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Master Thesis

Gastrointestinal parasites in sympatric reindeer (*Rangifer tarandus*) and sheep (*Ovis aries*)

- Evidence of spillover and consequences thereof

Master in Applied Ecology

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ABSTRACT

Understanding the role of gastrointestinal parasites for ecosystems and their potential impact on their hosts is valuable knowledge within wildlife management. In Norway, there is a long tradition mountain grazing for sheep, meaning that domesticated sheep and reindeer often share rangeland. This study aimed to investigate spillover of gastrointestinal parasites between domesticated sheep (*Ovis aries*) and wild and semi-domesticated reindeer (*Rangifer tarandus*) for the areas of Nordfjella zone 2, Forollhogna, and Knutshø, with medium to high, respectively, of sheep grazing intensity. Karasjok Vestre, a reindeer husbandry with very low overlap of sheep on the rangeland, was included as a control area. Parasite prevalence, abundance, intensity and richness for all study areas are reported. Parasite abundance and species richness as well as proportion of sheep parasites were statistically modelled in relation effect of temperature, precipitation, age and study area. In addition, abundance of abomasa nematodes in Knutshø and Forollhogna was compared with the last known historical record of nematode counts from these areas. I detected gastrointestinal spillover in all areas with medium to high sheep grazing intensity, namely Nordfjella sone 2, Forollhogna and Knutshø. Most importantly, I report the first detection of *Nematodirus battus* in this study. This invasive duodenum nematode was present in the three areas with medium to high sheep grazing intensity. This parasite is common in sheep, especially lambs, and can cause high morbidity and mortality in these hosts. It is unknown what occurs in reindeer, but pathological effects may be similar. I also detected *Spiculopteragia boehmi*, a parasite thought to host specific to red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), but has now been found in several other ruminate hosts as well as the semi-domesticated reindeer included in this study and within wild reindeer in Nordfjella sone 2. I conclude that gastrointestinal parasite spillover from sheep to reindeer in sympatric rangeland is enhanced by the intensity of sheep grazing. My management recommendations are to reduce sheep grazing in areas with sympatric grazing of reindeer to avoid future parasite spillover. I also recommend reconsidering the current practice of salt lick stones in these areas to avoid pathogen accumulation and, thus, hot spots of spillover. For future studies I also recommend investigations of the pathologic effects of *N. battus* on reindeer.

Keywords: *Rangifer tarandus, Ovis aries; reindeer; sheep; gastrointestinal parasites; cross-transmission; gastrointestinal nematodes; Ostertagia gruehneri; Teladorsagia circumcincta; Spiculopteragia boehmi; Nematodirus battus*

SAMMENDRAG

Forståelse for gastrointestinale parasitter i økosystemene og deres potensiale for påvirkning på vertene er verdifull kunnskap innenfor viltforvaltning. I Norge er det lang tradisjon med å la sau (*Ovis aries*) beite i fjellene, ofte innenfor leveområder til rein (*Rangifer tarandus*), som betyr at de deler felles beiteland. Dette studiet undersøkte potensiell smitte av gastrointestinale parasitter mellom sau og rein for villreinområdene Nordfjella sone 2, Forollhogna og Knutshø, med henholdsvis medium til høyt beitetrykk fra sau. Karasjok Vestre, et tamreinområde med veldig lavt beitetrykk fra sau, ble inkludert som kontrollområde i studiet. Parasittforekomst, overflod, intensitet og rikdom for alle studieområder rapporteres. Parasittforekomst og artsrikdom samt andel saueparasitter ble statistisk modellert i forhold til variablene temperatur, nedbør, alder og studieområde. I tillegg ble parasitt byrden av abomasal nematoder i Knutshø og Forollhogna sammenlignet med den sist kjente historiske registreringen av nematodetall fra disse områdene. Jeg oppdaget smitteoverføring av gastrointestinale parasitter fra sau til rein i alle områder med middels til høy beiteintensitet av sauer, nemlig Nordfjella sone 2, Forollhogna og Knutshø. Denne oppgaven representerer første rapportering *Nematodirus battus* detektert i rein. Denne invasive tynntarm nematoden ble oppdaget i de tre områdene med middels til høyt beitetrykk for sauer på villrein. Dette er en vanlig parasitt hos sauer, spesielt lam, og kan forårsake sykdom og har høy dødelighet hos spesielt lam. Det er ukjent hvilken effekt parasitten har på rein, men patologiske effekter kan være like mellom kalver og lam. Jeg oppdaget også *Spiculopteragia boehmi*, en parasitt som antas å komme fra hjort (Cervus elaphus) og rådyr (Capreolus capreolus), men har nå blitt funnet i flere andre drøvtyggere, samt tamrein som er inkludert i dette studiet og innen villrein i Nordfjella sone 2. Jeg konkluderer med at overføring av gastrointestinal parasitt fra sau til rein i felles beiteområder forsterkes av beitetrykket fra sau. Mine anbefalinger til forvaltningen er å redusere beitetrykket fra sau i områder med felles beite av villrein for å unngå fremtidig parasittutslipp. Jeg anbefaler også å revidere nåværende praksis angående saltslikkesteiner i disse områdene for å unngå patogenansamlinger og områder med høy risiko for smitteoverføring mellom disse artene. For fremtidige studier anbefaler jeg også undersøkelser av de patologiske effektene av N. battus på reinsdyr.

Nøkkelord: *Rangifer tarandus; Ovis aries; reinsdyr; sau; gastrointestinale parasitter; smitteoverføring; gastrointestinale nematoder; Ostertagia gruehneri; Teladorsagia circumcincta; Spiculopteragia boehmi; Nematodirus battus*

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1 INTRODUCTION

Parasites are important and complex factors within different ecosystems. Gastrointestinal parasites can supress the health of individual hosts and may influence the fitness of entire populations (Stien, et al., 2002). Shifts in temperature, rainfall patterns and habitat loss are all ongoing factors in the Sub-Arctic Norwegian ecosystems. This will have an impact on the development and transmission of endemic and introduced parasites, especially for northern ruminant parasite systems, where the ecological structure already has influenced the distribution for pathogens (Hoberg, Kutz, Galbreath, & Cook, 2003; Hoberg, 2005; Kutz S. J., Hoberg, Polley, & Jenkins, 2005). Sub-Arctic ruminants have a central position in the food web and can provide valuable insights for their role of ruminant infections as drivers and outcomes of trophic cascades (Jolles & Ezenwa, 2015; Kutz S. J., Hoberg, Polley, & Jenkins, 2005). Species-specific parasite surveys to detect and map the infection of gastrointestinal parasites is the first key to understanding this complex epizootiology in wildlife (Hoberg, Kocan, & Rickard, 2001).

Few animal species are more representative to Norwegian culture and tradition than the reindeer (*Rangifer tarandus*). Reindeer herding and hunting are traditional activities handed down through generations. In addition to the meat, skins, bones and antlers are regarded as important raw materials and products, especially for Saami culture and tradition. Semi-domesticated and wild reindeer are closely related but with some genetic differences between them; furthermore, there are genetic variations within the Norwegian wild reindeer populations (Røed, 1985). Reindeer are regarded as a nomadic species that require large continuous rangelands where they can migrate between seasonal grazing areas. Today the original migratory patterns for wild reindeer have been reduced drastically due to loss and fragmentation of habitats caused by human infrastructure development (Skogland & Mølmen, 1980; Jordhøy , Strand, & Landa, 1997).

Sheep and goats were the first domesticated livestock of importance in Norway. Sheep were introduced into Norway during the middle Neolithic B (2600-2200 BC) and became common livestock during the late Neolithic period (2200-1700 BC) (Helle, 1961). In 1830 the total number of sheep and lambs was one million and increased slowly to more than two million by 2005 (Hjelle, Hufthammer, & Bergsvik, 2006). Norwegian farmers have used mountain pastures for sheep grazing during late spring, summer and early autumn for generations.

Sheep are now the most common domesticated grazing animal in the Norwegian mountains and rangeland. While the number of sheep has increased the last decade, the number of sheep farmers has decreased (Statistics Norway, 2020). This has led to higher concentrations of sheep grazing in certain areas, and in some of these areas there can be up to 108 sheep per km^2 (Hillestad, Bunger, & Smedshaug, 2018).

Parasitology is often defined as an "ecological interaction where the parasite is physiologically depending on the host and at the same time has a negative impact on the host" (Crofton, 1971). The effect of parasites on the host population is complex and often a result of interactions between factors such as parasite species richness and burden, weather, predation and inter- and intraspecific competition (Holmes, 1982). Parasites can also be a regulating mechanism for the population dynamics of a species (Hudson, Dobson, & Lafferty, 2006; Stien, et al., 2002).

According to their location on the host, parasites may be divided into two categories, ectoparasites and endoparasites. The ectoparasites live on the host body while the endoparasite lives within the host body (Hendrix & Robinson, 2017). This study focuses on the relationship between reindeer and sheep endoparasites, primarily in the gastrointestinal tracts.

Gastrointestinal parasites may cause loss of productivity, unthriftiness and even mortality within both reindeer and sheep herds (Josefsen, Oksanen, & Gjerde, 2014B). Sheep are usually monitored and treated for gastrointestinal parasitic diseases (Gjerde, 2011). Semi-domesticated reindeer are treated with antihelmintics for ectoparasites, the medications of which also have an effect on gastrointestinal parasites. However, the treatment is usually not given at an optimal season for combating endoparasitic infections (Josefsen, Oksanen, & Gjerde, 2014B). Wild reindeer are not treated for parasites, and the general consensus is that wild reindeer do not harbour high burdens of gastrointestinal parasites. Nonetheless, the recent changes in sheep husbandry, rangeland infrastructure and even climate, warrants a survey of the epidemiology of gastrointestinal parasites of domesticated sheep and wild reindeer. These ruminants share a decreasing area of rangeland, possibly increasing the risk of pathogen spillover.

Ruminants have a polygastric digestive system, which consists of a four-compartment stomach. The four parts are the rumen, reticulum and omasum (together referred to as the

nonglandular forestomach) and the abomasum (the glandular stomach). The small intestine consists of three sections (in order of digestion): duodenum, jejunum and ileum. The large intestines has two parts: the caecum, or blind sac, where the small and large intestine meet, and the colon, which terminates as the rectum and anal canal. (Frandson, Wilke, & Fails, 2009).

Gastrointestinal parasites reside in the host's digestive tract, and includes both helminths and protozoa. Helminths are worms such as roundworms (nematodes), tapeworms (cestodes) and flatworms (trematodes). Protozoa are single-celled organisms.

Knowledge of gastrointestinal parasites in both semi-domesticated reindeer and sheep in Norway is high (Gjerde, 2011; Josefsen, Oksanen, & Gjerde, 2014A; Josefsen & Handeland, 2014). Gastrointestinal parasites may affect the hosts welfare, reproduction and production, depending on the intensity and complexity of the infection. In relation to livestock animals, these parasites also have a direct impact on the farmers economy. In general these parasites will cause a decrease in host body condition and fecundity rather than being the cause of mortality (Dobson, Hudson, & Lyles, 1992), but accumulating evidence suggests that they may also have an effect on mortality (Anderson & May, 1978; Gunn & Irvine, 2003; Hudson, Cattadori, Boag, & Dobson, 2006; Irvine R. J., 2006; May & Anderson, 1978).

Climate changes have the potential to alter host-parasite interactions by improving environmental conditions for parasite survival, viability and reproduction in intermediate hosts, such as higher temperatures, more rainfall and shorter winters (Hudson, Cattadori, Boag, & Dobson, 2006; Kutz S. J., Hoberg, Polley, & Jenkins, 2005). One of the alarming predictions are the estimated higher effect in Arctic conditions (Kattsov & Källén, 2006). Wild reindeer parasitology has not been studied extensively on mainland Norway, and the latest publication of studies on gastrointestinal parasites of wild reindeer is dated back to 1987 (Bye, 1987).

The complete lifecycle of nematodes with a direct lifecycle consists of the egg stage and 5 larvae stages before they end up at the final stage as the immature adult. After hatching, the first stage larvae (L1) emerge and go through two moults (L1- L2, L2 - L3) before reaching the third stage. These moults may either occur in the external environment or within an intermediate host, depending on if the life cycle is direct or indirect. The third larval stage is the infective stage when the larvae is ready to parasitize the definitive host (Taylor, Coop, &

Wall, 2015). When ingested by the definitive host, the larvae undergo two more moults before reaching the fifth stage, pre-adult nematode (L5). The process from fifth stage larva to the mature adult nematode generally takes place in the gut lumen or with small overlapping movement into the mucosa (Hendrix & Robinson, 2017; Taylor, Coop, & Wall, 2015). The lifecycle is complete when the nematode is sexually mature and capable of fertilising females or producing eggs. The eggs are shed into the gastrointestinal tract and exit the host with the faeces to the open environment (Taylor, Coop, & Wall, 2015).

Gastrointestinal nematodes transmit through the digestive intake of vegetation and have a direct life cycle. Until reaching the infective third larvae stage, the larvae can survive in the harsh climatic environments of the Sub-Arctic, through extreme dryness and below freezing temperatures before it is ingested by a grazing ruminant (Halvorsen, Stien, Irvine, Langvatn, & Albon, 1999). Gastrointestinal nematode species have different lifecycle strategies, whereby some larvae have a rapid reproduction strategy while others undergo an arrested development during the winter period in a hypobiotic state in the host. Arrested development could be an adaptation for the parasite to delay adult reproduction until environmental conditions are more favourable for eggs and larvae, and may also be an adaption to increase the chance of survival for the host animal during periods of poor environmental conditions (Kutz, et al., 2012).

In addition to gastrointestinal nematodes, it was of interest to include the infection rates from the Metastrongylid parasites *Dictyocaulus eckerti* and *Elaphostrongulus rangiferi* in reindeer for this study. Detection of these parasites within the reindeer samples will provide a greater understanding of the total parasite richness burdening the host. *Dictyocaulus eckerti* is commonly known as the “deer lungworm”. The adult worm resides in the cervid host’s lungs. Eggs are coughed up and swallowed. The eggs hatch as they pass through the intestinal tract and are excreted as first stage larvae with the faeces. Larvae go through two moults before reaching the infectious parasitic third stage. After the larvae have been digested, they moult twice again in the intestinal system before penetrating the intestine and traveling to the lungs (Mcnulty, Rosa, Martin, & Tyagi, 2016). Hatched larvae will most likely not survive the winter in the environment and, in addition, the parasite has a relatively short lifespan. Therefore, it has developed a survival strategy whereby the larva enters hypobiosis (hibernation) inside the host in larval stage four or early five (Josefsen, Oksanen, & Gjerde, 2014A).

Elaphostrongulus rangiferi, commonly known as "the reindeer brainworm" is a protostrongylid nematode that matures in the lungs and central nervous system and affects the central nervous system and skeletal muscles when the parasite burden is heavy (Bakken & Sparboe, 1973). *Elaphostrongulus rangiferi* has an indirect lifecycle and depends on a terrestrial gastropod intermediate host, a snail or slug, to develop from the first to the infective third larval stage (Josefsen & Handeland, 2014). *Elaphostrongulus rangiferi* may infect a variety of wild ruminant hosts, commonly reindeer and moose (*Alces alces*) (Stéen, Blackmore, & Skorping, 1997). Livestock animals such as sheep and goats may act as aberrant hosts (Handeland, Skorping, Stuen, & Slettbakk, 1994). Early stage larvae living free in the environment are extremely tolerant towards the harsh Arctic climate. A laboratory-based study detected larvae survival after a whole year frozen at -80°C (Lorentzen & Halvorsen, 1986). Halvorsen and Bye (1985) detected seasonal fluctuations in the parasite larvae production. These seasonal fluctuations make interpretation of faecal analyses uncertain in relation to the true prevalence and intensity of infection. Because of the parasite's need for an intermediate host, this parasite species is more dependent on climatic variables, such as temperature and especially precipitation to reproduce (Halvorsen, Skorping, & Hansen, 1985). The snail and slug species identified as intermediate hosts also have a habitat preference, favouring rich fen (Andersen & Halvorsen , 1984).

