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Parasitic infection risk for the Svalbard Reindeer (*Rangifer tarandus platyrhynchus*) in relation to temperature, host density, and grazing behaviors

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Ecology

Preface

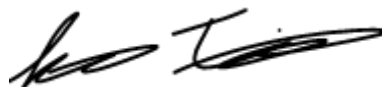
The following thesis is for the master's degree program in Ecology at the Norwegian University of Life Sciences. This project was carried out under the supervision of Professor Leif Egil Loe from the Norwegian University of Life Sciences, Professor Audun Stien from the University of Tromsø, and PhD candidate Tirza Moerman from the Norwegian University of Life Sciences.

I would like to thank all my supervisors for this opportunity to learn and work alongside them. As well as the grace that was shown to me during the unfortunate hurdle of Covid.

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Abstract

Climate change has the potential to disrupt phenological synchronization between parasitic nematodes and their hosts, which may have implications for host regulation. Understanding the parasitic-climatic relations within ecosystems that are vulnerable to climate change is crucial for disease management and conservation. Svalbard, an inherently simple ecosystem with a high susceptibility to climate change, serves as an ideal site to study the dynamic between parasites and hosts regarding climate. Historically the parasitic nematode *Ostertagia gruebneri* has regulated Svalbard reindeer (*Rangifer tarandus platyrhynchus*) populations by reducing fat reserves, thereby lowering fecundity, and limiting population growth. However, in the last two decades, reindeer populations have more than doubled, raising questions about potential changes in the parasites' life cycle. This study examines two potential factors that may explain the lack of regulatory impact on host populations due to changes in infection risk. First, a dynamic simulation model based on known parameters that govern nematode survival and developmental rates was used to examine whether the potential negative effects of warmer temperatures outweigh the positive effects of reindeer density, on seasonal abundance of the infective nematode stages in the pasture. Historical (1997), present (2022), and potential future (2070-2100) temperature data were examined alongside observed reindeer densities (1995-2021). Secondly, these simulated seasonal curves were compared to empirical grazing height data throughout the growing season (2022), to examine if a phenological mismatch may have occurred from reindeer feeding at higher strata during peaks in nematode availability, as feeding near moss levels may increase infection rate. This study revealed that temperatures representing the warmest year (2022) had a modest adverse impact on the availability of parasites in contrast to the coldest year (1997) when the reindeer population was held stable in the model. However, when factoring in the observed increase in reindeer densities from both cold (historic) and warm (recent) years, the large positive effect of increased number of hosts outweighed the small negative impact of temperature. Furthermore, infections that occur early in the season might be lessened due to potential shifts in vegetation season and growth, further distancing the infection risk of feeding near soil levels during predicted growth of nematode occurrence in the pasture, leading to a potential phenological mismatch. This study underscores the challenges inherent in comprehending parasitic-host relationships in the natural environment and emphasizes the need to adopt a holistic approach that considers multiple factors that may impact complex multi-species systems.

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1. Introduction

Population regulation of wildlife species is intricately linked to multiple factors, with an often-overlooked aspect being the role of parasitism, which is dependent upon the dynamics of infection risk. At individual level, parasites can induce modifications in the host's behavior (McElroy & De Buron, 2014), reproductive capacity (Newey & Thirgood, 2004), and survival rate (Lyonsdale et al., 2017). These alterations can precipitate cascading effects on the growth of host populations (Watson, 2013) and, by extension, significantly disrupt ecological food webs (Lafferty et al., 2006, 2008). Parasites, despite their substantial influence on both individual and ecosystem levels, are not immune to external influence. They can often be impacted by factors such as climatic conditions (Altizer et al., 2006; Molnár et al., 2013a), host abundance (May & Anderson, 1978), gregariousness's of hosts (Patterson & Ruckstuhl, 2013) host-induced mortality, density-dependent intraspecific conflicts (Stanko et al., 2006), and phenological mismatch (McDevitt-Galles et al., 2020), which can thereby alter infection risks. Comprehending infection risk is vital as it has the potential to profoundly influence the stability and resilience of ecosystems.

Infection risk can be intrinsically impacted by temperature, and therefore climate change. The Metabolic Theory of Ecology (MTE) aims to understand the influence temperature has in relation to metabolic rate and biological processes within individual organisms (Brown et al., 2004). These processes include changes in the rates of development and mortality, in addition to changes in the age at which maturity is reached and the totality of lifespans (Brown et al., 2004). This non-linear theory can be adapted into more complex models and simulations to understand the impacts of a changing climate. Since pre-industrial times, average global temperatures have risen approximately 0.8°C – 1.2°C degrees as of 2017 (Allen et al., 2022). Global average temperatures are only expected to further rise, with a warming of 0.3 - 5.7 °C by the end of the 21st century depending on global actions to combat climate change (J. Y. Lee et al., 2022). The changing climatic conditions observations have already been observed in parasitic species, with particular interest in helminths, or parasitic worms such as nematodes (Van Dijk et al., 2010). While theorized to be a potential boon to parasites (Harvell et al., 2002), newer studies indicate alternative negative impacts. In addition parasitic nematodes, such as *Ostertagia gruehneri*, appear to observe small benefits with warmer temperatures up until mortality rate kicks in due to thermal limits (Peacock et al., 2022). Furthermore *O. gruehneri* have been observed to exhibit shorter life cycles with warming temperatures (Peacock et al., 2022), which may alter the abundance and time the parasites are observed in the natural environment. Therefore, there is

considerable uncertainty of the effect of increasing temperatures on the free-living stages of *O. gruebneri*.

The risk of infection, in addition, can be influenced by indirect mechanisms. For example, alterations in host populations can increase parasite prevalence and intensity (Patterson & Ruckstuhl, 2013), as well as overall macro-parasite abundance (Arneberg et al., 1998). Another example is that of changes to the point of infection due to climate change. Parasitic species similar to *O. gruebneri* have been found to inhabit varying soil depths, root mats, and herbage (Al Saqur et al., 1982; Callinan, 1978), however the percentage found on vegetation is likely to be small as vertical ascension may be limited due to their finite energy reserves and the likely decrease in survival as they ascend to higher strata (Van Dijk & Morgan, 2011). It is assumed then that if hosts graze closer to ground level infection risk increases. However, with warmer climates a positive relationship to vascular canopy height can occur (Elmendorf et al., 2012) where hosts are then potentially grazing further from these reservoirs, potentially leading to a phenological mismatch and a resulting decrease in infection risk.

O. gruebneri provides the first empirical evidence of macro-parasites impacting fecundity of wild mammalian herbivores (Albon et al., 2002). When anthelmintic treatment was administered in adult female reindeer, an 11% increase in pregnancy rates was observed compared to that of the control group (Stien et al., 2002a). Considering the hosts' modest annual growth rate of 1-5%, the parasitic influence could negatively affect the overall population growth (Albon et al., 2002). The reduction in fertility is linked to deteriorating body conditions, with an observed increase in body mass of 0.9 kg, and an increase in 3.3 mm of back fat depth, in treated hosts (Stien, Irvine, Ropstad, et al., 2002). While historically parasitic regulation of *O. gruebneri* on the Svalbard reindeer have regulated population sizes, in the last two decades populations have more than doubled in size (Loe et al., 2021), indicating a potentially weakening of this regulatory effect. Gaining further insight on why the parasitic effect on fecundity appears to have weakened is important for understanding future conservation work of the Svalbard reindeer, their potential subsequent impacts on the ecosystem, disease management, and parasite-host interactions under climate change.

The Svalbard Archipelago provides an exemplary setting for the study of parasitism for three primary reasons. First, arctic regions are more susceptible to climate change, with an observed average increase of 4 °C degrees over the last forty years (Jansen et al., 2020), making it an ideal site to understand the profound impact of warmer temperatures on infection risk. Secondly, this remote Arctic region is characterized by a relatively simple ecosystem and terrestrial food web,

consisting of just three trophic levels (Jónsdóttir, 2005). The ecosystem's sole herbivore ungulate, the dwarf Svalbard reindeer, experiences limited predation pressure, albeit with the exception of rare polar bears predation (Derocher et al., 2000), and limited recreational hunting (Loe et al., 2021), in addition to a lack of intraspecific competition (Loe et al., 2016). The most substantial challenges these endemic reindeer encounter are in regards to parasites and climatic changes (Albon et al., 2002; Stien et al., 2002b). Leading into the third reason, there are two species of gastrointestinal nematodes that account for 95% of adult parasitic worms found within the Svalbard reindeer; *Marshallagia marshalli* and *Ostertagia gruehneri* (Irvine et al., 2000). There appears to be no negative correlation between these gastrointestinal nematodes, different life histories, and spatial-temporal dynamics (Irvine et al. 2000; Irvine et al. 2001), with genetic testing indicating that *O. gruehneri* are the predominant gastrointestinal nematodes within the abomasum lining throughout the summer months (Irvine et al. 2001). The simplicity of this ecosystem, combined with the control that can therefore be exerted and lack of additional confounding variables, offers an optimal setting to study parasite-host dynamics, allowing for a focused examination of the impacts in question.

