential role in disease pathogenesis, possibly through a synergistic interaction similar to what has been described for IBK in cattle (Schnee *et al.* 2015; Loy *et al.* 2021a). However, the exact mechanisms underlying such synergistic processes have not been fully described in cattle, and further investigation is therefore needed to clarify potential associations and interactions, including in reindeer.

Chlamydia spp. was rarely detected concurrently with CvHV2, and neither pathogen was associated with clinical signs of IKC. In contrast, *P. aeruginosa* and *S. aureus* were associated with clinical signs. Furthermore, the presence of CvHV2 was significantly associated with *P. aeruginosa* and *K. pneumoniae*, as well as with *Chlamydia* spp. (Paper II). This may suggest that environmental conditions in which reindeer are kept influence the bacterial community present, with certain bacteria tending to co-occur with specific pathogens. The composition of the ocular microbiota is known to vary with factors such as host age, environment, season, and sampling methods, and the normal flora plays an important role in maintaining ocular health through competition with pathogenic species (Gould *et al.* 2021). However, disruption of this balance, through immunosuppression, epithelial damage, or co-infection such as with CvHV2 or *Chlamydia* spp., may allow opportunistic bacteria to contribute to disease, potentially through cumulative or synergistic interactions. The findings in our studies (Paper I, II, IV) reinforce that IKC is a multifactorial condition influenced by a complex interplay of infectious agents, host factors, environmental stressors, and herd management practices.

5.2.1 Role of poxviruses

Poxvirus analyses were performed on a subset of samples selected based on the presence of periocular skin lesions (Paper II). Poxviruses were subsequently detected in 10 sampling episodes of IKC, including two episodes with PPV, six with CvPV, and two with both detected (Paper II). In some cases, such as episode six from October 2021 (Figure 7 and Paper II), the predominant clinical manifestations with epiphora and eyelid lesions observed in the herd were, in retrospect, attributable to CvPV, following its subsequent detection. This suggests that CvPV may have played a primary role in these outbreaks and indicates that the virus has been circulating since at least 2021 in this herd. It is therefore possible that several of the recorded episodes were mainly driven by CvPV, particularly during autumn when CvPV infections appear to be more common (Nymo *et al.* 2025). However, further studies with a more systematic sampling and analysis approach are required to assess the occurrence of CvPV in reindeer and to determine whether it may increase the risk of, or contribute to, the development of IKC.

In addition, 21.9% (68/310) of the conjunctival swabs were analysed for the presence of parapoxvirus (PPV), of which 10.3% (7/68) tested positive (Paper II). In contrast to CvHV2, PPVs are not considered enzootic in Norwegian and Swedish reindeer populations, as indicated by sporadic outbreak reports. Transmission of PPV through direct or indirect contact with sheep, goats, and cattle has been proposed as the main route of introduction (Tryland *et al.* 2001; Tikkanen *et al.* 2004). However, it remains unclear whether reindeer can act as subclinical carriers, although PPV has been detected in reindeer carcasses in Norway without clinical signs of contagious ecthyma (Tryland *et al.* 2005). The detection of PPV in conjunctival swabs (Paper II), including in animals without characteristic crusty and proliferative lesions on the muzzle, lips, and oral mucosa in reindeer with contagious ecthyma (Büttner *et al.* 1995; Tryland *et al.* 2001; Tryland *et al.* 2013), may suggest subclinical infection in some animals. This is comparable to findings of RDPV, which has been detected in the tonsils of apparently healthy red deer hunted in Germany, suggesting that subclinical infections may play a role in disease dynamics (Friederichs *et al.* 2015). However, the factors required to trigger disease outbreaks remain unclear in reindeer.

Recent findings further support the occurrence of subclinical infections, demonstrating the emergence of RDPV in reindeer, likely resulting from cross-species transmission and subsequent host adaptation. This is supported by the observation that the greatest genetic variation was found in regions associated with host interactions and virulence (Paper III). Furthermore, genetic evidence of recombination, including a unique genomic insert, suggests adaptation to the reindeer host and highlights the potential for previously unrecognised PPVs to circulate in reindeer populations. In affected reindeer where both CvPV and RDPV were detected, clinical signs included crusting and proliferative lesions on the muzzle, oral mucosa, and eyelids (Paper III).

In addition, PCPV was recently detected in a herd of free-ranging reindeer sampled during the first autumn gathering for slaughter in Norrbotten County, following the observation of clinical signs of IKC, including epiphora, purulent discharge, conjunctivitis, and keratitis (Olsson *et al.* 2026). This may indicate that reindeer can harbour subclinical PPV infection and that PPV may contribute to the development of IKC. Similarly, outbreaks in which contagious ecthyma, necrobacillosis, and IKC occurred concurrently have been reported, suggesting pathogen interactions enabling multiple infections (Tryland *et al.* 2019b). For example, mucosal damage induced by CvHV2 may facilitate the establishment of other pathogens, such as ORFV and *F. necrophorum*. Additionally, virus infection, such as CvPV and others, may lead to immunomodulation or suppression, paving the way for secondary infections.

Taken together, these findings indicate that poxviruses may be more common in reindeer than previously recognised. Moreover, parapoxvirus infections may be more dynamic and complex, involving cross-species transmission, host adaptation, and potential subclinical circulation in reindeer. However, their role in IKC development remains unclear, particularly regarding potential interactions with other pathogens. In addition, clinical signs associated with different poxviruses in reindeer may be difficult to distinguish based on clinical examination alone, further supporting the need for molecular diagnostics.

5.3 Perceptions and management of ocular diseases

Herders describing their perceptions of OD, including IKC (Paper IV), reported that primarily calves in enclosures were affected, in line with previous reports and Papers (I-III) (Tryland *et al.* 2009; Tryland *et al.* 2016; Sánchez Romano *et al.* 2019). At the same time, they described cases of OD that were either entirely novel or of an unfamiliar magnitude. Furthermore, OD was reported not only in calves but also in adult females, as well as in calves during summer marking (Paper IV), suggesting that the disease may affect a broader range of animal categories and occur outside the expected seasonal patterns (e.g., winter). Together, these observations point towards an apparent discrepancy between established risk factors, such as stress and primarily calves affected, and some field-based experiences, raising the possibility that current assumptions may not fully capture disease dynamics in contemporary reindeer husbandry.

However, the underlying causes of these few and specific observations remain uncertain, as the aetiology is not fully established. For instance, young calves observed during summer may reflect other ocular conditions presenting as "white eyes" with visual impairment, such as uveitis secondary to systemic inflammation or infection (Plummer *et al.* 2022). In addition, herders may first detect affected animals after periods of free ranging, when animals have not been closely observed, potentially leading to recognition at later stages of disease progression when chronic lesions predominate and primary infectious agents (e.g. viral pathogens) are no longer detectable. It is also possible that disease expression is influenced by interactions between multiple pathogens, such as poxvirus and different bacteria in the eye, as previously suggested (Sánchez Romano *et al.* 2019; Tryland *et al.* 2019b). Other causes of ocular clinical signs should also be considered, as cataracts may occur sporadically in reindeer and external trauma can result in similar clinical signs, typically affecting only single reindeer rather than on herd level (Laaksonen 2019).

5.3.1 The process of managing ocular disease

To synthesise the findings in Paper IV and provide a broader understanding of how OD is perceived and managed in practice, a conceptual model of OD-management in reindeer husbandry is proposed (Figure 8).

The findings of Paper IV suggest that the management of OD in reindeer husbandry can be understood as a dynamic and context-dependent process shaped by the interaction between three interconnected domains: (1) herd-level disease risk, (2) practical and emotional constraints, and (3) experiential learning and adaptation over time.

Figure 8. Conceptual model of ocular disease (OD) management in reindeer husbandry from a One Welfare perspective.

At the core of this model is the perception of OD as a threat to the herd rather than to the single reindeer. This perception directs management towards preventive and protective strategies aimed at limiting disease transmission, such as slaughter or culling, and isolation of affected reindeer. These are measures commonly performed according to Paper I and IV, and previous research (Tryland *et al.* 2016). However, these decisions are not made solely based on disease knowledge. Instead, they are strongly influenced by practical constraints, including labour availability, logistics, access to veterinary services, and the emotional burden associated with managing potential disease outbreaks, which in turn affects herders' well-being.

These interacting factors create a decision-making context in which herders must continuously balance animal welfare with what is practically feasible, while prioritising the protection and long-term stability of the herd over the outcome for individual animals. Over time, experiences of disease outbreaks contribute to learning processes that shape how clinical signs are interpreted and how management strategies are adapted. This includes changes in feeding practices, avoidance of transportation, risk assessment, and treatment decisions.

Importantly, the model also highlights that disease management is embedded within a broader social and organisational system. Factors such as trust, communication, stigma, and collaboration between herders, within and between RHDs, veterinarians, and other stakeholders influence both the implementation and effectiveness of disease control measures. This underscores the importance of veterinary knowledge of reindeer husbandry, reindeer health, and welfare to enable "contextualised care" and shared decision-making (Skipper *et al.* 2021). In addition, this highlights the need to improve access to veterinary care and strengthen communication and collaboration between herders and veterinarians. Such efforts are essential for building trust and effective collaboration, as noted in Paper I and IV, and in previous research (Tryland *et al.* 2016; Tryland 2022).

Together, this conceptual model illustrates that effective management of OD cannot be understood solely as a biological or clinical issue, but rather as a socio-ecological process consistent with a One Welfare perspective (Pinillos *et al.* 2016), where animal health and welfare, human well-being, and organisational conditions are closely interconnected.

5.3.2 Treatment strategies and prevention

Many herders already implement preventive measures to reduce the risk of IKC outbreaks (Paper I & IV). Minimising stress in reindeer is a key component in both the prevention and management of the disease, as stress is known to increase susceptibility to infectious diseases and may exacerbate clinical signs (Tryland *et al.* 2019a). Avoiding stressful handling procedures, particularly during high-risk periods such as winter feeding and gatherings, is therefore crucial. In addition, dispersing the herd and performing feeding on free-range reduces stress and contact between animals and limits the spread of infectious diseases (Paper I) (Rehbinder & Nilsson 1995; Riseth *et al.* 2020). Feed quality, feeding hygiene, sufficient access to feeding sites, and the design and size of enclosures are also important factors. During summer gatherings for calf marking, hot weather and dusty conditions should be avoided (Laaksonen 2019).

Preventive measures are especially important given the practical constraints of reindeer husbandry and the animals' sensitivity to repeated handling, which also influence treatment strategies (Paper IV).

Medical treatment strategies

When treatment is considered necessary, particularly in cases where the disease does not appear to resolve spontaneously but instead progresses rapidly, with the development of moderate to severe clinical signs such as corneal oedema and chemosis, treatment strategies must account for both disease severity and practical constraints.

Due to practical constraints, the sensitivity of reindeer to repeated handling, and the involvement of multiple pathogens in IKC, such as *Mycoplasma* spp. and *Chlamydia* spp., and various bacteria, long-acting injectable antibiotics may be preferred over repeated local treatments (Paper II & IV) (Sánchez Romano *et al.* 2019; Bonevik 2022). Prior to treatment, the eye should be cleaned with sterile saline, and in mild cases, antiseptic cleaning may be sufficient (Laaksonen 2019).

Tetracycline is considered a suitable treatment option in most cases in Sweden. However, in certain situations, particularly when only a few or relatively tame animals require treatment, local administration of penicillin (off-label use) may also be effective, provided that handling of the animals is feasible and does not cause excessive stress (Paper II & IV) (Laaksonen 2019). Local treatment with ophthalmic ointments is contraindicated in cases of deep corneal ulceration in horses and small animals and should therefore be used with caution in reindeer when more severe corneal lesions are suspected. In such cases, or when corneal rupture has occurred, culling may be considered the most appropriate management option (Paper II) (Läkemedelsverket 2025).

Mycoplasma spp. and C*hlamydia* spp. are not included in routine antimicrobial susceptibility testing; however, they are generally considered susceptible to tetracyclines and intrinsically resistant to penicillin (Gelatt & Plummer 2017; Sachse & Borel 2020).

In addition, non-steroidal anti-inflammatory drugs (NSAIDs) may be beneficial given the painful nature of IKC. When uveitis is present, local administration of atropine may also be considered, as described in cattle (Sheedy *et al.* 2021; Bonnevik 2022).

6. Conclusions

This thesis has contributed to an increased understanding of infectious keratoconjunctivitis (IKC) and periocular lesions in reindeer, including its epidemiology, associated pathogens, risk factors, and herders' perceptions within a One Welfare context. The identification of multiple pathogens, as well as the emergence of viruses, highlights the complexity of infectious diseases and their multifactorial nature in reindeer. Together, these findings provide a basis for improved preventive and treatment strategies, while also identifying key areas for future research.

- Infectious keratoconjunctivitis is a common herd disease, with peak occurrence during autumn and winter. Many herders were reluctant to contact a veterinarian, often due to the perceived lack of knowledge about reindeer diseases.
  Feeding in enclosures was associated with IKC outbreaks, whereas free-range feeding appeared protective. Results indicate that IKC is associated with feeding situations, particularly affecting calves. The challenging herding year 2019/2020 was significantly associated with IKC outbreaks and coincided with the highest reported use of feeding.

- Multiple pathogens were detected in reindeer with and without clinical signs of IKC, including *Mycoplasma* spp., not previously associated with IKC in reindeer in Sweden. Specific clinical signs of IKC were associated with different pathogens, with cervidpoxvirus (CvPV) linked to periocular lesions and *Chlamydia* spp. to conjunctivitis.

- Parapoxvirus red deer (RDPV) was detected for the first time in reindeer, associated with clinical signs resembling contagious ecthyma and showing evidence of host adaptation, cross-species transmission, and emergence in reindeer.

- Herders perceived ocular disease (OD) primarily as a herd-level threat, shaping management strategies towards preventive measures. Slaughter was the most commonly reported control measure, followed by isolation of affected animals from the herd to prevent disease spread.

- Disease management was strongly influenced by contextual factors, including access to veterinary support, labour availability, and logistical constraints. Outbreak experiences contributed to adaptive management, including adjustments in feeding practices and disease risk assessment. Effective prevention requires improved coordination, communication, shared guidelines, and strengthened trust between herders, veterinary services, and other stakeholders.

7. Future perspectives

The findings of this thesis demonstrate the need for further research on the occurrence, pathogenesis, epidemiology, and management of IKC in reindeer. Key areas for future studies are outlined and discussed in the following sections.

Epidemiology and microbial dynamics of IKC

A **systematic longitudinal sampling** approach, including conjunctival swab samples collected before, during, and after outbreaks within the same herd, including a balanced sampling of reindeer with and without clinical signs, could provide valuable insights into the dynamics of the ocular microbiota in reindeer. Studies in cattle have shown that the bacterial ocular surface microbiome changes during IBK, and that these alterations may persist beyond the acute disease phase compared to healthy eyes. Certain bacterial taxa, such as *Corynebacterium*, have been suggested to play a protective role, whereas others, including *Rothia nasimurium*, may be associated with disease development (Gafen *et al.* 2023).

In addition, geographic variation in **ocular microbiota** has been reported in cattle, both in healthy and diseased animals, which may reflect natural variation between subpopulations or differences in underlying aetiology. Host-related factors such as age and sex have also been shown to influence microbial composition in cattle (Cullen *et al.* 2017; Anis *et al.* 2023; Gafen *et al.* 2023). Applying similar approaches in reindeer could improve understanding of the role of the ocular microbiota in IKC, including potential protective or predisposing microbial communities, and whether differences exist between regions, herds, or management systems. Such knowledge may contribute to improved prevention strategies and a more refined understanding of disease aetiology.

To better assess prevalence and identify risk factors for IKC, more systematic and geographically representative sampling across herds is required. The current material is based on convenience sampling, with clustering of submissions from certain regions and herds, reflecting variation in reporting behaviour, veterinary contact, and engagement rather than true disease distribution. Consequently, the data represent primarily clinical cases rather than a population-based sample, and information on the total number of affected animals, as well as the stage of disease at sampling, is limited.

These limitations restrict the ability to draw firm conclusions on prevalence and risk factors. Future studies should therefore prioritise systematic study designs with balanced sampling across regions and herds, including detailed metadata on age, feeding practices, enclosure use, and other potential stressors such as body condition, weather events, and predation pressure. In addition, more observations are needed to enable robust multivariable analyses to disentangle the relative importance of different risk factors. A further challenge relates to the highly dynamic nature of reindeer populations, including contacts between herding districts and the introduction of new animals. Overall, prioritising structured data collection and improved representativeness will be essential to strengthen evidence on disease dynamics, risk factors, and control measures in reindeer populations.