Although reindeer may host a variety of different endoparasites (Bye & Halvorsen, 1983; Bye, 1987), the clinical importance of these parasites on reindeer health remains largely unknown (Rehbinder & Christensson, 1977; Oksanen A. , 1999). Nematodes located in the abomasa are regarded as the most significant gastrointestinal parasites of domestic ruminants (Fruetel & Lankester, 1989). However, studies that have detected *Nematodirus* and/or *Nematodirella* nematodes in the small intestine of reindeer calves (Bye, 1987; Oksanen, et al., 1990) indicate the need to include intestinal nematodes in studies of reindeer gastrointestinal nematodes. In the small intestine we expected to detect *Nematodirus tarandi* and *Nematodirella longissimespiculata,* which are regarded as nematodes specific to reindeer (Fruetel & Lankester, 1989).

Intensity and prevalence of most gastrointestinal nematodes fluctuate between seasons and with climatic variables, similar to the description of *E. rangiferi* but without the requirement for an intermediate host to complete their lifecycles (Taylor, Coop, & Wall, 2015). Studies on both wild and domestic ruminants show clear evidence of seasonal fluctuations of nematode

burden and parasite egg production (Crofton, 1971; Michel, 1969; Halvorsen & Bye, 1985; Hrabok J. T., 2006; Carlsson, et al., 2018). Before and around lambing or calving, female ruminants have a reduced immunity that in parasitology is referred to as "spring rise". The result from the suppression of the ewe or doe's immune status leads to maturation of arrested larvae and increased egg production by female nematodes (Animalia, 2013; Brown, 1992; Crofton, 1971). The result from this seasonal fluctuation leads to high infection pressure by larvae on pasture during mid-summer (Handeland & Slettbakk, 1994; Handeland, et al., 2019). Still, Halvorsen et al. (1999) found a high abundance of abomasal nematodes in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) during winter, implying the reindeer can also ingest infective larvae from snow-covered pasture during the Arctic winter.

Ostertagia gruehneri and *Ostertagia arctica*, the smaller morphotype, are the most common and dominant abomasal nematode species found in Norwegian reindeer (Bye, 1987; Bye & Halvorsen, 1983). These parasites are normally detected with high prevalence and the average intensity has been estimated in previous studies to be 1.300 adult nematodes in calves and 3.900 adult nematodes in adult reindeer (Josefsen, Oksanen, & Gjerde, 2014A). The abomasal nematodes *Teladorsagia circumcincta* and *Teladorsagia trifurcata*, the smaller morphotype, have also been detected in studies by Bye (1987) and Gammelsæter (1999) in wild reindeer abomasa samples from Norway.

Ostertagia. gruehneri and *Marshallagia marshalli* have been studied in Svalbard reindeer (Bye, Halvorsen, & Nilssen, 1987). Antihelmintic treatment of the reindeer led a to higher reproduction probability among the treated reindeer compared with the untreated reindeer group. The parasite worm burdens were found to regulate the reindeer population by 1-5% annually by weakening the body condition and reducing fecundity of female reindeer (Irvine, Stien, Dallas, Halvorsen, & Langvatn, 2001). *Marshallagia marshalli* was not a nematode we expected to find in this study as it has not been detected in ruminants on the Norwegian mainland.

Other intestinal nematodes are *Capillaria* sp., *Trichuris* sp. and the pinworms of genus *Skrjabinema* that could be expected to be detected in reindeer. Reindeer intestinal nematodes are not studied thoroughly enough to determine the exact life cycles, and their impact on hosts are uncertain (Rehbinder & Christensson, 1977; Oksanen A. , 1999).

We have a much broader knowledge of gastrointestinal parasites in sheep in Norway compared to wild ruminants (Gjerde, 2011; Josefsen, Oksanen, & Gjerde, 2014A). Lambs exposed to roundworms gradually develop immunity against most of these infectious parasites. Adult sheep are usually immune, but can still shed nematode eggs with faeces. Therefore, designed antihelmintic treatment targeted towards roundworms are important management implications to reduce the worm burdens. Lately there has been a greater focus on non-medical interventions in Norway, such as reducing grazing sheep per km^2 (achieved usually by expanding sheep rangeland), rotating grazing of an area between other ungulate species (e.g. horse and cattle) and developing breeding strategies to avoid development of antihelmintic resistance (Animalia, 2013).

Teladorsagia circumcincta and its smaller morphotype *T. trifurcata* are the most common gastrointestinal nematodes in Norwegian sheep. These parasites have a direct lifecycle with adult nematode, egg stage and five larval stages. They are also capable of overwintering in the pasture before hatching from the egg in the spring, and larvae may undergo hypobiosis in the abomasal mucosa. *Teladorsagia circumcincta* has been detected in sheep in all areas of Norway (Animalia, 2013).

Nematodirus battus is a species that we know much of in relation to infection in sheep, and it is believed that this nematode will benefit from climate changes in the temperate regions (Van Dijk & Morgan, 2008). This nematode has been identified in the small intestine, or more specifically the proximal duodenum, in lambs located in South- and Mid-Norway (Animalia, 2013). *Nematodirus battus* was introduced to Norway in 1961 as a result of import of infected sheep from Britain (Helle, 1961). The eggs from *N. battus* need a cold period to develop to the infective stage inside their sturdy eggs, and stage three larvae hatch synchronously during spring causing a larval boom in the environment when the average day temperature reaches ~11°C (Van Dijk & Morgan, 2008). The synchronous hatching of *N. battus* can cause high infection and severe diarrhoea, and in some cases severe los of condition of the host and even death (Scott, 2013; Helle, 1961). It is not known whether *N. tarandus* or *N. longissimespiculata* have the same lifecycle as *N. battus* but regarding the short summers in the Arctic, this could be a beneficial strategy (Oksanen A. , 1999).

Earlier studies have shown the potential for parasite cross transmission between sheep and reindeer where parasite spillover can affect both species (Manninen, Thamsborg, Laaksonen, & Oksanen, 2014; Bye, 1987; Halvorsen & Bye, 1985; Gammelsæter, 1999; Hrabok,

Oksanen, Nieminen, & Waller, 2006). As stated above, the long-term trend in Norway is a growing sheep population and fewer farmers (Statistics Norway, 2020) leading to higher concentrated areas of sheep grazing. In general, we have little knowledge about the real effects of the presence of sheep and reindeer on shared rangeland. During summer their diets overlap (Mysterud, 2000), but there are no indications to conclude that sheep are supressing reindeer from their summer food sources or vice versa (Rekdal, 2014). Areas with high concentrations of grazing animals are expected to have a higher risk of parasite contamination than areas with lower numbers of grazing animals. Potential risk of cross-transmission between sheep and reindeer are predicted to be highest in the areas where most sheep, and reindeer, share mutual rangeland. Furthermore, adult female ruminants with lambs or calves with reduced fitness and immune system and their offspring are vulnerable to infections from these parasites during "spring rise" (Crofton, 1954).

This study aimed to determine whether there is evidence for recent spillover of gastrointestinal parasites between sympatric wild reindeer and sheep by comparing reindeer rangeland areas with low to high concentration of sheep grazing.

To answer this question, I collected samples of abomasa, duodena, caeca and faeces from both species, quantified and identified gastrointestinal nematodes, and performed faecal egg counts. These current results were compared to that described by Bye (1987), the only other recent study of parasites in Knutshø and Forollhogna, two of my study areas.

2 MATERIALS AND METHODS

For this study, partial gastrointestinal tracts from field dressed reindeer were collected during the annual 2018 and 2019 hunting season from the areas of Nordfjella zone 2, Forollhogna and Knutshø in Norway (Figure 1 A, B and C). In addition, samples from slaughtered reindeer in Karasjok Vestre (Figure 1 D) and from sheep that had been grazing in Nordfjella zone 2, Forollhogna and Knutshø were collected. All samples were analysed using general parasitology methods to collect, speciate and quantify parasites from the abomasa, proximal duodena, caeca and faeces.

2.1 Host populations

2.1.1 Wild reindeer

The total Norwegian wild reindeer population located on the mainland was estimated to be between 30 000 and 35 000 animals in 2018. This population is regarded as the last remaining viable population of wild European reindeer (Norwegian Environment Agency, 2018). The population is divided into 23 sub populations due to habitat fragmentation as an effect of human infrastructure development. The Norwegian wild reindeer can be divided into three categories based on the genetic influence by semi-domesticated reindeer; (1) low-, (2) medium- and (3) high grade of influence. These classifications are based on observational and genetic studies (Reimers, 2007).

2.1.3 Semi-domesticated reindeer

Norwegian reindeer herding has been practiced by the Saami population for generations for meat and skin production. Reindeer herding is now limited mainly to Northern Norway, Trøndelag, Møre and Romsdal and Hedmark. These herding areas cover almost 40% of the Norwegian landscape. The total population of semi- domesticated reindeer in Norway is approximately 240 000 animals counted during the spring (County Governor, 2020), and the majority of this number are found in Finnmark, the northernmost county of Norway. The average age of semi-domesticated reindeer herd will be on average lower compared to a wild reindeer herd, as most animals are slaughtered at the peak of their production.

Reindeer samples from Karasjok Vestre / Kárášjoga Oarjjabealli were included as controls for this study. The Karasjok Vestre area is also known as reindeer grazing district nr. 16. These reindeer graze on the coastal area during the summer and are moved to the inland during the

winter, where the conditions are dryer, colder and usually have less amounts of snow and ice (Kulseng, Tveraa, & Hætta, 2019). The reindeer grazing area within district 16 has had a low overlap of grazing areas with sheep (Figure 1 D), which made Karasjok Vestre an ideal control area for this study.

According to the official numbers, the population of semi-domesticated reindeer in Karasjok Vestre was 31 068 during the 2011/2012 season but was reduced to 23 363 for the 2018/2019 season. Based on official papers, the slaughter weights reported from Karasjok Vestre were lower than average, but during the last three year period (2016-2019) the calf and adult male slaughter weights have been average or a bit above average (Kulseng, Tveraa, & Hætta, 2019).

2.1.3 Sheep

The winter population of sheep in Norway was approximately 1 million (lambs excluded) in 2018 but was reduced to approximately 930 000 in 2019 (Statistics Norway, 2020). The highest regional populations are found in Rogaland, Trøndelag, Vestland, Innlandet and Nordland. Our study area in Karasjok has one of the lowest numbers of grazing sheep that overlap with reindeer grazing (Norwegian Institute of Bioeconomy Research, 2019), with the remaining grazing areas consisting of high grazing populations of sheep. The grazing overlap in the study areas are described by km^2 overlap in Table 1 and visually presented in Figure 1.

2.2 Study areas

Study areas were classified as having a “low”, “medium” or “high” grazing overlap based on rangeland areal overlap and number of sheep in the rangeland (Table 1, Figure 1). Low was set for Karasjok with low numbers of sheep and low percentage of overlap with the semi-domesticated reindeer rangeland. Medium was set for Nordfjella zone 2, even if it had high percentage of overlap, not many sheep were grazing in the wild reindeer rangeland. High was set for Forollhogna and Knutshø. Both areas had high percentage of overlap and many sheep within the wild reindeer rangeland. Knutshø had a bit lower percentage overlap than Forollhogna, but higher numbers of sheep within the rangeland.

2.2.1 Karasjok Vestre / Kárášjoga Oarjjabealli

Reindeer district 16, Karasjok Vestre is located in Finnmark, Northern Norway and has a total area of 76.473km^2. Forest makes up a total area of 1.190 km^2 (68.9 %), for the southern

grazing area within the rangeland. Rangeland located above the treeline make up a total area of 305 km^2 (17.6%) for the southern rangeland area. Recently, reindeer numbers have been reduced, and the grazing habitat has improved in the period between 2011-2018 due to a resulting higher production of lichen (Johansen, Tømmervik, Bjerke, & Davids, 2019).

Karasjok Vestre has a lower altitude compared to the other study areas but is located at a higher northern latitude. The altitude range is between 0-450 meters above sea level. There were sheep grazing in the coastal areas around the town Lakselv. The sheep rangeland was small, with a high density of sheep (Table 1). Even if this area was included in the reindeer rangeland there were reasons to conclude, based on literature, that the reindeer preferred the southern grazeland (Johansen, Tømmervik, Bjerke, & Davids, 2019). Overlapping grazing areas between sheep and reindeer were therefor set as "low" in the Karasjok Vestre study area (Figure 1D; Table 1).

2.2.2 Nordfjella

Nordfjella zone 2 is the neighbour area to Nordfjella zone 1 where the prion disease, chronic wasting disease (CWD) was detected in wild reindeer in 2016 (Ytrehus, et al., 2018). The wild reindeer population located in Nordfjella zone 2 is ranked as a category two, with various genetic influence from semi domesticated reindeer (Reimers, 2007). Nordfjella has a high-altitude range including mountain peaks over 1.900 meters above sea level. The lower reindeer rangeland in Nordfjella is located at approximately 1.200 meters above sea level, very little rangeland is located beneath the treeline. Nordfjella is the smallest study area regarding reindeer rangeland. There was high overlap with sheep rangeland but most of this rangeland is located outside of the reindeer rangeland (Figure 1C; Table 1). Overlapping grazing areas between sheep and reindeer were therefore defined as "medium" in the Nordfjella study area.

2.2.3 Forollhogna

Forollhogna is known as the wild reindeer area with highest production in Norway and has large bulls within the population where most of the reindeer rangeland is located within Forollhogna national park (Norwegian Environment Agency, 2020). The rich and nutritious vegetation in Forollhogna is a result of its geology which is dominated with mica schist and lime (Rekdal, 2014). Forollhogna is, therefore, a prioritized grazing area for sheep as well as wild reindeer in Norwegian management regulations. The estimated total potential number of

sheep grazing in Forollhogna has been set to a maximum of 68.000 individuals based on forage quality (Linell, et al., 2015).

The altitude range in Forollhogna is from 950 meter above sea level to the highest mountain top located at 1.332 meters above sea level. The wild reindeer population in Forollhogna is ranked as category three, with high genetic influence from semi-domesticated reindeer (Reimers, 2007). Reindeer rangeland has high overlapping intensity with sheep rangeland. The estimated sheep grazing intensity within reindeer rangeland was set to "high", even though there are overlapping sheep grazing areas outside of the reindeer rangeland (Table 1; Figure 1B).

2.2.4 Knutshø

Knutshø is located close to Forollhogna and has many similarities. Knutshø's geology is dominated with cambrosiluric schist and lime which gives an ideal foundation for a rich and nutritious vegetation (Knutshø villreinutvalg, 2018). The reindeer rangeland area of Knutshø was re-established between 1960 and 1970 when flocks from Snøhetta and/or Rondane migrated into the vacant rangeland (Jordhøy , Strand, & Landa, 1997). The area was grazed historically by semi-domesticated reindeer in the late 1800s and early 1900s (Strand, et al., 2015).

Genetically the Knutshø wild reindeer are closer to reindeer located in Snøhetta, but it is known that semi-domesticated reindeer have migrated into Knutshø from Røros and Trollheimen (Jordhøy , Strand, & Landa, 1997). It is therefore uncertain whether Knutshø belongs to the same genetic reindeer category as Rondane and Snøhetta, which are known to be the genetically closest to the original European wild reindeer populations (Reimers, 2007). Regardless of this uncertainty, the Knutshø and Forollhogna herds are identified as separate populations of wild reindeer for Norwegian wildlife management. This, together with their potential genetical differences, were the main reasons to treat Knutshø and Forollhogna as separate study areas.

Altitude for Knutshø's reindeer rangeland varies from 900 meters to the highest mountain peak at 1.676 meter above sea level. The area has the highest intensity of sheep grazing among the study areas (Table 1). In addition, reindeer rangeland in Knutshø has high overlap of sheep rangeland where the sheep goes outside that of the reindeer (Figure 1A). Therefore, the overlap of sheep grazing intensity was set as "high" in Knutshø.

Table 1. Data describing Figure 1, (Norwegian Institute of Bioeconomy Research, 2019; Norwegian Mapping Authority, 2019).