The primary objective of this thesis is to investigate potential reasons behind the diminishing regulatory effect of *O. gruehneri* within the populations of the Svalbard reindeer, given the unprecedented rise in population densities within recent years (Loe et al., 2021). Given that no discernable immune response in regard to *O. gruehneri* is observed within the host (Irvine et al., 2000), this study proposes to explore alternative factors that may be impacting the infection risk and potential abundance of *O. gruehneri*. The approach is twofold; first, the study aims to determine if elevated temperatures may contribute to the reduction of the potential parasite abundance and whether increased host populations can counteract temperature influences. Second, this study examines the potential correlation between the seasonality of grazing heights and the simulated projected seasonality and peaks of infective larvae.

To address the first objective, a dynamic model was developed to simulate the predicted abundance of the free-living stages of non-infective and infective larvae within the pasture. A simulation-based methodology is critical due to the dynamic and non-linear relationship between the free-living stages of *O. gruehneri* and key factors within the environment, which include temperature-dependent developmental rates, mortality rates, and nematode egg production as influenced by feces production of hosts. Moreover, there are no current established methods, or previous research endeavors, capable of accurately ascertaining the abundance of these parasitic nematodes within the pasture through collection, largely due to the overwhelming complexity and time-consuming nature of such an endeavor. Due to these restrictions, this makes a

simulation-based approach a practical alternative in understanding parasite dynamics. To address the second objective, the simulated seasonality abundance of the parasitic nematodes from the first portion are juxtaposed with the second portion of this study, which examines the seasonal variation in vegetation height and grazing patterns of the host through the collection of empirical data collected in the field. By aligning these seasonal curves, the study evaluates the potential risk of infection during the summer months regarding how close the host is grazing to the moss level in relation to simulated nematode abundance. Higher infection risk is expected during periods where host grazing behavior near moss levels coincides with elevated simulated nematode abundance, with lower infection expected in the contrary scenario.

The research questions are described succinctly below:

RQ1: Utilizing the empirical range of temperatures and reindeer densities; does the model simulation predict that a negative temperature effect outweighs the positive effect of more hosts?

- i. Increasing temperatures may lead to a decrease in nematode abundance. The temperature stress may have limited the abundance of both infective and non-infective stages.
- ii. The infective stage may be further compounded due to the limited pre-infective stage, leading to a two-fold pressure on this later stage.

RQ2: Are reindeer grazing on tall vegetation before L3 larvae are predicted to develop on the pasture?

- i. Warmer springs temperatures lead to earlier growing seasons and higher vascular plant height (Elmendorf et al., 2012). If infective larvae abundance peaks occur at the time reindeer are grazing on tall vegetation at higher strata, further from the moss where *O. gruebneri* are thought to reside, potentially causing a phenological mismatch.

2. Methods & Materials

2.1 Study Area

The study was conducted within the Svalbard Archipelago (76°26' N - 80°50' N) on the main and largest island of Spitsbergen (37,673 km²). Data collection occurred within two valley systems within the southwest of Spitzbergen, accessible from Longyearbyen. Reindalen (77.9° °N, 15.8° °E), is located within Nordenskiöld Land, a protected reserve established in 2003. Adventdalen (78.2° °N 16.3° °E), runs 30 km in length, opening to Longyearbyen and Isfjorden.

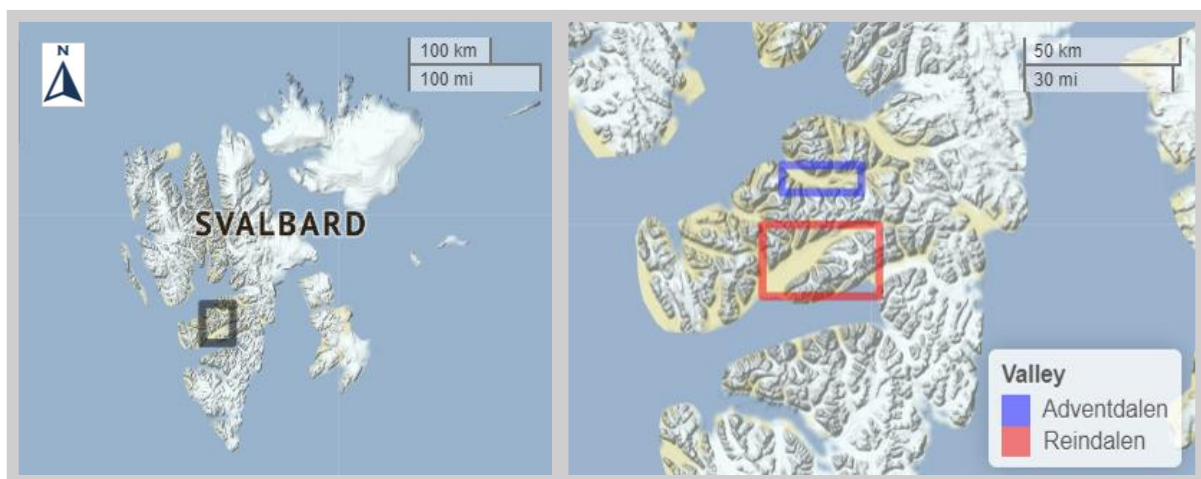


Figure 1: Map of Svalbard Archipelago. The grey box indicates the study area within the greater Svalbard region. Highlighted are the two study sites of Adventdalen (blue) and Reindalen (red) within the main island of Spitsbergen. Map was created using leaflet in R studio version 4.2.2 with Stamen.Terrain.

The study sites fall within the Middle Arctic Tundra Zone (MATZ), defined by mean July temperatures of 5-7°C degrees (Hanssen-Bauer et al., 2019). Throughout the study period of 1995-2022, mean daily temperatures ranged from -34.3°C degrees to 17.8°C with mean summer temperatures of 4.9°C and mean winter temperatures of -7.7°C degrees. Climate change is creating higher seasonal variations in winter months (October-May) over that in summer months (June-September) (Hanssen-Bauer et al., 2019), as observed in our temperature records (Figure 2). Precipitation is highest during winter months and lowest during summer months, with a yearly average of 791 mm in the study region, expected to increase 3-4 percent each decade (Hanssen-Bauer et al., 2019). The MATZ is notably marked by its denser and richer vegetation, made possible by warm waters from the Atlantic Current along western Spitsbergen (Johansen et al., 2012). The vegetation is characterized by its distinct lack of trees (Jónsdóttir, 2011), yet is home to over 173 vascular plants (Jónsdóttir, 2005), 380 bryophytes (Prestø et al., 2014), and 742 lichen species (Øvstedal et al., 2009). The window for seasonal growth varies annually but typically spans the months of June - August (Albon et al., 2017). The region hosts three

terrestrial mammal species alongside a considerable diversity of invertebrates at 937 species (Jónsdóttir, 2005). Overall, the terrestrial food web is simple, with a slight increase in complexity over summer as a result of migratory birds (Jónsdóttir, 2005).

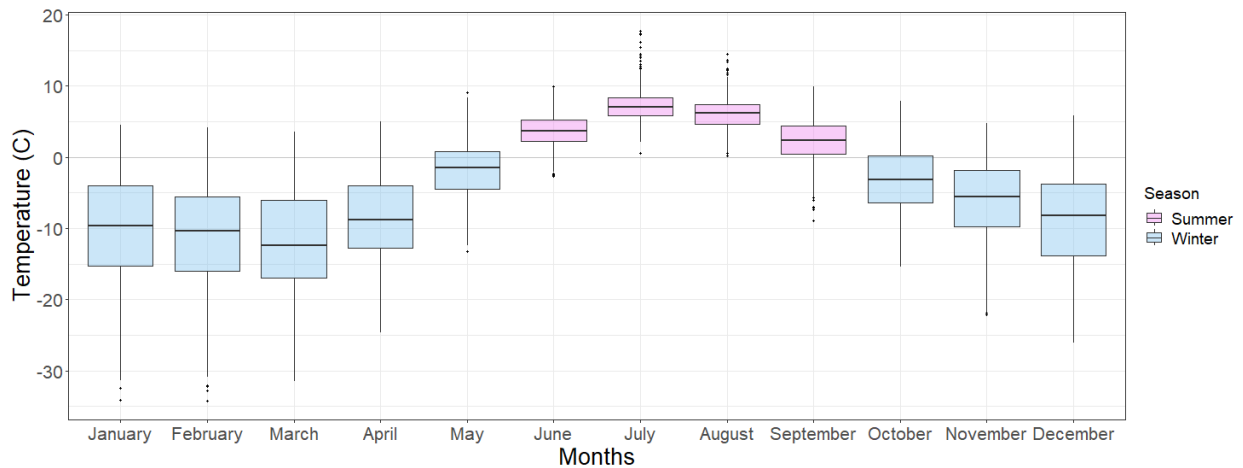


Figure 2: Daily mean temperatures (24 h) from 1994-2022 categorized by month. Season is noted in color. Temperatures are taken from the weather station in Longyearbyen, Svalbard, and provided by met.no, with 83 supplemental dates by Yr.no. Whisker-box plots display the interquartile range (IQR), the line within the box is the 50% percentile (median), the whiskers represent the variability outside the upper and lower quartiles, extending 1.5 times the upper and lower interquartile range. Outliers are represented by dots.