Metagenomic sequencing and **other complementary molecular approaches**, alongside traditional bacteriological culture and qPCR, could further elucidate the microbial findings in the reindeer eye. Given recent reports on the pathogenic properties of *Mor. bovoculi* in cattle (Loy *et al.* 2021b), the pathogenic potential of *Mor. bovoculi* isolates from reindeer warrants further investigation. Recently, a novel *Moraxella* species has been identified in cattle with IBK using 16S rRNA gene sequencing and has been tentatively named *Moraxella oculi* sp. nov. (Wilkes *et al.* 2024). In addition, serological screenings of herds with IKC, for example, targeting CvHV2 and *Chlamydia* spp., could contribute to a better understanding of exposure, transmission patterns, and immunity.

Further investigation into potential **genetic variation among CvHV2 isolates** from different geographical regions may be of interest. Species of alphaherpesviruses in cattle are associated with a range of distinct clinical manifestations, including respiratory disease, abortion, and venereal infections (MacLachlan & Dubovi 2017). Exploring whether similar variation in viral strains may influence disease expression in reindeer could therefore provide important insights into the pathogenesis and epidemiology of IKC.

Additional studies are warranted to validate the findings on *Mycoplasma* spp. from EVL, including confirmation at the species level by sequencing and assessment of antimicrobial resistance patterns. Corresponding studies are also needed for *Chlamydia* spp., alongside the development of more accessible tools for monitoring resistance in these bacteria, such as sequencing or PCR assays targeting specific resistance genes. To date, tetracycline resistance has only been reported in *Chlamydia suis*, and not in other *Chlamydia* species (Sachse & Borel 2020).

Management and prevention of IKC

Since signs of OD have interconnected impacts on animal welfare and herders' well-being, and its management is often described as both labour-intensive and emotionally demanding, there is a need to strengthen support systems, consistent with a One Welfare framework. Improved communication within and between RHDs, as well as increased trust and collaboration with veterinary services, are essential.

Participatory research approaches could support the identification of effective ways of working and improving collaboration by incorporating herders' perspectives, needs, and preferences. For example, the development of a structured reindeer health service, including regular herd visits, training courses, and workshops to strengthen knowledge exchange and collaboration. Innovative approaches, such as remote digital necropsies, have already shown promising results in Finland, and a similar approach has also been explored in Sweden, which may represent a valuable tool in reindeer health management (Itkonen *et al.* 2026).

In addition, strengthening veterinary knowledge of reindeer husbandry and disease is crucial. Establishing a more consistent definition of IKC and recognising it as a herd-level diagnosis may enhance awareness of the disease and support more timely, appropriate, and context-adapted treatment and management responses to outbreaks, as has previously been suggested in cattle (Kneipp 2021). In general, there is a need for further studies, with **follow-up of treatments**, to support evidence-based treatment recommendations for both antibiotic and non-antibiotic interventions in IKC, and, in the longer term, to explore the potential for vaccine development, as has been suggested in cattle (O'Connor *et al.* 2021).

Currently, there is a lack of a structured reindeer health management system in Sweden. Developing such a framework, alongside continued professional training in reindeer medicine, would be important steps towards increasing veterinary competence and understanding of reindeer diseases and reindeer husbandry, and the Sámi cultural context in which it is embedded. This, in turn, is essential for building trust and strengthening collaboration between herders and veterinary services, ultimately supporting both reindeer health and welfare and sustainable management in reindeer husbandry (Baker *et al.* 2022). **Strengthening a structured reindeer health**

management system in Sweden is therefore of key importance, not only for improving animal health and welfare, but also from a broader preparedness perspective, as reindeer husbandry represents an important resource in an increasingly uncertain subarctic and arctic environment.

In this context, **emerging infections**, such as poxviruses in reindeer, further highlight the value of coordinated support systems. Improved access to veterinary services, effective communication, and facilitated sample submission from the field to diagnostic laboratories are essential components of enhanced passive surveillance. Such systems enable early disease detection, support research, and contribute to discoveries, while also identifying knowledge gaps requiring further investigation.

Future studies should aim to determine the prevalence and distribution of RDPV and CvPV, assess their genetic variation, and identify viral determinants of host specificity. Furthermore, the role of potential vectors, such as insects, ticks, and small mammals, in the transmission of infections to reindeer and other cervids warrants further investigation.

In addition, there is a need to improve understanding of **subclinical infections** and their potential impact on both reindeer welfare and herd productivity, as these may represent a substantial but under-recognised burden compared to overt disease outbreaks. This includes infections caused by CvHV2, *Chlamydia* spp., and zoonotic microbes, such as PPVs, but also reindeer pestivirus, as well as parasites, together with their interactions with environmental and management-related stressors (Tryland *et al.* 2022; Tryland & Buhler 2025).

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Popular science summary

Reindeer husbandry is a fundamental part of Sámi society and central to Sámi culture. It is based on the reindeer's natural adaptation to the environment and their ability to utilise natural grazing resources. Over the past few decades, access to pasture has declined due to competing land uses such as forestry, mining, infrastructure development, tourism, and predators. In addition, climate change has led to increased temperature fluctuations, with freeze–thaw events causing ice formation on the ground or within the snow, resulting in "locked pastures" that limit access to forage.

These changes have led to an increased use of supplementary feeding in both Sweden and Norway. Feeding may occur either on natural pastures or in enclosures, and common feed types include grain-based compound feed, grass silage, hay, and lichen. While feeding may be necessary to ensure reindeer survival, it often results in animals being kept at higher densities, which may increase the risk of infectious disease transmission. One such disease is infectious ocular disease, a painful eye infection that affects both animal welfare and the working conditions of reindeer herders. However, knowledge about its causes, occurrence, and effective prevention and management remains limited.

The aim of this thesis was therefore to improve understanding of the microorganisms and risk factors associated with eye infections in reindeer, as well as how herders perceive and manage ocular disease in practice.

The thesis is based on four studies. A questionnaire survey investigated the occurrence of the disease, associated risk factors, and herders' perceptions in Norway and Sweden. A field study involved the collection of eye swab samples from both clinically affected and apparently healthy reindeer to identify the presence of different microorganisms. A third study focused on describing clinical signs and a virus detected in reindeer for the first time. The fourth study consisted of interviews with herders about their experiences of managing ocular disease.

The results show that eye infection is commonly observed at herd-level, particularly during autumn and winter. Outbreaks were more frequent in association with feeding in enclosures, and calves were the most affected group. Multiple pathogens were detected in the eyes, including viruses, bacteria, and opportunistic microorganisms, highlighting the multifactorial nature of the disease. An important finding was the first detection of a parapoxvirus in reindeer previously associated with red deer, suggesting host adaptation and the possibility of cross-species transmission.

The interviews showed that ocular disease is primarily perceived as a herd-level problem rather than an individual animal issue. Disease management is strongly influenced by practical factors such as labour availability, access to enclosures, logistics, and access to veterinary services. Many herders described disease management as both time-consuming and emotionally demanding.

Overall, the findings demonstrate that infectious ocular disease in reindeer is a complex condition influenced by pathogens, environmental factors, and management practices. The study highlights the need for increased knowledge, improved communication, and strengthened collaboration between herders, veterinarians, and other stakeholders to support animal health, welfare, and sustainable reindeer husbandry in a changing environment.

Populärvetenskaplig sammanfattning

Renskötseln är en grundläggande del av det samiska samhället och central för den samiska kulturen. Den bygger på renarnas naturliga anpassning till miljön och deras förmåga att utnyttja naturliga betesresurser. Under de senaste decennierna har tillgången på bete minskat till följd av konkurrerande markanvändning, såsom skogsbruk, gruvor, infrastruktur, turism och rovdjur samt till följd av klimatförändringen. Varmare vintrar, mer nederbörd och att det växlar mellan tö och kyla leder till isbildning på marken eller i snön, vilket leder till "låsta beten" som betyder att renarna inte kan komma åt sin naturliga föda. Detta har lett till att utfodring, antingen som stöd på naturbetet eller i hägn, har blivit allt vanligare i både Sverige och Norge. Även om utfodring kan vara nödvändig för att säkerställa renarnas överlevnad, innebär den ofta att djuren samlas tätare och blir stressade, vilket kan öka risken för spridning av infektionssjukdomar. En sådan sjukdom är ögoninfektion, en smärtsam åkomma som påverkar både djurens välfärd och renskötarnas arbete. Kunskapen om sjukdomens orsaker, förekomst och hur den bäst kan hanteras och förebyggas är fortfarande begränsad. Syftet med denna avhandling var därför att öka förståelsen för vilka mikroorganismer och riskfaktorer som är kopplade till ögoninfektion på ren. Vidare undersöktes hur renskötare uppfattar och hanterar ögonsjukdom i praktiken, för att på bästa vis kunna behandla och förebygga sjukdomen.

Avhandlingen bygger på fyra delstudier. En enkätstudie undersökte hur vanlig sjukdomen är och vilka riskfaktorer som finns samt hur den uppfattas av renskötare i Norge och Sverige. I en fältstudie samlades ögonsvabbprover in från både sjuka och till synes friska renar för att kartlägga förekomsten av olika mikroorganismer. En tredje studie fokuserade på att beskriva synliga symtom och ett virus som påvisades hos ren för första gången. Den fjärde studien bestod av intervjuer med renskötare om deras erfarenheter och upplevelser kring att hantera ögonsjukdom.

Resultaten visar att ögoninfektioner är vanligt förekommande på hjordnivå, särskilt under höst och vinter. Utbrott av sjukdomen i en hjord var vanligare i samband med utfodring i hägn och kalvar var den mest drabbade gruppen. Flera olika smittämnen påvisades i ögonen, bland annat virus, bakterier och opportunistiska mikroorganismer, vilket visar att sjukdomen har många olika orsaker som samverkar. Ett viktigt resultat var att kronhjortens parapoxvirus påvisades hos ren för första gången. Fyndet tyder på att viruset kan ha anpassat sig till ren och att smitta kan ske mellan olika djurarter.

Intervjuerna med renskötare visade att ögonsjukdom främst uppfattas som ett problem på hjordnivå snarare än hos enskilda djur. Hur sjukdomen hanteras påverkas i stor utsträckning av praktiska förhållanden såsom tillgång till hjälp, inhägnader, logistik samt kontakt och tillgång till veterinär. Många renskötare beskrev sjukdomshanteringen som både tidskrävande och känslomässigt belastande.

Sammantaget visar resultaten att ögoninfektion hos ren är en komplex sjukdom där både smittämnen, miljö och skötsel samverkar. Studien understryker behovet av ökad kunskap, bättre kommunikation och stärkt samarbete mellan renskötare, veterinärer och andra aktörer för att förbättra djurhälsa, djurvälfärd och en hållbar renskötsel i en föränderlig omvärld.

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Infectious keratoconjunctivitis in semi-domesticated reindeer (*Rangifer tarandus tarandus*): a questionnaire-based study among reindeer herders in Norway and Sweden

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Abstract

Background The effects of climate change, loss of pastureland to other land usage and presence of large carnivores are the main reasons for the increase in supplementary feeding of semi-domesticated reindeer (*Rangifer tarandus tarandus*) in Fennoscandia over the last decades. Feeding might expose reindeer to stress and increased animal-to-animal contact, leading to an increased risk of infectious disease transmission, such as infectious keratoconjunctivitis (IKC). As it can develop rapidly and be very painful, IKC is described as an important animal welfare concern and a potential source of economic loss. The aim of this study was to investigate the current presence of IKC and potential associations between IKC and supplementary feeding through an online questionnaire survey, distributed among reindeer herders in Norway and Sweden in 2021.

Results Seventy-six reindeer herders (33 from Norway and 43 from Sweden) responded to the questionnaire, representing 6% and 4% of the registered reindeer herding groups in Norway and Sweden, respectively. Infectious keratoconjunctivitis was common, with 54 (71%) of the 76 herders that responded having observed clinical signs during the past 10 years. These signs were mainly observed as increased lacrimation, causing "wet cheeks", but also as keratitis and conjunctivitis. Autumn and winter were the seasons in which IKC was observed most. The herders reported several measures, such as slaughter and isolation of affected reindeer, to counteract the spread of disease. The herding year 2019/2020 was associated with reports of outbreaks of IKC in herds as well as being the herding year where most herders (80%) had performed supplementary feeding. A significant association was found between IKC and feeding performed in an enclosure (odds ratio = 15.20), while feeding on free-range areas had a non-significant, negative, relationship with the appearance of IKC outbreaks (odds ratio = 0.29). Finally, there was a trend in the data suggesting that IKC affected calves especially.

Conclusions Infectious keratoconjunctivitis is a common disease, mainly observed in winter and autumn. It usually has mild to moderately severe clinical signs. Our results imply that IKC is associated with stress and feeding situations

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and that calves might be more susceptible than adults, however, this needs to be confirmed with further studies, preferably at an individual animal level.

Keywords Climate change, Eye disease, Free-range, Infectious disease, IKC, Natural pastures, Reindeer husbandry, Supplementary feeding

Background

Semi-domesticated Eurasian tundra reindeer (*Rangifer tarandus tarandus*) in Norway and Sweden are mostly free-ranging and dependent on access to natural pastures. Ongoing climate change is causing a warmer climate with an increase in precipitation and fast changes in snow depth. This has resulted in winters with more frequent rain-on-snow and freeze–thaw events, causing ice-locked, inaccessible pastures, challenging the traditional methods used in reindeer husbandry [1–5]. The effects of climate change in combination with the loss of pastureland due to other land uses (forestry, infrastructure, mining, wind power parks, and tourism) and the presence of large carnivores (e.g., wolves, bears, lynxes, wolverines and eagles) are the main reasons for the increased need for supplementary feeding, in natural pastures or full feed rations in enclosures, given over several weeks or months in the wintertime seen in Fennoscandia over recent decades [6, 7].

In Norway and Sweden there are different types of reindeer herding districts, based on migration patterns and geography. In Sweden, there are three types of districts; mountain, forest, and concession herding districts. Mountain herding districts are the dominant form in both countries, whereas forest herding districts only exist in Sweden. The Swedish Sámi concession herding district resembles the forest district type with limited seasonal migration restricted to the boreal forest year around. The right to reindeer husbandry is an exclusive right to the Sámi people in both countries. However, special legislation allows non-Sámi ownership in the concession areas [8].

The present use of supplementary feeding and general feeding practices differs between countries and regions in Fennoscandia, and it varies considerably between years. Emergency feeding, to prevent starvation, is practiced in all countries, while regular feeding for several months is mostly practiced in the southern parts of the reindeer herding districts in Finland; it occurs only sporadically in the northern parts of reindeer herding districts in Finland and in Norway and Sweden. In addition, temporary feeding during gathering and migration periods has been commonly practiced for decades in areas in Sweden but does not seem as common in Norway. Grass silage, hay, and grain-based pellets are commonly used [6, 9–12]. The winter season during the herding year 2019/2020 was reported by many herders in Fennoscandia as being very challenging with ice crust formation in the snow, ice layers on the ground, and deep snow leading to unavailable winter pastures. Because of this, many herders had to implement supplementary feeding [6].

Supplementary feeding is conducted either by bringing the feed to the reindeer pastures or by feeding the animals in enclosures [6]. Gathering and feeding might expose the animals to stress, which could negatively affect the immunological status of the animals and increase their susceptibility to infections. In addition, intensified herding associated with supplementary feeding will often increase animal-to-animal contact and may contribute to unfavourable hygienic conditions on feeding spots, with an increased risk of infectious disease transmission [2, 13–16]. It is also known that supplementary feeding is associated with increased risk of feeding related disorders, changes in reindeer behaviour, as well as increased financial burden and workload for the reindeer herder.