	Karasjok	**Nordfjella**	**Forollhogna**	**Knutshø**
Number of sheep (2018)	1058	20374	39186	48039
Reindeer rangeland	76473 km^2	11270 km^2	23380 km^2	20671 km^2
Overlapping sheep rangeland	1544 km^2	78075 km^2	3398 km^2	2210 km^2
Sheep pr. km^2 in sheep rangeland	7.35	0.26	11.53	21.74
Sheep pr. km^2 in reindeer rangeland	0.01	1.81	1.68	2.32
Percent overlapping rangeland	2 %	80 %	89 %	87 %
Overlapping sheep grazing intensity	Low	Medium	High	High

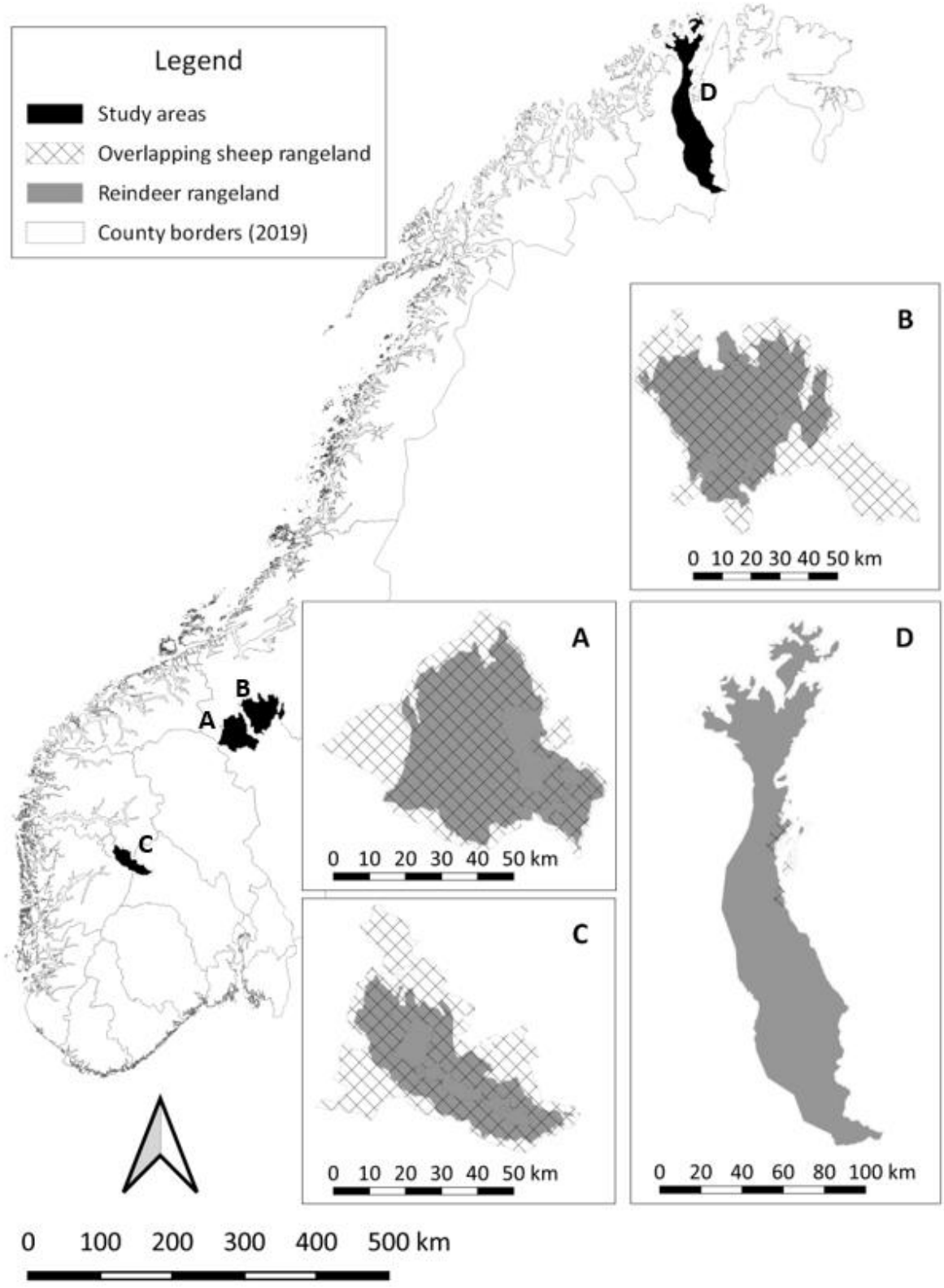

Figure 1. Map of Norwegian county borders (2019) with the four study areas from the reindeer populations. The study areas are shown in smaller boxes including the overlap from sheep grazing areas for the 2018 season (A= Knutshø, B= Forollhogna, C= Nordfjella zone 2 D=Karasjok). Estimated sheep grazing inside reindeer rangeland; A=86.9%, B=89.7%, C=81% and D=2%. All maps were constructed using QGIS Development Team, 2009. QGIS Geographic Information

System. Open Source Geospatial Foundation. Sheep grazing areas are collected from NIBIO (Norwegian Institute of Bioeconomy Research, 2019), domesticated reindeer maps and wild reindeer maps were both collected from GeoNorge (Norwegian Mapping Authority, 2019).

2.3 Data collection

Data were collected in collaboration with wildlife officials (local rangers), sheep farmers and Norwegian Institute for Nature Research (NINA) personnel from field and slaughterhouses during autumn and winter (August – December) 2018 and autumn 2019. Table 2 presents an overview of the gastrointestinal samples collected.

Due to miscommunication with some slaughterhouses and farmers, only faecal samples were available from some sheep collected in 2018. In addition, one wild reindeer gastrointestinal sample from Forollhogna was not possible to include in the lab analysis. Table 3 presents an overview of the total faecal samples collected.

Before fieldwork started, bags were prepared containing necessary sampling sets. These sets contained cable ties, plastic bags, a 100ml formalin container and a 100ml empty container. A scissors, a knife and a box with disposable gloves was also included for each fieldworker.

Hunters were addressed in a pre-hunting meeting arranged by the local wildlife rangers and hunter management, where they were invited to collaborate with us. This was important for the study to successfully sample sufficient gastrointestinal tracts from the field dressed reindeer. Hunters and the local rangers were asked to send GPS coordinates of the field dressing spots to the respective study fieldworker located in the area. Information was put out on information boards located at the most used parking spots within the study area. After receiving GPS coordinates the positions were plotted on a Garmin GPS unit for specific location of each sample. If no GPS coordinates had been received before arriving in the study area, the larger reindeer flocks were located with the local rangers and observed from a distance until the hunters had been successful. Hunters were then approached to collected samples.

2.3.1 Sample collections in the field

From the abomasum we collected a tissue sample (~ 4 x 4 cm) to preserve in a 100ml formalin container for a future study. The rest of the abomasum and proximal duodenum was bagged in a plastic bag. The caecum and duodenum were bagged in separate plastic bags. Faecal samples were collected directly from the reindeer's rectum to avoid contamination

with free-living soil nematodes and put into tubes. Each sample was marked with a unique sample number, study area and sample age category (calf or adult).

The samples collected in Forollhogna and Knutshø were transported back to the lab within 72 hours after collection from the field. The samples from abomasum, caecum and small intestine were frozen at -8°C and faecal samples were stored in a fridge at 4°C. The abomasum tissue samples in formalin were stored at room temperature. Samples collected from Nordfjella were more complicated logistically and resulted in longer time between field sampling until proper storage in the lab.

2.3.2 Sample collections from slaughterhouses

Gastrointestinal samples of semi-domesticated reindeer from Karasjok Vestre were collected in December 2018 at Min Boazu slaughterhouse in Karasjok, Finnmark. Due to logistics at the slaughterhouse we were not able to collect data regarding sex and age of the animals. Due to the timing of the year the slaughter reindeer would be either close to 1 year old calves or adults; thus, these samples were all treated as adults in the further analysis and discussion. The samples were collected directly after the entrails were discarded into a waste container outside the slaughterhouse through a hatch, then carried in separate containers to a clean area where the abomasum was disconnected from the forestomach and bagged together with the small and large intestine for each sample. The samples from Karasjok vestre were transported back to the lab within 12 hours after sampling.

Sample collections for sheep were arranged with local slaughterhouses in Oppdal and Florø. The samples from Oppdal and Florø were in collaboration with sheep farmers within the study areas. Samples from sheep that had been grazing in the Nordfjella study area were collected from the Florø slaughterhouse. The slaughterhouse in Oppdal provided samples for both Forollhogna and Knutshø. The sheep samples from these two slaughterhouses were collected in September and October 2018 and 2019. It was not possible to obtain data regarding sex and age of the sheep as the sheep as the logistical challenge was almost identical as described for Karasjok Vestre. The samples from Oppdal were transported back to the lab within 4 hours after sampling. Samples from Florø took approximately 48 hours before they came to the lab. In the lab the abomasum, proximal duodenum, and caecum were bagged separately. Faecal samples were sampled in a small box. All the sample bags and boxes were marked with a unique sample number and study area before they were bagged in a larger

plastic bag that were labelled with the unique sample number. The abomasum, caecum and small intestinal samples were frozen at -8°C. The faecal samples were stored in a fridge at 4°C.

Table 2. Total number of sheep and reindeer sampled for gastrointestinal parasites. Semi-domesticated reindeer (S-D).

	S.D. Reindeer	Sheep	Wild reindeer	Total
Forollhogna	*1*	*15*	*19*	*35*
Karasjok	*19*			*19*
Knutshø		*10*	*22*	*32*
Nordfjella		*6*	*8*	*14*
Sum	*20*	*31*	*49*	*100*

Table 3. Total number of sheep and reindeer where faecal samples were collected. Semi-domesticated reindeer (S-D)

	S.D. reindeer	Sheep	Wild reindeer	Total
Forollhogna	*1*	*25*	*20*	*46*
Karasjok	*19*			*19*
Knutshø		*20*	*22*	*42*
Nordfjella		*10*	*8*	*18*
Sum	*20*	*55*	*50*	*125*

2.3.3 Climatic variables

Temperature and precipitation from the three study areas and the control area were collected for the summer periods (May-June) in 2018 and 2019. Mean temperature and mean

precipitation for each study area was calculated based on reported values from the collected periods at each respective weather station located closest to the study area (Table 4).

Table 4. Mean of precipitation (millimetres) and temperature (degrees Celsius) per year from weather stations corresponding to each study site. Data from Karasjok 2019 were not collected because no sampling was done in Karasjok that year.

	Knutshø	Forollhogna	Nordfjella	Karasjok
2018				
Precipitation	0.6 mm	1.2 mm	2.2 mm	0.1 mm
Temperature	6.6°C	11.6°C	8.7°C	11.8°C
2019				
Precipitation	0.1 mm	2.2 mm	0.1 mm	-
Temperature	7.8°C	8.7°C	7.7°C	-
Weather stations				
Precipitation	Hjerkin	Lillebudal bru	Finsevatn	Karasjok
Temperature	Driva	Ålen	Finsevatn	Karasjok

2.4 Preparation and laboratory analyses of faecal samples

2.4.1 McMaster flotation method.

McMaster analysis was performed after maximum one week from collection. Faeces were kept at 4° until examination.

A 3 g sample was homogenized in 57 ml water and sieved through a sieve with pore diameter ~1000 µm. The suspension was divided into two 15 ml tubes and centrifuged at 1550 relative centrifugal force (rfg) for 3 minutes, after which the supernatant was discarded.

The concentrated pellet from one of the tubes was resuspended in $NaCl/ZnCl_2$ solution (specific gravity 1.3 *g*). McMaster counting chambers (Whitlock Universal, Australia) were filled with 2.5 ml of this suspension and the whole slide read at 10x-20x magnification for detection of parasite eggs and oocysts in the case of *Eimeria* spp. The eggs were identified based on morphological features to either genus or species level. Some eggs were could only be identified to category of parasites (i.e. strongylids) (Gjerde, 2011; RVC, 2018; Josefsen, Oksanen, & Gjerde, 2014A). Results were reported as eggs per gram (EPG) for each genus,

species or category and oocytes per gram faeces for *Eimeria* spp. Together these results were reported as faecal egg counts.

2.4.2 Baermann method

Due to work load at times of data collection, only reindeer faeces were examined using the Baermann method. Faeces were weighed and wrapped in a piece of gauze. The sample was suspended over a plastic champagne glass with a hollow stem, filled with lukewarm tap water (37 - 40° C), and left submerged in the water for a minimum of 15 hours.

After a minimum 15 hours, the faeces were removed as well as the water from the top of the glass, ensuring not to disturb the bottom ~10 ml of the remaining suspension. The bottom ~10 ml was transferred to 15 ml centrifugation tubes and centrifuged at 1500 rfg for 5 minutes. The supernatant was then aspirated to the 1 ml mark and a 100µl subsample of the sediment was examined at 100x magnification for larvae. If no larvae were observed, the centrifugation tube was left to sediment for ~15 minutes, and 100µl of precipitation was again examined. Larvae were recorded as hatched GIN larvae, the lungworm *Dictyocaulus eckerti*, or *Elaphostrongylus rangifer* larvae based on morphology. The number of larvae per gram faeces (LPG) was estimated from the subsample count (number of larvae detected in 100µlx10/the weight of the faeces in the faecal sample).

2.5 Post-mortem examination

In this study, we examined the contents of the abomasum, duodenum (proximal small intestine), and cecum using principally the procedures described by Hansen and Perry (1994). The data collection described in this chapter are always collected after the animals are dead, though faecal samples obviously have the potential to be collected from living animals.

2.5.1 Abomasum

After thawing at room temperature, the abomasa content and wall were washed with tap water, and the volume was adjusted to 2 L. Four 50-ml centrifuge tubes (4 x 2.5 % aliquots) were then removed from the middle of the bucket while stirring to get a homogenous suspension. The tubes were left to sediment for 30 minutes, and the supernatant thereafter carefully removed with a 10 ml syringe. The tube was again topped off with tap water. If the subsamples were not examined the same or next day, the subsamples were frozen at -8°C until examination.

The rest of the abomasa were stored in the freezer at -8°C for future analysis of arrested larvae in the mucosa. The 50 ml subsamples were examined under a stereomicroscope. Adult nematodes were picked out and counted, and, due to work load, the examination for each aliquot was stopped when the worm count reached >90 worms. The total estimate was, thus, based on subsamples representing 2,5% to 10% of the total abomasa content.

The worms were stored in petri dishes containing 70% ethanol and examined on an object glass with a drop of physiological saline solution under a cover slip to determine both sex and species. The male and female worms were counted. Males belonging to different species and morphotypes were grouped and speciated according to the features of the male bursal organs, such as spicules and other bursal features (Taylor, Coop, & Wall, 2015; Dróżdż, 1965; Dróżdż, 1995). If the worm species was not identifiable, the male was cut in half and the bursal portion placed in polyvinyl lactophenol for 2-5 minutes to clear the parasite. If species identification was still not possible, the upper half of the worm were stored in an Eppendorf tube containing 70% ethanol for sequencing.

2.5.2 Duodenum

The proximal part of the duodenum was cut longitudinally and the content washed with tap water. The suspension was poured through a sieve with a pore diameter of 116µm, and the sieve was inspected visually. Structures resembling worms of the Nematodirinae family were picked out with fine tweezers and further examined under the microscope at 40x and 100x magnification for speciation using the same procedure as described for abomasal nematodes and stored at 70% ethanol before DNA extraction.

2.5.3 Cecum

The cecum was opened with scissors and the content spread out. As nematodes of the large intestines are generally easily seen, visible nematodes were picked off with forceps and placed in a petri dish containing 70% ethanol before further examination with a stereomicroscope and then a compound microscope at 40x.

2.6 Statistical analysis

Data were analysed using Excel and R x64 -3.6.2 (R Development Core Team, 2019) programs. A significance level of $p < 0.05$ was used for all the statistical models analysed. When variables were compared together, the data from one faecal sample collected from a

wild reindeer in Forollhogna was removed as only information related to the faecal parasite counts were available. My data also include one semi-domesticated reindeer from Forollhogna. The results from the statistical analysis did not differ when tested with or without this observation.

2.6.1 Terminology

The ecological terms used in this study are according to the defined terminology established by Margolis et al (1982) and Bush et al (1997). Parasite intensity, or parasite infection intensity, is defined by Bush et al (1997) as the count of a certain parasite species located in the hosts. In this study the parasite intensity refers to quantified adult nematode count (total individuals) in the abomasum or the quantified parasite egg counts (EPG and OPG) detected from the McMaster method or larva count from the Baermann method (LPG).

The difference between parasite intensity and abundance is that abundance includes the non-detections (zeros) in the count, while intensity only uses positive observations. Mean abundance is the average of the total count of a specific parasite from either abomasum nematode count or faecal parasite counts in a specific host species divided by the count of total hosts. As a result of grouping all parasites within abomasa and faecal samples for the statistical analysis, abundance is referred to as the count from a specific group of parasites in this study.

Parasite prevalence is the number of infected hosts divided by the number of total hosts examined. Prevalence is commonly presented as proportion or percentage. When calculating the proportion of sheep parasites in reindeer, a reindeer was considered positive for sheep parasites if I detected a sheep parasite in any of the different parts of the reindeer gastrointestinal tract.