2.2 Study Species

2.2.1 Reindeer

The Svalbard reindeer, a unique subspecies endemic to the Svalbard Archipelago, is presumed to have migrated from mainland Eurasia approximately 6,500 years ago (Kvie et al., 2016). This subspecies are notably different from their mainland counterparts, exhibiting distinct characteristics such as smaller stature, rounder faces, shorter legs, along with pronounced sexual dimorphism (Tyler, 1987b). Unlike their migrating mainland relatives, Svalbard reindeer remain relatively stationary, likely a result of the region's fragmented landscape (Le Moullec et al., 2019). Group sizes within these segmented regions often range from two to five individuals, rarely exceeding twenty (Reimers, 1977).

Lifespans vary by gender, with males typically living up to twelve years, and females reaching seventeen years (Pedersen et al., 2019). Population dynamics are largely driven by two main factors, parasitism and climatic variation (Albon et al., 2002; Stien et al., 2002), and to a lesser extent density-dependence (Albon et al., 2017). Within the last two decades populations have more than doubled (Figure 3; Loe et al., 2021), suggesting a change in regulatory factors.

The diet of Svalbard reindeer mainly comprises of various graminoids (Hiltunen et al., 2022), *Salix polaris* (Van Der Wal et al., 2000), and uniquely include moss consumption, a rarity among vertebrates (Prestø et al., 2014; Prins, 1982). Svalbard reindeer pivotally alter vegetation communities through top-down regulations, by grazing, trampling, and manuring, altering the plant composition to increase graminoids (Hansen et al., 2007), and reduce moss (van der Wal et al., 2001b) and lichens (van der Wal et al., 2001a).

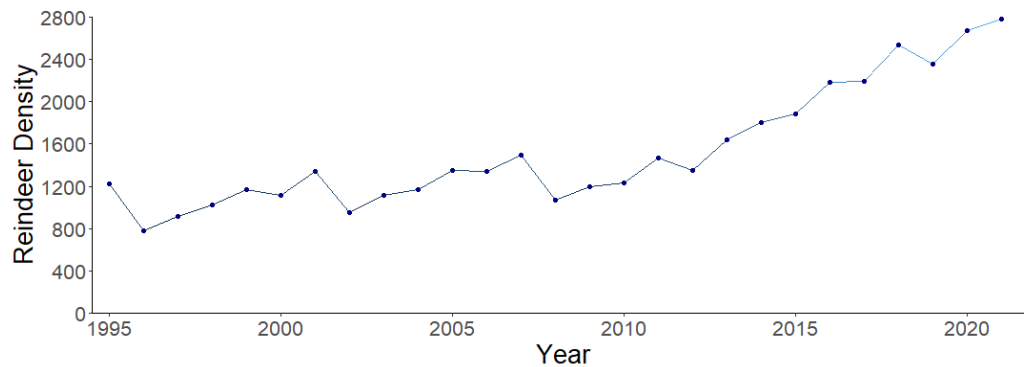


Figure 3: Reindeer densities recorded for the population located in Reindalen valley from 1995 – 2021 (Løe et al. 2021). Reindeer density is the total reindeer count by 361 km² surface area of the Reindalen valley, calculated each July after calving season (Reimers, 2011, Løe 2021). Reindeer density for 2022 is not yet released.

2.2.2 The Nematode *O. gruebneri*

O. gruebneri, a member of the Trichostrongylidae family, primarily inhabits the Northern Hemisphere, particularly the Arctic and High Arctic regions (Hoberg et al., 2012). In comparison to other gastrointestinal nematodes, *O. gruebneri* is the most pervasive in the Holarctic region and prevalent amongst all Rangifer sub-species (Kutz et al., 2012), with the exception of a small population within Greenland (Korsholm & Olesen, 1993; Steele et al., 2013).

O. gruebneri, exhibits a direct life cycle, transitioning through six stages (L0-Adult), with life cycles ranging from one to three years (Peacock et al., 2022). Initial stages (L0-L3) reside in the pasture as free-living entities. These early stages are categorized as non-infective (L0-L2), developing from eggs deposited through host feces into the pasture, and infective (L3), when the ability of host infection occurs (Aleuy & Kutz, 2020). Upon ingestion, the parasitic nematode settles into the abomasum, or lining thereof, further undergoing development until adulthood is attained and reproduction begins (Irvine et al., 2000). The cycle of egg release begins in spring, peaks within summer (July-September), decreasing through the fall, tapering in spring (Hrabok et al., 2006). It is at this point the cycle begins anew (Figure 4).

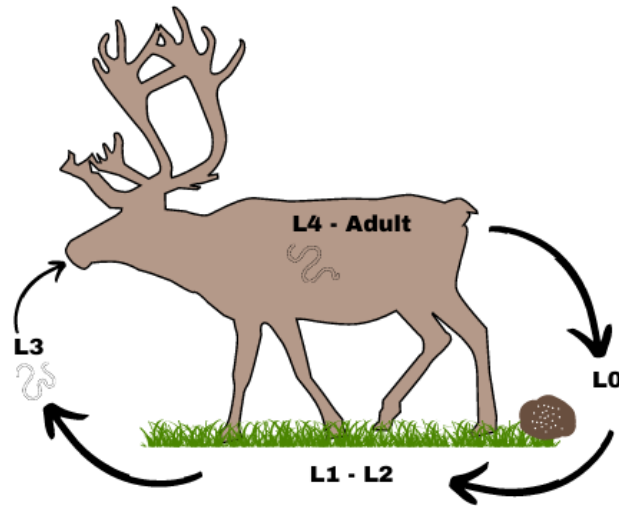


Figure 4: Depiction of host-parasite cycle between the parasitic nematode *O. gruebneri* and The Svalbard reindeer. Each stage and how the parasite interacts with the host is shown. Parasitic L3 consumed while foraging, mature within the host, and shed eggs through the host's feces, starting the cycle again. Image is made using Canva.

2.3 Modelling

2.3.1 Model

Using R studio version 4.2.2 for Windows 10, a simulation model was developed to predict nematode abundance and seasonality curves. The model utilized parameters established in earlier studies consisting of nematode egg production per gram of host feces, mortality rates, and developmental rates of the free-living *O. gruebneri* stages (Figure 5; Irvine et al., 2000; Peacock et al., 2022; Stien et al., 2002). The model requires two inputs: temperature and reindeer density (Figure 5). Temperature influences the mortality rate of both groups in addition to the developmental rate. Reindeer density influences the egg output of the parasitic nematode in the pasture. The model output includes the non-infective (L0-L2) and infective (L3) stages. Both the non-infective and infective groups are subject to environmental conditions outlined in the model, with reindeer density directly impacting non-infective stages.

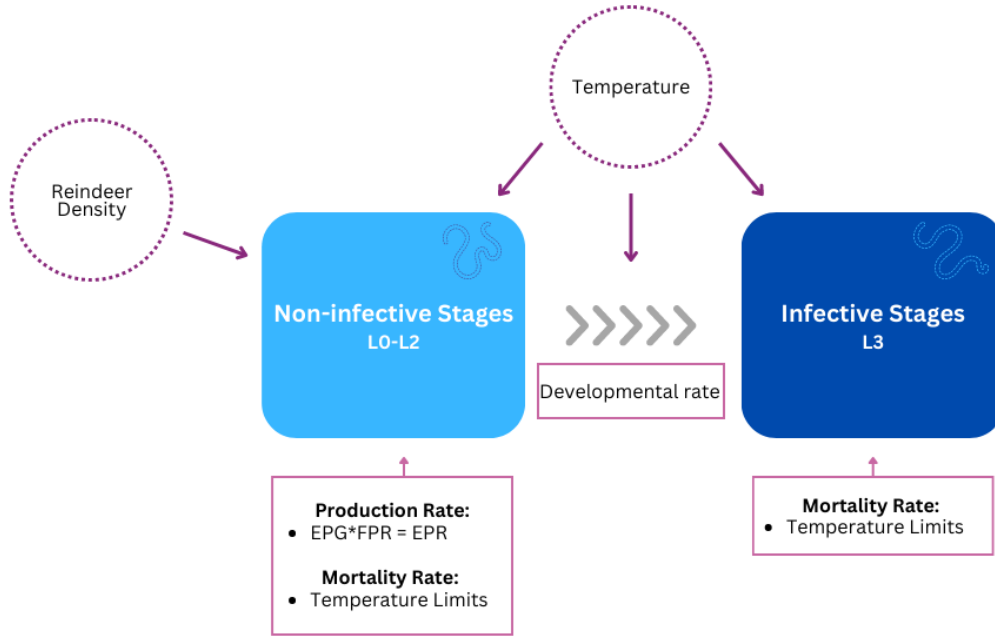


Figure 5: A simplistic overview of the model used to predict both non-infective (L0-L2) and infective (L3) larvae abundance in the environment. The circles represent the independent variables, temperature, and reindeer density, with temperature affecting both non-infective and infective stages directly. Non-infective in turn affects abundance of Infective larvae abundance as they develop over time. Controlled variables consist of temperature limitations in terms of minimum and maximum temperature survivability for both stage groups, and developmental rate affects how the larvae develop through stages L0-L3. Created using Canva. Model created by Dr. Audun Stien (unpublished manuscript).