A disease with a major impact on animal welfare in reindeer husbandry is infectious keratoconjunctivitis (IKC) ("Čalbmevikke" in Sámi), which is a multifactorial disease that has been known for more than a century [17, 18]. Regional and seasonal differences in management have been described as contributing factors in previous studies [19, 20]. Stress associated with herding, gathering, transport, and translocation to new environments, as well as environmental conditions and management factors, has been associated with large outbreaks of IKC, primarily affecting calves and yearlings. Recently, cervid herpesvirus 2 (CvHV2) was established to be a primary pathogen for IKC [21–24]. The virus remains latent in the animal after infection and is enzootic in most reindeer populations in Fennoscandia, with a typically higher prevalence of antibodies in adults than in calves [25–30]. Other microbiological agents, like *Chlamydia* spp., *Moraxella bovoculi, Listeria monocytogenes*, and Pestivirus, have been identified as possible causes or co-infections contributing to IKC [14, 21, 22, 31]. Due to CvHV2's ability to cause mucosal lesions in the eye and mouth, CvHV2 can facilitate secondary infections caused by other pathogens, as well as co-infections [32]. An additional pathogen, enzootic in Norway and Finland, that could have a pathological impact and may potentially present ocular signs in reindeer is gammaherpesvirus (malignant catarrhal fever virus group; MCFV)

[25, 33], but the clinical impact of this virus in reindeer needs to be investigated further. Infectious keratoconjunctivitis severely affects animal welfare as the condition is very painful and follows a potentially rapid course which could lead to blindness. Furthermore, this causes difficulties for the reindeer when following the herd and finding feed, and, consequently, can lead to stress, potential starvation, and an increased risk of injury or death by predators. Non-infectious causes, such as insect bites and trauma, can give rise to clinical signs similar to IKC (i.e., keratitis, conjunctivitis, increased lacrimation) but are unlikely to cause outbreaks of IKC.

Tryland et al. [34] conducted a questionnaire survey around 10 years ago. The questionnaire was distributed among reindeer herders in Norway and Sweden and revealed that IKC was common in reindeer. Since then, climate change and the restricted availability of reindeer pastures, combined with economic support for feeding as compensation, has led to an additional increase in supplementary feeding in Norway and Sweden [6, 7, 14]. This may have potential effects on health and the transmission of infectious diseases, such as IKC, and an updated and extended investigation of the herders' perspectives, traditions, and experiences over the recent decade was warranted. Hence, the objective of this study was to obtain an overview of the current presence of IKC in semi-domesticated reindeer in Norway and Sweden, and the potential association between IKC and supplementary feeding. Our hypothesis was that occurrence of IKC is associated with supplementary feeding practices.

Methods

Questionnaire survey

The study was conducted as a questionnaire survey. A link to a digital questionnaire together, with information about the study, was distributed by e-mail to a contact person for each herding district (siida/sijte) in Norway (n=82) and to the chairperson of each herding district (Sameby) in Sweden (n=51). The contact person and chairperson for each district was further urged to distribute and invite all their members to the questionnaire. In 2020, 535 and 1048 reindeer herding groups were registered in Norway (siida-shares) and Sweden (usually representing a family), respectively, meaning a total of 1583 active groups of reindeer herders could be reached. In addition, the questionnaire was accessible through the Sámiid Riikkasearvi's (Sámi Reindeer Association, SSR) webpage to the members of 44 herding districts and 17 Sámi associations, and members of one private Facebook group (n=87) engaged in reindeer health. The survey was accessible from the 16th of April 2021 in Norway, and from the 26th of April 2021 in Sweden, until the 6th of September 2021 for both countries. Monthly reminders were sent out by e-mail. In Sweden, the chairperson of each herding district was also reminded by phone. All the respondents in this study are hereafter referred to as herders. Information regarding the handling and storage of data and written informed consent was provided to all respondents at the start of the questionnaire. In addition, a permit from the Norwegian Social Science Data Services was obtained for the collection and handling of personal data (Approval No. 457339). Similar declarations were not required in Sweden, based on instructions from the Swedish Ethical Review Authority.

Development of the questionnaire

The questionnaire was available in Swedish, Norwegian and Northern Sami (Additional files 1, 2, 3). It was generated in the web-based service Questback Essentials (Questback Sweden Ltd., Stockholm, Sweden, version number 38, 2021). The questionnaire contained 139 questions of various types, including simple yes/no and multiple-choice questions, and some supplemented with images. A few mandatory questions, mainly at the start of each section, were followed by questions based on the answer to the previous question (conditional branching). The respondents were able to add comments continuously. The questions referred to observations made over the past five or 10 years, or during the herding year 2019/2020. The questionnaire was divided into six sections: demographics, IKC, contagious ecthyma, oral necrobacillosis, other diseases, and feeding. This study has focused on the responses to questions from three parts, e.g., demographics, IKC, and parts of the feeding section.

Demographics and herd data

The first part of the questionnaire concerned herd data, including country, region, and herd size (divided into eight intervals from <50 to >3000, Additional files 1, 2, 3). For Sweden, the type of reindeer herding district, i.e., mountain, forest, and concession herding district, was also included. Demographic data included gender and age.

Presence and clinical signs of infectious keratoconjunctivitis

In the second part of the questionnaire, three images of different clinical stages of IKC were presented (Fig. 1). The questions addressed whether similar clinical signs had been noticed over the last 10 years, and the respondent's level of certainty related to such observations. Further questions on this topic were: when IKC was last observed; the most common clinical signs observed; the season of the year when clinical signs were observed; and the age category, calf (<1 year old), young (1–3 years

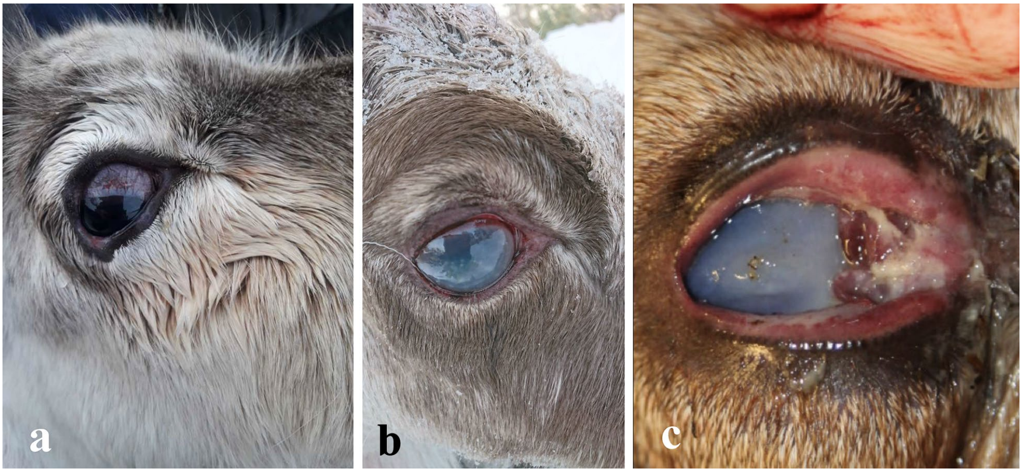

Fig. 1 Images showing the clinical signs of infectious keratoconjunctivitis (IKC) in reindeer used in the questionnaire distributed to Norwegian and Swedish reindeer herders. **a** Increased lacrimation (epiphora) causing "wet cheeks", which are a sign of the early and mild stage of IKC. **b** Conjunctivitis and corneal oedema, indicated as bluish/whitish discoloration of the cornea, which are both typical clinical signs of IKC at a moderately severe stage. **c** A very severe and often irreversible stage of IKC, including clinical signs like peri-orbital oedema and swelling (chemosis) and shedding of pus. Images from: Sámiid Riikkasearvi (Sámi Reindeer Association) and Farm and Animal Health's image archive

old), and adult (> 3 years old), and number of reindeer with IKC. We also asked if the respondents had experienced an outbreak of IKC. In the questionnaire, an outbreak was defined as an evident increase in the number of clinical cases observed over a period of time, it could be over longer (season) or shorter (few weeks) periods of time. Furthermore, questions about herding year and herding conditions, e.g., supplementary feeding or not, and if so, whether this was in an enclosure or free-range, were asked. This was followed by questions about any observed changes in the presence of the disease over the past 5 years, and for what reasons, followed by questions regarding what management interventions were used when IKC was last observed. We also asked if the respondents had experienced economic consequences in relation to IKC (e.g., loss of reindeer, increased workload or veterinary expenses), and if they had any traditional name or traditional knowledge associated with the disease.

Supplementary feeding

In the third part of the questionnaire, the use of supplementary feeding was addressed. Feeding was defined as giving supplementary feed to a winter herd for more than 2 weeks. The feeding section of the questionnaire was divided into the following four sections: (1) A general part, involving when and where (enclosure and/or free-range) feeding took place over the past five herding years; (2) The reason why feeding was conducted; (3) The effects of feeding; and (4) The detailed feeding routines for the herding year 2019/2020 and general feeding routines over the past 5 years. From this part of the questionnaire, only certain data from the general questions (section 1) are presented in this study.

Data management and statistical analysis

Initial exploratory data analysis was performed using Questback Essentials (Questback Sweden Ltd., Stockholm, Sweden, version number 38, 2021). Further data management, maps and graphs were produced and analysed in R, version 4.1.0 (R Core Team, 2021), and demographic data was calculated as percentages and presented in tables. The quotations presented in the results are based on written comments from the respondents and are thus not verbatim, but the meaning and essence of the respondents' words have not been altered.

To evaluate the potential association between supplementary feeding and the appearance of IKC, mixed effect logistic regression, using the "lme4" package was done on survey questions that covered multiple herding years, from 2015–2016 to 2020–2021. In each regression model, the outcome variable was the observed presence of an IKC outbreak in the herd for a given herding year (yes or no; 1/0), with each observation under analysis being a herding year per herd. The exposure variables of interest were three binary dummy variables related to feeding. The first two dummy variables were feeding in an enclosure and free-range feeding. The third dummy variable, feeding overall, is a variable created based on the two prior ones (feeding in an enclosure and free-range feeding). These were investigated in separate univariable models. Herd ID was used as a random effect to account for the repeated nature of this data over time, and thus the lack of independence between observations from the same herd at different points in time. A simple multivariable model selection was conducted considering these main exposures as well as some spatiotemporal and demographic covariates (herd size, region, country, and herding year). Since several Norwegian counties had very few herds surveyed, these were aggregated for modelling, with Nord-Trøndelag, Sør-Trøndelag, and Hedmark forming one region, and Nordland and Troms forming another. Model selection was done in a two-way approach, starting from an empty model and using the Akaike Information Criterion (AIC) with a likelihood ratio test (LRT). Given the small sample size, a P-value of 0.1 was used on the LRT to include a variable in the final model. Similarly, $P=0.1$ was used to identify a significant association, with $P\leq0.05$ being considered "significant" and $P>0.05$ and <0.1 being considered "borderline significant".

Results

Demographics, herding district, and herd data

In total, 134 herding district representatives in Norway and Sweden received the link to the questionnaire, and 76 reindeer herders responded to the questionnaire, 33 from Norway and 43 from Sweden (Table 1), representing 6% and 4% of the registered reindeer herding groups in Norway and Sweden, respectively. Responses were received from all reindeer herding regions, except for the county of Møre og Romsdal in Norway, which is hosting only a restricted number of semi-domesticated reindeer. In Sweden, nine respondents were from concession districts (21%), 10 from forest districts (23%), and 24 from mountain districts (56%, Fig. 2). The distribution of gender, age and herd size are presented in Table 1. The herd size distribution varied both between, and within the countries (Table 1, Additional file 4).

Table 1 General demographic data for the 76 herders that responded to the questionnaire survey distributed in Norway and Sweden in 2021 regarding the health and supplementary feeding of semi-domesticated reindeer

Parameter	Category	Norway n (%[a])	Sweden n (%[a])	In total n (%[a])
Respondents	In total	33 (43)	43 (57)	76 (100)
Gender	Female	6 (18)	21 (49)	27 (36)
	Male	27 (82)	19 (44)	46 (61)
	Unspecified	0 (0)	3 (7)	3 (4)
Age (years)	< 20	0 (0)	0 (0)	0 (0)
	20–39	9 (27)	13 (30)	22 (29)
	40–59	19 (58)	24 (56)	43 (57)
	> 60	5 (15)	6 (14)	11 (14)
Herd size	1–499	13 (39)	10 (23)	23 (30)
	500–999	6 (18)	11 (26)	17 (22)
	1000–1999	4 (12)	12 (28)	16 (21)
	> 2000	10 (30)	10 (23)	20 (26)

[a] Since decimals were omitted, the sum is not necessarily 100 (%) for each parameter

Presence and clinical signs of infectious keratoconjunctivitis

In total, 51 of the 76 respondents (67%) had observed clinical signs of IKC over the past 10 years, whereas three (4%) answered that they were unsure or had seen other clinical signs than presented in Fig. 1. Results per country show that 20 (61%) of the 33 respondents in Norway and 34 (79%) of the 43 respondents in Sweden had observed IKC over the past 10 years. Most of the respondents had observed clinical signs of IKC in the last year (Table 2).

The most observed clinical signs in both countries, observed sometimes or often, were epiphora/increased lacrimation causing a "wet cheek" (Fig. 1a) and conjunctivitis and bluish/whitish discoloration of the cornea due to oedema (Figs. 1b, 3). Of the 54 respondents that had observed IKC or other clinical signs in the past 10 years, 47 (87%) observed clinical sign A sometimes or often, with 46 reporting clinical sign B (85%). The least frequently observed clinical signs were C (periorbital oedema and swelling (chemosis), and shedding of pus, Fig. 1c), and clinical sign D, representing clinical signs 'other' than A–C (Fig. 3). Other clinical signs mentioned in the comments were ruptured eyes, purulent secretions and white spots on corneas.

Observed clinical signs related to season and age

Clinical signs of IKC were mainly observed during the autumn and winter season for all three age categories: calf, young and adult (Fig. 4). A minority of respondents reported IKC all year round or in spring. In Sweden, calves and young reindeer were the only age categories observed with clinical signs during the summer. Comments to this set of questions reported that all three stages of eye disease were observed, the most common being increased lacrimation in calves during autumn and winter. Respondents also stated that dust from the feed was a cause of IKC, and finally, that clinical signs mostly appeared in calves and during supplementary feeding.

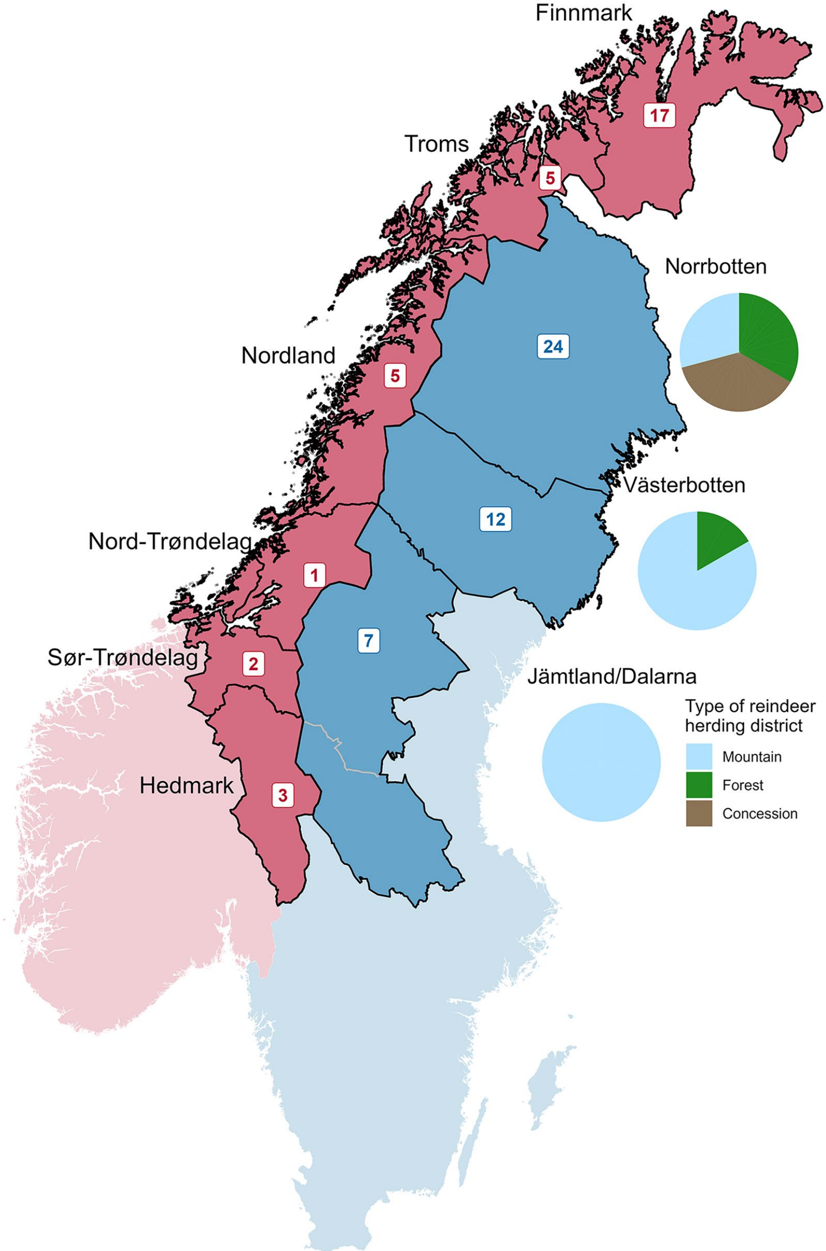

Fig. 2 Number of respondents to the questionnaire survey regarding the health and supplementary feeding of semi-domesticated reindeer, divided per county, Norway (in red; designated as before 2020 when several counties were merged) and Sweden (in blue; where Jämtland and Dalarna are merged). The pie charts show the distribution of type of reindeer herding district (mountain, forest, and concession districts) in the four Swedish counties