Parasite species richness is the number of different parasite species detected in a collection. In this study parasite species richness was calculated using the different species identified from abomasa samples, duodenum samples, caecum samples and faecal samples. Therefore, the total parasite species richness was determined by the number of parasite species detected in the whole gastrointestinal tract.

2.6.2 Correlation between Strongylid eggs and adult female nematode counts

The relationship between faecal egg count (FEC) from strongyle-type eggs and the egg producing (adult female) nematodes was investigated using a Spearman's rank test. This analysis was performed to give a better foundation to understand and to discuss the correlation between parasite worm counts from adult female Strongylid nematodes and parasite egg counts from faecal samples.

2.6.3 Parasites in reindeer samples

Faecal parasite count in the models include all results extracted from the faecal samples (egg per gram + Oocyst per gram + larvae per gram) while faecal egg counts only include nematode eggs.

In order to select which explanatory variables were important for parasite abundance, parasite species richness and the proportion of sheep parasites, I used backward selection to choose the most parsimonious model. For backward selection, I used the drop1 function, which drops a single variable and compares the model with/without this variable with a Chi-square test.

Abundance

Abundance is measured by the level of infection in all hosts, including non-infected individuals (Bush, Lafferty, Lotz, & Shostak, 1997). The parasite abundance was measured by the total worm count in the abomasa and the total egg count that we could identify as nematode species, from the faecal analysis. Because of highly overdispersed data, both in abomasa counts and faecal parasite counts, the parasite abundance was modelled using negative binomial general linear models (GLM) regressions, using the package 'MASS'. Both models were fitted with area as the explanatory factor to detect variation between the study areas. Karasjok Vestre was set as intercept.

Parasite species richness

Parasite richness was analysed by defining whether the parasite was detected or not detected in the abomasa, duodena, caeca or faecal samples. To get a measure of total parasite species richness, I excluded the parasites that I was not able to determine to species level: *Nematodirus* spp., *Nematodirinae* spp. and *Strongylid* spp. Parasite species that were detected in more than one sample were counted only once. Parasite richness was modelled using GLMs with Poisson errors and a log link function. All models were fitted with area as the

explanatory factor to detect variation between the study areas. Karasjok Vestre was set as intercept.

Proportion of sheep parasites

The proportion of sheep parasites (number of detected sheep parasite species / total number of detected parasite species) in the abomasa-, faecal- and duodena samples were modelled using GLMs with a binomial error and logit link function. Non-infected individuals were excluded to be allowed to calculate and model the proportions. The fitted explanatory variable for this model were study areas with Karasjok Vestre set as the intercept. Because there was no detection of parasites in the reindeer caecal samples located in Karasjok Vestre, a model for counted sheep parasites in the caecum was fitted using a Poisson error and a log link function to determine effects of sheep parasites between the study areas and the control area.

2.6.4 Comparison between Knutshø and Forollhogna in 1987 and 2020

The distribution of adult abomasal nematode counts from the reindeer in Knutshø and Forollhogna showed a Poisson distribution for the resulting three comparable parasite species. To test whether the mean values from Bye (1987) were equal or not to my findings, I used an 'Exact poisson test' to test the mean abomasal nematode count from the reindeer in Knutshø and Forollhogna in this study against the means from 1987. The p-value from the test determine if the two means are equal or not.

3 RESULTS

3.1 Gastrointestinal parasites

A total of 70 gastrointestinal samples from reindeer (14 calves and 56 adults) were collected from the study and control areas, and 69 of these samples were included in this study. One sample was decayed and thus removed from the study. All 70 faecal samples were included in the study. In addition, 32 gastrointestinal samples and 55 faecal samples from sheep samples were collected from the three study areas.

I found 9 different abomasal nematode species in the abomasa samples, 7 nematode species from the duodena samples, 3 nematode species from the caeca samples and 9 nematode species and types from the faecal samples. All gastrointestinal parasite species and types are listed and defined as commonly found in sheep, reindeer or "non-defined" parasites in Table 3. Parasites listed in brackets represents detection in a gastrointestinal part where they are not usually found.

Table 5. All gastrointestinal parasites identified in sheep and reindeer found during this study. Detected parasites are defined either as typical "sheep parasites", "reindeer parasites" or "non-defined parasites" if we can assume that they are commonly detected in both host species. These determinations are based on existing literature (Gjerde, 2011; Josefsen, Oksanen, & Gjerde, 2014A). Parasites are sorted according to which gastrointestinal part they were detected in. Nematode species with their smaller morphs are numbered in superscript.

	Sheep parasites	**Reindeer parasites**	**Non-defined parasites**
Abomasum	*T. circumcincta*[1]	*O. gruehneri*[2]	*S. boehmi*[3]
	T. trifurcata[1]	*O. arctica*[2]	*S. mathevossiani*[3]
	(*T. colubriformis*)	*(N. tarandi)*	
		(N. longissimespiculata)	
Duodenum	*N. battus*	*N. tarandi*	*Monezia* sp.
		N. longissimespiculata	*Nematodirus* sp.
			Trichuris sp.
			Skrjabinema sp.
Caecum			*Oesophagostomum* sp.
			Trichuris sp.
			Skrjabinema sp.
Faeces	*N. battus*	*E. rangifer*	*Trichuris* sp.
		D. eckerti	*Strongyles* spp.
			Nematodirus spp.
			Monezia sp.
			Capillaria sp.
			Eimeria spp.

Adult nematodes in the abomasum

I found *T. colubriformis* in one sheep abomasum from Forollhogna. I also found *Nematodirus longissimespiculata* and *N. tarandi* in one reindeer abomasa sample each from the study areas of Nordfjella and Karasjok. These parasite species are expected to be found in the small intestine and may have moved into the abomasum post mortem during sample collection and handling.

Three species were detected in the sheep abomasa. The two most common parasites detected in sheep was T. circumcincta *and its smaller morph* T. trifurcata*. Seven nematode species were detected in the reindeer abomasa. I found* O. gruehneri *in 54 infected reindeer, which was the parasite with the highest prevalence in both the wild and semi-domesticated reindeer samples.* Teladorsagia circumcincta *was found in 37 reindeer. This parasite was not detected in the control area of Karasjok, but had the highest prevalence and intensity in the three study areas among the wild reindeer samples.* Spiculopteragia boehmi *was detected in Karasjok and Nordfjella with high prevalence in reindeer.* Spiculopteragia boehmi *was also detected in a semi-domesticated reindeer located in Forollhogna but had a low intensity (100 worms). I also detected the* S. boehmi *minor morph* S. mathevossiani *(Liénard, Depaquit, & Ferté, 2006) in one semi-domesticated reindeer in Karasjok with low intensity (186 worms) (*A total of 70 gastrointestinal samples from reindeer (14 calves and 56 adults) were collected from the study and control areas, and 69 of these samples were included in this study. One sample was decayed and thus removed from the study. All 70 faecal samples were included in the study. In addition, 32 gastrointestinal samples and 55 faecal samples from sheep samples were collected from the three study areas.

I found 9 different abomasal nematode species in the abomasa samples, 7 nematode species from the duodena samples, 3 nematode species from the caeca samples and 9 nematode species and types from the faecal samples. All gastrointestinal parasite species and types are listed and defined as commonly found in sheep, reindeer or “non-defined” parasites in Table 3. Parasites listed in brackets represents detection in a gastrointestinal part where they are not usually found.

Table 5). (Liénard, Depaquit, & Ferté, 2006). *Spiculopteragia boehmi* was not detected in any sheep samples. The typical sheep nematodes *T. circumcincta* and the minor morph *T. trifurcata* were both detected in reindeer abomasa samples in all the three study areas with medium-high sheep intensity (**Error! Not a valid bookmark self-reference.**).

Table 6.Parasite intensity of adult nematodes detected in reindeer abomasa samples, classified by adult/calves from 69 reindeer sampled during the annual hunt in Nordfjella, Forollhogna and Knutshø 2018 and 2019 and from the reindeer slaughterhouse in Karasjok 2018. Median, mean and min-max values are calculated from all samples where the parasite was found.

		Adult				**Calves**		
	n-positive / n-total	Median	Mean	Min-max	n-total / n-positive	Median	Mean	Min-max
Knutshø								
T. circumcincta	11 / 14	1785	1648	60-3696	8 / 6	324	359	86-999
T. trifurcata	4 / 14	410	369	93-562	8 / 1	51	51	51-51
O. gruehneri	11 / 14	825	1066	26-3956	8 / 1	26	26	26-26
O. Arctica	2 / 14	68	68	52-84	8 / 2	25	25	25-26
Forollhogna								
T. circumcincta	14 / 16	698	1390	28-8308	4 / 4	713	1510	410-2450
T. trifurcata	7 / 16	128	268	76-1024	4 / 2	172	172	67-277
O. gruehneri	15 / 16	995	1034	92-3019	4 / 1	92	92	92-92
O. Arctica	5 / 16	202	207	43-472	4 / 1	152	152	152-152
Nordfjella								
T. circumcincta	0 / 5	-	-	-	3 / 2	105	105	28-182
T. trifurcata	1 / 5	41	41	41-41	3 / 1	23	23	23-23
O. gruehneri	5 / 5	1081	1107	461-1878	3 / 3	64	64	46-83
S. boehmi	5 / 5	42	49	27-82	3 / 1	16	16	16-16
Karasjok								
O. gruehneri	18 / 19	3598	3509	434-6205	0	-	-	-
S. boehmi	18 / 19	2702	2440	195-6618	0	-	-	-

Adult nematodes in the duodenum

Five nematode species were detected in the reindeer duodenum samples. Both *N. tarandi* and *N. longissimespiculata* were detected in reindeer duodenal samples from Knutshø and Nordfjella. *Nemotadirus longissimespiculata* was also detected in one reindeer located in

Forollhogna. *Teladorsagia colubriformis*, which was found in a sheep sample from Forollhogna, was not detected in any samples from reindeer. *Monezia* sp. and *Nematodirus* spp. were detected in reindeer samples from Knutshø and Forollhogna. *Nematodirus battus* was detected in reindeer samples from Knutshø, Forollhogna and Nordfjella. *Nematodirus battus* and *Monezia* sp. were also detected in sheep samples from Knutshø and Nordfjella, but not in Forollhogna. No parasites were detected in the duodena of the Karasjok reindeer samples. The parasite prevalence in the duodena is equal to the prevalence detected for the egg, oocyst and larva count (Table 7) except for two additional detections within calves in Forollhogna. I detected adult *Nematodirus battus* in 1 adult reindeer and 12 calves in total. Calves were detected with high prevalence of *N. battus* in the duodena: Nordfjella 100%, Forollhogna 50% and Knutshø 87%. *Nematodirus battus* were the only typical sheep parasite found in the duodena from reindeer samples (Table 5).

Adult nematodes in the caecum

Three parasite species were detected from the caeca samples. *Trichuris* sp. was the only parasite detected in sheep samples from Knutshø and Nordfjella. *Trichuris* sp. was detected in reindeer samples from Knutshø and Forollhogna. *Skrjabinema* sp. was detected in reindeer samples from Knutshø, Forollhogna and Nordfjella. *Oesophagostomum* sp. was detected in one reindeer caecum sample from Forollhogna. No parasites were detected in the caeca from the Karasjok reindeer samples. The parasite prevalence in the caeca is equal to the prevalence detected for the egg, oocyst and larva count (Table 7). I detected no parasites in the caecum samples from reindeer that I could determine morphologically as a typical sheep parasite (Table 5).

Total egg, oocyst and larva count

Two nematode species were detected in the Baermann analyses of the reindeer faecal samples. *Dictyocaulus eckerti* was detected in samples from Knutshø, Forollhogna and Karasjok. *Elaphostrongulus rangiferi* was detected in samples from Forollhogna, Karasjok and Knutshø. There was a detection of a total of six parasite groups from the McMaster analysis from the faeces samples. *Nematodirus battus* eggs were detected in sheep faeces from Knutshø and Nordfjella and in reindeer faeces from Knutshø, Forollhogna and Nordfjella. *Trichuris* sp. was found in sheep faeces from Nordfjella, Knutshø and Forollhogna. High prevalence of *Eimeria* sp. was found in sheep faecal samples from

Knutshø, Forollhogna and Nordfjella. Reindeer faecal samples from Nordfjella, Forollhogna and Knutshø were also *Eimeria* sp. positive, but with a lower prevalence and intensity. *Nematodirus battus* was the only parasite detected in the faeces samples from reindeer that can be categorized as typical sheep parasite based on egg morphology (Table 7). In two reindeer calves from Nordfjella, the faecal analysis was negative for *N. battus*, but adult nematodes were detected in the duodena. *Nematodirus battus* was also detected in one adult reindeer from Nordfjella.

Table 7. Prevalence of parasite eggs, oocysts and larvae based on McMaster and Baermann analysis of reindeer faeces from the study areas sampled during the reindeer hunt, August- September 2018 and 2019, and the control area Karasjok sampled during the reindeer slaughter in October 2018. Median, mean and range are calculated from the parasite intensity (eggs, oocysts and larvae per gram faeces),

Knutshø [n=22]	**n-positive**	**% positive**	**95% CI**	**Median epg/opg**	**Mean epg/opg**	**Range of epg/opg**
Strongylid spp.	22	100	85 – 100	85	158	10 - 1015
Nematodirinae spp.	6	27	11-50	20	70	10 - 330
N. battus	7	32	15 – 55	50	53	10 - 150
Trichuris sp.	1	5	0.1 – 23	10	10	10 - 10
Capillaria sp.	1	5	0.1 – 23	10	10	10 - 10
Eimeria sp.	3	14	3 – 35	200	17333	200 - 51600
Dictyocaulus eckerti	5	23	8 – 45	22	47	4 - 88
E. rangifer	1	5	0.1 – 23	2	2	2 - 2
Forollhogna [n=21]						
Strongylid spp.	20	95	76 – 100	95	160	30 - 790
Nematodirinae spp.	4	19	5 – 42	30	95	10 - 310
N. battus	3	14	3 – 36	20	37	10 - 80
Capillaria sp.	6	29	11 – 52	20	67	10 - 300
Eimeria sp.	1	5	0.1 – 23	400	400	400 - 400
Dictyocaulus eckerti	7	33	15 – 57	75	118	10 - 396
E. rangifer	6	29	11 – 52	2	23	1 - 151
Nordfjella [n=8]						
Strongylid spp.	4	50	16 – 84	20	20	0 - 30
Nematodirinae spp.	1	12.5	0.3 – 52	30	30	30 - 30
N. battus	1	12.5	0.3 – 52	40	40	40 - 40
Eimeria sp.	1	12.5	0.3 – 52	300	300	300 - 300
Karasjok [n=19]						

Strongylid	12	63	38 – 84	40	82	10 - 360
Capillaria sp.	5	26	9 – 51	20	26	10 - 50
Dictyocaulus eckerti	2	10	1 – 33	17	75	4 - 339
E. rangifer	16	84	60 – 97	2	6	2 – 10

3.2 Correlation between Strongylid eggs and adult female nematode counts

The correlation between the *Strongylid* spp. egg counts and the estimated numbers of adult female strongylid parasites found in the abomasa showed a weak positive relationship (Spearman's rank r=0.270, p=0.004; Figure 2). The low number of strongylid eggs detected in the samples indicate low *Strongylid* spp. infection.