Part 1: Reproduction

Model step 1: Egg abundance

EPG defines the expected number of parasitic eggs per gram of reindeer feces. This concept is outlined in Irvine (2001) and Stien (2002) papers, with the equation as follows:

$$\text{Eqn 1:} \quad \text{EPG} = \lambda I^{1+\beta}$$

I is the intensity of infection within the reindeer, β represents the parameter controlling density dependence in regards to the egg output from the parasites, and λ defines the egg output from a single parasitic nematode, with the equation as follows:

$$\text{Eqn 1a:} \quad \lambda = \alpha_1 + \frac{\alpha_2}{\sigma \sqrt{2\pi}} e^{-\frac{(t-\mu)^2}{2\sigma^2}}$$

λ is influenced by seasons. Both α represent the seasonal maximum and minimum nematode egg count, with α_1 being the winter egg count (minimum) and α_2 the summer egg count (maximum). The length of the season is defined as σ , with the time of the seasonal peak occurring at μ . Time, t , is a continuous non-leap year.

FPR defines the grams of feces per day per individual reindeer. This equation is outlined in Stien (2002) paper. The equation is as follows:

$$\text{Eqn 2:} \quad \text{FPR} = \alpha_{1f} + \frac{\alpha_{2f}}{\sigma_f \sqrt{2\pi}} e^{-\frac{(t-\mu)^2}{2\sigma_f^2}} \quad \text{grams per day}$$

α_{1f} represents seasonal maximum and minimum feces output, with α_{1f} being the winter feces count (minimum) and α_{2f} as the summer feces count (maximum). The length of the season is defined as σ , with the time of seasonal peak occurring at μ . Time, t , is a continuous non-leap year.

These two equations, eggs per gram feces (EPG) and feces production rate (FPR), are then multiplied together to form the formula $\text{EPG} \times \text{FPR} = \text{EPR}$, with EPR representing the nematode egg production rate per reindeer. Therefore, this portion of the model is directly impacted by reindeer density. It should be noted that the empirical data is weak for this section (Stien et al., 2002a). This is the only step in the model impacted by reindeer density.

Part 2: Mortality and Development

To calculate the mortality and developmental rate two key equations were utilized. The first a variant of the Arrhenius equation, typically used to calculate chemical reaction rates dependent upon temperature (McCoy & Gillooly, 2008), was applied to interpret the developmental of mortality rates of *O. gruebneri*. The second a variant of the Sharpe-Schoolfield equation, traditionally used to describe the upper and lower thresholds within temperature-dependent biological rates, thereby providing insights on thermal ranges and thermal extremes upon potential parasitic abundance (Molnár et al., 2017; Schoolfield et al., 1981).

The formulas in this section convert the input of Celsius into Kelvin, as is standard with both these equations. Each variable labeled “temp” is the input for the daily average temperature recorded.

Model step 2: From egg to L2 larvae

The mortality rate of egg, L1, L2 stages are influenced by temperature. These non-infective stages fair best at 5°C, and are more susceptible to increasing temperature, having ten times higher mortality rate than the infective stage (Peacock et al. 2022). The formula μ_0 takes temperature as an input and returns the corresponding predicted mortality rate. Temperature influences the physical and biological constants and relationships between these stages and the ability to survive. The equation is listed below:

Eqn 3:

$$\mu_0(temp) = 0.068 \cdot e^{\frac{-0.884}{8.62 \times 10^{-5}} \cdot \left(\frac{1}{temp+273.15} - \frac{1}{15+273.15} \right)} \cdot \left(1 + e^{\frac{2.928}{8.62 \times 10^{-5}} \cdot \left(\frac{1}{temp+273.15} - \frac{1}{-3.377+273.15} \right)} \right)$$

The coefficient 0.068 represents the baseline mortality rate at 15°C, estimated from a fitted model in the Peacock paper (2022).

Model step 3: From non-infective to infective L3

The transitions between stages require time which can be altered by temperature, as in line with thermal biology (temperature-dependent development) under the metabolic theory of ecology. Generally speaking, the higher the temperature the faster the developmental rate, up until a certain threshold is met, at which point the developmental rate slows, creating a peaked response to temperature, with mortality often followed closely. The peaked response to temperature signifies that the developmental rate increases with temperature up to an optimal point, beyond which it starts to decrease due to physiological stress or other factors. The formula ρ_0 estimates the number of individuals that transition into the parasitic larvae stage per day. This model acknowledges that the metabolic rate can change with increasing temperature, and developmental rate can decrease at specific thresholds (Peacock et al, 2022).

Eqn 4:

$$\rho_0(temp) = 0.032 \cdot e^{\frac{-0.686}{8.62 \times 10^{-5}} \cdot \left(\frac{1}{temp+273.15} - \frac{1}{15+273.15} \right)} \cdot \left(1 + e^{\frac{7.957}{8.62 \times 10^{-5}} \cdot \left(-\frac{1}{temp+273.15} + \frac{1}{30.568+273.15} \right)} \right)^{-1}$$

The coefficient 0.032 is the estimated developmental rate regarding the baseline reference temperature of 15°C, which was determined from a fitted model in the Peacock paper (2022).

Model step 4: L3 larvae

The last step of the model focuses on the mortality rate influenced by temperature on the last stage of the free-living parasites, the infective L3 larvae. Survival rates for L3 fare best at 25°C and decrease significantly after 30°C (Peacock et al. 2022). The equation μ_3 within the model, which is temperature dependent, estimates the mortality rate of the infective larvae per day.

Eqn 5:

$$\mu_3(temp) = 0.0211 \cdot e^{\frac{-0.208}{8.62 \times 10^{-5}} \cdot \left(\frac{1}{temp+273.15} - \frac{1}{15+273.15} \right)} \cdot \left(1 + e^{\frac{3.409}{8.62 \times 10^{-5}} \cdot \left(\frac{1}{temp+273.15} - \frac{1}{-19.318+273.15} \right)} + e^{\frac{3.5543}{8.62 \times 10^{-5}} \cdot \left(-\frac{1}{temp+273.15} + \frac{1}{27.6+273.15} \right)} \right)$$

The coefficient 0.0211 represents the base mortality rate at 15°C. The next portion of the formula represents the Arrhenius variation modelling the exponential increase or decrease of the mortality rate in reference to temperature. The final two portions are based off the Sharpe-Schoolfield model aiming to better understand the mortality rate at low and high temperature thresholds, -19.318°C and 27.6°C respectively.

2.3.2 Model Inputs

Population Densities

Historical and contemporary population densities of reindeer were estimated from capture-recapture data and census counts collected from 1994 through 2021 in Reindalen, Svalbard (Figure 3; Lee et al., 2015; Loe et al., 2021). These data counts occurred in a two month window spanning July – August, a strategic timing as it follows the birthing season which typically occurs the initial two weeks of June (Tyler, 1987a). The reindeer densities only consider females, yearlings, and calves. The recoding time frame allowed for a comprehensive counting of the reindeer population at the commencement of their annual life cycle.

Temperature

Temperature data for historical and contemporary periods were obtained through a collaborative initiative which involves the Norwegian Centre for Climate Services, the Norwegian Meteorological Institute, the Norwegian Water Resources and Energy Directorate, Norwegian Research Centre, and Bjerknes Centre for Climate Research. Svalbard Lufthavn weather station.

Temperature was recorded as the mean daily temperature over a 24-hour period. Over the span of 1995-2022, there was a total of 83 days lacking temperature data. These gaps were filled using mean daily values available from Yr, a public service provided by the Norwegian Meteorological Institute. In addition, as the model strictly factors a year as 365 days, all leap year dates were systematically removed from the dataset.

To account for potential bias in initial nematode counts, a burn-in period of one year was incorporated into all models. This measure was designed to eliminate any potential bias resulting from the model initiating nematode count at artificially zero in the beginning of the simulation.

2.4 Vegetation Study

Vegetation heights for grazed and un-grazed shoots were recorded within Adventdalen. To observe the seasonal curve, observations were conducted over nine days spanning from June – September.

To track reindeer grazing activity, data collection occurred by two-person teams. One team member, referred to as the spotter, utilized a spotting scope or binoculars to locate grazing sites, and at which point would guide the second team member, referred to as the recorder, towards the identified position. Upon reaching the site, the recorder verified the presence of grazed marks before signaling the spotter to join. Once marks were located, the team would unite to begin data collection, with the recorder acting as a scribe and the spotter measuring vegetation height.

While the study primarily focused on general graminoids, other vegetation types were also observed and recorded, however, due to a scarcity of data, seasonal comparisons for these types were not feasible. Graminoid species recorded are the following: *Poa*, *Luzula*, *Dupontia*, in addition to a category for general graminoid when exact species was undiscernible. Notably, *Salix polaris* was frequently found grazed to the roots, or entirely consumed, making the recording of this species unfeasible.

2.4.1 Grazed Vegetation Height

At the site, a 10 x 10 cm wooden frame was set over areas with noted fresh grazing marks. Only freshly grazed marks were recorded that fell within this quadrant. Fresh grazing marks were defined by recently bitten or torn looking ends with little to no yellowing or fading colors. Yellow discoloration of shoots indicating aged grazing marks were not recorded. The vertical height was taken from the top of the moss layer to the free-standing height of the grazed shoot. The aim was to record a minimum of 3 quadrants for each grazing site. Vegetation type, sex of the grazing reindeer, GPS coordinates, and species type were all recorded alongside the vegetation height.

2.4.2 Un-grazed Vegetation Height

Control height was taken alongside grazing height. Un-grazed shoots were recorded, containing no bite marks of any sort, old or new, and appeared to be undamaged. The vertical height was taken from the top of the moss layer to the free-standing height of the un-grazed shoot.