Table 2 General distribution of answers related to when infectious keratoconjunctivitis was last observed over the past 10 years, from 54 herders surveyed in the questionnaire regarding health and supplementary feeding of semi-domesticated reindeer in 2021, with 20 and 34 respondents from Norway and Sweden, respectively

Question	Category	Number and frequency[a] of answers		
		Norway	Sweden	Total
When did you last observe eye disease?	Last year	11 (55)	23 (68)	34 (63)
	Not last year, but in the last 5 years	5 (25)	6 (18)	11 (20)
	> 5 years ago	3 (15)	2 (6)	5 (9)
	Don't know	1 (5)	3 (9)	4 (7)

[a] Since decimals were omitted, the sum is not necessarily 100 (%) for each parameter

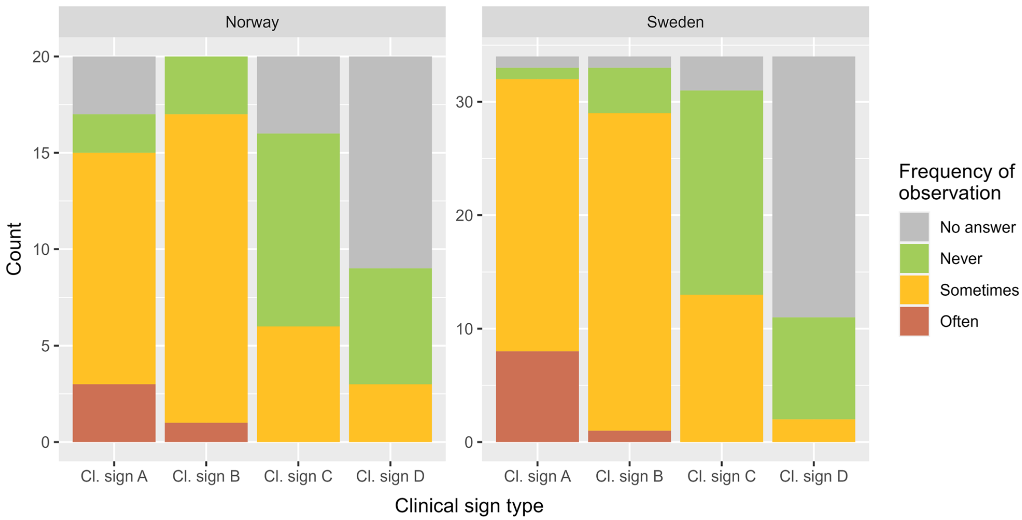

Fig. 3 Frequency of clinical signs associated with different stages of infectious keratoconjunctivitis identified by 54 respondents, 20 from Norway respective 34 from Sweden, in the questionnaire survey regarding health and supplementary feeding of semi-domesticated reindeer. Clinical sign A represents increased lacrimation (epiphora), causing a "wet cheek" (mild stage); B represents conjuctivitis and bluish/whitish discoloration of the cornea due to edema (moderately severe stage); and C represents periorbital edema and swelling (chemosis) and shedding of pus (very severe stage). D represents clinical signs'other' than A–C

Some direct quotes (opinions) from free text comments (voluntary to fill out) by respondents in the questionnaire, related to IKC were:

> *"I often observe wet cheeks all year round."*
> *"We rarely observe eye diseases but have experienced all clinical signs given in the questionnaire, most common is tear flow from calves during autumn and winter."*
> *"Mostly observed in calves during supplementary feeding."*
> *"It can spread rapidly among reindeer whatever their condition."*

Supplementary feeding

In total, 66 (87%) of the respondents had performed supplementary feeding from time to time over the past 5 years, 27 (82%) of the Norwegian respondents, and 39 (91%) of the Swedish respondents. In general, over the past five herding years, free-range feeding was most common, followed by a mix of free-range feeding and in enclosure feeding for a single herd during the herding year. The least common was feeding in enclosures only (Fig. 5). The herding year in which most of the respondents performed feeding was 2019/2020, in

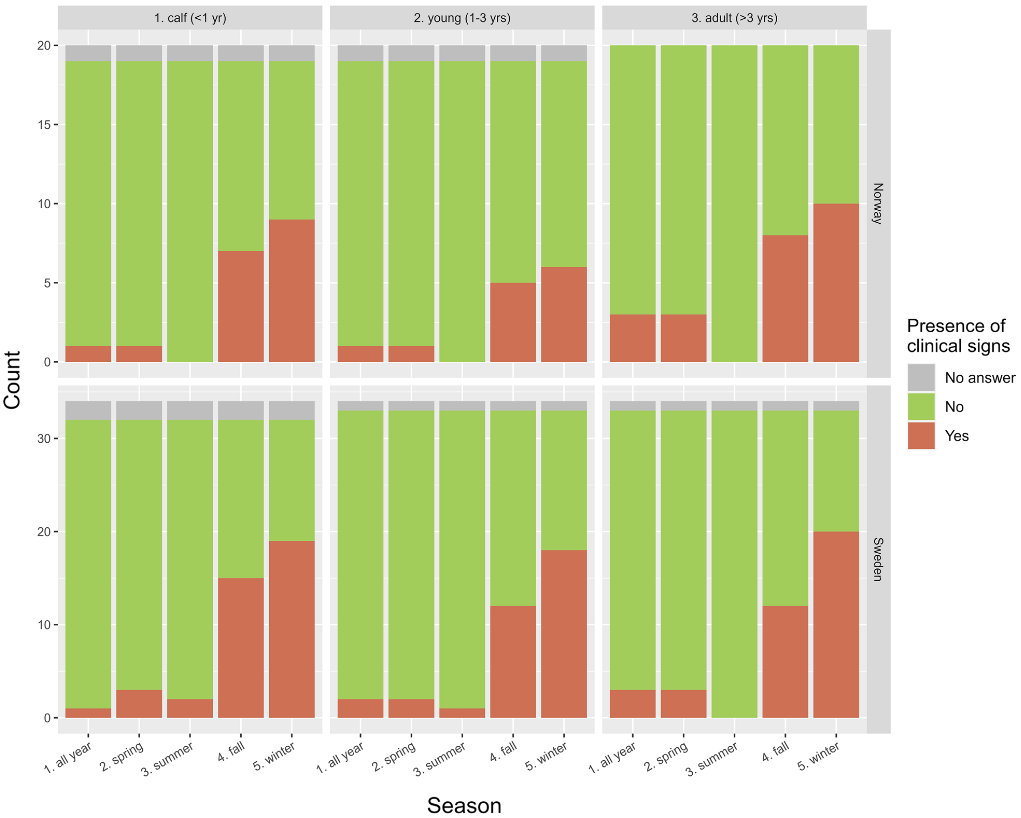

Fig. 4 Reported observations of infectious keratoconjunctivitis over the four seasons of a year, in age categories: calves (< 1 year), young reindeer (1–3 years), and adults (> 3 years), from 54 herders surveyed in the questionnaire regarding health and supplementary feeding of semi-domesticated reindeer, 20 respondents from Norway and 34 from Sweden

which 61 (80%) out of 76 respondents fed their reindeer (Fig. 5).

In general, larger groups of reindeer (≥ 300) were commonly free-range fed, while smaller groups of reindeer (< 300) were fed in enclosures more often, only investigated for the herding year 2019/2020. In addition, it was more common (n = 15; 35%) to only feed calves in enclosures in Sweden, compared to feeding the whole group (n = 3; 7%). This was in contrast to Norway where it was unusual to feed calves as well as the whole group in enclosures (Table 3). None of the respondents specified that they had exclusively fed reindeer over 1 year of age. Additional comments mentioned that certain groups of reindeer were fed each year, including calves, weak animals, animals selected for slaughter, reindeer involved in tourism and tame reindeer, while the rest of the group was not fed.

Some direct quotes (opinions) from free text comments (voluntary to fill out) by respondents in the questionnaire, related to supplementary feeding were:

> *"I feed a few reindeer every winter."*
> *"The majority are free-range fed."*
> *"Some winters, we separate the calves to feed them in enclosures, and the rest of the herd are free-range fed."*

Outbreak of infectious keratoconjunctivitis per herding year and number of affected reindeer

For each herding year in the period 2015/2016–2020/2021, the majority of the respondents had not

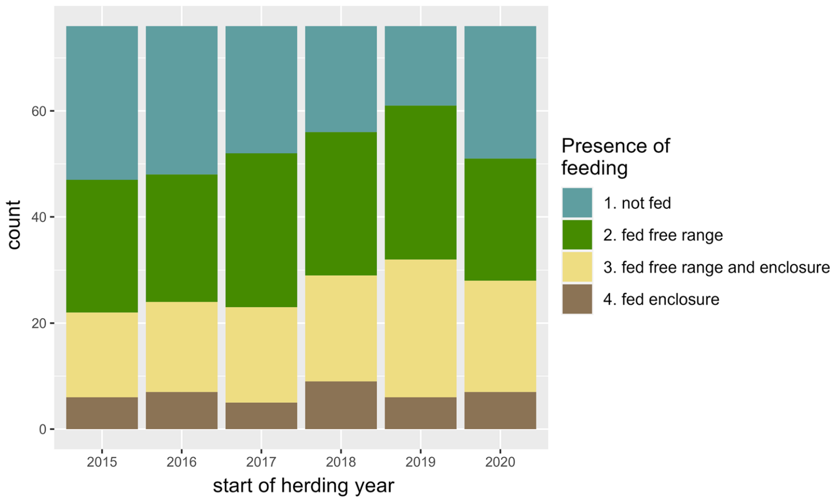

Fig. 5 Distribution of feeding practices over six herding years, from 2015/2016 to 2020/2021, based on answers from herders who responded to the questionnaire survey regarding the health and supplementary feeding of reindeer in Norway and Sweden. Sixty-six respondents, 27 from Norway and 39 from Sweden, had performed supplementary feeding at some time over the past 5 years, whereas ten respondents answered that their animals were free-range with no supplementary feed at all

Table 3 Distribution of the number of reindeer and the animal category (e.g., calves or whole group) fed in an enclosure or free-range fed, investigated for the herding year 2019/2020. Presented per country out of the 76 reindeer owners from Norway (n=33) and Sweden (n=43) who responded to the questionnaire survey regarding health and supplementary feeding of reindeer

Question	In enclosures			Free-range		
	Norway n (%[a])	Sweden n (%[a])	Total n (%[a])	Norway n (%[a])	Sweden n (%[a])	Total n (%[a])
Number of animals fed						
No answer	1 (3)	5 (12)	6 (8)	1 (3)	5 (12)	6 (8)
None	22 (67)	16 (37)	38 (50)	7 (21)	11 (26)	18 (24)
< 300	7 (21)	10 (23)	17 (22)	3 (9)	5 (12)	8 (11)
≥ 300	3 (9)	12 (28)	15 (20)	22 (67)	22 (51)	44 (58)
Animal category						
No answer	2 (6)	5 (12)	7 (9)	2 (6)	5 (12)	7 (9)
None	24 (73)	20 (47)	44 (58)	7 (21)	12 (28)	19 (25)
Calves only	3 (9)	15 (35)	18 (24)	0 (0)	0 (0)	0 (0)
Whole group	4 (12)	3 (7)	7 (9)	24 (73)	26 (60)	50 (66)

[a] Decimals are omitted and therefore the sum is not 100 (%) for each column

reported an outbreak of IKC (Fig. 6). Outbreaks of IKC were most commonly reported during the herding year 2019/2020, when 20 (26%) of the 76 respondents reported an outbreak. During the same year, there was no difference in the number of reported outbreaks among herds in enclosures compared to free-range herds, 11 (15%) responders reported outbreaks under one of the two conditions, while just four respondents (6%) reported outbreaks in both enclosure and free-range (Fig. 6). In general, the same pattern was repeated each herding year; outbreaks were most commonly observed in enclosures or in free-range herds and were less commonly reported in both enclosure and free-range, independent of whether the reindeer were fed or not. The proportion of affected reindeer varied greatly, from 0.2 to 100% of reindeer being affected in one group. In general, calves (< 1 year) and young reindeer (< 3 years) were reported to be affected in greater numbers, spanning

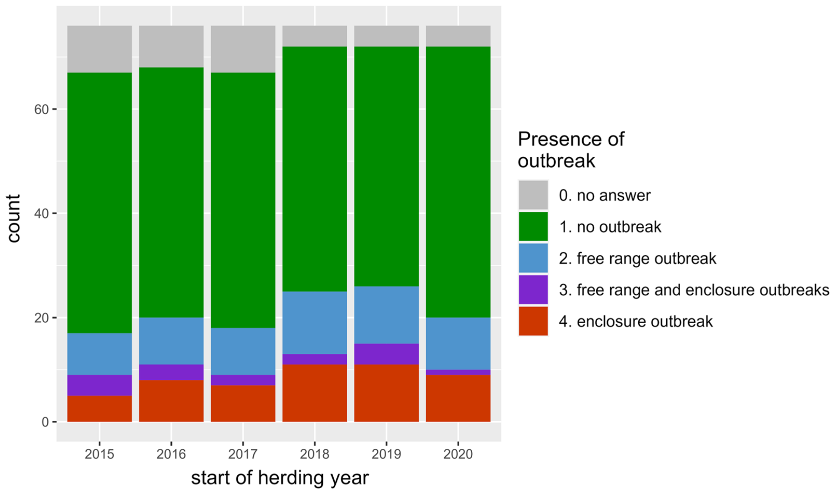

Fig. 6 Observations of outbreaks of infectious keratoconjunctivitis at herd level, distributed as free-range and/or enclosure, independent of whether the reindeer were fed or not, over six herding years, from 2015/2016 until 2020/2021. The figure is based on answers from 76 herders who responded to the questionnaire survey regarding the health and supplementary feeding of reindeer in Norway and Sweden

from 0.2 to 100%, compared to adult reindeer (3 years or more), spanning from 0 to 20%. Since information on the age composition of the total herd from which the affected reindeer were part was missing, the true proportion of affected calves/young and adult reindeer could not be calculated. However, herders with herds up to around 100 animals tended to report a higher proportion of affected reindeer (20–100%) compared to herders with larger herd sizes (around 2000), who reported a lower proportion of affected reindeer (0.1–1%). Several of the respondents commented that they had seen individual animals with IKC but had not experienced an outbreak.

Some direct quotes (opinions) from free text comments (voluntary to fill out) by respondents in the questionnaire, related to outbreaks of IKC and season were:

> *"I have observed reindeer with clinical signs but not experienced an outbreak during 2020/2021, the disease does not seem as contagious this year."*
> *"It has been more or less common for one year depending on where the reindeer were located during the autumn."*
> *"We usually observe a few reindeer with clinical signs of different severity, it is easier to observe the disease during the winter."*

Relationship between feeding and outbreak of infectious keratoconjunctivitis

When considering the year-based questions, there were 456 herd-year observations. However, due to non-answers from some herders to the year-specific herd question, 418 complete observations were available for regression modelling.

Univariable mixed effect regression models showed no evidence of an association between feeding overall and the presence of outbreaks in a herd. However, when separating feeding by location, e.g., free-range versus enclosure, we observed that feeding in enclosures was significantly associated with higher odds of IKC outbreak (Odds Ratio = 11.59, P = 0.011). Free-range feeding had a negative, but non-significant, relationship with the appearance of an IKC outbreak (Table 4).

The multivariable model selection led to the inclusion of the location specific feeding in enclosures variable described above as well as the herding year. The association with feeding practice was similar when seen in the multivariable model, with an OR of 15.20 for feeding in enclosures (P = 0.009). The herding years 2018–2019 and 2019–2020 were associated with a higher likelihood of an outbreak of IKC compared to the reference year 2015–2016, with 2019–2020 having the highest likelihood (OR = 13.04, P = 0.027). The other 3 years (2016–2017, 2017–2018, and 2020–2021) were not significantly different from 2015–2016 (Table 5).