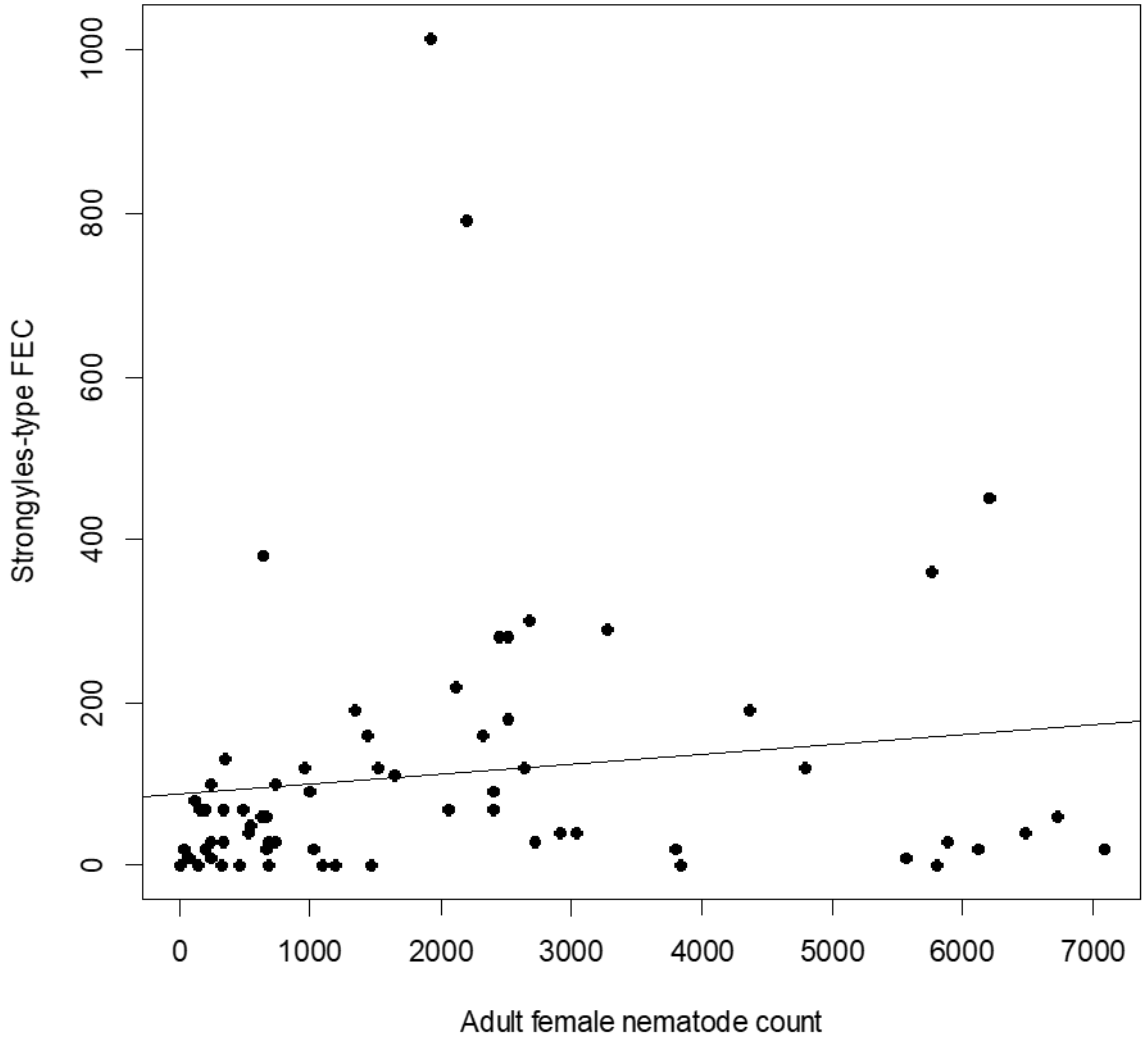

Figure 2. The correlation between the number of female strongylid nematodes counted in the abomasa and the strongyle-type fecal egg count from the reindeer faeces samples (n=69) from all study areas.

3.3 Parasite abundance in reindeer samples

Karasjok Vestre had a significantly higher parasite abundance than the other areas (Figure 3Table 3; Table 8). Adults had a significantly higher parasite abundance than calves in the abomasum samples (Table 4; Table 8). Precipitation (slope ± SE= -13.34 ± 5.75; Table 8Table 7) and temperature (slope ± SE= -4.94 ± 2.04; Table 8Table 7) had both a significant negative correlation with adult abomasal nematode abundance.

The faecal parasite counts also varied among study areas (Table 8Table 7; Figure 3). Karasjok had the highest counts and Forollhogna the second highest counts of faecal eggs, while Nordfjella and Knutshø had the lowest counts of faecal eggs (Figure 3). The egg count from the faecal analysis had one extreme outlier (Forollhogna 1.091). The model for the total egg count showed a significant difference between the study areas both with and without the outlier removed (Figure 3; Table 8). Precipitation (slope ± SE= -15.63 ± 6.55;Table 8) and temperature (slope ± SE= -5.76 ± 2.34; Table 8Table 7) affected the faecal egg count from the reindeer faeces negatively (Table 8). There was no statistically significance between calves and adults.

Table 8. Summary of the model for area (Karasjok, Nordfjella, Forollhogna and Knutshø), age (calf and adult), precipitation and temperature were fitted against parasite abundance in the reindeer abomasa nematode count and faecal egg counts

	Area	**Age**	**Precipitation**	**Temperature**
Abomasum	$\chi^2_{3,61}$=17.70; p< .001	$\chi^2_{1,61}$=11.93; p< .001	$\chi^2_{1,61}$=5.48; p=.019	$\chi^2_{1,61}$=<5.95; p= .015
Faeces	$\chi^2_{3,61}$=17.07; p< .001	$\chi^2_{1,61}$=0.02; p=.881	$\chi^2_{1,62}$=5.37; p= .021	$\chi^2_{1,63}$=7.75; p= .017

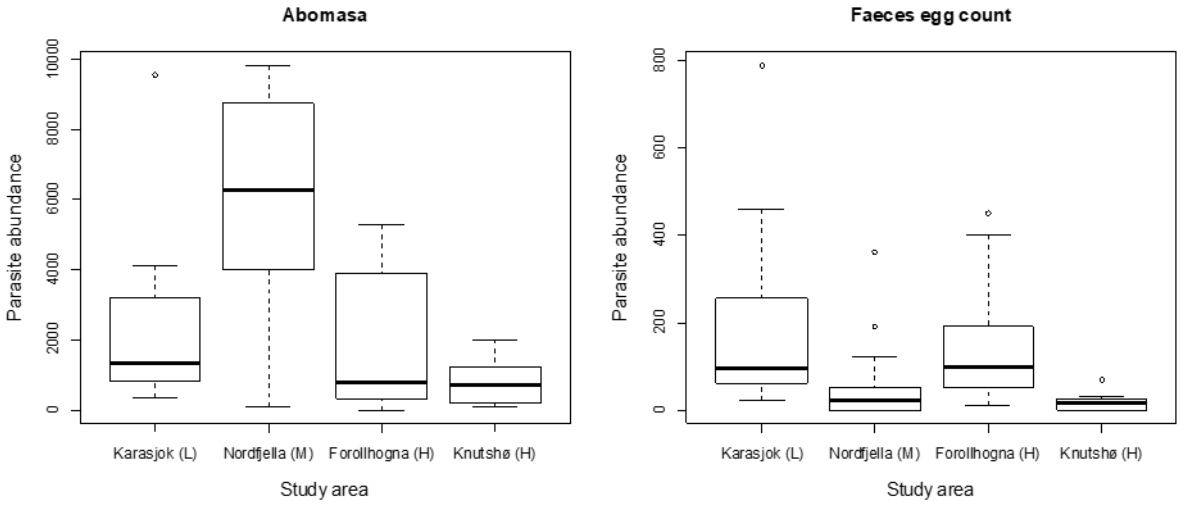

Figure 3. Abomasa parasite count and faecal egg count from faecal samples from the study areas (Forollhogna, Knutshø and Nordfjella) and the control area (Karasjok Vestre). Sheep grazing intensity, low – medium – high, are indicated in brackets behind each study area. The solid black line represents the median. Boxes show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles for both the abomasa worm count and faeces egg count. Outliers from the data are plotted with individual points. The extreme outlier of 1.091 in Forollhogna was excluded from the faeces egg count figure and model.

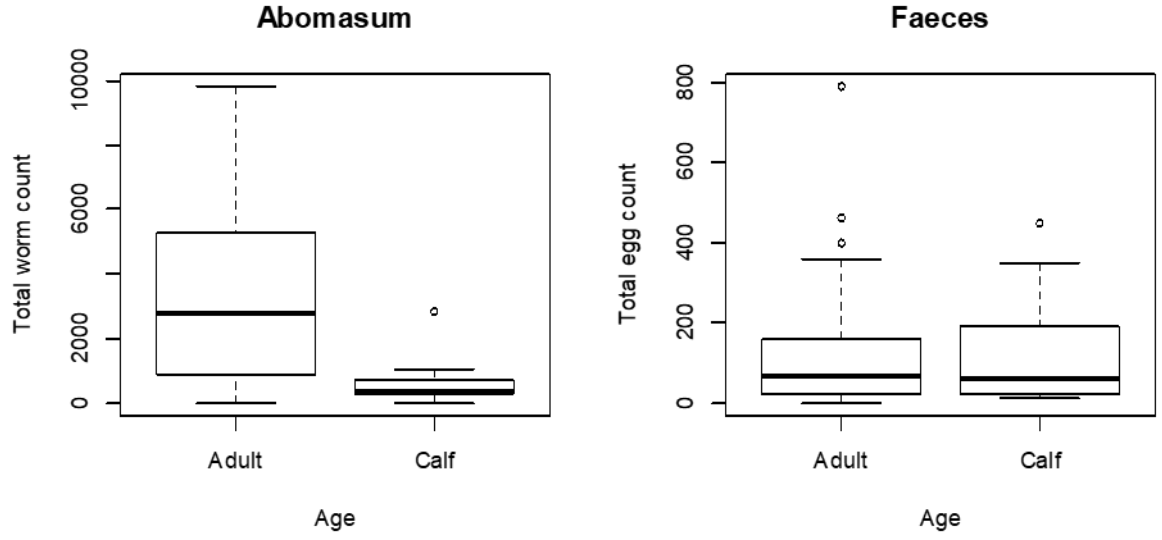

Figure 4. Parasite abundance divided between adult and calves in the reindeer abomasa samples and faecal samples. The solid black line represents the median. The boxplots show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles for the abomasa worm count and faecal egg count. Outliers from the data are plotted with individual points.

3.4 Parasite species richness

Area, age, precipitation and temperature showed no significant relationship for parasite species richness in the reindeer abomasum samples (Table 9). There was no statistically significant effect from the variables on parasite diversity in the total reindeer gastrointestinal samples (Table 9; Figure 6).

Caecum samples from the study areas were slightly statistically significant with Karasjok Vestre having a lower parasite species richness than the other study areas (Table 9; Figure 5). Temperature (slope ± SE= 77.78 ± 17946.20; Table 9Table 9) and precipitation (slope ± SE= 224.87 ± 52043.99;Table 9) both had a positive significant effect on the reindeer caecum samples. Parasite species richness in the reindeer caecum samples showed no difference between the other variables (Table 9; Figure 6, Figure 7)Figure 5.

Area and age both had a significant effect on duodena parasite richness in the reindeer samples (Table 9; Figure 5). Karasjok Vestre showed a significant lower parasite richness than the other areas and calves showed a significantly higher parasite species richness than adults for the duodenum samples (Table 9; Figure 7).

The faecal samples showed a significant difference with Nordfjella and Karasjok Vestre having a lower parasite richness than Knutshø and Forollhogna (Table 9; Figure 5). Age, precipitation and temperature showed no significant relationship for parasite species richness in the reindeer faecal parasite count (Table 9; Figure 5, Figure 7).

Table 9. Summary of the model for area (Karasjok, Nordfjella, Forollhogna and Knutshø), age (calf and adult), precipitation and temperature fitted against parasite species richness in the reindeer gastrointestinal tract sample counts and faecal egg count.

	Area	Age	Precipitation	Temperature
Abomasum	$\chi^2_{3,62}$=1.37; p= .713	$\chi^2_{1,62}$=1.50; p= .220	$\chi^2_{1,67}$=2.74; p= .098	$\chi^2_{1,65}$=<0.01; p= .980
Caecum	$\chi^2_{3,63}$=8.12; p= .436	$\chi^2_{1,62}$=0.43; p= .515	$\chi^2_{1,63}$=5.04; p= .025	$\chi^2_{1,63}$=<4.96; p= .026
Duodenum	$\chi^2_{3,62}$=11.07; p= .089	$\chi^2_{1,62}$=30.42; p< .001	$\chi^2_{1,62}$=0.35; p= .555	$\chi^2_{1,63}$=0.36; p=.548
Faeces	$\chi^2_{3,65}$=7.85; p= .049	$\chi^2_{1,64}$=1.37; p= .242	$\chi^2_{1,62}$=0.05; p= .819	$\chi^2_{1,63}$=0.74; p= .388
Total	$\chi^2_{3,64}$=3.39; p= .336	$\chi^2_{1,63}$=0.57; p= .449	$\chi^2_{1,62}$=0.14; p= .704	$\chi^2_{1,63}$=0.11; p= .736

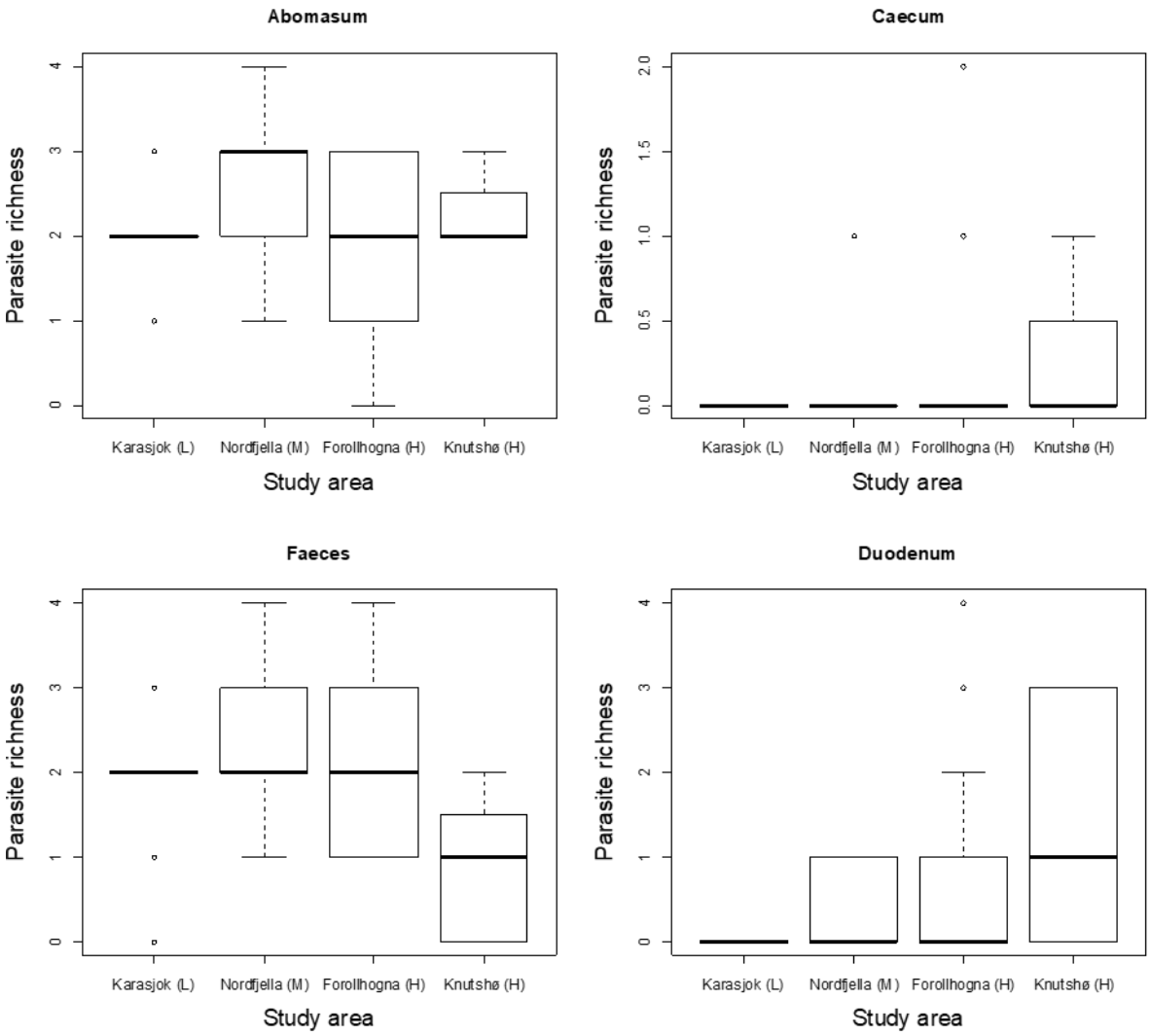

Figure 5. Parasite species richness for the number of parasite species detected in the different parts of the reindeer gastrointestinal tract compared between the different study areas. Sheep grazing intensity, low – medium – high, is indicated in brackets behind each study area. The solid black line represents the median. The boxes show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles from the abomasa nematode species count and faecal species count. Outliers from the data are plotted with individual points.

