Worms on the brain: Modelling parasitic disease transmission in reindeer

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ABSTRACT

Elaphostrongylus rangiferi is a protostrongylid nematode responsible for cerebrospinal elaphostrongylosis, or 'brainworm' disease in reindeer (*Rangifer tarandus* ssp.) and co-grazing small ruminants. Although the parasite is endemic and infection normally occurs at a low level, recently there have been severe outbreaks with high levels of mortality. This impacts on the livelihoods of the Sami people who herd reindeer across Norway.

Outbreaks of brainworm disease have been linked to the climatic conditions in preceding years, and development rates of the larvae within the intermediate host are known to vary dependent on environmental temperature. This information could therefore be used to predict the risk of elaphostrongylosis based on environmental conditions. Forecasts of disease risk could be used by Sami herders to aid in decision making regarding planning and enacting disease mitigation measures. The aim of this project was to development models with the potential to be used in this manner.

As transmission can only occur where there is overlap in the ranges of the intermediate (gastropods) and definitive (reindeer) hosts, and the extent of the suitable habitat for gastropods within Norway is currently unknown, species distribution models were developed for multiple slug and snail species with the potential to act as intermediate hosts and projected onto different climate change scenarios. They predicted an overall decrease in future probability of presence of gastropods across Europe, but an increase in some areas of the Norwegian reindeer range. A degree-day model representing development of first to third stage larvae within the intermediate host was also applied to climate change projections and predicted an increase in thermal suitability in the coming decades, under all emissions scenarios and for all time periods. This, combined with the increase in probability of presence for the intermediate hosts, may result in an increase in potential risk of *E. rangiferi* transmission to reindeer.

The degree-day model was also applied on a finer scale to an individual reindeer herd and combined with reindeer movement both to assess monthly availability of infectious third-stage larvae (L3) and to demonstrate the applicability for its use as a predictive tool. This predicted L3 availability from July in this herd with little variability year-on-year.

A more complex model of the extra-mammalian lifecycle stages was also developed to incorporate more lifecycle processes and provide a better representation of the infectious L3 availability. With this model annual variation in the highest period of risk was predicted.

The models developed provide a framework that could be used on local or national scales to predict spatiotemporal risk of *E. rangiferi* infection of ruminants. Additional data collection for refinement of the model parameters and model validation is needed before this can be further developed.

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CHAPTER 1: INTRODUCTION

The world is currently facing significant change induced by the human population and this is affecting ecosystems worldwide. There are many ways in which environmental changes can affect parasite populations, including the expansion or translocation of host or parasite ranges. Examples include the introduction of bank voles to Ireland (Stuart et al., 2020), or the introduction of non-native freshwater fish in South Africa (Smit et al., 2017). Environmental changes have led to the emergence of parasites in areas they were not previously found, for example the Asian longhorned tick *Haemaphysalis longicornis* (Egizi et al., 2020) and *Angiostrongylus vasorum* (Kistler et al., 2014) in the USA. Similarly a resurgence in previously low levels of parasitic infection have been recorded, for example the lungworm *Ummingmakstrongylus pallikukensis* in Canadian Muskoxen (Kutz et al., 2004), and *Sarcoptes scabei* in American black bears (Niedringhaus et al., 2019). Finally there is evidence that environmental change is leading to a change of hosts for some parasites, for example *Eimeria* spp. that normally parasitise *Apodemus* spp have been recorded in different species of rodents (Macova et al., 2018), and Apicomplexan parasites have been shown to switch from birds and primates to bats (Duval et al., 2007).

Globally, much of the land use change, and therefore changes in risk of parasitism, is due to direct anthropogenic factors such as deforestation causing a reduction in habitat size, but at northern latitudes and in the Arctic, habitat change is primarily due to climate change (Jetz et al., 2007). It is widely acknowledged that climate change and the increase in frequency of extreme weather events is going to have serious effects on infectious disease, including parasitic disease. This could be in the form of outright increases in incidence, occasional severe outbreaks, or shifts in distribution and emergence. It is a situation that needs careful monitoring (Brooks and Hoberg, 2007; Harvell et al., 2002; Kovats et al., 2001; Lafferty, 2009; Sutherst, 2001). There are many examples where climate change has already been linked to changes in parasitic disease risk. There are multiple cases studies of endoparasites on sheep farms in South-East Scotland that have started showing alterations from their normal epidemiology resulting in parasitic disease of unusual intensities and at unexpected times, which