Both teams measured grazed shoots locally with slight variation only in terms of where the control shoots were determined. The first part of summer team A recorded un-grazed shoots in

the same area by randomly tossing an object in the same local vegetation type and setting down the 10 x 10 cm square and counting all un-grazed shoots in that area. This process was ideally carried out 3 times at each site. Team B, in the latter half of the season, would count 10 un-grazed shoots directly around the 10 x 10 cm square they placed down to record grazing marks, taking the closest 10 un-grazed shoots to the right, and left of the square. As both teams recorded un-grazed shoots locally in the same vegetation type on the same day and hour, this should not be cause for observer bias.

2.5 Data Visualization and Variable Justification

2.5.1 Seasonal Parasitic Curves

To analyze the relationship between nematode abundance and seasonal variations, along with yearly variability, the model was employed using temperature data spanning the entire study period (1995-2022) and the total average reindeer density (1531). This approach allowed for a simulation of predicted daily nematode abundance throughout the length of the study period if reindeer densities remained consistent.

For visualization of the seasonal curve, the nematode output for the first day of each month was extracted, of which the median values were subsequently plotted with variation visualized by plotting 10th and 90th percentiles as the lower and upper bounds. This was repeated for both infective and non-infective stages.

2.5.2 Temperature Based Seasonal Parasitic Curves

To evaluate the impact of temperature differences on the predicted nematode output, the coldest year (1997) and the warmest year (2022) from the study period of 195-2022 were selected for comparison. These years were determined based on daily temperatures throughout summer months, primarily June – August, as this time frame is typically associated with the onset of infection (Albon et al., 2002a) and aligns with the growth season of vegetation (S. Karlsen et al., 2014). To isolate the effects of climate, reindeer density was set to the average throughout the study period (1531).

2.5.3 Temperature and Density Based Parasitic Curves

To further the analysis, the scope of section 2.5.2 was enhanced by incorporating actual reindeer densities for each specific year as opposed to relying on the average density over the study period. The graph was therefore constructed on the same basis as the previous section, with the modification of specific reindeer densities, with 914 for the year 1997 and 2779 for the year

2022. This approach allowed for a better assessment of host density ability to impact simulated nematode abundance in accordance with temperature.

2.3.4 Future RCP Seasonal Parasitic Curves

Projected temperatures for the end of the century (2070-2100) were obtained by applying the Representative Concentration Pathways (RCPs) derived from various climate scenarios for the Longyearbyen area. The specific RCP models employed were sourced from the “Climate in Svalbard 2100 Report”, which drew upon the research conducted by Isaksen (2016, 2017). In this study RCP 4.5 and 8.5 scenarios were utilized, which correspond to medium and high greenhouse gas emissions, respectively. The RCP 2.6 scenario, associated with lower greenhouse gas emissions, was excluded from this study due to the lack of necessary corresponding policies which were required to be implemented three years prior, making it obsolete for the purposes of this study, and therefore irrelevant.

For each RCP, potential temperature increases were provided for all four seasons, thereby providing four data points. Daily temperatures were extrapolated from these seasonal data points using a Loess regression model. The resulting daily values were then added to the daily (24h) average temperature from 1971-2000, as this was the baseline period for the RCP models. This allowed for the ability to generate realistic daily fluctuations in future potential temperature scenarios (Figure 5). This data was then incorporated into the nematode abundance model, in conjunction with average reindeer density (1531) from the study period of 1995-2022, as there is no current reliable method to predict future reindeer densities, and this approach allows for a more direct comparison between past, current, and potential future scenarios.

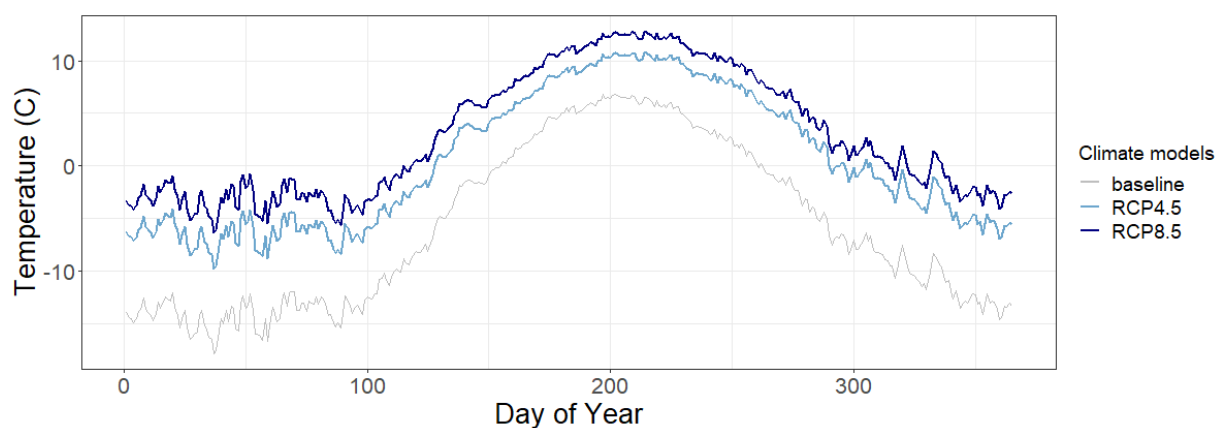


Figure 6: Daily predicted temperature increase for 2070-2100 based off the average seasonal temperature from 1971-2000, using RCP estimate models for future climate change predictions. The moderate estimate for both the RCP 4.5 and RCP 8.5 model were used to predict end of century (2070-2100) potential average daily temperatures. The baseline represents the daily average temperature between 1971-2000, which the RCP models are based on.

2.3.5 Seasonal Vegetation Curves

To effectively illustrate the variation in vegetation height throughout the growing season, a whisker-box plot was utilized, allowing for a clear visual representation of how frequently shoots were recorded near the moss layer, in addition to the median per date. Additionally, a line graph of the median recorded height per date was superimposed upon the box plot to illustrate the seasonal curve throughout the growing season. The use of median values aided in minimizing the influence of outliers. This was repeated for both grazed and un-grazed heights.

Combined, this superimposed graph allows for a comprehensive, yet easy to interpret representation of the data, with the line graph allowing for a straightforward comparison between vegetation height and the simulated predicted nematode abundance from the previous sections.

3. Results

3.1 Parasitic Seasonal Curves

3.1.1 Median Seasonal Curve of the Study Period

The simulated number of infective larvae (pink line) peaked in September while non-infective larvae (blue line) peaked in August (Figure 7). The model predicts that infective larvae are able to overwinter in a normal year, with the lowest predicted abundance seen in late May to early June. However, in February and March some years reach total eradication, as shown by the tenth percentiles. Non-infective larvae do not appear to overwinter, with the length of seasonal abundance stretching from May – December. Infective stages show greater variability in winter months, while non-infective stages show greater variability in summer months.

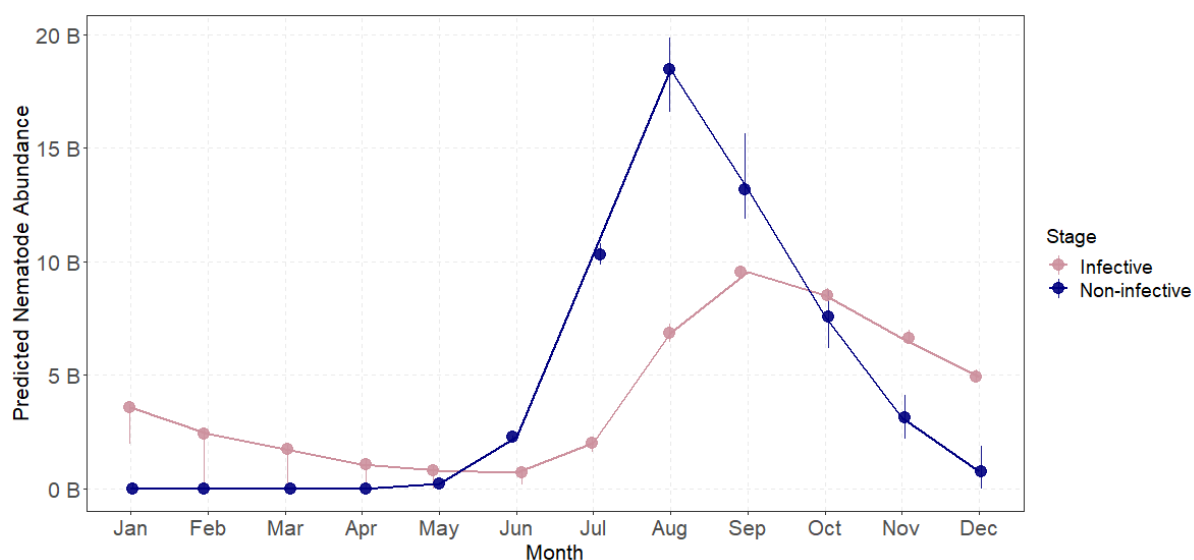


Figure 7: Model predicted nematode abundance in the natural environment throughout an averaged year. Daily mean temperature (24 h) from 1995 to 2022 was used to get an average seasonality curve of both predicted infective L3 stages and non-infective stages. Reindeer density was set as the average of the study period, 1531.522. A burn-in period of one year (using temperature values from 1994) was used but not depicted here. To show the distribution of nematode abundance the 10th and 90th percentiles are displayed.