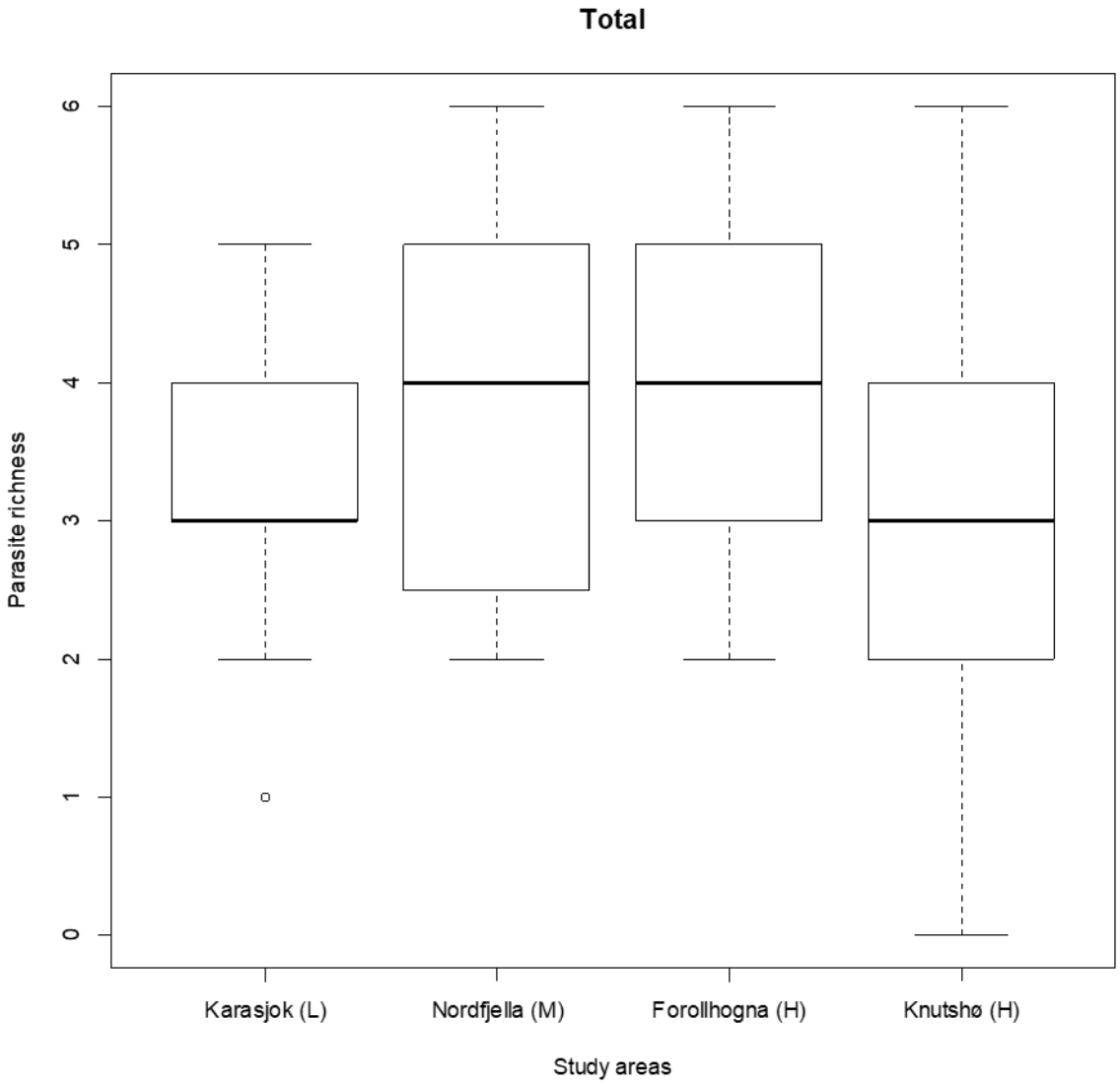

Figure 6. Total parasite species richness between the different study areas. Parasite richness is calculated from total parasite richness in the reindeer gastrointestinal tract. Sheep grazing intensity, low – medium – high, is indicated in brackets behind each study area. The solid black line represents the median. The boxes show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles from the abomasa nematode species count and faecal species count. Outliers from the data are plotted with individual points.

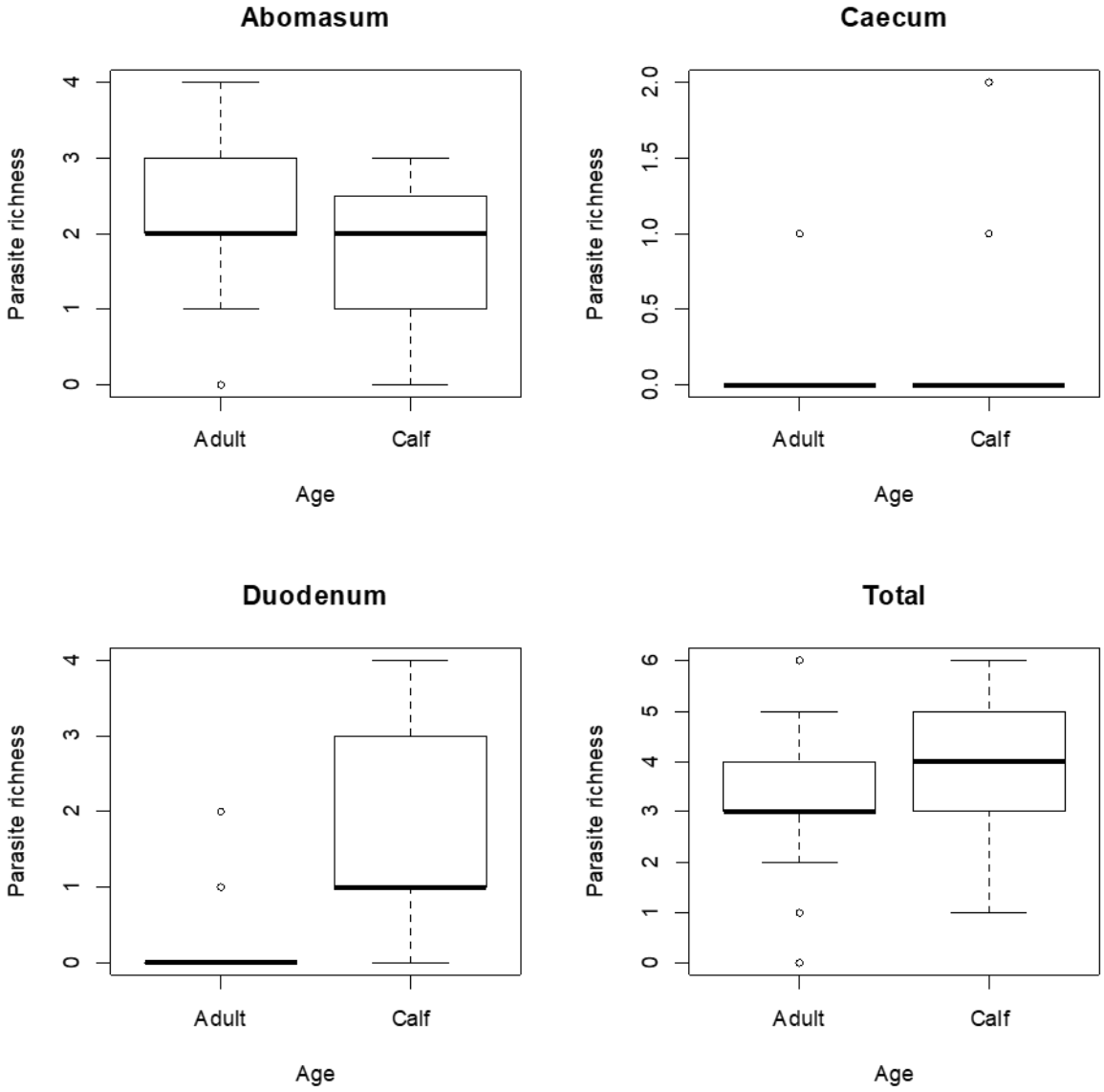

Figure 7. Parasite species richness presented for both adult and calf in the different parts of the reindeer gastrointestinal tract. The solid black line represents the median. The boxes show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles from the abomasa nematode species count and faecal species count. Outliers from the data are plotted with individual points.

3.5 Proportion of typical sheep parasites found in reindeer samples

No typical sheep parasites were detected in the gastrointestinal tract samples from reindeer in Karasjok Vestre, but sheep parasite spillover was detected in the all the other study areas. The proportion of sheep parasites in reindeer abomasa from the other study areas was statistically significantly when compared to the control area (Table 10; Figure 8). Calves showed significant higher values than adult reindeer (Table 10; Figure 9). The proportion of typical

sheep parasites found in the reindeer abomasa showed a relation with all explanatory variables. Precipitation (slope ± SE= -18.67 ± 9.06; Table 10) and temperature(slope ± SE= -6.88 ± 3.20; Table 10) had a significant negative effect on the proportion of sheep parasites in the abomasa samples.

Calves showed a significant higher proportion of sheep parasites in the duodena samples (Table 10; Figure 9). Precipitation and temperature show no significant effect on the proportion of sheep parasites in the reindeer duodena samples (Table 9). It was not possible to run a proportion test for the Karasjok (area with low sheep intensity) duodena samples, as no sheep parasites were detected in these samples (Table 9).

Calves had a significantly higher proportion of sheep parasites than adults for the faecal samples (Table 10; Figure 9). Area, precipitation and temperature did not have a statistically significant effect on proportions of sheep parasites from the reindeer faecal samples (Table 10).

The proportion of sheep parasites found in the reindeer gastrointestinal tract (total) from each of the study areas was statistically significantly when compared to the control area (Table 10; Figure 8). Calves had significant higher proportions of sheep parasites than adults (Table 10; Figure 9). Precipitation and temperature showed no significant effect on the proportion of sheep parasites in the total reindeer gastrointestinal tract.

Table 10. Summary of the model analysing factors affecting the proportion of sheep parasites in reindeer samples. No sheep parasites were detected in Karasjok duodenum samples; hence the table only includes results for duodenum samples tested by positive detection of sheep parasites as response variable from only 3 study sites.

	Area	**Age**	**Precipitation**	**Temperature**
Abomasum	$\chi^2_{3,58}$= 21.64; p< .001	$\chi^2_{1,58}$= 5.29; p= .022	$\chi^2_{1,58}$= 4.11; p= .036	$\chi^2_{1,58}$= 4.80; p= .029
Duodenum	$\chi^2_{3,31}$= 0.27; p= .965	$\chi^2_{1,36}$= 13.48; p< .001	$\chi^2_{1,35}$= 2.86; p= .091	$\chi^2_{1,31}$<0.01 ; p= .957
Faeces	$\chi^2_{3,58}$= 0.71; p= .871	$\chi^2_{1,62}$= 20.08; p< .001	$\chi^2_{1,61}$= 0.66; p= .415	$\chi^2_{1,62}$= 1.41; p= .235
Total	$\chi^2_{3,63}$= 44.10; p< .001	$\chi^2_{1,63}$= 5.34; p< .020	$\chi^2_{1,61}$= 1.49; p= .264	$\chi^2_{1,62}$= 2.42; p= .120

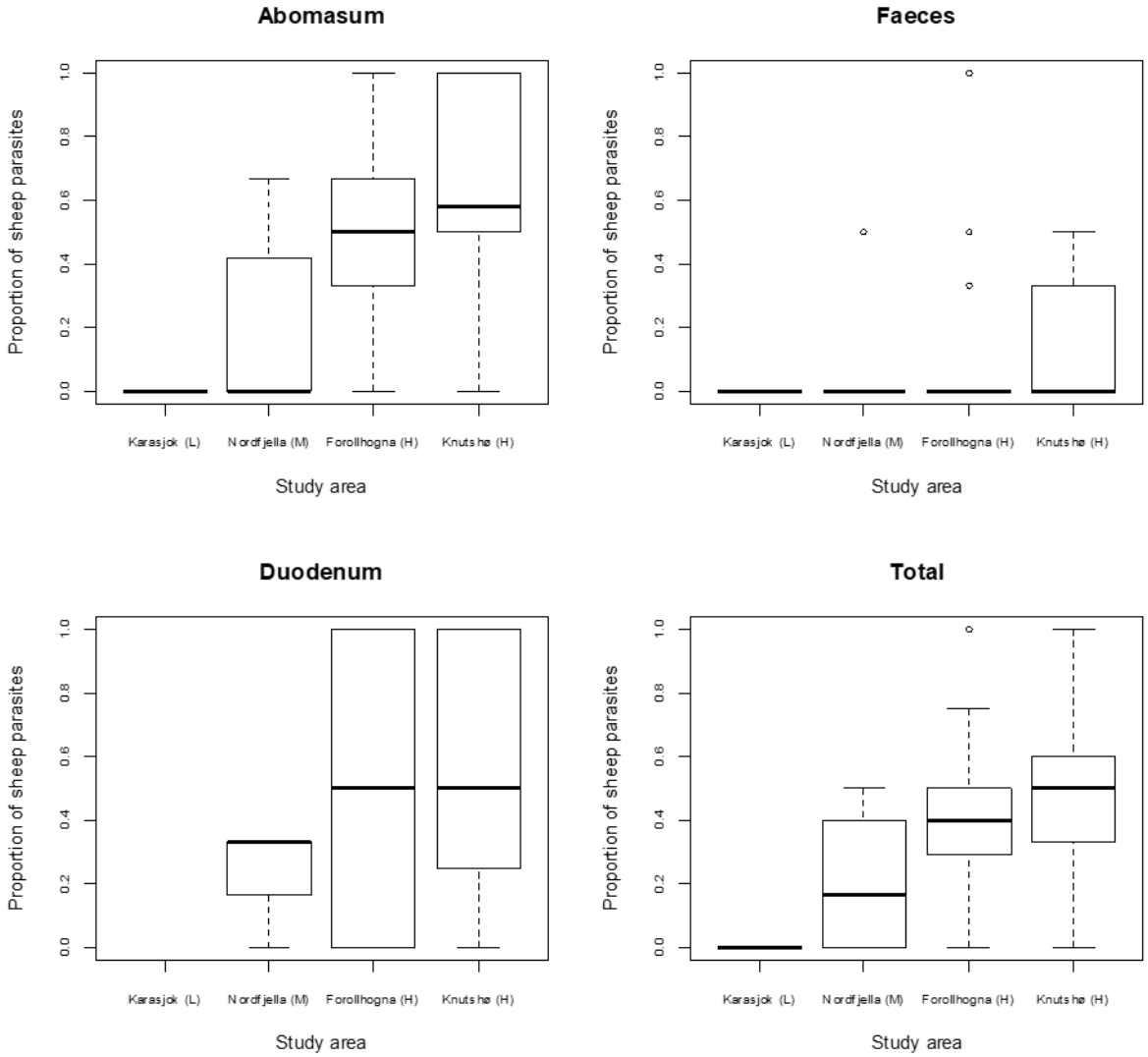

Figure 8. Proportion of sheep parasites in reindeer calculated by detection of sheep parasite species in reindeer abomasa, faeces and duodena samples. "Total" represent total sheep parasite proportion in the reindeer gastrointestinal tract. I detected no parasite in the duodena samples from Karasjok. Sheep grazing intensity, low – medium – high, are indicated in brackets behind each study area. The solid black line represents the median. The boxes show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles from the abomasa nematode species count and faecal species count. Outliers from the data are plotted with individual points.