have been putatively linked to climate change (Kenyon et al., 2009). Predicted climate-driven environmental suitability for development of *Fasciola hepatica* has increased over time, particularly since the year 2000, and this has been matched with an increase in observed incidence of infections in livestock. This increase is predicted to continue with a variable seasonal pattern across Europe; in Northern Europe there are expected to be peaks in risk of fasciolosis in Autumn and Spring, whereas in Southern Europe it is expected in the winter (Caminade et al., 2015). For the tick *Hyalomma marginatum* the environmental suitability for its habitation within its current range in Southern Europe has been estimated to have increased since 1970 based on thermal and hydrological variables, along with new areas having become suitable (Fernandez-Ruiz and Estrada-Pena, 2021). Retrospective analysis has also predicted changes to its lifecycle dynamics over this time in relation to the same environmental factors by increasing development rates and decreasing mortality in immature larval and nymph stages but increasing mortality in questing adults. This was predicted to make it more likely that *H. marginatum* could colonise new areas (Estrada-Peña et al., 2015). A generalised model of nematode infections in livestock predicts a tipping point in temperature driven larval development rate at which peak parasite burden starts to rapidly increase (Fox et al., 2015). The same processes apply for parasites of wild and semi-domesticated ungulates grazing in herds. The focus of this thesis is the impact of climate on the epidemiology of the reindeer brainworm (*Elaphostrongylus rangiferi*) which affects wild and semi-domesticated reindeer throughout Norway.

1.1 REINDEER – *RANGIFER TARANDUS* SSP.

In Arctic regions across North America and Europe, reindeer (*Rangifer tarandus* ssp.) are one of the most abundant large herbivores and are important ecologically and culturally. The ecology of reindeer is very important as the ecosystem in Fennoscandia has developed alongside large herds of reindeer. Grazing reindeer have the potential to act as ecosystem engineers by way of grazing and trampling of vegetation and snow, which exposes the underlying vegetation to the air (Moen and Danell, 2003; Suominen and Olofsson, 2000). They have been found to increase vegetation species richness and decrease gastropod abundance and species richness (Suominen, 1999). This could be due to changes in the environment to which these gastropods are susceptible, or

increases in predators of the gastropods (Suominen, 1999). In Sweden where reindeer numbers have stayed relatively constant over the past century, there is no evidence of over-exploitation of the environment by reindeer (Moen and Danell, 2003). However, elsewhere there have been changes to the environment induced by reindeer herding at unsustainable levels. In Finnmark county in Norway there was a doubling of the reindeer population in the 1980s and these high grazing densities have been associated with loss of lichen carpets, which then has the effect of removing protection of the ground from hard freezing, leading to increased soil erosion (Moen and Danell, 2003). Nutrient cycling was also found to have decreased in tundra that was only moderately grazed (Suominen and Olofsson, 2000).

The Sami are an indigenous people to Fennoscandia and north-west Russia. Reindeer are an important part of the society and industry of the Sami people and reindeer herding has been part of Sami culture since at least the 17th Century, and probably at a smaller scale long before this (Emanuelsson, 1987). There are many challenges faced by the Sami people. Although some of these are related to the climate, there have also been some anthropogenic changes which are affecting the way reindeer are managed across Fennoscandia. During the 19th and 20th Centuries political borders in Fennoscandia were gradually closed to the movement of reindeer (Lantto, 2010). This, alongside changes in the climate, resulted in extreme changes to the management of reindeer in Finland where they are now mainly confined to enclosed areas of pasture (Turunen and Vuojala-Magga, 2014). However, in Norway the majority of herds are still managed in the traditional manner with reindeer herds free ranging over defined areas and rounded up twice yearly. Over recent years the industry has become less profitable and herd productivity has become less resilient to forces of change, and now rely more on state intervention and outside funding (Hausner et al., 2011; Reinert and Benjaminsen, 2015). An increase in the frequency of outbreaks of brainworm (*E. rangiferi*) further threatens the livelihoods of the Sami. Wild reindeer herds also remain in Norway in the national parks and mountains of the south (Figure 1.1).

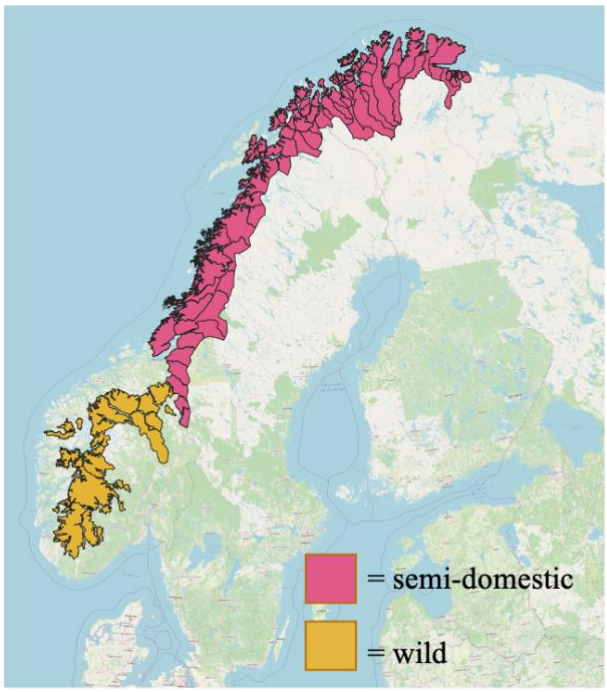


Figure 1.1 The location of reindeer herds across Norway. The wild reindeer range is shown in yellow and the semi-domesticated reindeer range in pink, with the demarcations showing the individual herd ranges.