Table 4 Results from a univariable mixed-effect logistic regression, where the observed presence of an outbreak of infectious keratoconjunctivitis in a herd for a given herding year was the outcome, with each observation under analysis being a herding year per herd (number of herd-years). Based on the 76 herders surveyed in the questionnaire regarding health and supplementary feeding of reindeer, 33 respondents from Norway and 43 from Sweden

Variable	Category	Numbers of herd-years	Numbers of herd-years with outbreak	Proportion	OR univariate	95% CI	*P*-value
Feeding overall	No	134	33	0.25	Reference		
	Yes	284	93	0.33	1.30	0.15–11.58	0.82
Feeding in enclosure	No	276	68	0.25	Reference		
	Yes	142	58	0.41	11.59	1.75–77.01	0.01
Free-range feeding	No	167	43	0.26	Reference		
	Yes	251	83	0.33	0.29	0.05–1.72	0.17
Herd size	< 500	134	40	0.30	Reference		
	500–999	83	29	0.35	1.54	0.02–123.80	0.85
	1000–1999	82	16	0.20	0.88	0.01–102.49	0.96
	> 1999	119	41	0.35	1.14	0.02–71.51	0.95
Regions	Norrbotten	129	45	0.35	Reference		
	Västerbotten	56	15	0.27	1.33	0.01–211.03	0.91
	Dalarna/Jämtland	36	6	0.17	0.21	0.00–305.97	0.68
	Finmark	102	30	0.29	0.50	0.01–38.98	0.76
	Nordland/Troms	59	24	0.41	1.23	0.01–213.52	0.93
	Trondelag/Hedmark	36	6	0.17	0.21	0.00–305.94	0.68
Country	Norway	197	60	0.31	Reference		
	Sweden	221	66	0.30	1.48	0.06–36.36	0.81
Herding year	2015–2016	67	17	0.25	Reference		
	2016–2017	68	20	0.29	3.21	0.42–24.73	0.26
	2017–2018	67	18	0.27	1.36	0.17–11.02	0.77
	2018–2019	72	25	0.35	6.83	0.89–52.29	0.06
	2019–2020	72	26	0.36	10.14	1.29–79.90	0.03
	2020–2021	72	20	0.28	0.81	0.11–6.15	0.84

OR, odds ratio; CI, confidence interval

Forcing the free-range feeding variable into the multivariate model, led to similar results for the prior two variables and a negative borderline significant association between free-range feeding and the presence of an IKC outbreak (OR = 0.17, *P* = 0.0996).

Changes in the occurrence of infectious keratoconjunctivitis, management, and access to veterinary assistance

Twenty-three (43%) of the respondents, nine from Norway and 14 from Sweden, stated that they had not observed any changes in the occurrence of IKC over the past 5 years. Six herders (11%) answered that the disease had decreased, and 12 (22%) stating that they did not know. Answers were distributed equally between Norwegian and Swedish respondents. Thirteen (24%) respondents, one from Norway and 12 from Sweden, stated that the number of IKC cases had increased. Comments on why IKC had increased included an increase in

Table 5 Results from multivariable model selection, where the observed presence of an outbreak of infectious keratoconjunctivitis in a herd was the outcome, based on 76 herders surveyed in the questionnaire regarding health and supplementary feeding of reindeer, 33 respondents from Norway and 43 from Sweden

Variable	Category	OR multivariate	95% CI	*P*-value
Feeding in enclosure	No	Reference		
	Yes	15.20	1.95–118.53	0.01
Herding year	2015–2016	Reference		
	2016–2017	3.65	0.41–32.78	0.25
	2017–2018	1.17	0.13–10.64	0.89
	2018–2019	7.40	0.81–67.70	0.08
	2019–2020	13.04	1.34–127.37	0.03
	2020–2021	0.80	0.09–7.28	0.84

OR, odds ratio; CI, confidence interval

supplementary feeding, stress, and climate change, which had caused warmer and wetter weather conditions.

Some direct quotes (opinions) from free text comments (voluntary to fill out) as to why IKC had increased:

> *"Limited access to natural pastures has led to feeding in enclosures the last couple of years."*
> *"Dust from the feed and close contact between the reindeer."*
> *"Warmer and wetter weather."*

Comments on why IKC had decreased focused on the use of better enclosures, better monitoring and awareness, and the reduction of stress in their reindeer.

Some direct quotes (opinions) from free text comments (voluntary to fill out) as to why IKC had decreased:

> *"We are more careful and aware, sick reindeer are isolated and we change clothes between handling sick and healthy reindeer."*
> *"It depends on how much stress there is, from mosquitos and from other sources, we also perform free-range feeding."*

Forty-one (76%) of the respondents, 13 from Norway and 28 from Sweden, usually acted when IKC was observed in their reindeer. Different measures were performed when clinical signs of IKC were last observed by the herders. Slaughter was the most common measure (n = 30; 56%), followed by grouping and isolation of affected reindeer (n = 20; 37%), for both countries (Fig. 7).

Three herders commented in the comment field that they performed eye washing. The majority of the respondents (n = 37, 70%) had not heard about any traditional treatments other than the slaughter of calves, eye washing, or other antimicrobial or antibiotic treatment administrated locally in the affected eye. Three herders also mentioned snuff in the eye as a treatment performed in the past.

Most of the respondents (n = 39, 74%), distributed equally between Norway and Sweden, did not think or did not know whether IKC had brought any economic consequences to them. Only 14 herders (26%), three from Norway and 11 from Sweden, stated that IKC had brought economic consequences. Thirty-eight of the respondents (14 from Norway and 24 from Sweden, a total 58% of the 76 respondents) were able to get the help they needed from a veterinarian. The other 42% answered that they could not get the help they needed from a veterinarian. The answers were distributed equally between Norwegian and Swedish respondents. The lack of knowledge of reindeer diseases among veterinarians was a frequently stated cause in the comment field.

Some direct quotes (opinions) from free text comments (voluntary to fill out) by respondents in the questionnaire, related to access to veterinary assistance were:

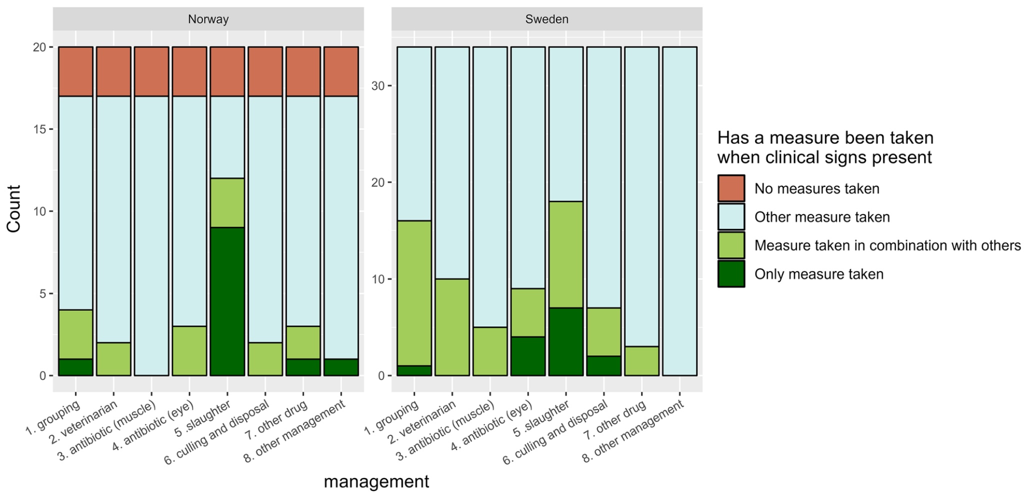

Fig. 7 Reported measures when observations of clinical signs of infectious keratoconjunctivitis were last made, from the 54 herders that had observed clinical signs of IKC over the past 10 years, surveyed in the questionnaire regarding health and supplementary feeding of semi-domesticated reindeer, with 20 respondents from Norway and 34 from Sweden

> *"It is difficult to get hold of a veterinarian with knowledge of reindeer."*
> *"Often the veterinarian does not know what to do, nor can they help to determine the cause of the sick reindeer."*
> *"I think I can get help if needed, but they are too far away and too expensive."*
> *"Lack of availability and knowledge."*

Finally, the Sámi traditional names for IKC mentioned in the comments were: "Golgii čalbmi" (tearflow), "Deiggan" (white eye), "Čalbme vihkki" (eye disease), and in Swedish "Blåöga" (blue eye).

Discussion

This study presents an overview of the current presence of IKC in Norway and Sweden, as reported by the reindeer herders, and confirms that IKC is frequently or sporadically observed. We also found a significant association between outbreaks of IKC and feeding when performed in an enclosure. However, free-range feeding seemed to have a potentially protective influence on IKC.

Presence and clinical signs of infectious keratoconjunctivitis

Our study revealed that a high proportion (n = 54, 71%) of herders had observed clinical signs of IKC, being mostly mild to moderately severe (images a and b in Fig. 1). This finding is in line with the previous survey performed in 2011 [34], where 55% of the herds reported signs of IKC. Clinical signs like "wet cheeks" are easily seen from a distance on freely grazing animals. This may represent a bias and reason why this is most often observed and reported in our study. Moreover, the reindeer herders might have learnt that this is an early clinical sign of IKC that needs further attention. Autumn and winter were the two seasons when most cases of IKC were reported. The animals are exposed to stress and are kept at a higher density during these seasons, which could potentially initiate IKC and its transmission. In the questionnaire survey performed in 2011 [34], the main seasonal appearance of the disease was from September to November, corresponding to autumn in our study. However, the potential shift towards IKC being mostly observed in winter may be associated with the reported increase in emergency feeding practices to prevent starvation which have taken place in recent years in both countries due to unfavorable weather conditions, as well as loss of pastureland because of competing land use [6, 7]. Yet, another potential explanation to differences in the seasonal appearance of IKC would be the different pathogens which could be involved, some of which may be more suited to different settings, herds, or seasons. For example, *Listeria monocytogenes* has been reported in outbreaks as a causative agent of IKC in Finland and are known to be associated with feeding silage [31]. In addition, co-infections can appear, with CvHV2 able to facilitate secondary infections caused by other pathogens, e.g., *Fusobacterium necrophorum*, an obligate anaerobic bacterium causing the disease necrobacillosis, as well as orf virus (ORFV; genus *Parapoxvirus*, family *Poxviridae*), which causes contagious ecthyma [32]. In a recent study, all three pathogens were identified during the same IKC outbreak, indicating that they may have interacted with each other or caused co-infections [31]. A novel gammaherpes virus (*Rangiferine gammaherpesvirus 1*) has recently been identified in reindeer in Norway, and a high seroprevalence of gammaherpes virus was found in reindeer in Finland, with unknown pathological potential in either country [25, 33]. Viruses from this group could play a part in the pathogenesis of IKC. Microbiological studies are, however, warranted to further clarify the pathological impact and potential associations between gammaherpes viruses and ocular disease in reindeer. One possible constraint is the responders' inability to distinguish between different causes, like trauma, insects or microbial agents leading to clinical signs similar to IKC. However non-infectious causes should affect single cases rather than outbreaks of IKC.

Supplementary feeding

Supplementary feeding was commonly performed by the herders, where 66 (87%) had fed their reindeer at sometime during the past 5 years, most often free-range feeding. Our results significantly point to the herding year of 2019/2020 as having the highest number of reports of herds with outbreak of IKC and being the time when most of the herders (80%) had performed supplementary feeding. This is in line with several sources reporting this winter as catastrophic because of the lack of availability of winter pastures, causing many herders to apply for economical support because of costs related to supplementary feeding [6]. Our results are in contrast with the previous survey in 2011 [34], where environmental factors, e.g., supplementary feeding, were not associated with clinical signs of IKC, suggesting there has been an increase of outbreaks of IKC associated with feeding over the last decade. However, in the previous study, the distribution of respondents between Norway and Sweden was different, with only 15 respondents from Sweden (24%), limiting the comparability of the results. The majority of respondents in our survey stated that they had not observed any changes in the occurrence of the disease. In Sweden, however, the number of herders reporting an increase was almost as many as reporting a decrease, whereas this was not the case in Norway. This could potentially mean that there are differences between the countries, and that IKC might have increased in Sweden. One explanation for this could be that herders in Sweden more commonly fed calves in enclosures compared to Norway, where feeding in enclosures was less common overall (Table 3).

The present study showed a trend of a higher proportion of calves reported with clinical signs of IKC, than adults. Also, herders with smaller groups of reindeer (≤100) seemed to be reporting a higher proportion of affected animals than herders with larger herds. In addition, our results revealed that smaller groups of reindeer (<300) were more often fed in enclosures compared to larger (>300) groups (Table 3). Several herders, however, commented that they had observed isolated cases of IKC but had not experienced an outbreak. This could mean that the herder's ability to detect IKC has improved rather than there has been an increase in outbreaks of IKC.

Association between feeding and outbreak of infectious keratoconjunctivitis

Another possible explanation for why feeding in enclosures was associated with reports of outbreak of IKC in a herd could be that calves and young reindeer are more sensitive to stress and susceptible to infection and are more likely to be fed whole rations in enclosures compared to adult reindeer and the whole winter group. This is in line with previous studies that point to management factors, increased animal density, stress, and challenging hygienic conditions as risk factors for transmission and outbreak of IKC, primarily affecting calves and young reindeer [21–23]. The separation of mother and calf further adds to stress that could lead to reactivation of CvHV2 [23, 24]. Hence, we find it likely that the potential increase in the animals' stress levels, combined with the increased contact between infected and immunologically naïve animals, could have a greater impact on the occurrence of IKC than supplementary feeding itself. The density of animals in an enclosure is higher compared to free-range, despite the fact that herders reported a smaller group size in total in enclosures. While for free-range animals, it is easier to keep better hygienic conditions, with a regular change of feeding site, access to clean snow or water, and where natural pasture is not restricted to the same extent as in an enclosure [6, 14]. However, in this study, questions about the enclosures such as animal density, size, and topography were not included, which are factors that could play a role in the development of infectious diseases like IKC. This needs to be further studied, especially when it is getting more challenging to keeping reindeer in enclosures due to climatic changes [1].

In our study, dust from the feed was mentioned in the comments as a contributing factor for IKC. Early studies suggest that both summer and autumn, as well as spring, were seasons where clinical signs of IKC could be observed. This was reported mainly in forest reindeer because of corralling in dusty environments and heavy loads of insects leading to foreign bodies and corneal lesions, and eyelid irritation (caused by insect bites) as initial causes, paving the way for secondary infections, leading to IKC. The herding conditions for mountain reindeer differed and could be used as an argument as to why they seemed to have fewer cases of infected eyes in this herding district type [18, 19]. However, another study reported an outbreak of IKC in calves supplementary fed during winter, with management factors causing stress and feed particles from pellets being suggested as the main contributors leading to secondary infections and, consequently, IKC [20]. The present research still addresses the disease as multifactorial, where stress (associated with herding, gathering, transport, and translocation to new environments), environmental conditions and management factors are associated with IKC. Dust and other sorts of trauma can harm the eye without being the direct cause of IKC. In addition, CvHV2 has recently been established as a primary, causative agent, while other agents, like *Chlamydia*, and their role in the pathogenesis of IKC need to be further clarified [21–23].

Unexpectedly, free-range feeding had a non-significant, but negative relationship with the presence of an outbreak of IKC. Thus, feeding on free-range could potentially be protective against the presence of an outbreak of IKC in a herd. Our results revealed that larger groups of reindeer (>300) and the whole winter group were most often free-range fed (Table 3). Access to natural pastureland, better hygienic condition due to larger areas to utilize, and no additional stress because of handling and separation of female and calf when free-ranging could be potentially important prophylactic factors against an outbreak of IKC. In addition, nutritional status and general condition are crucial for the survival of the animals. Supplementary feeding, conducted in the right manner, such as with a gradual introduction to the diet under good hygienic conditions, and with high quality feed suited to reindeer, contributes to increased body weight and general health condition. Consequently, better resilience against stress and diseases, increased reproduction success, and a decrease in calf mortality is expected and has been documented [10, 35].

However, it should be noted that this information regarding season and location in association with IKC could be biased, since most reindeer are handled and inspected at close range due to management practices during winter and autumn. Reindeer kept in enclosures are also observed more closely, thus it is easier to detect signs of IKC compared to free-range reindeer, which limits the interpretation of our results. Future studies investigating the relationship between the presence of outbreaks in an enclosure compared to free-range outbreaks in more depth and on an individual animal-level are therefore warranted. This could be investigated by performing in-depth interviews specifically addressing these issues.