3.1.2 Effects of Temperature: Coldest & Warmest Year, Average Reindeer Density

The warmest year, 2022, for infective (dark pink) and non-infective (brown) larvae are shown to have a slight negative association in simulated abundance, whereas the coldest year of 1997 for infective (dark blue) and non-infective (light blue) larvae are shown to fair better (Figure 8). The temperature difference appears to have the largest impact on the non-infective larvae than that of the infective. Furthermore, the simulated infective larvae for the warm year were the only stage capable of overwintering. The length of seasonal availability for warm temperature non-infective stages ranged from early May – mid December. For colder temperatures non-infective stages ranged from early May – early November, and for colder infective stages from early June – mid-January. Infective nematode abundance peaks for both cold and warm years were relatively close in time, with a slight offset earlier in the season for colder years, peaking in August, with the colder year infective stage peaking in early September.

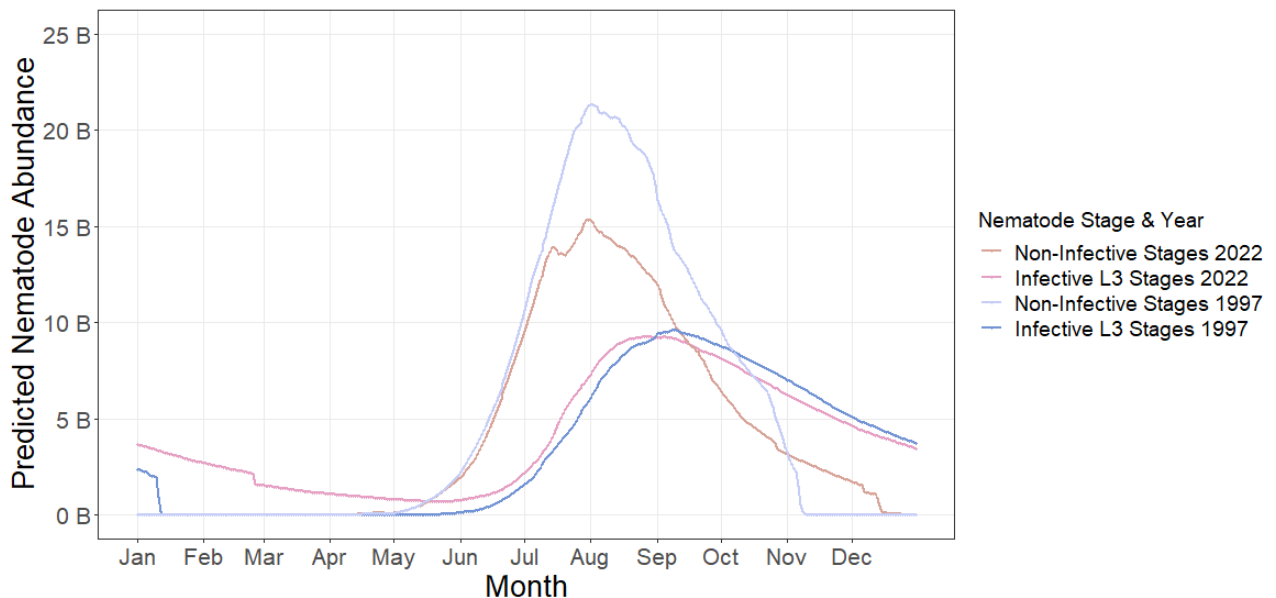


Figure 8: Model predicting nematode abundance for the coldest and warmest year defined by the summer average. Daily mean temperatures (24h) for 1997 and 2022 were used to calculate seasonality curves for both infective L3 stages and non-infective stages. Reindeer density was set to the average of the study period, 1531.522. A burn-in period of one year (using temperature values for 1996 before 1997, and 2021 before 2022) were used but not depicted here.

3.1.3 Effects of Temperature & Density: Coldest & Warmest w/Actual Densities

This figure displays the warmer (2022) and colder (1997) year temperatures with the actual reindeer densities for each year, 2,779 and 914 respectively (Figure 9). Non-infective peaks occurred at the beginning of August for both 1997 (light blue) and 2022 (brown). Infective peaks occurred in the beginning of September for 1997 (dark blue) and mid-August for 2022 (pink). Overall simulated seasonal lengths for 1997 infective larvae were mid-June – mid-January, for 1997 non-infective stages were early May - early November, and for 2022 non-infective larvae from beginning of May - mid-December. The 2022 infective stages were the only group able to overwinter when actual temperature and reindeer density were considered (Figure 9).

The actual reindeer densities inverted the relationship from temperature effect alone (cf. Figure 8), resulting in a larger predicted L3 abundance in 2022 (warm) compared with 1997 (cold). The increase in reindeer densities also saw an increase in overwintering abilities for infective stages in 2022. The inclusion of the actual reindeer densities appears to not lead to any changes in terms of the duration of the seasons or the occurrence peaks for the nematodes.

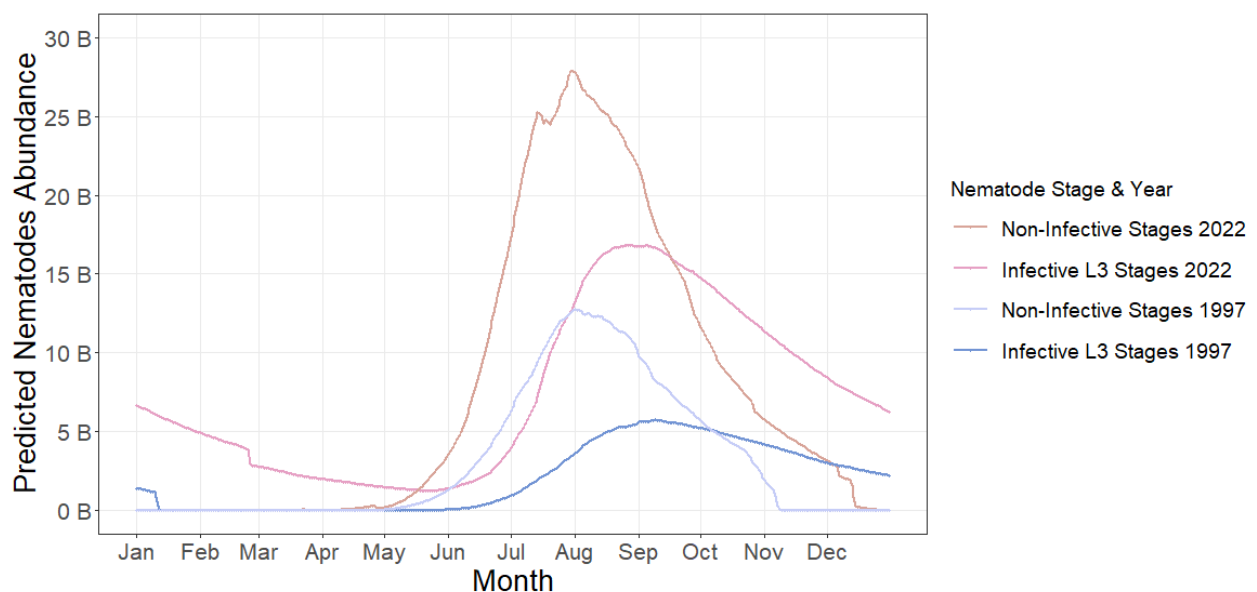


Figure 9: Model predicting nematode abundance for the coldest and warmest year defined by the summer average and actual reindeer densities. Daily mean temperatures (24h) for 1997 and 2022 were used to calculate seasonality curves for both infective L3 stages and non-infective stages. Reindeer density for 1997 was calculated as 913.8713, and for 2022 calculated as 2779.1713. A burn-in period of one year (using temperature values for 1996 before 1997, and 2021 before 2022) were used but not depicted here.

3.1.4 Future RCP Seasonal Curves

Simulated nematode abundance for the end of the century (2070-2100) are displayed with RCP values of 4.5 and 8.5 for the Longyearbyen area (Figure 10). Simulated infective peaks occur in late August for RCP 4.5 (blue) and mid-August for RCP 8.5 (pink), displaying a slightly earlier peak with slightly lower minimum abundance in the warmer prediction. Both infective stages had overwintering capabilities, with a slightly higher capability for the cooler RCP 4.5 predictions. Non-infective stages exhibited very minimal overwintering capabilities. This follows similar trends for current and historic years. However, non-infective peaks are lower than that of current and historical years (Figure 8). Infective larvae peaks, while showing a slight difference between all scenarios, are approximately similar to one another.