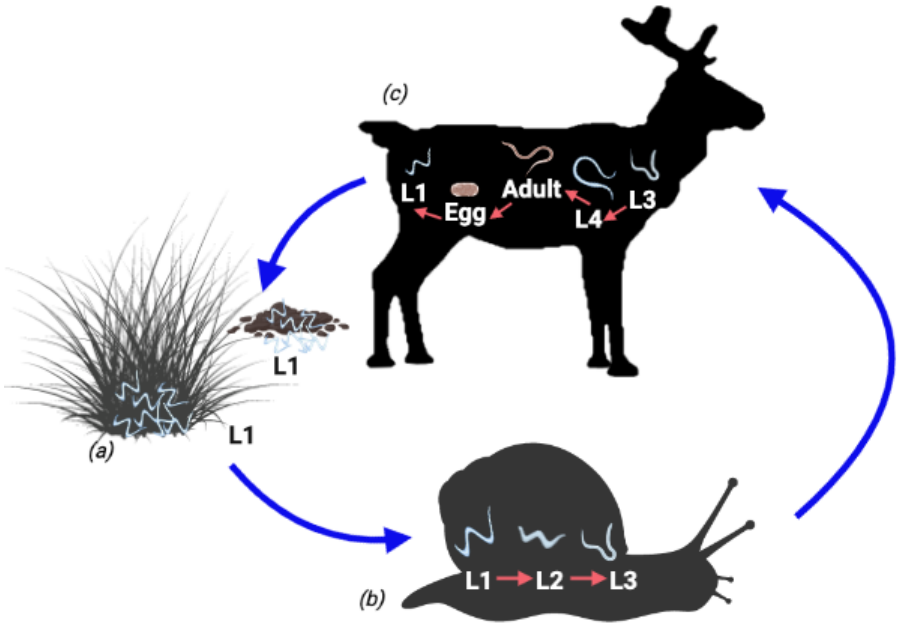


Figure 1.2 The lifecycle of Elaphostrongylus rangiferi. (a) L1 are deposited in faeces and may migrate onto pasture. (b) L1 infect gastropod intermediate hosts where they develop to L3. (3) Reindeer ingest gastropods with infective L3, these develop to L4 then adults which produce eggs that develop into new L1. Image created with BioRender.com

1.2 REINDEER BRAINWORM – *ELAPHOSTRONGYLUS RANGIFERI*

Elaphostrongylus rangiferi is an important parasite of reindeer in Norway and one in which changes in outbreak frequency are suspected to be related to climate change (Davidson et al., 2020). *E. rangiferi* is a protostrongylid nematode which uses gastropods as intermediate hosts and infects reindeer after ingestion of these (Figure 1.2). Third stage larvae (L3) from ingested infected gastropods migrate out of the reindeer abomasum and through blood vessels to the meninges where they develop through L4 stage to adult, taking a minimum of 48 days to reach the central nervous system (CNS). From there the adults migrate to the skeletal muscle where they produce eggs, with the earliest finding of adults in skeletal muscle at 90 days post infection (Hemmingsen et al., 1993). The eggs travel via blood vessels to the lungs where they hatch to L1 and cause a verminous pneumonia (Handeland, 1994). The L1 are then coughed up and swallowed before passing through the digestive tract to be deposited on pasture in the faeces. The pre-patent period as a whole takes 4-4.5 months (Handeland, 1994). The majority of the clinical signs are caused by the worms in the meninges where infection can cause paralysis or paresis of the hind limbs leading to wasting, or less commonly they can cause death by damaging the central nervous system directly (Handeland and Norberg, 1992).

There are regular, often incidental, findings of brainworm infection in reindeer carcasses and samples submitted to the Norwegian Veterinary Institute, although no wide scale surveillance has been conducted to ascertain prevalence levels (Davidson et al., 2020). Serious outbreaks are seen only sporadically, with large outbreaks seen in the 1980s, and recurrence seen in 2018 (Davidson et al., 2020). Outbreaks in the 1980s were strongly correlated with above average temperatures the previous summer and higher than average levels of rainfall (Handeland and Slettbakk, 1994).

Seasonal infections are seen in goats in regions with large migrant reindeer populations (Handeland and Sparboe, 1991). Goats are thought to be highly susceptible to infection (Handeland and Skorping, 1992), with outbreaks possible within herds; 25% of surveyed farmers reported disease occurrence within a two-year period (Handeland and Slettbakk, 1995). Sheep have also been shown to become infected experimentally (Handeland et al., 1993) but natural infection only occurs

sporadically (Handeland and Slettbakk, 1995). Although pathological changes associated with infection (Handeland and Skorping, 1992) and adult *E. rangiferi* have been recovered from muscles and spinal cord of sheep and goats (Handeland et al., 1993), the parasite is not thought to be capable of completing its lifecycle since no larvae were detected in faeces 5 months post infection in either species (Handeland and Skorping, 1993; Handeland et al., 1993). Outbreaks in small ruminants have also been associated with higher than average temperatures the preceding summer (Handeland and Slettbakk, 1995). It is therefore suspected that outbreaks of clinical disease may become more frequent in the future due to the changing climatic conditions.