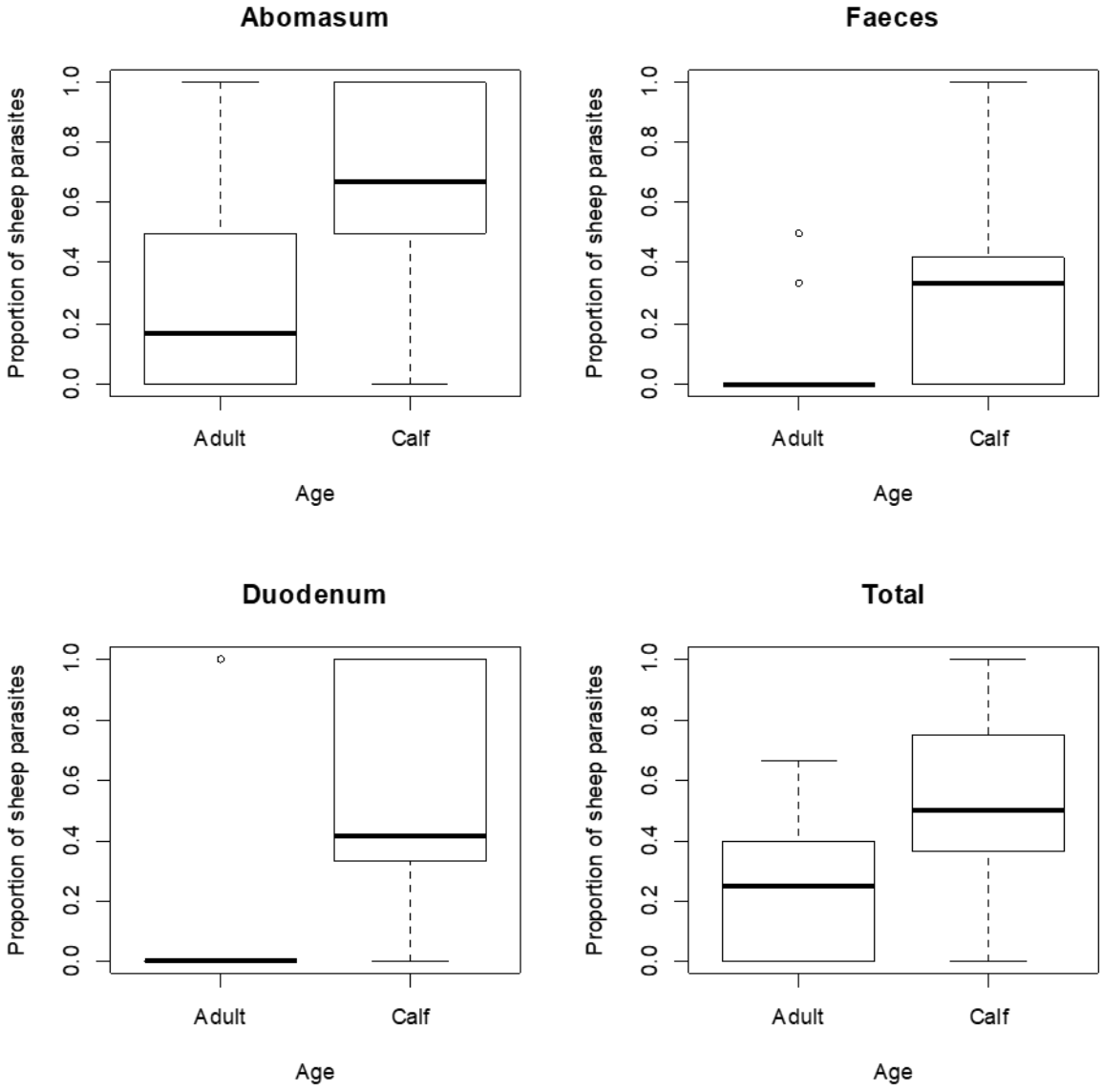

Figure 9. Proportion of sheep parasites presented for adults and calves in the different parts of the reindeer gastrointestinal tracts. The solid black line represents the median. The boxes show the quartiles and the whiskers (lines extending from the boxes) represent the variability outside the quartiles from the abomasa nematode species count and faecal species count. Outliers from the data are plotted with individual points.

3.6 Comparison between Knutshø and Forollhogna in 1987 and 2020

Although Bye (1987) detected low abundance of the parasites *T. axei* and *T. davtiani*, I did not detect these parasites in the reindeer abomasa samples. The only parasite Bye detected in Forollhogna was *Teladorsagia davtiani*. Bye did not detect *S. boehmi* or *T. Trifurcata* in his study in 1987, but these parasites were detected with low prevalence in this study.

The comparison between our studies showed a large increase in intensity of *T. circumcincta* between 1987 to 2018/2019 for reindeer in Knutshø. *Teladorsagia circumcincta* also had a high increase in abundance for reindeer in Forollhogna. The minor morph *O. Arctica* showed low abundance for both our studies. Still, I detected an increase in Forollhogna and a decrease in Knutshø for this parasite. Comparing results between Bye (1987) and this study show that our resulting means are significantly different (Table 11).

Table 11. Mean parasite abundance for abomasum nematodes collected from adult reindeer in Forollhogna and Knutshø from Bye (1987) compared with the mean ± CI from the results in this study. Growth values represent the parasite species increase or decrease for the current parasite abundance compared to the reported intensity for Bye 1987. P-values from the exact poisson test show if the relationship between the two compared means are significantly different or not.

	95% CI low	Mean Bye (1987)	95% CI high	95% CI low	Mean (2020)	95% CI high	Growth	p-value
Forollhogna								
T. circumcincta	173.6	519.5	865.4	1199.0	1216.1	1233.3	2.3	< .001
O. gruehneri	642.6	954.8	1267.0	1012.4	1028.0	1043.8	1.1	< .001
O. arctica	27.7	40.6	53.5	60.9	64.8	68.9	1.6	< .001
Knutshø								
T. circumcincta	20.2	30.2	40.2	1275.9	1294.6	1313.6	42.9	< .001
O. gruehneri	528.8	668.4	808.0	822.9	838.0	853.3	1.3	< .001
O. arctica	22.5	23	23.5	8.2	9.7	11.5	0.4	< .001

4 DISCUSSION

I found clear evidence of gastrointestinal nematode spillover between reindeer and sheep in the areas with medium-high sheep grazing intensity (list your study areas here). I found no typical sheep nematodes in the reindeer gastrointestinal samples located in the area with low grazing intensity (Karasjok Vestre). This study has also revealed other significant findings. Perhaps most important was the detection of *N. battus* in both duodena and faecal samples from wild reindeer in Nordfjella, Forollhogna and Knutshø. *Nematodirus battus* is a pathogen listed as a pathogen with "potential high risk of spreading" and causing "unknown ecological effects" and which "has been detected in moose, musk and now wild reindeer in Norway" by the Norwegian Biodiversity Information Centre (2020).

Another important result was the weak relationship between the parasite abundance detected from faecal Strongylid egg counts and adult female nematode counts in the abomasa. This is a strong indication that faecal samples collected during the fall hunt, has low explanatory value for parasite nematode burden (see further discussion below). These results are similar to other findings where seasonal fluctuations of gastrointestinal nematode egg production have been documented (Hrabok, Oksanen, Nieminen, & Waller, 2006; Taylor E. L., 1935) as well as studies documenting the influence of climatic variables, such precipitation and temperature (Chattopadhyay & Bandyopadhyay, 2013). Understanding the different gastrointestinal parasites' epidemiology and lifecycle is, therefore necessary to interpret the results, especially for the faecal egg counts for parasite species that have high seasonal fluctuations (Halvorsen & Bye, 1985; Carlsson, et al., 2018). The samples collected from Karasjok Vestre were collected during winter. During winter it would be expected to find low numbers of both adult worms and thus eggs and oocysts in the gastrointestinal tract of reindeer, as the majority of nematodes in the abomasa undergo hypobiosis overwintering in the mucosa as larval stages during this season (Hrabok, Oksanen, Nieminen, & Waller, 2006; Rehbinder & Christensson, 1977; Bye & Halvorsen, 1983). I found low faecal egg counts in the samples from Karasjok Vestre, as I expected, but the adult nematodes count from the abomasa was high. This may be explained by the fact that the dominant nematode species, *T. circumcincta*, would be in hypobiosis (hibernation) during the time of sampling and not shedding eggs.

I detected abomasal nematodes in all reindeer samples except two calves and one adult in Knutshø, and one presumed adult from Karasjok Vestre. In one of the Karasjok Vestre

samples, *N. tarandi,* was detected in the abomasum, which I suspect had floated into the abomasum from the duodenum post mortem. This is also a likely explanation for the findings of *N. longissimespiculata* in a calf abomasum from Forollhogna. Both of these parasites are expected to be found in the duodena.

Stien et al. (2002) found seasonal fluctuations for *O. gruehneri* with a variation between 5.000 to 10.000 adult nematodes per reindeer host the first year and 9.000 to 17.000 adult nematodes per reindeer host the second year. In my study, the samples from Karasjok Vestre had the highest intensity of adult nematodes, and the two dominant species detected in these were *O. gruehneri* and *S. boehmi,* with medium intensity. Reindeer samples from Karasjok Vestre had a high intensity with 58% of the reindeer positive with < 5.000 nematodes and a further 21% with < 9.000 nematodes. The dominant abomasal nematode species found in the samples from Knutshø and Forollhogna was *T. circumcincta,* and in Nordfjella it was *O gruehneri*. In Knutshø 22% of the dominant nematode had counts < 2.000 and 20% in Forollhogna. The highest number of abomasal nematodes in samples from Nordfjella was 1.878. Compared to Stien et al. (2002), these results indicate that the reindeer included in my study had medium abomasal nematode infection intensity, but that the results from the semi-domesticated reindeer samples from Karasjok Vestre had a higher abomasal nematode infection intensity, particularly compared to the other study areas.

It is estimated that a burden of 12.000 to 15.000 adult *Ostertagia ostertagi* could potentially induce mortality in cattle calves, but adult cattle could tolerate burdens of more than 40.000 adult nematodes (Hoberg, Kocan, & Rickard, 2001). However, even if the host nematode count may be high, it is important to include other relevant factors such as nematode species, species, weight, age, immune status, and nutrition status of the host, as well as environmental variables such as climate and forage availability when evaluating possible pathological effects from worm burden (Hoberg, Kocan, & Rickard, 2001). Unfortunately, I do not have data for the above factors listed, except nematode species and count and the relative age. This limits the possibility to discuss the pathological effects, but I can extrapolate from available literature in the following discussion.

In ungulate populations, nematodes are often found with higher abundance in male compared to female hosts, see for example Armour (1989) and Halvorsen and Bye (1999). Acquired immunity may also limit the nematode infection intensity of older ungulates, see for example Armour (1989). However, in this study, adults had higher abundance of abomasal nematodes

compared to the calves. Sheep can also develop immunity towards some abomasa nematodes, for example *N. battus* (Animalia, 2013). In Svalbard reindeer, the abundance of *O. gruehneri* adult worm in abomasa were found to increase until the age of 3 – 5 years, and then decline, suggesting that reindeer do not develop an efficient immune response against this particular parasite (Halvorsen, Stien, Irvine, Langvatn, & Albon, 1999) . In addition, the life expectancy of an *O. gruehneri* worm is 2 years, in contrast to 3-4 months to its "domestic" counterpart, *O. ostertagi* (Smith, Grenfell, & Anderson, 1986), which may lead to an accumulating of *O. gruehneri* in the host.

Temperature and humidity are primary factors for nematode free-living larvae survival, but nematodes adapted to the Arctic, e.g. *O. gruehneri* and *O. arctica* are able to survive and develop in more harsh and extreme conditions (Crofton, 1971; Josefsen, Oksanen, & Gjerde, 2014A). In this study I found a negative relationship in relation to both temperature and precipitation for abomasal nematode abundance. I also found a negative relationship for these factors in relation to proportion of typical sheep parasites. Both 2018 and 2019 were dry and warm summers compared to the average summer temperature and humidity in the study areas, and this may have affected these results. I did find a positive relationship between temperature and precipitation with the parasite richness of caecal nematodes supporting my predictions.

Two typical sheep abomasal nematodes, *T. circumcincta* and its smaller morph *T. trifurcata*, were detected in my study and have previously been detected in reindeer in North America (Low, 1976; Dikmans, 1939). Bye and Halvorsen (1983) also detected small numbers of *T. circumcincta* and *T. trifurcate* in reindeer on Svalbard and, almost 20 years later, Irvine et al. (2001) detected a medium prevalence of *T. circumcincta* and low prevalence of *T. trifurcata* in Svalbard reindeer.

Two typical sheep abomasal nematodes were detected in samples from my study areas, *T. circumcincta* and its smaller morph *T. trifurcata* , which have previously been detected within reindeer in North America (Low, 1976; Dikmans, 1939). Bye and Halvorsens (1983) study of Svalbard reindeer abomasal nematodes also detected small numbers of *T. circumcincta* and *T. trifurcata*. Irvine et al. (2001) detected a medium prevalence of *T. circumcincta* and low prevalence of *T. trifurcata*. The origin of the Svalbard reindeer is unknown, but it has been hypothesized that the founder animals came from Nova Semlja, Russia (Norderhaug & Reimers, 1976). How these reindeer were potentially infected by gastrointestinal nematodes of domestic livestock is, however, uncertain. Either they carried these parasites from the

mainland when they first arrived or they were infected on Svalbard. We know that there have been agriculture activities in Svalbard, which included sheep livestock for a short time period in a farm established in the town Pyramiden in 1972 (Vikan, 2014). The areas of agricultural activity in Svalbard could be a potential spot where cross-transmission occurred. The current lack of sheep on Svalbard is a clear indication that these nematode species are capable of surviving on Arctic rangeland and adapting to reindeer as the only available ruminant host. Therefore, it is interesting that I have detected these parasites in all the study areas with overlapping sheep grazing but not in Karasjok Vestre, where the number of sheep grazing may be considered negligible compared to the number of reindeer in the same area. It is unclear why these sheep parasites are not present in reindeer here despite the presence of some sheep, but the anthelmintic treatment of sheep (Gjerde, 2011) may partly explain the absence of these parasites in combination with the minimal rangeland overlap.

I found high prevalence for *T. circumcincta* in reindeer abomasa in both Forollhogna and Knutshø. This may be related to the high degree of overlap between sheep and reindeer rangeland, but may also be related to temperature and potential for larval development. Hoar (2012) measured the survivability of infective stage 3 larvae for both *O. gruehneri* and *T. circumcincta* and found higher survival for stage three larvae for *T. circumcincta* for all temperatures. *Teladorsagia circumcincta* had a high upper development threshold and could continue to develop in temperatures up to 35-40°C with a peak larvae stage three production at 41°C (Hoar, 2012). *Ostertagia gruehneri* had a similar development with larva starting to develop at 5-15°C, but *T. circumcincta* developed more rapidly (Hoar, 2012). Also, in contrast, larvae development of *O. gruehneri* ceased at temperatures greater than 31-34°C and had a 100% larvae mortality at 35°C. These results suggest that *T. circumcincta* has a higher production capacity and survival than *O. gruehneri* at higher temperatures and will benefit from a warmer climate. The high amount of *T. circumcincta* in my results is could suggest that this nematode has benefitted from the warm and dry summers during my study, compared to *O. gruehneri*.

Ostertagia gruehneri is the most commonly found reindeer abomasal parasite, often detected with 100% prevalence and high intensities, see for example Pedersen, et al. (2014). These observations are also supported by my study, as I found *O. gruehneri* with high intensity in samples from all areas. It also had a high prevalence in Karasjok, Nordfjella and Forollhogna, albeit a somewhat lower prevalence in Knutshø. Furthermore, *O. gruehneri's* smaller morph,

O. arctica, had medium prevalence and low intensity found in samples from Forollhogna and Knutshø.

It should be noted that *O. gruehneri* and *O. arctica* are regarded to be conspecific (Josefsen, Oksanen, & Gjerde, 2014A). The lack of detection of *T. trifurcata* in 2018 and *O. arctica* in 2019 could be due to the close morphological resemblance between these two minor morphs. It may be that *O. arctica* was identified as *T. trifurcata* in the 2019 samples, and opposite the preceding year. These minor morphs were found in small numbers and do not have a significant impact on the results. The most obscure, difficult to identify nematodes have been sent for sequencing and the results are pending. Still, these results should not have any influence my current results as the parasite species were grouped in total nematode and faecal parasite counts or categorised as typical sheep parasites or not sheep parasites.

Another interesting finding in this study was the high prevalence of *S. boehmi* in Karasjok Vestre and Nordfjella. This nematode was also detected in one adult reindeer sample from Forollhogna belonging to a semi-domesticated reindeer that was culled by the local wildlife official and included in this study. *Spiculopteragia boehmi* is an abomasal nematode thought to be host specific for red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) (Liénard, Depaquit, & Ferté, 2006) but has also been found in southern Norwegian moose (Kongsbak, 2005). *Spiculopteragia boehmi* has also been detected in reindeer that have been sharing grazing areas with elk (*Cervus canadensis*) in North America (De Bruyn, 2010) and in Swedish semi-domesticated reindeer (Nesbakken, 1987). Red deer, roe deer and moose could be a potential source for the distribution of this parasite to the wild reindeer rangeland areas as well as to semi-domesticated reindeer. These results in addition to my findings seem to suggest that *S. boehmi* is a host generalist among wild ruminants. In my study I found no *S. boehmi* nematodes in sheep. Therefore, the dispersion of *S. boehmi* to Nordfjella is likely related to infections from other wild ruminant populations. The detection of the *S. boehmi* in the semi-domesticated reindeer in Forollhogna gives a strong indication that this abomasal nematode could be well established in semi-domesticated reindeer populations. However, further studies should be carried out before any conclusions are made related to *S. boehmi* prevalence and impact on wild ruminants in Norway.