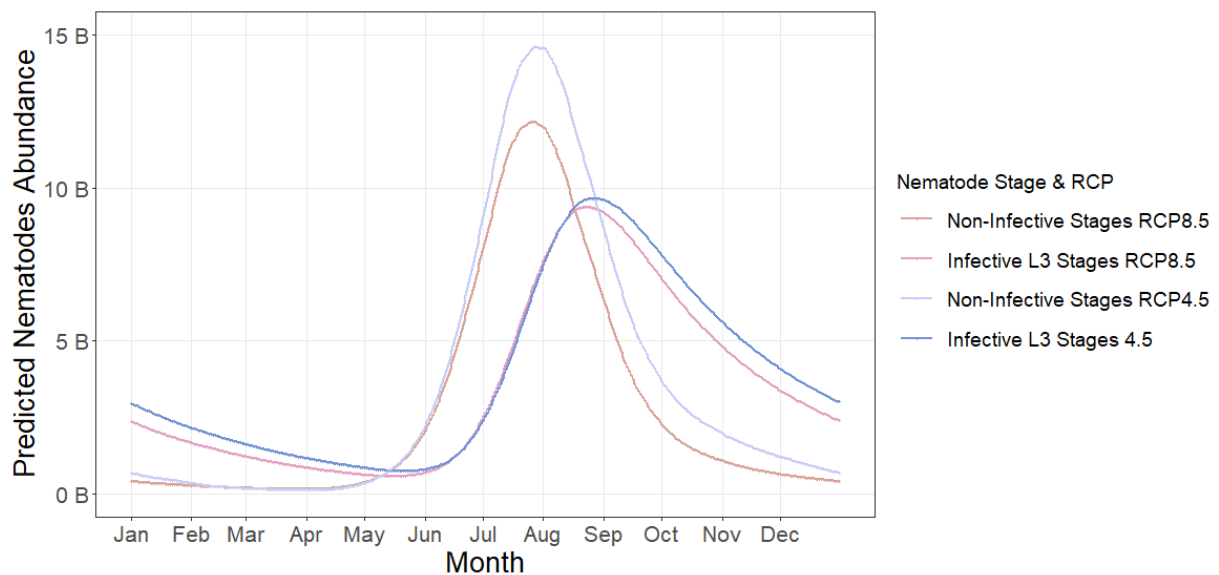


Figure 10: Model predicting nematode abundance for future potential climate scenarios at the end of the century, 2070-2100 based on the RCP median models for 8.5 and 4.5 outlined in the climate report Svalbard Climate 2100. RCP 4.5 is defined as “medium emissions” and RCP 8.5 is defined as “high emissions”. Reindeer density was set to the average of the study period, 1995-2022, of 1531.522. A burn-in period of one year (repeating yearly values for RCP 4.5 and 8.5) was used but not depicted here.

3.2 Vegetation Seasonal Curves

The seasonal grazed vegetation curve begins increasing from the beginning of June through July, at which point there is a small dip and then plateaus until the beginning of September where it decreases back towards soil height at the end of September. The increase of vegetation height aligns with the increase in infective nematode abundance on the pasture (Figure 8, Figure 9). The final decrease in vegetation height is similar in time to the peak of simulated infective larvae, however the grazed vegetation height decreases while simulated infective larvae remain elevated in the pasture.

There was only one day recorded during the season where vegetation height was recorded at moss level, and the lowest median was also the same day at 6 mm (07/07/2022). The highest recorded median height occurred relatively early in the growing season, measuring 24.5 mm (07/07/2022). Both the end date and start date of our data recorded similar medians, 9 mm (06/06/2022) and 10 mm (27/09/2022).

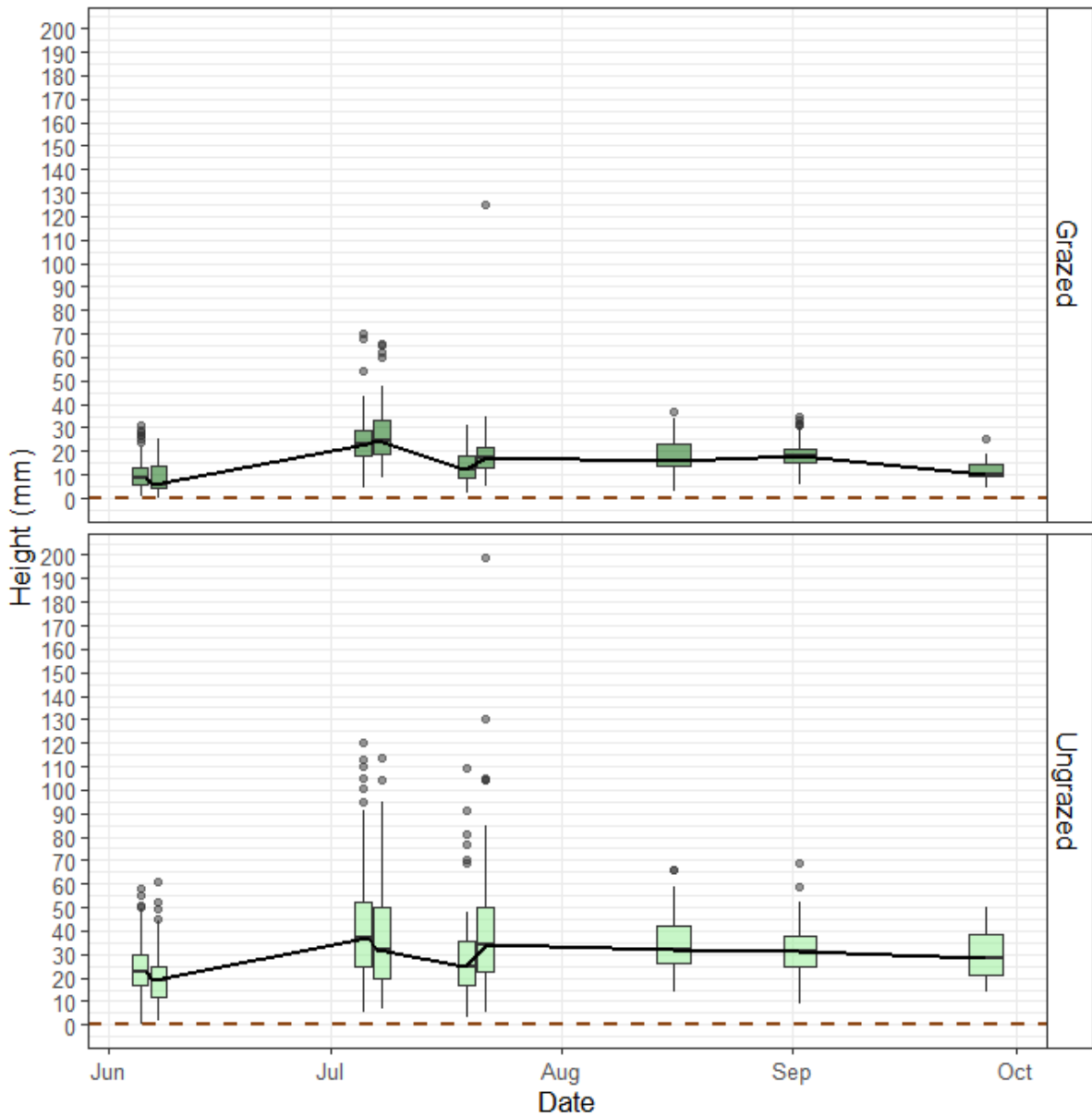


Figure 11: Recorded graminoid height (mm) for grazed and un-grazed vegetation recorded in Adventdalen throughout the 2022 growing season. The overlay line represents the seasonal curve according to the median graminoid height in millimeters per day sampled. The whisker-box plot shows the variation within the sampled data per date, with the median plant height represented by the solid black lines, the shaded boxes representing the interquartile range (IQR), and the whiskers representing the variability outside the upper and lower quartiles, extending 1.5 times the upper and lower interquartile range. Outliers are represented by circles. The brown dashed line represents the soil and moss level as heights were recorded starting at the moss level if present, or the soil level if mosses were absent.

4. Discussion

This study aimed to investigate the factors contributing to the reduced regulatory effect of the parasitic nematode *O. gruebneri* on the Svalbard reindeer population, which has experienced remarkable population growth since the 2000s (Loe et al. 2021). To assess potential dynamic change, a dynamic model was utilized to predict nematode abundance in the pasture, considering the influence of temperature and reindeer density. The simulated predictions of nematode abundance and seasonality were subsequently compared with seasonal grazing height to determine if a phenological mismatch may be leading to a lower infection risk and rate. The findings of this study suggest that temperature, when isolated, had small negative effects on infective larvae and a more noticeable impact on non-infective larvae peaks, with warmer temperatures altering the peaks slightly earlier in the year. When accounting for variation in reindeer density, the observed increase in host populations far exceeded temperature effects, suggesting that infection risk may remain relatively high even with a changing climate that led to warmer temperatures. When simulated seasonal abundances were compared alongside grazing height a slight overlap occurred in the beginning of the growing season to the initial ramp up of simulated infective larvae in the pasture. This may suggest a partial phenological mismatch occurring, which may be responsible for a reduction in the regulatory effect of parasites. The insights of the study have notable implications for understanding ecological responses in the face of climate change and emphasize the need to not only consider the dynamics of climatic and host population factors, but also indirect factors such as changes in plant communities, including seasonal growth, impacting infection risk and our understanding of disease ecology.

4.1 Simulated Nematode Abundance

4.1.1 Factors of Nematode Abundance

This study found that although warmer conditions were initially associated with a slight reduction in parasitic abundance in the pasture, this is overshadowed by the positive association with increased host availability. The infective nematode abundance increased by approximately three times when accounting for actual host densities, overturning the simulated temperature impact. This aligns with an assumption made that host population densities may be a more important factor than environmental conditions in regards to parasitic abundance (Stien et al., 2002). This further aligns with a meta-analysis on parasitic nematodes suggesting that host densities are an integral part of parasite transmission risks (Arneberg et al., 1998).