1.3 THE IMPACT OF CLIMATE CHANGE ON *E. RANGIFERI*

Three criteria have been suggested to determine whether changes to parasitism are induced by climate change: 1) evidence of meteorological climate change; 2) evidence of sensitivity of the organisms to climatic factors; 3) evidence of epidemiological change in association with the climate (Kovats et al., 2001).

1.3.1 Meteorological change in the Arctic

The Arctic is one of the areas of the globe facing the biggest climatic changes, with the highest rates of change being found at northern latitudes (Kovats et al., 2001). Arctic ecosystems are particularly sensitive to the effects of climate change, with tundra, boreal forest and mountainous areas all being identified as particularly susceptible (Solomon and IPCC, 2007). Changes happening in the Arctic region also compound the effects of climate change globally as changes in snow and ice cover have knock-on effects due to their reflective capacity and influence on sea levels and salinity (Bintanja and van der Linden, 2013; Polar Research Board, 2011).

Overall the global temperature has risen approximately 1ºC since the end of the 19th century and is predicted to increase by up to 5.7 ºC by the end of the current century (IPCC, 2021). The Arctic has seen rises in temperature at twice the rate of the rest of the world over recent decades, with an acceleration predicted over the coming decades (Hassol, 2004). In Arctic regions, winter warming exceeds summer warming by a factor of four (Bintanja and van der Linden, 2013). The rising temperatures mean the

winter season will become shorter, with freezing happening later in the season and snow melt occurring earlier. This will have knock-on effects to the hydrological system as peak river flow will shift earlier in the spring, along with increased levels of river run off (Hassol, 2004). Along with the winter freeze occurring later there will be more days during which the temperature crosses the freezing point threshold, and an increase in the number of thaw days (Jylhä et al., 2008). Rainfall has increased by 8% over the past century and this is expected to continue, along with increasing frequency of heavy rainfall events, however periods of drought are also expected to become more frequent during the summer months (Hassol, 2004; Solomon and IPCC, 2007). All these factors will combine to affect the suitability of the habitat for different species and will alter ecosystem dynamics. However, current models have not accurately predicted the observed changes, for example the level of sea ice decline (Polar Research Board, 2011), therefore these predictions may be an underestimation of the true magnitude. Another downside is that the majority of climate change models use mean predicted increases; they have not predicted the seasonality that has been observed, often over predicting summer warming and underpredicting winter warming (Bintanja and van der Linden, 2013). They also fail to account for occasional extreme weather events (Thompson et al., 2013), which could have a different impact on parasite ecology compared to a uniform change in temperature.

There is an additional stressor in the Arctic in the form of ozone depletion leading to increased UV radiation at the Earth's surface in this region. This is likely to be strongest in the spring, during the time when ecosystems are more vulnerable to the effects, as increased UV radiation can interfere with photosynthesis of plants. This will be compounded by the reduced snow cover which would normally provide protection for sensitive species (Hassol, 2004).

1.3.2 Sensitivity of *E. rangiferi* and its intermediate and definitive hosts to climatic factors

Climate change affects all trophic levels of an ecosystem, and the distribution of both the intermediate and definitive hosts of *E. rangiferi* are determined by habitat and land type. Changes have already been observed in the vegetation of Arctic regions, with satellite observations revealing 'browning' of boreal forests, along with 'greening' of

tundra areas as forests move northwards (Polar Research Board, 2011), and the spread of tundra vegetation into polar deserts has also been observed (Hassol, 2004). Along with the expansion of the tree range northwards and towards higher elevations (Hassol, 2004), there are stresses induced in the native tree populations within their current range due to alterations in climate outside the range to which these species are adapted. A tipping point is expected at which these boreal forest populations die off, as climate changes move at a faster pace than arboreal migration rates. This could result in decreased species diversity and decreased genetic diversity within species leading to a reduction in resilience of Arctic species in the face of altered conditions (Hassol, 2004). These changes in flora will also have a large impact on herbivores as they could result in changes in habitat and grazing patterns. This will have knock-on effects at all trophic levels. Increased tree growth in tundra areas is likely to contribute to regional warming, as well as changing the habitats for native fauna and flora. The increase in forested area also increases the risk of forest fires, and in outbreaks of insects (Hassol, 2004).

Due to their close relationship with environmental conditions, ectotherms are highly susceptible to environmental changes. Gastropods are particularly sensitive to climate change due to their limited scope for movement, their requirements for moisture and their sensitivities to changing temperature. Very little is known about physiological changes induced by such pressures but there is evidence that they are having effects. Reduced winter dormancy periods induced by increasing winter temperatures has been associated with reduced reproductive capacity of gastropods, as has increasing summer temperatures (Nicolai and Ansart, 2017).