Even if there was a weak positive correlation between Strongylid egg count and adult female nematode count, the Strongylid egg count from this study still indicated low levels of parasite intensity. Nordfjella and Karasjok had the lowest abundance of faecal egg count. Faecal

parasite counts should be performed as soon as possible after sampling, to avoid egg hatching before analysing the sample. The Nordfjella faecal samples had unknown time lag and suboptimal storage conditions. The 2018 faecal samples were kept frozen with the gastrointestinal samples, and the 2019 samples were kept separate at room temperature between sampling and lab analysis. Freezing could potentially have decreased the faecal egg counts from Nordfjella, this would cause the eggs to deform or crack, causing detection and species identification difficulties. Regardless of sample handling, using faecal parasite counts as a proxy for parasite intensity and abundance should be done with caution. The presence of parasite eggs in the host faeces is ultimately a reflection of the presence of an adult female nematode in the host, a female of the same species as the egg. However, the relationship between adult female nematode count and Strongylid egg count has been a debate for some time and evidence of this relationship seems to be rather weak in ruminant parasitology (Michel, 1969; Davidson, Ličina, Gorini, & Milner, 2015; Halvorsen, Stien, Irvine, Langvatn, & Albon, 1999; Hrabok, Oksanen, Nieminen, & Waller, 2006; González-Garduño, Mendoza-de Gives, & Torres-Hernández, 2013). Differences in faecal egg shedding depends on season, parasite fecundity and host immunity (Houtert & Sykes, 1996; Stien, et al., 2002). As in our study, most parasite surveillance of wild ungulates is conducted in conjunction with the seasonal autumn hunt. This is a period which overlaps with wild ungulates male rutting season. In addition to the above listed factors, rut causes a reduction of feeding among the males, this will affect the relative proportion of eggs in the faeces positively, due to the lower faecal production. Furthermore, many of these nematodes choose to begin hypobiosis through winter at this stage and produce few eggs at this time of year (Miquelle, 1990; Josefsen & Handeland, 2014).

Elaphostrongylus rangiferi, or the reindeer brainworm, is one of the reindeer parasites that has been studied most extensively in Norway (Bakken & Sparboe, 1973; Handeland & Slettbakk, 1994). I detected this parasite at high prevalence and abundance in Karasjok Vestre, and at a lower prevalence and abundance in the other study areas. The well documented pathogenic effect of *E. rangiferi* spillover, such as ataxia and mortality (Josefsen & Handeland, 2014; Halvorsen, 2012) from semi-domesticated reindeer to sheep and especially to goats may be of concern for livestock farmers with grazing ruminants in these areas (Handeland, Skorping, & Slettbak, 1993; Josefsen & Handeland, 2014). Because *E. rangiferi* is not capable of completing its lifecycle within sheep, I did not search for this worm

within sheep. Detecting the adult nematode of *E. rangiferi* requires a pathological examination of the sheep spinal nerve roots and the central nervous system as well as liver, lungs, myocardium and kidneys (Handeland, Skorping, & Slettbak, 1993), which was not performed.

Manninen et. al (2014) detected parasite spillover of the typical reindeer abomasa parasite *O. gruehneri* to sheep, which shared a corral with reindeer. This study was performed in an area where reindeer were the dominant grazing ruminant. In my study, I included three study areas with medium and high sheep grazing intensity, where sheep was the dominant ruminant within the common rangeland. This was opposite in Karasjok Vestre where there are low numbers of sheep within the semi-domesticated reindeer rangeland, and therefore was not surprised to detect no typical sheep parasites within this area. For the other three study areas, I detected a high degree of parasite spillover of abomasal nematodes and the total gastrointestinal tract as evidenced by the proportion of common sheep parasites detected in the reindeer samples. The significant relationship between the proportion of typical sheep parasites and host age in the reindeer abomasa, duodena, faecal and the total gastrointestinal tract suggests that sheep parasites infecting reindeer are more likely to infect calves than adults. I also found evidence that the proportion of typical sheep parasites within the reindeer abomasa and in the complete gastrointestinal tract were dependent on sheep grazing intensity where study areas with medium or high sheep grazing had higher proportion of typical sheep parasites.

In addition to the aforementioned parasite species, I also detected *N. tarandi, N. longissimespiculata, Monezia* sp., *Trichuris* sp. and *Skrjabinema* sp. in the reindeer duodena samples for this study, as well as *D. eckerti*, *Eimeria* sp. and *Capillaria* sp. in the faecal samples. These were all detected with a low prevalence and intensity in this study. These parasites were expected to be found (see for example ref), but still provided valuable information about parasite species richness within the reindeer populations examined. I have, however, chosen to focus this study and the discussion on parasite species that may not be regarded as typical findings in reindeer in Norway.

4.1 Changes in abomasal parasite fauna over time

My findings suggest that the nematode fauna in wild reindeer located in Forollhogna and Knutshø has changed during the last 30 years. I found two nematode species (S. boehmi and

T. trifurcata) that were not detected in wild reindeer in this area in previous studies. Furthermore, two nematode species (*Trichostrongylus axei* and *Taleadorsagia davtiani*) previously detected by Bye 1987 were not identified in my samples. Compared with the results of Bye (1987), there was an increased intensity of the abomasal nematodes *T. circumcincta* and *O. gruehneri* in both Forollhogna and Knutshø. *Ostertagia arctica* intensity was increased in Forollhogna and decreased in Knutshø. The increased intensity of *T. circumcincta* in both areas should be treated with concern with regard to the general health of the reindeer populations. Although we know from sheep that this parasite causes lowered body condition and often diarrhoea (Gjerde, 2011), we do not know what if any pathological effects exist in reindeer. Whether this increased intensity is related to changing ecological conditions within these study areas or anthropogenic alterations are difficult to answer within the scope of this study. However, the increased summer population of sheep in these areas is a clear indicator of a change of ecological conditions caused by human alterations.

As mentioned above, Hoar (2012) found that *O. gruehneri* had a significantly lower temperature threshold for development. This could explain the decrease of *O. gruehneri* within the Forollhogna and Knutshø samples. Even if air temperatures are low there can be a significantly different temperature in the soil surface temperatures. Field studies in arctic areas show that soil surface temperature frequently exceeded 30°C during mid-summer (Kutz S. J., Hoberg, Molnár, Dobson, & Verocai, 2014). If the study areas within this study had records of soil temperatures above *O. gruehneri'*s upper threshold for larvae development this may have led to lower recorded intensity. Although this is an interesting hypothesis, to my knowledge, these data have not been recorded or investigated, but we know that both summers were warm and dry, and could have had a large influence on my data. The changes of reindeer abomasal nematode fauna between 1987 and 2018/2019 has the potential to support the theory of a warmer climate altering the parasite fauna of Arctic ruminants. Kutz et al. (2014) in reference to parasite distribution states "extended summers and extremes in heat will alter habitat and host ecology". Further investigations are needed to support or negate these hypotheses in my study areas.

4.2 Potential health risks for ruminants in sympatric grazing areas

Sheep in Norway today are not continuously watched over by herdsmen. As a result, to encourage sheep to stay where they want them, farmers put out mineral lick-stones in strategic places (Mattilsynet, 2019). These salt lick-stones have a potential to be "hot spots" for

transmission of diseases and parasites between sympatric ruminants. Both wild and domestic ruminants are attracted to the salt lick itself and the salty soil around it. When gathering and spending time around these licks enjoying their salty treat, these ruminate also defecate, urinate and salivate in the adjacent areas potentially releasing parasites into the environment (Ytrehus, et al., 2018). When the ruminates sample the salty soil, they also take up parasites and other pathogens. Cross transmission of, for example, *N. battus* or other gastrointestinal parasites with a high pathological effect are thus of higher risk in these areas.

To my knowledge, this study reports the first observation of *N. battus* adult worms in reindeer duodena. The detection of this sheep parasite in samples in the study areas with medium – high of sheep grazing intensity overlap is an important concern for wild reindeer health. Based on the treatment recommendations for sheep by Animalia (2013) and the known disease caused by high *N. battus* infections in lambs, indicates a challenge for wild reindeer management in the affected areas (Gjerde, 2011). Although I did not quantify the *N. battus* intensity or abundance for the duodena samples, the faecal egg counts revealed low to moderate abundances for *N. battus* in wild reindeer. The parasite prevalence for *N. battus* was low in adult reindeer with only one sample from a reindeer located in Forollhogna as positive. As lambs develop immunity to *N. battus* 4 – 6 weeks after infection, the same pattern has been speculated for *N. tarandi* and *N. longissimespiculata* infection in reindeer calves (Hrabok, Oksanen, Nieminen, & Waller, 2006). It is, therefore, also possible that reindeer calves develop immunity after exposure to *N. battus* as well. Prevalence for calves in Forollhogna was 50%. Prevalence in Knutshø was higher at 87%, and prevalence in Nordfjella was 100%. In two of the calves from Nordfjella, adult *N. battus* males were found in the duodena, but no eggs were detected in the faecal analysis. Again, this may be due the time lag and storage conditions of these faecal samples, but may also indicate a low intensity of infection, as Nematodirinae female worms are not high egg producers (Gjerde, 2011).

My results show that both Knutshø and Forollhogna showed a shift in dominant abomasal nematode species from 1987. *Teladorsagia circumcincta*, a sheep parasite, had a higher abundance than the common reindeer parasites altogether. With regard to the findings of the CWD in the wild reindeer population in Nordfjella zone 1 in 2016 (Ytrehus, et al., 2018), the focus on factors that could contribute to spread CWD is currently of high priority for Norwegian wildlife managers. Among these factors' are sheep as they have been mentioned as a species which could potentially transmit CWD (Ytrehus, et al., 2018). By using

gastrointestinal parasites as a proxy for infection, patterns of oral-faecal disease transmission (including disease caused by both parasites and prions) between sheep and reindeer could be elucidated. (Ytrehus, et al., 2018). In this study, the shift of dominant abomasal nematode species richness in wild reindeer towards species commonly found in domestic sheep in Norway, and the novel finding in wild reindeer of an invasive duodenal nematode (*N. battus*) responsible for high morbidity and even mortality in sheep, indicates a change in the disease ecology in the study areas. Most importantly, it demonstrates, that domestic and wild ruminants are in closer contact and are sharing far more than common rangeland.

4.3 Management implications

The pathological impact and effect of *N. battus* in the wild ruminants, especially juveniles, needs further investigation. The detection of *N. battus* in wild-reindeer is the third wild ruminant species in Norway where this invasive species is detected. Even if the detection levels in wild ruminants may so far be considered low, this does not exclude that *N. battus* has the potential to spread to other wild ruminants, just as we note that *S. boehmi* has already done. *Nematodirus battus* can cause severe morbidity and even mortality in highly infected lambs, and, if assuming the same effects on juvenile wild ruminants, this can be an alternative or additive explanatory factor for the low production rate in certain wild ruminant populations. In addition, when *N. battus* is introduced to a naïve sheep flock, these parasites outperform the endemic duodenal *Nematodirus* spp within 4 – 5 years (Gjerde, B. 2014). This this could be the scenario for endemic reindeer Nematodirines as well. The higher morbidity caused by *N. battus* may have unknown consequences for an already vulnerable wild reindeer population. Until necessary knowledge is obtained, collaboration between the management for both wildlife and domestic livestock is needed to establish clear strategies to prevent *N. battus* from spreading to new ruminant populations and possibly to limit the current trend. Reducing sheep grazing intensity within wild-reindeer populations should be a priority.

However, a reconsideration of salt lick stone management within wild ruminant rangeland would be my highest recommendation for management changes based on this study and my results showing evidence of parasite spillover in areas with both medium and high sheep grazing intensity. Salt lick stones have the potential to be “infectious hot spots” where parasite spillover is likely to occur. Farmers have been advised by Norwegian agriculture authorities since 1967 to be cautious regarding where they establish these salt licks in the landscape, recommending, in particular, bare rock-face areas which animals will leave after salt

consumption (Nasjonalbiblioteket, 1967). Based on personal observations during fieldwork, many salt lick stones were established in vegetation areas with soil ground. These areas had clear signs of intensive grazing around the salt lick stones. If these stones are moved to an area with bare rock-face, the parasite eggs and larvae may not accumulate or flourish as much as they might in the vegetation. This is a potential strategy to reduce the parasite dispersal for more than just the *N. battus* nematode, as it would be just as efficient for all the gastrointestinal parasites.

4.4 Potential scientific errors in the study

Gastrointestinal samples that had been left exposed too long in the field were difficult to extract necessary data from. I experienced that rainfall and temperature alone could affect a sample in less than 24 hours after field dressing. Ravens, crows and eagles were efficient scavengers, and in some cases the proximal part of the duodenum was missing from the sample upon arrival probably due to quick scavenging. The most successful collection method was to follow the largest reindeer flocks from a distance and wait until hunters had made a kill. Usually several reindeer were shot when the flock tried to run off. The hunters had mostly disappeared from the sampling site before I arrived. The ideal sample number for this study could have been at least five calves, five adult females and five adult males from each area with wild reindeer in both 2018 and 2019. However, the sampling approach was time consuming and dependent on hunters to be successful in the area that was chosen. Therefore, the sampling was done opportunistically to be as efficient as possible.

The parasites of reindeer in Norway that have received the most attention are the warble fly, *Hypoderma tarandi* and the nose bot fly, *Cephenemyia trompe*, both of which are ectoparasites causing damage by burrowing into the skin and nasal sinuses, respectively. Botflies cause panic and flight in reindeer herds, resulting in reduced grazing and resting time and thus impacting herd productivity, health and welfare (Tryland & Kutz, 2018). Semi domesticated reindeer may get treatment for ectoparasites that also have an effect on endoparasites as well (Josefsen, Oksanen, & Gjerde, 2014B). Whether semi-domesticated reindeer in this study were given parasite treatment is unknown. However, it was performed, the treatment was likely given before summer and would not have caused a long-term effect that would have affected the gastrointestinal parasite load seen during the slaughter season. My results showed a higher abomasal nematode intensity for the control area (semi-domesticated reindeer) compared with the study area; therefore, I do not believe treatment

status of our sampled animals had any obvious influence on the results. It would also have been ideal for the study to include a wild-reindeer population with no, or minimum, overlap of sheep grazing in the study as a control area, but due to logistics, this was not possible.

I included temperature and precipitation data from weather stations close to, or within the study areas, but this was not the ideal data for this study. An average of maximum soil temperature in grazing areas for the summer months would have been a better scientific approach. This was discussed before the study started but was not prioritized. Temperature and precipitation were both excluded and included within the combined models with minimum effect on the parsimonious model in either case.

5 CONCLUSIONS

My results support the conclusion that spillover from sheep to reindeer is normal for abomasal strongylides in areas with sympatric grazing ruminants like Manninen et al. (2014). I found that this spillover is influenced by the intensity of sheep grazing. The spillover of potential pathogenic species from sympatric ruminants could influence the structure of gastrointestinal parasites in wild reindeer populations. It may also represent a health risk, though we can only speculate as to what these risks may be as of today. The typical sheep nematode *T. circumcincta* dominated the reindeer abomasal nematode fauna. The pathological effects of presence of this sheep abomasal nematode *T. circumcincta* as well as *S. boehmi* in wild ruminants should be investigated further. Most importantly, I detected the duodenal sheep nematode *N. battus*. If *N. battus* has the same impact in wild ruminants as in sheep, especially lambs, it should be included as an important explanatory factor for increased morbidity and mortality of juveniles within wild reindeer populations.

In addition to climate change, the decline and fragmentation of reindeer rangeland have reduced the grazing flexibility for both wild and semi-domesticated reindeer. With increasing infrastructure barriers, reindeer and wild ruminants migrate less and stay within concentrated rangelands. More stationary populations increase the build-up of pathogens in soil and vegetation, leading to increased risk for disease spread. This is a general concern for gastrointestinal parasites as well as other pathogens. Actions to reduce parasite spillover from sheep to wild reindeer should be applied. Reducing the sheep grazing intensity and reconsideration of salt lick stones as a practice as well as increasing wild ruminant rangeland are recommended management efforts based on the results from this study.

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