However, this simulation contradicts the observed increase in host populations, as with higher simulated nematode abundance in the pasture, it could be assumed the regulatory effect parasites have on host populations would be observed as it was in the past. Therefore, it is unlikely that warmer temperatures alone can explain the observed lack of regulatory effect on the host. In addition, it appears that host density-dependent mechanisms are not a driving factor in infection risk of Svalbard reindeer. Signifying other factors may be at play impacting infection risk.

4.1.2 Future Nematode Abundance

In this study, despite the average increase in summer temperature between historic and RCP 8.5 conditions of 7.92°C degrees, the simulation predicted similar infected nematode peak abundance for all yearly temperature conditions, albeit with a slight negative association with warmer temperatures. On the contrary, the non-infective stages exhibited a greater variation between yearly temperatures. These findings are consistent with the different sensitivity levels to temperatures for both stages (B. M. Hoar et al., 2012; Peacock et al., 2022).

Interestingly, non-infective larvae develop into infective larvae yet there was no discernable difference between the predicted infective nematode abundance regardless of the changes in the non-infective abundance. This could suggest either the developmental rate is increasing in a manner to offset mortality rate, or that developmental rate is relatively stable. With increasing temperatures, developmental rates are expected to increase up until a threshold, as in line with the metabolic theory of ecology (Brown et al., 2004). This applies to mortality rate as well, however with non-invasive stages being more susceptible the rates can differ under the same temperatures. Alternatively, a paper by Hoar et al, (2012a) suggested that this phenomenon may be the result of developmental rate remaining fairly consistent due to *O. gruebneri*'s ability to handle a wide range of temperatures.

Additionally, although not as pertinent to this study's main premise, the overwintering capabilities of non-infective larvae when comparing future, historic, and current climate scenarios with average reindeer density, fare better under the RCP scenarios. This is likely a result of L2 larvae having a more robust temperature threshold compared to other earlier stages of non-infective larvae, which is what is likely observed in the graph (Hoar et al., 2012a).

4.2 Vegetation

4.2.1 Grazing Height

As warmer temperatures do not overpower reindeer density in simulated nematode abundance, an alternative explanation may lie in a phenological mismatch impacting infection risk.

This study found that reindeer began grazing on taller vegetation coinciding with the increase of simulated abundance of infective nematodes in the pasture. However, simulated infective nematode abundance remained elevated throughout the fall and early winter, whereas grazing height began to decrease quickly after the start of September. Overall, the main overlap of increased grazing height occurring at the same time as elevated simulated infective larvae is from June – September. Even with the shortage of historical data on grazing height, there has been a demonstrated increase in canopy height and biomass of arctic graminoids with warmer temperatures (Elmendorf et al., 2012; Wahren et al., 2005). With Svalbard experiencing the fastest rate of increased warming throughout the circumpolar Arctic (Descamps et al., 2017), an assumption can be made in regards to a variation of vegetation height from historical to current years of the study period. Based off these assumptions this may indicate a potential partial phenological mismatch occurring within the start of summer. Similar phenomena of phenological mismatches have been observed throughout parasitic ecology, so it is not unfounded (MacDonald & Brisson, 2022; McDevitt-Galles et al., 2020)

An additional change in the vegetation community in recent years is the decline in mosses, which are declining alongside warmer temperatures (Prestø et al., 2014). Whereas little is known about *O. gruebneri* specifically in terms of location within the Svalbard soil and vegetation strata, nematodes in general have been found to prefer moss as they may pervade a moist space, which aids in prevention of desiccation (Glimme, 2021). This reduction in bryophytes, and their subsequent reduction within the diet of Svalbard reindeer (Hiltunen et al., 2022), may therefore be further mitigating infection risk, however it is not considered within the model.

4.2.2 Seasonal Vegetation Shifts

The lack of historical data on grazing height poses a challenge to directly ascertain if a phenological mismatch is occurring. Nevertheless, by utilizing Normalized Difference Vegetation Index (NDVI) data, and the known results of climate change on plant growth, it is possible to estimate on the occurrence of a mismatch.

The average vegetation seasonal onset for the entirety of Svalbard between 2000-2020 shows a 0.1% of growth before June 16th, with 25.3% by June 16th-30th (Karlsen et al., 2020). However, there are documented instances of growth onset occurring as early as late May to early June (Le Moullec et al., 2019). As of 2013-2020, vegetation onset began equally as early if not earlier compared each year in central Spitsbergen, with the entire island showing an approximate twelve-day increase in vegetation onset from 2000-2020, however, there is no statistically

significant trend seen in the onset of the growing season (S. Karlsen et al., 2014; S. R. Karlsen et al., 2020).

Nematode L3 seasonal peaks begin elevating in mid-June as seen both historically and in recent years, suggesting little shift in seasonal nematode peaks on the pasture. With no significant trend in the onset of growing season, it is difficult to say whether the early season phenological mismatch is due to earlier growing seasons. However, it is likely primarily due to temperature influences on vegetation growth.

4.2.3 Future Potential Vegetational Shifts and Height

The forecasts under RCP 4.5 and 8.5 models for temperatures at the end of the century are expected to result in milder winter temperatures (-3.37°C to -1.03°C) and warmer summer temperatures (3.37°C to 5.67°C). The trend of warming conditions is already evident within Svalbard, with observations of summers elongating and winters reducing over time (Førland et al., 2011; Loe et al., 2021).

In the context of this study, delayed autumns and increased access to vegetation, in addition to higher plant biomass with warming temperatures (Elmendorf et al., 2012), could potentially increase the phenological mismatch in the future. However, when accounting for simulated infected nematode abundance at the end of the century, the overwinter ability is accelerated. This may offset any additional length in the growing season.

It should be noted, however, that this is an oversimplification of the plant communities' prospects in the future as other factors come into play (e.g., loss of permafrost, invasive species, disturbed dormancy, increased precipitation, rain-on-snow events, amongst others) (Bartlett et al., 2021; S. R. Karlsen et al., 2020; Vincent et al., 2017). This makes it difficult to fully predict plant community structure at the end of the century.

4.3 Model Limitations

Models are a vital tool in predicting nematode population dynamics, a feat that would be difficult to do in the field. While useful in comprehending interactions between complex dynamics, there are limitations to consider when employing a model. The assumed nematode egg production per feces is based on weak empirical evidence (Stien et al., 2002a). Given the uncertainty of whether egg production per feces is underestimated or overestimated, it remains uncertain whether a more precise estimate would increase or reduce estimated nematode abundance. This is bias, but with unknown direction. Furthermore, the reindeer densities only account for the female individuals and does not distinguish reindeer age. Yearlings and calves

have been noted to have lower levels of infection (Irvine et al., 2000), and therefore have lower egg per gram feces, resulting in a bias that is overestimating feces. The current model is therefore an example of a transition from low to high density state, and not an exact representation of total animals. Future models may be further refined by incorporating additional factors of influence on the survival of *O. gruebneri*, such as humidity and precipitation, which is expected to increase with climate change (Hanssen-Bauer et al., 2019). Increased humidity, up until a threshold, can bolster the survival of gastrointestinal nematodes by preventing desiccation (Perry, 1999) and facilitates the hatching and developmental stages thereby aiding infection rate (Hoar, 2012b). Increase in precipitation may further mitigate desiccation and larval dispersal during short rainfall events (Grønvold & Høgh-Schmidt, 1989), with heavy rainfall increases chances of larvae being picked up in runoff (Stromberg, 1997). Hence, the integration of additional influential factors will enhance the understanding of infection risk and how it may change with a changing climate.

4.4 Vegetation Source Error

Vegetation sampling was limited as a result of covid related restrictions. A total of nine days were sampled throughout the study period, and a low sample size may result in a limited view of the seasonal vegetation curves and height. Each day also recorded varying graminoid species, and not consistent throughout the season. This could lead to a bias in data if taller graminoid or shorter graminoid species were accidentally favored that day due to location variation within the valley or patch type.

However, the data obtained still provides an overview of a seasonal trend. Future studies may benefit from a set weekly schedule throughout the growing season for further insights. In addition, ensuring equal measures of graminoid species recorded per day could aid in accounting for bias. Overall, this may help with outliers and provide a more reliable and clear seasonal vegetation curve.

5. Conclusion

The challenges posed by climate change significantly complicate the prediction and management of parasite-host interactions and infection risks, especially considering the complexities involved in studying these dynamics in the natural environment. This study's findings illustrate a slight negative association between rising temperatures and simulated parasite abundance, with an increased impact on non-infective stages. Counteracting these effects, increasing host densities appear to overcome the slight negative impact of temperature, increasing nematode abundance in the pasture. This has led to a simulated increase in parasitic nematodes in current years than historical years, which is counterintuitive to the apparent decrease ability in the regulatory influences occurring as a result of the parasite-host relationship. Therefore, the possibility of a phenological mismatch may result in the decrease of this phenomena. This study found that vegetation heights increased during the increase of parasitic nematodes on the pasture, possibly leading to a lowered infection risk as grazing behaviors occurred further from the parasitic reservoirs. This potential inhibition may only increase in strength as warmer climates are expected to increase plant height and plant biomass into the fall. This study is the first to investigate the impacts of grazing throughout the season in context of infection risk. Future research should continue to monitor vegetation grazing to substantiate the theory of diminished infection risk, as the current understanding is based on a single season of data collections with assumptions derived from historical NDVI comparisons.

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