Management of infectious keratoconjunctivitis

Forty-one (76%) out of the 54 respondents who had experienced IKC usually took measures to address it, with the most commonly practiced action being slaughter, but antibiotic treatment and contact with a veterinarian was also reported. Furthermore, herders reported that reindeer with IKC were isolated from the rest of the herd (Fig. 7). This is in contrast to the results in the previous study by Tryland et al. [34], where none of the herders isolated affected reindeer. This change in management might be due to increased awareness and knowledge of the disease. We also noted that several herders reported a general lack of access to veterinarians with thorough knowledge of reindeer diseases as a reason for not getting adequate help from a veterinarian. Although an increase was observed, from 7 (12%) to 12 (22%) of the respondents in the previous survey from 2011 and in our survey, respectively, it may still be regarded as uncommon to contact a veterinarian when IKC appears. Antibiotic treatment administered locally was reported to be used to a higher extent than systemic administered antibiotics. There are no approved eye ointments for reindeer, so all use is off-label [36, 37].

Most of the respondents from Norway were from Finnmark (51%) but the reported herd size in Vest-Finnmark was high, with herd sizes of over 2000 reindeer. In Norway, 70% of all semi-domesticated reindeer and 75% of all reindeer owners are located in Finnmark (Vest- and Øst-Finnmark included), and the average number of reindeer is about 65 per owner. However, 80% of the owners in this area have less than 50 reindeer, and the highest proportion of small herd size is in Vest-Finnmark. In addition, the reindeer number of each reindeer herding group (siida-share) varies within each region [8]. This might influence our results and the respondents might be less representative of that specific region. Most of the respondents from Sweden were from Norrbotten (56%), where the stated herd size varied significantly and may not be representative of general reindeer owners in the region. There are more owners and reindeer in Norrbotten, mostly made up of small enterprises with fewer reindeer per herder than in Västerbotten, Jämtland and Dalarna [8].

We know that there are great variations between regions within each country with regards to geography, herding area, herd size, number of reindeer owners and herders, other land users, and density of different predators, all affecting profitability and production. Therefore, we investigated differences between regions in each country when possible. There are also differences in reindeer herding between Norway and Sweden (e.g., differences in governance, economic support system, geography, herding area, predator management policies, legislation, access to veterinarians, and management practices) that could influence our results, considering our relatively few respondents. However, there are also similarities, for example, some mountain districts in Sweden migrating to Norway for summer pasture. In addition, reindeer pastoralism in Fennoscandia faces the same kind of challenges due to climate change and competing land use in the reindeer herding area [8]. Our findings showed no association between the appearance of IKC and herd size, region, or country.

Limitations

Besides the potentially questionable geographical representativity of our respondents, the population of reindeer herds is relatively small in both countries, and of this, we only got an approximately 5% response rate in each country. Since we found an equal distribution of data between the two countries, we decided to present the data as one population (Norway and Sweden together), and most results are presented using a descriptive approach. The relatively small number of respondents could be the reason why this study potentially lacked the power to reveal certain associations, such as the non-significant negative relationship between outbreaks of IKC and supplementary free-range feeding. Another possible challenge may be recalling bias, as we go back 5–10 years for many of our questions. In addition, potential selection bias should also be considered, since herders more experienced with IKC and/or supplementary feeding might have been more motivated to respond to our survey. This could lead to several biases in the data. For example, herders responding to the questionnaire could have observed IKC more often than the general herder and therefore made more measures to stop the transmission of the disease. In addition, the respondents might have recognized early clinical signs more than general herders or may have had more experience in feeding their animals. Also, clinical signs of IKC are not specific for infectious agents and could also be caused by insects and trauma. Therefore, we cannot rule out that the reported cases of IKC in our study might be of a non-infectious origin. However, the questions in the questionnaire pointed out that we are interested in outbreaks, not single cases. Because the study was retrospective and covered several years, we could not ask for detailed information about where and when feeding was practiced in relation to outbreaks of IKC, and there was a lack of information at the animal level. Therefore, we could only investigate associations between outbreaks and feeding on a herd level and not on an individual level. Thus, we may have missed information on whether the same animals that have experienced an outbreak, or had been observed with IKC, had also been supplementary fed or not, and in what environmental conditions. Follow up studies, such as in-depth interviews, to investigate this closer and, if possible, to do so at an individual level would further clarify the relationship between IKC and feeding in enclosures compared to free-range.

Conclusions

Clinical signs of IKC were commonly observed at a herd level, and the main seasonal appearance of IKC were during the autumn and winter. Mild to moderate clinical signs were most commonly observed, and slaughter, followed by isolation of affected animals from the herd, was the most common measure taken by the herders. This could indicate an increased awareness and knowledge of the disease today compared to a decade ago. However, herders were reluctant to contact a veterinarian and a common reason mentioned was that veterinarians had restricted knowledge about reindeer diseases. In addition, feeding in enclosures, which is performed mainly during the winter season, was associated with an outbreak of IKC in a herd, whereas free-range feeding could potentially be protective. The known catastrophic herding year 2019/2020, which had inaccessible winter pastures, was significantly associated with the presence of an outbreak of IKC in a herd, as well as being the herding year where most herders had performed supplementary feeding. Results imply that infectious diseases like IKC are associated with the feeding situations, affecting calves especially. In-depth studies focusing on the animal level could further clarify these associations.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13028-023-00694-x.

Additional file 1: The Questionnaire in Swedish.

Additional file 2: The Questionnaire in Norwegian.

Additional file 3: The Questionnaire in North Sámi.

Additional file 4: Specified herd size per reindeer herding region in each country from 76 respondents, 33 from Norway and 43 from Sweden.

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Author contributions

MT and YP secured funding for the study and MT initiated the collaboration of the study between Norway and Sweden. KWP, HR, JSR, YP, JF, MT, IHN and AO planned and designed the questionnaire. KWP and HR distributed the questionnaire in Sweden, and JSR in Norway. KWP, JB, and JF organized the data. JB conducted modelling, statistical analysis, and produced all the figures in the results section. JB, JF and KWP performed the epidemiological analysis. KWP wrote the first draft of the manuscript and all authors contributed to discussions and interpretation of results, as well as reading and approving the final version of the manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request. The questionnaire, for Swedish, Norwegian, and Northern Sámi, used in the study is to be found in additional files (Additional files 1, 2, 3).

Declarations

Ethics approval and consent to participate

A permit from the Norwegian Social Science Data Services, Approval No. 457339, was obtained. Similar declarations were not required in Sweden, based on instructions from the Swedish Ethical Review Authority. The study did not contain questions interfering with personal integrity, or animal experiments, therefore this study did not require official or institutional ethical approval.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Prior publication

Data has not been published previously.

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First report of a parapoxvirus red deer infection in reindeer (*Rangifer tarandus tarandus*): clinical presentation and full-genome characterization

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Abstract
In September 2023, five semi-domesticated reindeer calves (*Rangifer tarandus tarandus*) from Norrbotten County, Sweden, displayed clinical signs resembling contagious ecthyma. Samples were collected from the lesion sites, including the skin of the muzzle, eyelids, and oral mucosa. The samples were analysed via real-time PCR (qPCR) for parapoxviruses (PPV) and cervidpoxviruses (CvPV). Both viruses were detected in samples from several calves. Full genome sequencing of the PPV strain 23-MIK191411 revealed close similarity to the parapoxvirus red deer (RDPV) strain HL953 from a red deer (*Cervus elaphus*) in Germany but with a novel 2,187 bp insert in the right terminal third of the genome. This insert carried two open reading frames (ORFs) that, while divergent, presented sequence homology with several other PPVs. Analysis of amino acid differences relative to the sequence of the RDPV HL953 strain revealed that proteins implicated in host interactions and virulence presented the greatest differences. Thus, comparative sequence analysis indicates that an RDPV has recombined with an ancestor of 23-MIK191411 and adapted to the reindeer host. This study represents the first detection of RDPV, with a unique insert likely originating from an unknown PPV in reindeer, indicating its emergence beyond the red deer host range. Clinical signs are consistent with those caused by other poxviruses, including CvPV also detected in the investigated animal group, making it difficult to diagnose the causative agent solely via clinical observation. In the sequenced sample, RDPV was confirmed as the predominant variant. These findings underscore the importance of molecular diagnostics for accurate pathogen identification and highlight the need for continued health surveillance of reindeer. Further investigations are needed to determine the clinical impact of RDPV in reindeer.

Keywords Eurasian tundra reindeer, Full genome, Host adaptation, Parapoxvirus, P*arapoxvirus reddeerpox*, RDPV

†Karin Wallin Philippot and Mikael Leijon eqally contributed in this work.

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Introduction

The genus of parapoxviruses (PPVs), a member of the family *Poxviridae* and subfamily *Chordopoxvirinae*, causes contagious pustular dermatitis and stomatitis in various host species. This genus is currently divided into five recognized species: *Parapoxvirus orf* (orf virus, ORFV), *Parapoxvirus bovinestomatitis* (bovine papular stomatitis virus, BPSV), *Parapoxvirus pseudocowpox* (pseudocowpox virus, PCPV), *Parapoxvirus sealpox* (seal parapoxvirus, GSEPV), and *Parapoxvirus reddeerpox* (parapoxvirus red deer, RDPV) [1]. In addition, a related, unclassified horse parapoxvirus was recently isolated from horses with dermatitis in Finland [2, 3]. All PPVs are known or considered zoonotic, although the host range for the specific PPV species varies. ORFV is considered to have a broad host range and is distributed worldwide, causing contagious ecthyma (CE) (*syn.* contagious pustular dermatitis, scabby mouth) in domestic sheep and goats. Notably, ORFV has also been detected in naturally infected domestic and wild ruminants, such as reindeer, caribou, muskoxen, Alaskan mountain goats, and camelids [4–7]. Bovine papular stomatitis virus and PCPV infect mainly cattle, and RDPV has previously not been detected in species other than red deer (*Cervus elaphus*) [4, 8, 9].

Clinical signs of RDPV, mainly scabs on velvet antlers, ears, muzzles, and lip margins, were first described in farmed red deer in New Zealand (NZ) in 1985–1986 [10]. Red deer were imported to NZ from Europe in 1851, and just before the first reports of clinical signs, red deer farming had undergone a period of intensification [9]. The first report of RDPV outside of NZ was in wild red deer with severe stomatitis in Italy from 2008–2009. The virus is closely related to the RDPV found in NZ [11]. In Germany, a similar virus was found in tonsil swabs from apparently healthy red deer hunted in the Bavarian Alps, confirming RDPV as a separate species within the PPV genus [8]. In addition, the results suggest that subclinical infection in animals could play a role in disease dynamics. Sheep experimentally infected with RDPV have only displayed mild clinical signs, similar to lesions induced by ORFV [4, 9].

Chordopoxviruses generally consist of a core region of 88 well-conserved genes [12, 13]. Genus- or species-specific genes are located outside the core region and are of particular importance to virulence and virus–host interactions. To date, only two isolates of RDPV, RD86 and HL953, have been successfully propagated in cell culture, and only the full genome of RDPV HL953 is available [8, 9].

In semi-domesticated reindeer (*Rangifer tarandus tarandus*), ORFV and PCPV have been described as the causative agents of outbreaks in Fennoscandia [7, 14–17]. Clinical signs include severe crusty lesions, especially on the muzzle and in the oral mucosa. These lesions may lead to secondary bacterial infections, impairing the ability to eat, and consequently, starvation and mortality [7, 14, 16, 18–20]. In addition, a cervidpoxvirus (CvPV) was first described in semi-domesticated reindeer from Norway and Sweden in September 2023, inducing somewhat similar clinical signs as PPV, such as crusty lesions around the eyes and genitalia [21].

Infectious diseases in reindeer are driven by multiple factors, including climate change and the loss of grazing land due to habitat fragmentation [22, 23]. These developments have increased the need for supplementary feeding, leading to intensified husbandry practices, increased animal density, and stress [24]. Cumulatively, these changes increase the exposure and susceptibility of reindeer to pathogens and exacerbate the spread of existing diseases [18, 24–27].

The occurrence of RDPV-associated disease in semi-domesticated reindeer in Sweden, as described in this study, exemplifies cross-species transmission and viral host adaptation. Moreover, reindeer may serve as reservoirs for zoonotic parapoxviruses, with potential implications for both reindeer health and humans in close contact. These findings underscore the need for continued health surveillance in reindeer populations. This study aimed to document the clinical signs associated with RDPV and to genetically characterize the virus at the full-genome level to enhance the understanding of its origin and potential implications for reindeer health.

Methods

Study herd and sampling of animals

The diseased reindeer came from a reindeer herd consisting of approximately 2,000 reindeer herded year-round in the taiga region of Norrbotten County, Sweden. The herders performed winter feeding on natural pastures when needed. The herd was assembled multiple times per year: during summer for calf earmarking, in autumn for the selection of adult males for slaughter, and from November to December, primarily for the slaughtering of calves. Animals showing clinical signs of disease or any health issues, including signs of eye diseases, were consistently sorted for slaughter, a practice the herders believed to have long-term positive effects on herd health.

Historically, three red deer farms were located within the pastureland of the herding district, overlapping with reindeer grazing areas. These farms were phased out ten to twenty years ago; however, one farm had been repurposed for sheep farming. For several years, herders observed crusts and skin lesions on the heads of individual calves, yearlings, and some adult reindeer, including a castrated male, particularly affecting the muzzle and eyelids. With experience, herders have become more proficient in identifying lesions. However, crusts and lesions in the skin around the eyes and muzzle were believed to be associated primarily with heavy insect activity from July to September.

During a herd gathering in September 2023, ten out of approximately 150 reindeer were observed with skin lesions and crusts on the head, primarily on the muzzle and eyelids. Five calves were isolated and examined further. The calves were sampled by gently rubbing an eSwab™ (Copan Diagnostics, Brescia, Italy) under and on crusts; on lesions on the muzzle (Calf 2 and 5); over the conjunctival fornix of eyes with affected eyelids (Calves 1, 3, 4 and 5); and on lesions in the oral cavity (Calf 5) (Table 1). Sampling was conducted in accordance with institutional and national guidelines (see Ethics statement). Calf 5 was the most severely affected animal with an affected general appearance and was therefore euthanized and necropsied. Tissue samples from the eyelids, oral mucosa, muzzle, spleen, and one submandibular lymph node were collected from Calf 5. Hygienic precautions were implemented to prevent cross-contamination between animals and from the environment. Disposable gloves were changed between each animal, and all samples were collected and handled individually in sterile containers. The samples were packed in separate bags and sent at 4 °C to the Swedish Veterinary Agency (SVA) and the Norwegian Veterinary Institute (NVI).

Histopathology

Histopathology was performed on tissue samples from Calf 5. The tissue samples were fixed in 10% neutral buffered formalin, embedded in paraffin, cut at approximately 4 µm, and mounted on glass slides. All the tissue sections were stained with hematoxylin and eosin (H&E) and coverslipped in an automated Dako Coverstainer (Agilent Technologies, Santa Clara, CA, USA). The recommended standardized staining protocol from the vendor was used.

Real-time polymerase chain reaction

Nucleic acids were extracted from swab samples collected from lesion sites on the five calves via the IndiMag Pathogen Kit (INDICAL BIOSCIENCE GmbH, Leipzig, Germany) and subsequently analysed via real-time PCR (qPCR) for the presence of PPV and CvPV as previously described [21, 28]. For PPV, the forward primer PPV up 5'-TCGATGCGGTGCAGCAC-3', reverse primer PPV do 5'-GCGGCGTATTCTTCTCGGAC-3', and the probe PPV TMGB 5'-FAM-TGCGGTAGAAGCC-MGB-3' targeting the B2L gene were used [28]. For CvPV, forward primer reVir-F 5'- TCTCCAACCATTCCCTGAAC-3', reverse primer reVir-R 5'- GGTGCRCCTGTAAGAAAGAG-3', and probe reVir-pr 5'-FAM- ACCATTTGTTACCGCTTGCA-BHQ1-3' targeting the virion core protein gene were used [21]. In brief, total nucleic acids from 0.2 ml of swab mixture were extracted and eluted in 0.1 ml of AVE buffer according to the manufacturer's instructions. Real-time PCR for PPV was performed with PerfeCTa qPCR Toughmix (Quantabio, Beverly, MA, USA) in a total reaction volume of 15 µl using 2 µl of sample extract with 0.5 µM of each primer and 0.1 µM of the probe. Real-time PCR for CvPV was performed with Brilliant III Ultra-Fast QPCR Master Mix (Agilent) using 0.9 µM of each primer and 0.6 µM of the probe and 5 µl of sample. Both PCRs were run for 45 cycles with annealing at 60 °C. A clear curve with a cycle threshold (Ct) value $\leq$ 40 was considered positive. Both qPCR assays have been validated and show no cross-reactivity [21].