Changes to the ranges of gastropods over time have become evident. An increase in the upper elevational limit of the snail *Arianta arbustorum* over a period of 95 years has been found in an Alpine region, and in a protected area untouched by human activity. This is presumed to have occurred due to climatic changes (Baur and Baur, 2013). However, it is unknown whether the movement of the snails follows or is associated with any change in the vegetation on the slope i.e., changes in the range of the suitable habitats for the snails. On a larger scale, the removal of climatic barriers is predicted to facilitate species invasions (Solomon and IPCC, 2007); this has been seen across Europe as climate change has also been implicated in the establishment of

A. arbustorum in areas further north and east than its historic range (Bondareva et al., 2020). In Fennoscandia the suitability for the snail is currently restricted to the western coastal edge of Norway and southern Sweden and Finland, but is predicted to expand northwards across Fennoscandia by 2050 due to increases in moisture levels and milder summers (Bondareva et al., 2020). As *A. arbustorum* is a potential intermediate host of *Elaphostrongylus* spp. this could have implications in expanding the range of the parasite into areas where it is not currently seen to be a problem.

Changes that have been predicted or observed in one intermediate host (IH) species may not apply to them all. Although some models have been produced to predict the distribution of certain gastropods under climate change in certain environments (Willis et al., 2006), the responses of gastropods to climate change are variable, even in closely related species, which highlights the need for species specific information regarding adaptations (Nicolai and Ansart, 2017). For example, Arctic species may be adapted to colder conditions, and invasive generalist species such as *A. arbustorum* may be more resilient to the changes taking place. However, there are some factors which are conserved across gastropods, such as the upper thermal tolerance limit. This does not appear to vary by much between different populations or species of terrestrial ectotherms at differing latitudes (Sunday et al., 2011). All these factors highlight the uncertainties about the effects of climate change on gastropods and the difficulties in predicting these. This adds an extra layer of complexity to predicting the dynamics of *Elaphostrongylus* in changing climates due to the wide range of gastropods that have been found to be suitable intermediate hosts (Skorping and Halvorsen, 1980). There may also be changes in the population diversity and the species that prevail under climate change.

As well as the effect of warming, the change in the seasonal dynamics will have an effect on the ecosystem cycle (Bintanja and van der Linden, 2013). Climate induced changes in animal phenology have been observed; at northern latitudes these are linked to temperature rather than precipitation which is the predominant influencer at lower latitudes (Cohen et al., 2018). Invertebrates advance their phenology at higher rates than large vertebrates, probably due to ectotherms' greater sensitivity to environmental temperatures (Cohen et al., 2018). Herbivores also advance their phenology more than carnivores, probably due to their association with plant

phenology (Cohen et al., 2018). This is exemplified in the relationship between great tit reproductive phenology and that of their prime food source the caterpillar. Although synchrony between maximum caterpillar biomass and maximum chick energy requirements creates the best chick growth, and timing of this peak in caterpillar biomass and egg laying are both strongly related to temperature, there are differences in the extent to which each of these variables has been found to advance in the face of the warming climate. This has resulted in an asynchrony leading to reduced growth of the chicks. The great tits have failed to adapt to the changing climate in order to maximise their reproductive potential unlike the caterpillars (Visser et al., 2006).

In recent years, reindeer populations have been decreasing throughout their range, which is thought to be due to a combination of climate-related factors (Vors and Boyce, 2009), and observed changes to reindeer weights may reduce their resilience to external stressors (Reinert and Benjaminsen, 2015). This loss of resilience can cause decreased over-winter survival, both due to direct causes and reduced ability to avoid predation (Hausner et al., 2011). There are several ways in which this can be influenced by climatic factors. There can be a direct reduction in the amount of food, for example lichen is an important source of nutrients over the winter, a reduction in access to lichen has been associated with decreased over-winter survival and reduced reproductive success (Vors and Boyce, 2009). A trophic mismatch can arise in the spring where climate-induced changes to the vegetation growing season induce an asynchrony between the time of reindeer peak requirements for nutrients around calving, and the time of highest nutrient availability in forage plants (Post and Forchhammer, 2008). This occurs due to different factors influencing the processes involved; although the timing of the growth of the plants is dependent on sunlight and is highly variable, reindeer migration is determined by day length, and despite birth being correlated with mean temperature it is minimally variable year on year (Post and Forchhammer, 2008). Another example by which climate impacts on reindeer foraging is through ‘rain on snow’ events. These are thought to be one of the most significant climatic changes affecting reindeer populations as they change snow pack properties and the resultant formation of ice obstructs access to forage plants (Descamps et al., 2017). These events have been found to be associated with high levels of ungulate mortality (Hansen et al., 2014; Putkonen and Roe, 2003), and

decreases in population growth rates (Hansen et al., 2011). Reduced availability of, or access to, forage plants can cause nutritional insufficiency leading to immunomodulation and increased levels of parasitism and its consequences (Coop and Kyriazakis, 1999).