Table 1 Results from real-time PCR analysis for parapoxvirus (PPV) and cervidpoxvirus (CvPV) in five reindeer calves

Calf ID (swabbed lesion site)	PPV, (Ct value)	CvPV, (Ct value)
1 (conjunctiva)	Positive (34.0)	Negative
2 (muzzle)	Negative	Positive (23.8)
3 (conjunctiva)	Negative	Positive (35.8)
4 (conjunctiva)	Negative	Positive (23.3)
5 (conjunctiva)	Positive (19.6)	Positive (29.2)
5 (oral mucosa)	Positive (18.4)	Positive (34.9)

Ct = cycle threshold. A clear curve with a Ct value $\leq$ 40 was considered positive

Next-generation sequencing and bioinformatics

Library preparation and metagenomics were carried out at the Clinical Genomics Stockholm facility at the Science for Life Laboratory (Stockholm, Sweden), where 96.5 M 2 × 150 nucleotide paired-end reads were acquired via a NovaSeq X sequencer (Illumina, Inc., San Diego, CA, USA). The paired-end reads were quality trimmed via Trimmomatic v. 0.39 [29] with a sliding window of four nucleotides, and an average quality score of 15 was obtained. The trimmed reads, including singletons, were assembled via SPAdes v. 3.15.4 in standard mode [30]. The assembled contigs were then classified via DIAMOND v. 2.0.9 [31] with the NCBI nr database of GenBank release 248 and the corresponding NCBI taxonomy databases. The last 384 nucleotides of RDPV HL953 (accession NC_025963.1) were identical to the inverted repeat of positions 670–1053 of the SPAdes de novo assembled contig obtained from the strain 23-MIK191411 data. Inverted repeats are expected at the termini of PPVs, but short-read assembly is unable to account for this because all reads originating from the end repeats will end at a single end of the contig. Therefore, the following approach was used. The de novo assembled contig was merged with the last 384 nucleotides of NC_025963.1. Read mapping was then carried out with random selection if a read mapped to more than one site. This ensured equal mapping to both ends. Finally, a consensus sequence was extracted from the map and subjected to the criterion that at least 10 reads should cover each position. A coverage of less than 10 × was indicated with an 'N' in the sequence in the interior and was cropped if it was at the end of the sequence. This procedure, as well as the detection of inverted repeats, was carried out with CLC Genomics Workbench v. 24.0.1 (QIAGEN, Aarhus, Denmark). Annotation was carried out with PROKKA v1.14.5 [32] via RDPV HL953 with the GenBank accession NC_025963.1 as a reference. In a few cases, in which there were alternative start codons, the prediction of PROKKA and the open reading frame (ORF) given in NC_025963.1 differed, and a longer ORF was selected.

Phylogenetic analysis

The parapoxviruses (with GenBank accession shown within parentheses), RDPV (NC_025963), reindeer RDPV (PV021465), BPSV (NC_005337), PCPV (NC_013804), ORFV (NC_005336), and GSEPV (NC_035188) were subjected to maximum likelihood phylogeny analysis using the CLC Genomics Workbench. Ten parapoxvirus core proteins (the denotation of the Vaccinia virus Copenhagen strain homologues shown within parentheses): poly-A polymerase catalytic subunit (E1L), DNA polymerase (E9L), RNA polymerase associated protein RP94 (H4L), RNA polymerase subunit RPO132 (A24R), IMV protein VP55 (H3L), DNA topoisomerase type 1 (H6R), EEV envelope phospholipase (F13L), serine/threonine kinase (F10L), DNA helicase (A18R), and RNA helicase (I8R) were individually aligned and then concatenated before being subjected to maximum likelihood calculation using a neighbour-joining starting tree with the WAG protein substitution model. Four substitution rate categories were used. The gamma distribution parameter was set to 1. The bootstrap analysis utilised 1000 replicates.

The same parapoxviruses listed above were also used to carry out recombination analysis using the RDP software version 5.76 beta [33]. The full viral genome sequences were aligned with the CLC genomic workbench, and the alignment was subsequently analysed by RDP5 using the default set of analyses.

Results

Clinical presentation

During a gathering in September 2023 to select adult males for slaughter, several reindeer calves displayed clinical signs of disease. Ten out of approximately 150 reindeer were observed to have multiple skin lesions and crusts on the head, primarily on the muzzle and eyelids, and some exhibited ocular discharge. Five calves with the most extensive clinical signs were isolated for clinical examination and sampling. All these calves exhibited multiple crusts and skin lesions around one or both eyes, the muzzle, or elsewhere on the head. Three calves (Calves 1, 3, and 4) had mild to moderate lesions on the eyelids of a single eye, crusts with pus, and moderate epiphora. Calf 2 had a focal lesion on the muzzle, one lesion dorsally from the muzzle, and no eyelid lesions (Supplementary Fig. 1). Calf 5 appeared generally affected upon examination, was euthanized and necropsied, and an oral mucosal swab was later selected for sequencing. Multiple crusts and lesions were observed on the eyelids around both eyes, on the muzzle, and on the lips. Similar and proliferative lesions were detected in the oral cavity on mucous membranes, including the hard palate, tongue, and gingiva (Fig. 1). In addition, one submandibular lymph node was mildly enlarged with hyperemic areas. The body condition was normal.

Histopathology of tissue samples from Calf 5

In the oral cavity, there was an ulceration in the epithelium, and in the adjacent epithelium, vacuolar degeneration of keratinocytes was observed. In the connective tissue below the ulceration area, there was moderate infiltration of inflammatory cells, with a dominance of

Fig. 1 Crusts and proliferative lesions on the muzzle, in the oral cavity, on mucous membranes, and on both eyelids of the most severely affected calf (Calf 5) among five isolated semi-domesticated reindeer calves (*Rangifer tarandus tarandus*). The animals originated from a gathering of approximately 150 reindeer in September 2023 in Norrbotten County, Sweden. Photo: Veronica Lengquist, SLU

lymphocytes and plasma cells (Fig. 2A). The epidermis of the muzzle was focally ulcerated. In the adjacent epidermis, keratinocytes were necrotic or swollen with signs of degeneration. In the area of ulceration, there was abundant infiltration of inflammatory cells, with neutrophils dominating the epidermis and lymphocytes, plasma cells, and macrophages in the underlying dermis (Fig. 2B-C). Examination of the eyelid revealed a hyperplastic and hyperkeratotic epidermis close to the conjunctiva, with moderate to occasionally abundant infiltration of inflammatory cells and a dominance of lymphocytes and plasma cells in the underlying dermis (Fig. 2D). Abundant reactive lymphatic follicles with germinal centers were observed in the lymph node. The lymph nodes contained numerous apoptotic cells and cavities that were believed to have contained apoptotic cells (Fig. 2E). The spleen contained many reactive lymphatic follicles with germinal centers and relatively extensive apoptosis (Fig. 2F).

Real-time polymerase chain reaction of parapoxvirus and cervidpoxvirus

Samples from five reindeer calves were analysed for PPV and CvPV by qPCR (Table 1). Two of the calves were positive for PPV, with the lowest Ct values, indicating the highest viral load, in the samples from the eyelid and oral mucosa of Calf 5. Four calves were positive for CvPV, indicating that both viruses were present in the herd. Both viruses were detected in Calf 5.

Whole-genome sequencing

A 143,682 bp sequence of the reindeer RDPV isolate 23-MIK191411 (hereafter referred to as reindeer RDPV; GenBank accession PV021565.1) was assembled directly from nucleic acid extracted from an oral mucosal swab of Calf 5 without virus isolation or cultivation. All, except for a 384 nt portion (see Methods), of the sequence was obtained by de novo assembly with read coverage above 500x. No sequences of CvPV were detected in the sample, indicating a lower viral load than that of PPV.

Sequence comparison with RDPV HL953

The RDPV HL953, 139,981 bp in length, with the GenBank accession NC_025963.1, is the current reference sequence for the RDPV. The reindeer RDPV described in this study is closely related to RDPV HL953, and the following sections detail the genomic differences between the two isolates. The GC contents are 64.9% and 65.0% for reindeer RDPV and RDPV HL953, respectively, whereas the reindeer RDPV sequence is 3,701 bp longer than RDPV HL953. This difference is mainly due to a 2,187 bp insert in the right terminal third of the sequence (Fig. 3), and more of the right and left terminal regions are determined in reindeer RDPV, including parts of the inverted terminal repeats. All 130 ORFs predicted in RDPV HL953 are also present in the reindeer RDPV. In addition, using reindeer RDPV ORF numbering, two left terminal ORFs, ORF1 and ORF2, are predicted in reindeer

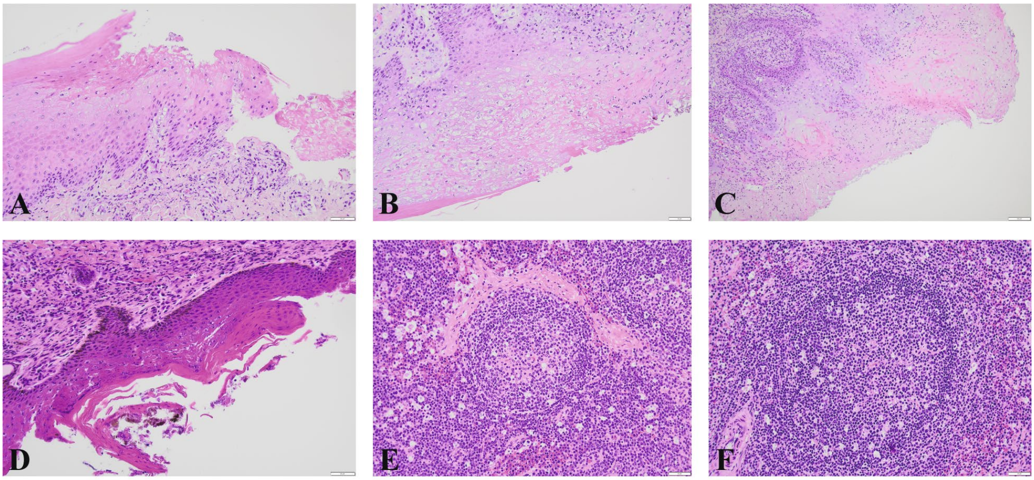

Fig. 2 Histopathological findings in tissue samples from the most severely affected reindeer calf (Calf 5). The samples were fixed and stained with hematoxylin and eosin (H&E). Scale bar = 50 µm unless otherwise indicated. **A** Ulceration in the epithelium, with swollen and necrotic keratinocytes, in the oral cavity. **B** Necrotic area in the epidermis of the muzzle. The presence of inclusion bodies was not confirmed but cannot be entirely excluded. **C** Hyperplastic epidermis (to the right) of the muzzle with swollen, degenerated keratinocytes and necrosis. Infiltration of inflammatory cells in the epidermis and dermis. Scale bar = 100 µm. **D** Hyperkeratotic epidermis and infiltration of inflammatory cells in the underlying dermis in eyelid tissue. **E** Reactive lymphatic follicle with apoptotic cells in the surrounding lymph node. **F** Reactive lymphatic follicle with scattered apoptotic cells in the spleen. High-resolution images are provided in the supplementary materials (Supplementary Fig. 2A-F)

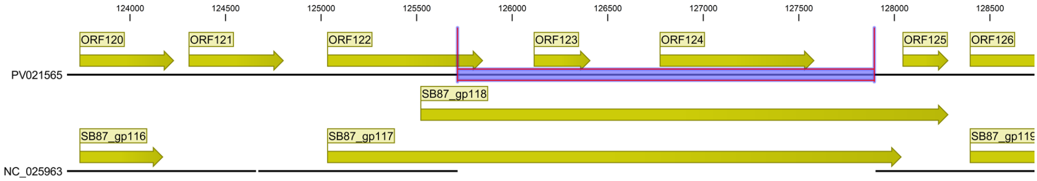

Fig. 3 The region of the sequence alignment of parapoxvirus red deer (RDPV) HL953 (bottom) and reindeer RDPV isolate 23-MIK191411 (reindeer RDPV) (top), showing the insert region, with the insert marked in blue. Open reading frames (ORFs) are indicated with yellow bars with ORF numbers for the reindeer RDPV and with locus tags (SB87_gp###) for the RDPV HL953. The two sequences are marked by their GenBank accession numbers. At the left end, ORF120/SB87_gp116, where ORF120 is longer due to a mutation in the stop codon, is shown. The hypothetical protein ORF121 is not annotated in RDPV HL953. ORF122 and SB87_gp117 are putative GM-CSF/IL-2 inhibitory factors, where for ORF122, a large part is altered by the insert. ORF123 and ORF124 (the latter of which is a putative NF-κB inhibitor) are contained in the insert. For RDPV HL953 (without an insert), the corresponding putative GM-CSF/IL-2 inhibitory factor (SB87_gp117) has a large ORF overlap with SB87_gp118 — a feature uncharacteristic of poxviruses — which encodes a hypothetical protein. Finally, at the right end of the reindeer RDPV genome, ORF125 encodes a closely related but truncated version of SB87_gp118

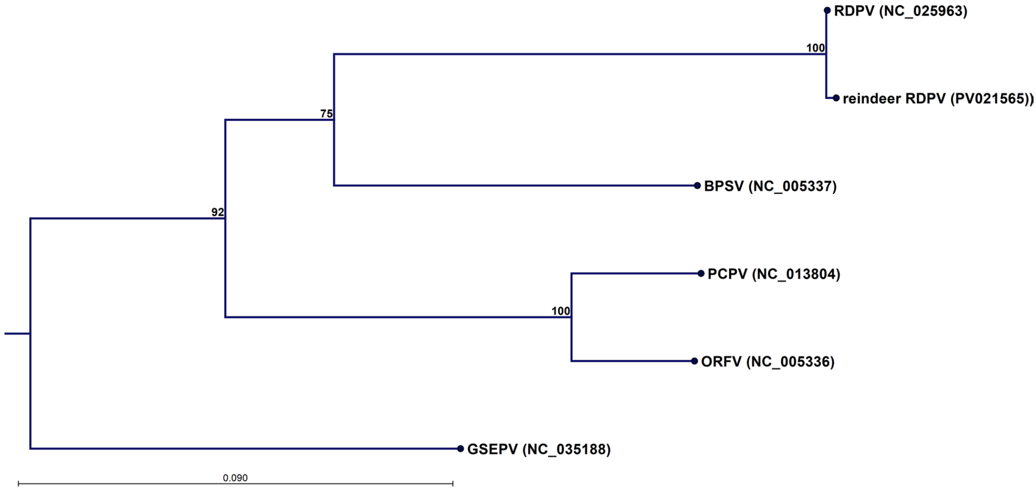

Fig. 4 Maximum likelihood phylogenetic tree based on the amino acid sequence of the concatenated alignments of the ten parapoxvirus core proteins: poly-A polymerase catalytic subunit, DNA polymerase, RNA polymerase associated protein RP94, RNA polymerase subunit RPO132, IMV protein VP55, DNA topoisomerase type 1, EEV envelope phospholipase, Serine/Threonine kinase, DNA helicase, and RNA helicase for isolate 23-MIK191411 (reindeer RDPV) and various other parapoxviruses (BPSV = bovine papular stomatitis virus, ORFV = orf virus, PCPV = pseudocowpox virus, GSEPV = seal parapoxvirus, and RDPV = parapoxvirus red deer)

RDPV, where ORF1 shares approximately 50% nucleotide sequence identity with ORF1s predicted in other PPVs. Three ORFs, ORF17, ORF30, and ORF121, carry the corresponding stop and start codons but were not predicted in RDPV HL953. A codon deletion in ORF17 relative to the sequence in RDPV HL953 provides some evidence that this ORF may be expressed. Similarly, ORF121 has a 4-codon insert relative to the unannotated sequence of RDPV HL953. The 2,187 bp insert introduces two ORFs, ORF123 and ORF124, with ORF124 tentatively encoding an NF-κB inhibitor. Thus, in total, 137 ORFs are predicted in reindeer RDPV. The amino acid sequences of the 130 commonly predicted ORFs are identical for 55 ORFs (42%) and have fewer than four amino acid differences for 115 ORFs (88%). Three ORFs, ORF25, ORF75, and ORF126, were identified as hypothetical proteins in RDPV HL953, but their sequence homology suggests that these ORFs are putative NF-κB inhibitors. Likewise, sequence homology suggests that ORF29, designated as a hypothetical protein in RDPV HL953, might be an ERK1/2 activator protein.