Another factor that can reduce resilience in reindeer is harassment from biting insects during the summer months, which can result in decreased body condition (Vors and Boyce, 2009). This is also impacted by climate and is likely to increase as years become warmer (Callaghan et al., 2004). This can also impact on disease transmission and has already been associated with outbreaks of the arthropod transmitted *Setaria tundra* in Finnish reindeer, which were strongly correlated with increased temperatures the summer prior to the outbreak occurring (Laaksonen et al., 2010).

1.3.3 Evidence of *E. rangiferi* epidemiological change in association with climate

Indirectly transmitted nematodes such as *E. rangiferi* are likely to be more resistant in the face of global warming than those directly transmitted, such as *Ostertagia gruehneri*, due to behavioural thermoregulation of the gastropod intermediate hosts creating a 'shelter effect'. The larval stages of protostrongylids (and other strongylid nematodes with gastropod IHs) within gastropods may be protected from extreme temperatures, which might otherwise lead to their deaths, by movement of the gastropod to a more suitable microclimatic area (Molnár et al., 2013a). Parasites adapted to areas with wide temperature ranges are less affected by small increases in temperature. In the Arctic although the overall temperature range is wide, the majority of this is below 0°C, and the range of temperatures at which parasites can develop is relatively small, therefore parasites are more likely to be affected by smaller increases in temperature (Aleuy and Kutz, 2020). Outbreaks of clinical elaphostrongylosis and increased levels of excreted larvae have been correlated with higher than average temperatures and rainfall in the preceding year (Halvorsen, 2012; Handeland and Slettbakk, 1994) and this is supported by model predictions suggesting an increase in thermal suitability for larval development may be associated with outbreaks (Rose Vineer et al., 2021).

There are many examples of indirectly transmitted parasites whose transmission dynamics and lifecycles are affected by the changing climate, including several from Arctic North America. For example, the muskox protostrongylid nematode, *Umingmakstrongylus pallikuukensis*. Like *Elaphostrongylus* spp., it typically has a 2-year life cycle involving gastropod intermediate hosts (Kutz et al., 2002), but it was found that with warmer temperatures it was possible for the L1 deposited on pasture to develop to L3 within the same year. Analysis of historical weather data revealed that the required number of days above the minimum developmental temperature required for the development of larvae to L3 has been exceeded more often in recent years, such that a 1-year cycle is now predominating (Kutz et al., 2005). This recent shift from a 2-year to 1-year lifecycle has also been found to be true for *Varestrongylus eleguneniensis*, a protostrongylid lungworm of Muskox in Canada (Kafle et al., 2020). In Norway a 1-year transmission cycle is seen in *Elaphostrongylus cervi*, along with a high prevalence and intensity of infection (Handeland et al., 2019). The red deer this parasite infects are found at lower altitudes than the wild reindeer. Modelling suggests a two-year lifecycle is still predominating for *E. rangiferi* in wild reindeer, however within locations where the semi-domesticated reindeer herd graze, a similar pattern is seen to that observed in Canada, with the accumulated degree-days surpassing the number required for development within one year more often in recent years than historically (Rose Vineer et al., 2021).

Where *U. pallikuukensis* larvae developed to L3 within the same summer as infection of the slugs, infectious larval load was much higher in these slugs than in overwintered slugs, and there was minimal loss due to slug mortality (Kutz et al., 2002). This could lead to infection pressure being much higher, resulting in increased infection prevalence and intensity within the muskox herds. A similar pattern was observed in red deer in southern Norway (Handeland et al., 2019). There is a caveat to this in that higher rates of synchrony of larval development have been found at higher environmental temperatures, meaning a more synchronised development of parasites and a higher infectious dose over a short time period may occur compared to events at lower temperatures (Kutz et al., 2001). It is possible for this emergence of parasites to be asynchronous with the definitive host life and movement cycles, limiting transmission (Gethings et al., 2015). If this emergence can be predicted it could be

used to inform avoidance strategies in the management of animals in order to induce an asynchrony in the lifecycle.

Increases in host density have been associated with increases in parasitism. For example, increasing *Teladorsagia boreoarcticus* infections have been seen in herds of Canadian muskox with increased density. The increased density is thought to have worked synergistically with climatic conditions conducive to accelerated development of the parasites (Kutz et al., 2004), although it is difficult to separate out the relative importance of these two factors. However, no correlation was found between *E. rangiferi* L1 abundance in faeces and reindeer density in herds in Canada (Ball et al., 2001) or Norway (Halvorsen, 2012). In summer pastures above the treeline there are thought to be minimal areas containing gastropod hosts, so even though the overall density of reindeer may not affect transmission the clustering of reindeer in areas with high densities of infected gastropods could have an effect; in these areas gastropods have been found within calcium-rich bogs where large densities of reindeer have been seen to aggregate (Halvorsen et al., 1980).

Range expansion has been observed for several Arctic parasites; *Umingmakstrongylus pallikuukensis*, and *Varestrongylus* spp. have expanded their range in the Canadian Arctic and are now found on an island that was previously free of infection (Kutz et al., 2013). The reasons for this related to the changing climate are two-fold. The warming has altered the range of the muskox and caribou hosts, leading them to travel from southern infected areas northwards in search of better environments. Also, changing conditions have provided a better environment for the development and maintenance of the parasite after its introduction (Kutz et al., 2013), with a tipping point appearing where there was a transition between the minority of years being suitable for parasite development to the majority being suitable (Kafle et al., 2020). Parasite range expansion could also be facilitated by climates changing to favour populations of intermediate hosts, for example with the predicted changes leading to increased range of *A. arbustorum* across Fennoscandia (Bondareva et al., 2020).

Hoberg et al., (2002) identified *Protostrongylus stilesi*, a protostrongylid previously associated with *Ovis spp.*, in introduced muskox (*Ovibos moschatus wardi*) for the first time, violating the previous assumption of host specificity. This implied that

sympatry between different host species, which were previously assumed to have separate parasite populations, may not have such clear definitions as originally thought. It is possible that there is an increased risk of parasitism associated with changing host habitat ranges and population expansions or translocations, which can also be associated with climate change. Introduced host species could also provide a bridge between different native species for which previously there was no overlap in either range or parasite populations. This can have serious management implications for the populations involved. However, this has to be interpreted with care as it is possible that detected host switches are not new but due to previous sympatry which has not been seen recently due to changes in host ranges and interactions (Kutz et al., 2004). This lack of baseline and historic data represents a major limitation to the study of the effects of climate change on Arctic parasites. Nematodes of the *Elaphostrongylus* genus were thought to be associated with hind limb ataxia in muskoxen in Norway but were not definitively speciated (Holt et al., 1990), and it has been shown experimentally that *E. rangiferi* is able to infect and complete its lifecycle in moose (Steen et al., 1997). Moose have their own species of *Elaphostrongylus*, *E. alces* (Gibbons et al., 1991) but the potential for them to become infected with *E. rangiferi* could be important in outbreaks of clinical disease in moose as reindeer, and thus *E. rangiferi*, are at a much higher abundance in Norway. Therefore, surveillance of these species in the wild could provide useful data regarding the host specificity of *E. rangiferi* and the potential for host switching.

Although *Elaphostrongylus* spp. and other protostrongylid nematodes are predominantly transmitted by terrestrial gastropods, under changing conditions there may be increased potential for aquatic gastropods to act as intermediate hosts. It is known that *E. rangiferi* can infect and develop in the freshwater snails *Lymnea stagnalis* at similar rates to in terrestrial snails (Skorping, 1985), however controlled infection scenarios can facilitate infection in a way that is not representative of natural scenarios and lifts many of the geographical constraints. It is also difficult to prove whether it is possible for infection to be transmitted to the definitive host (Morley, 2010). However with the predicted changes to the hydrological system and locations of wetlands (Hassol, 2004) this route of transmission cannot be ignored.

1.4 PREDICTING PARASITE TRANSMISSION TO INFORM CONTROL

In order to mitigate risk of parasite infection and disease a range of strategies can be employed. One of these strategies is simply to avoid areas where infection is a high risk. Sami herders have reported brainworm clinical signs being seen more commonly after warm summers, and herders have been known to move herds to pastures at higher elevation in response to outbreaks of disease in order to reduce risk (reported in Davidson et al., 2020). Similarly, in Canada local knowledge has been found to be valuable in monitoring health in wild caribou and muskoxen (Tomaselli et al., 2018). However, there are limitations to the predictive capabilities of this knowledge, which is based on historic conditions. Reindeer herders interviewed in Finland predicted that the reduction in the snow cover period induced by climate change would be favourable for their herding making longer periods of grazing possible. However in reality there will also be changes to the amount of ground ice which could lead to unfavourable conditions, and will be more evident in open areas than forested areas (Turunen et al., 2016). In addition this will affect the length of the growing season, and longer growing seasons and the subsequent changes in grazing pattern have been putatively linked to increases in levels of infection with gastrointestinal nematodes in sheep farms in Scotland (Kenyon et al., 2009). There is the possibility of this effect being seen in wild ruminants as well.

In order to cope with changing conditions reindeer herders are adjusting their management practices; the development of predictive tools would aid in this decision making. The prediction of *E. rangiferi* risk over different geographical areas throughout the year could inform herding strategies and parasite avoidance strategies. This can be done via the use of quantitative models.

1.4.1 Modelling approaches

Models are generally acknowledged as the only way to predict future patterns of infectious disease, but there are many different methods and approaches possible (Woolhouse, 2011). There are two general types of model that can be used. Empirical models look for correlations between environmental variables and disease or host presence, while mechanistic models mathematically describe the underlying processes of the disease system (Rose Vineer, 2020). Different models may be chosen depending

on the data available for their development. Mechanistic models can vary in their complexity but generally have a much higher data requirement than empirical models and demand a detailed understanding of the physiological processes underlying the system, making them much more challenging to develop. However, they are the preferable model to use when modelling novel situations such as climate change scenarios as they are better equipped for extrapolation of data and use for future projections (Fox et al., 2012).