Phylogenetic analysis

Figure 4 presents the maximum likelihood phylogeny based on the concatenation of ten proteins from the conserved PPV core genome and shows that the reindeer RDPV is highly similar to RDPV HL953. The RDPVs form a clade together with their closest relative BPSV, separate from the clade formed by PCPV and ORFV. The most genetically divergent PPV is the GSEPV.

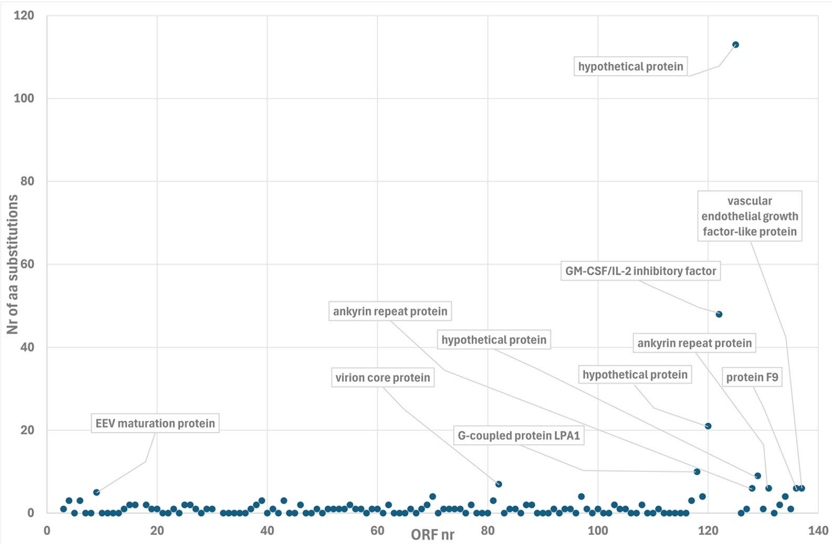

Fig. 5 The number of amino acid substitutions in parapoxvirus red deer from the reindeer isolate 23-MIK191411 (reindeer RDPV) relative to RDPV HL953 for each common open reading frame (ORF) along the sequence. Open reading frames with five or more amino acid alterations are indicated. Differences in length are considered alterations except when they are caused by alternative start codons available in both sequences

In Fig. 5, the number of amino acid substitutions per ORF in reindeer RDPV relative to RDPV HL953 is shown along the sequence for each of the 130 common ORFs. The number of substitutions is highest at the termini of the sequence, especially at the right terminal. ORFs with five or more substitutions are indicated. The only ORFs reaching this level at the left terminal and central regions are putatively encoding an extracellular enveloped virus maturation protein and a virion core protein homologous to the vaccinia virus protein A4, respectively. At the right terminal region, the following ORFs with five or more amino acid substitutions putatively encode two of three ankyrin repeat proteins in this region: a vascular endothelial growth factor-like protein, a protein homologous to the vaccinia virus protein F9, a GM-CSF/IL-2 inhibitory factor, and a G-coupled protein LPA1, in addition to three hypothetical proteins. The largest change is caused by the insert, which cleaves the ORF of a 191 amino acid hypothetical protein present in RDPV HL953, and at the right terminus of this protein, an ORF encoding a 79 amino acid hypothetical protein (ORF125) is left. At the left end of the insert, the GM-CSF/IL-2 inhibitory factor is strongly affected, leading to the substitution of 48 amino acids relative to the RDPV HL953 counterpart. Moreover, the hypothetical protein encoded by ORF120 undergoes substantial alteration due to a mutation of a stop codon, which leads to the addition of 19 amino acids, partly constituted by a duplication of an SSSSSSSL-motif and the addition of a positively charged RRRK tail.

Open reading frames introduced by the insert

The two ORFs on the insert, ORF123 and ORF124, as well as the truncated ORF125, have homologous counterparts in other PPVs. For example, for BPSV, PCPV, and ORFV with accessions PP565898, JF792399, and NC_005336, ORF118-120, with accessions WZD65462-64, AEL20653-55, and NP_957895-7, respectively, have BLASTp (Basic Local Alignment Search Tool for proteins) amino acid sequence identities in the range of 35.7–57.14% with a query (other PPVs) coverage in the range of 67–100%, except for the truncated ORF125, which naturally has a lower query coverage in the range of 22–36%. The GSEPV, with accession NC_035188, also has counterparts to ORF123 and ORF124, namely, the hypothetical proteins with locus tags CGV_gp196-7, which have sequence identities of 43.6 and 50.4%, respectively, with corresponding query coverages of 73 and 77%. However, GSEPV appears to lack an ORF producing a protein homologous to ORF125 (ORF120 in the other PPVs). Since there were simultaneous cases of CvPV infections in the herd and weakly positive PCR results for CvPV in Calf 5 (Table 1), the insert was initially hypothesized to have originated from this CvPV. Recently, a partial genome of CvPV was reported by Nymo et al. 2025 [21]. Sequence comparison between the insert and the CvPV genome revealed that the insert did not originate from this CvPV genome (unpublished data). This finding is also consistent with the fact that the ORFs of the insert only have sequence homology with other available PPVs.

Attempts to detect recombination using RDP5 [33] with representative donor PPV genomes from RDPV, BPSV, ORFV, PCPV, and GSEPV were unsuccessful.

Discussion

This study reports the first detection of RDPV in reindeer, suggesting a host shift from red deer.

Clinical examinations were performed on five out of ten affected reindeer calves. Real-time PCR analysis detected PPV in two of the calves and CvPV in four calves. Both viruses were identified in calf 5, where no contigs were classified as CvPV, indicating that this virus was present below the detection limit of the NGS run, consistent with the high Ct-value of 34.9. The affected calves in the herd displayed clinical signs similar to those of CE [7, 16, 19], characterized by crusts and lesions on the muzzle, lips, and oral mucosa (Fig. 1 and Supplementary Fig. 1). Histopathology confirmed nonspecific hyperkeratosis with infiltration of inflammatory cells in the cutis and subcutis, which is not indicative of a specific pathogen (Fig. 2). Similar histopathological findings were reported in an experimental infection study of ORFV in reindeer [34]. In addition, most PPV lesions in reindeer are mainly observed in the oral mucosa and not in the skin around the mouth, including secondary bacterial infections [7, 19, 34].

Therefore, the exact cause of the lesions remains unclear, as several factors could have contributed. Herders suspected insect harassment, especially around the eyelids, as a possible trigger. Additionally, the recently described CvPV, detected in four calves with clinical signs, causes lesions in the skin of the eyelids and external genitalia [21]. It is therefore plausible that both the reindeer RDPV and CvPV contributed to the observed clinical signs. Insects may contribute to disease transmission, as demonstrated in lumpy skin disease, a capripoxvirus infection of cattle, where flies, mosquitoes, midges, and ticks act as vectors [35]. Additionally, rodents are reservoirs for other poxviruses [36], and their role in reindeer poxvirus ecology cannot be excluded. Thus, the potential involvement of insects and rodents in the transmission and spread of reindeer RDPV and CvPV warrants further investigation. In addition, the intensification of reindeer husbandry due to pastureland loss, leading to supplementary feeding, increased animal density, and stress levels, might facilitate the spread of infectious diseases [24]. Regular and sporadic disease outbreaks of CE have been reported in Finland since the early 1990s, including several severe epidemics with high mortality, thought to be associated with supplementary feeding, severe winter weather conditions, introduction of a new virus, and secondary bacterial infections linked to fatal cases [7, 14]. Routes of transmission of PPVs to reindeer are thought to be either via direct contact with sheep, goats, and cattle, or indirectly through sharing pastures, corrals, transport vehicles, and roughage, as PPVs are highly stable in the environment [7, 37]. Remnants of fencing from former red deer farms persist within reindeer pastures used by the reindeer in this study and may have served as an indirect route of transmission, in addition to potentially shared pastures and direct contact when the farms were still operational. Moreover, climate change may influence the ecology of potential vectors and reservoirs, geographic distribution, and temporal persistence of various pathogens [38]. Together, these factors may increase reindeer susceptibility to infectious pathogens, such as reindeer RDPV and CvPV, resulting in enhanced pathogen shedding and more severe clinical manifestations. Transmission of parapoxvirus from cervids to humans during slaughter has been reported [39, 40]. Even though RDPV was not the cause in these cases, the zoonotic potential of PPVs poses a potential occupational health risk for humans in contact with reindeer.

The phylogenetic comparison of ten concatenated conserved genome core proteins (Fig. 4) shows that reindeer RDPV is highly similar to the RDPV HL953 [8]. The resulting overall tree topology is concordant with the one previously obtained using 47 conserved proteins [41]. Only eleven out of the 130 common ORFs presented more than 5 amino acid alterations, including changes in length (Fig. 5). The majority of these eleven ORFs are located at the right terminal region of the genome. The terminal regions of poxviruses contain genes that affect host range and pathogenesis [42, 43]. In a genomic comparison of ORFV and BPSV [42], ORF80 (ORF82 in the present reindeer RDPV numbering, c.f. Figure 5), which is a homologue of Vaccinia virus A4L and encodes a virion core protein, was pinpointed as a gene of significant variability. The corresponding gene in the reindeer RDPV is indeed one of the ORFs most different from RDPV HL953 (Figs. 4 and 5). This gene was also shown to be particularly variable in orthopoxvirus genomes [43]. Similarly, right terminal ankyrin repeat proteins have also been shown to be particularly variable [42, 43], a pattern that was likewise observed in the present study (Fig. 5). Ankyrin repeat proteins are typical of poxviruses and are implicated in host interactions [44]. ORF118 is also markedly different from its counterpart in RDPV HL953, with ten amino acid substitutions (Fig. 5). The homologue of ORF118 in ORFV, ORF113, has been shown to interact with the G protein-coupled receptor lysophosphatidic acid receptor 1 (LPA1) to increase p38 phosphorylation, which strongly promotes virus replication in infected cells [45]. The putative GM-CSF/IL-2 inhibitory factor (ORF122) combats the host immune response, and ORF136 is a homologue of Vaccinia virus protein F9, which is known to be required for cell entry [46]. The final ORF at the right terminal (ORF137), with six amino acid substitutions relative to RDPV HL953 (Fig. 5), encodes a viral analogue to vascular endothelial growth factor (VEGF), which also varies greatly between ORFV and BPSV [42]. Parapoxviral VEGF has been shown to be a pathogenicity factor associated with vascularization and lesion proliferation [47], which are likely to be host dependent as well. Thus, the vast majority of the ORFs with a comparatively large number of substitutions relative to RDPV HL953 encode proteins involved in host interactions and pathogenesis.

The insert contains two ORFs (ORF123 and ORF124). Both of these ORFs have homologues located in approximately the same genomic region in four other PPV species (ORF118–19 in ORFV, PCPV, and BPSV, locus tags CGV03_gp106–7 in GSEPV) but are absent from RDPV HL953. Interestingly, in a PCPV infecting reindeer, the loss of a 5,431 bp sequence encompassing ORF116–121 was observed after serial passage in cell culture [48]. Notably, this region includes the corresponding region of the whole insert in the present study. This observation suggests that, rather than an insert in the sequence obtained in the present study, there is a deletion in RDPV HL953, since the RDPV HL953 genome sequence was obtained from a virus collected after five passages in cell culture. However, the large alteration of the GM-CSF/IL-2 inhibitory factor (ORF122) at the left terminal of the purported insert and the truncation of ORF125 at the right terminal, which is only 79 amino acids in reindeer RDPV but 139 amino acids in BPSV (PP565898), 194 amino acids in ORFV (NC_005336), and 204 amino acids in PCPV (JF792399), strongly indicate that there has been an insertion in the reindeer RDPV. Notably, there may still be a deletion in RDPV HL953, which led to the loss of the ORFs corresponding to ORFs 123–24. The sequence identity of ORF123 to the other PPVs ranges from 43.6–46.5% over approximately 70% of the target, and that of the putative NF-κB inhibitor (ORF124) is 50–57.1% over 70–97% of the target. This low sequence identity suggests that the insert may derive from a previously unknown PPV species native to reindeer, rather than from any currently described PPVs. This is consistent with Tryland et al. (2019) [18], who found no evidence of a specific reindeer ORFV circulating in Fennoscandia based on GIF gene phylogeny. Attempts to detect a recombination event with currently characterized PPVs (RDPV, BPSV, PCPV, ORFV, and GSEPV) as potential donors using RDP5 were unsuccessful (data not shown). This is not unexpected since the sequence homology between the insert and any of these PPVs is very low.

The novel reindeer RDPV thus systematically displays a comparatively large number of amino acid alterations relative to the RDPV HL953 isolate in proteins involved in host interactions and pathogenesis. In addition, a unique insert was found that could play a key role in regulating the immune response. These observations suggest that the virus has adapted to the reindeer host for some time. The insert carries two ORFs, both with weak sequence homology to putative ORFs in all other currently known PPVs, except RDPV, at roughly the same genomic location. A currently unknown PPV likely recombined with RDPV, adapted, and established itself as a novel PPV in reindeer. This could indicate that previous red deer populations in the herding district introduced the RDPV to the reindeer herd in the same area, enabling the RDPV to recombine with an unknown PPV already circulating in the reindeer herd. These events may significantly affect reindeer health, particularly in conjunction with climate change and the intensification of reindeer husbandry, which may facilitate the emergence and spread of disease. The potential zoonotic risk underscores the importance of continuous health surveillance to monitor emerging diseases and guide management strategies.

Conclusions

This is the first report of a full-genome-sequenced RDPV in reindeer associated with clinical lesions, and the first detection of RDPV in a species other than red deer. The clinical signs were indistinguishable from previously reported lesions caused by other PPVs in reindeer as well as CvPV, which highlights the challenges in determining the causative agent of an outbreak based solely on clinical observations, and emphasizes the need for molecular methods such as sequencing and qPCR. The novel reindeer RDPV shows evidence of long-term adaptation to reindeer, including unique genetic changes likely resulting from recombination with an unknown PPV. This finding suggests cross-species transmission, possibly involving red deer, and highlights the risk of emerging diseases in reindeer, underscoring the importance of continued health surveillance.

Abbreviations

PPV	Parapoxvirus
ORFV	Orf virus
BPSV	Bovine papular stomatitis virus
PCPV	Pseudocowpox virus
GSEPV	Seal parapoxvirus
RDPV	Parapoxvirus red deer
CE	Contagious ecthyma
CvPV	Cervidpoxvirus
ORF	Open reading frame

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12985-025-03046-5.

Supplementary Figure

Supplementary Figure 2A

Supplementary Figure 2B

Supplementary Figure 2C

Supplementary Figure 2D

Supplementary Figure 2E

Supplementary Figure 2F

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Author contributions
KWP, ML, and JJW contributed to the study design and wrote the original draft of the manuscript. FS and BS conducted the PCR analysis of CvPV. TJ conducted the PCR analysis of PPVs and partial sequencing of RDPV. FB prepared the samples for NGS, ML carried out the bioinformatic analyses, visualized the data, and designed all related figures in the results section. VL conducted the clinical examinations and sampling of the reindeer, which were supervised by UR. YL performed the histopathological examinations and documented the findings through photomicrography. IHN, CAB, and BS developed and interpreted the PCR analysis of CvPV. All the authors contributed to discussions and interpretations of the results and reviewed, edited, and approved the final version of the manuscript.

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Data availability
The complete genome of the parapoxvirus red deer presented in this paper has been deposited in GenBank with the accession number PV021565.1. The authors confirm that all supporting data, code, and protocols have been provided within the article or through supplementary data files.

Declarations

Ethics statement
During the relevant time, any severely affected reindeer calves were euthanized by their owners to prevent further spread of the potentially contagious disease. Hence, no permit was required for the use of the animals in this research. The samples were then sent for postmortem examination and analysis and stored in the laboratory biobank system. These samples and results were subsequently used for this study. Field euthanasia of the reindeer was carried out in accordance with the European Council Regulation (EC) 1099/2009 to protect the animals at the time of death (49); a captive bolt gun or a rifle was used for stunning, followed by exsanguination to ensure the rapid death of the animal.

Competing interests
The authors declare no competing interests.

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Infectious eye diseases pose a significant challenge to reindeer welfare and husbandry. This thesis explores the pathogens involved, associated risk factors, and current management practices. The findings show that such diseases are common in reindeer herds, particularly in autumn and winter, and are associated with enclosure feeding. Multiple pathogens were identified, including a parapoxvirus not previously described in reindeer. Together, the results highlight the complexity of these infections and underline the need for improved collaboration, communication, and disease management strategies.

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