Due to their relative simplicity, and the ease at which correlative models can be developed using limited data, empirical models have been used to provide risk maps to advise on farm animal management, for example the Ollerenshaw model used to predict risk of exposure to *Fasciola hepatica* in the UK. This model utilised a simple correlation between meteorological data and disease incidence observed in Anglesey and was applied in a predictive manner across England and Wales at a large spatial scale (Ollerenshaw, 1966; Ollerenshaw and Rowlands, 1959). However, although maps such as these can give a broad indication, risk of infection depends on more local environmental factors. McCann et al., (2010) expanded on the Ollerenshaw model by using GIS mapping and a combination of environmental and climatic variables in a multiple regression model to determine the factors of importance and produce spatial maps of fasciolosis risk based on landscape. Although several landscape factors were identified as strong predictors of fasciolosis risk it is not clear how these influence transmission processes. This demonstrates one of the limitations of this model type in that the predicted niche of the parasite may not be representative of the realised niche. A mechanistic understanding of the requirements of parasites for certain conditions can be used to expand upon simple correlative models and provide predictive tools with better spatial and temporal resolution. For example, the water requirements for liver fluke development were used alongside detailed hydrological data to produce a finer scale risk map that accounts for long term data rather than considering each month individually, and the resulting predictions were found to be robust across two different case studies, demonstrating the applicability of the model to differing areas (Beltrame et al., 2018).

Degree-day models are simple mechanistic models of the thermal requirements for development of invertebrates. They have a low data requirement and can be used when

data pertaining to other system variables is lacking. This makes them suitable for modelling parasites in challenging environments where data collection is difficult, and due to this they have been used extensively in modelling Arctic protostrongylid nematode development (e.g. Jenkins et al., 2005; Kafle et al., 2020). They can also be developed to incorporate other environmental variables such as rainfall and evapotranspiration (Haydock et al., 2016).

Mechanistic models can also become much more complex by including multiple different lifecycle stages and parameters. Molnár et al., (2013b) integrated the metabolic theory of ecology (MTE) into a model of a directly transmitted Arctic parasite in a method that improves on the degree-day model by being able to account for temperature driven effects on multiple parasitic transmission parameters at once. However the MTE has only been established for free-living animals, not parasites (Molnár et al., 2017), and there will be additional difficulties in applying it to indirectly transmitted parasites such as *Elaphostrongylus* spp. due to the shelter effect of the intermediate host reducing mortality levels in high temperatures (Molnár et al., 2013a). This will affect the conclusions drawn from their model which found that the one summer season of transmission may be replaced by a two-peaked transmission with a decrease in summer when temperatures are becoming too high and leading to increased mortality in free living parasites (Molnár et al., 2013b). The main functional difference between the metabolic theory model and degree-day models is the use of a thermal performance curve in the former, whereas in the latter a linear relationship between temperature and development is assumed (Molnár et al., 2017). The use of a non-linear relationship in degree-day models has also been advocated by Moore and Remais (2014). Although the use of a known thermal performance curve may improve a model, in this case there are several confounding factors, including the unknown and unmeasured microclimatic factors. An example of this is the difference between soil surface temperature, which is the actual dependent factor, and air temperature, which is measured. At a range of temperatures, the linear model is valid as part of the development ‘curve’ is also linear. Additionally, behavioural thermoregulation of snails will change the temperature the parasites are at relative to the air temperature so the use of a horizontal cut-off in maximum temperature above which development proceeds at the same rate at all higher temperatures is biologically appropriate for this system, meaning the degree-day model is less likely to over-estimate development at

higher temperatures. This is a method commonly used for Arctic protostrongylids (Kafle et al., 2020; Kutz et al., 2005; Rose Vineer et al., 2021).

Another type of model incorporating the entire lifecycle of a parasite is the Q_0 model; these are based around the same principle as the R_0 (the basic reproductive quotient) in infectious disease but simulate the reproductive capacity of the parasite, therefore giving an indication of the level of infection pressure. This method was initially developed for *Teladorsagia circumcincta* (Roberts and Heesterbeek, 1995), using the 'density of infective larvae on the pasture' and 'the mean number of adult parasites per host' as state variables. Its use was developed and expanded on for *Haemonchus contortus* to include environmental stochasticity and allow future projections under climate change (Rose et al., 2016). Due to the incorporation of variables relating both to the parasite in the environment and in the definitive host the Q_0 model has a very high data requirement meaning it is not possible to produce this for many species currently. An alternative method to this is to model either the intra-mammalian or extra-mammalian lifecycle stages independently. An example utilizing the stages within the definitive host is the GLOWORM-PARA model, a lifecycle model which provides a framework for modelling the effect of host immunity on parasite populations (Rose Vineer et al., 2020). Another example is a stochastic individual-based model predicting the impact of the combination of grazing behaviour and development of immunity on gastrointestinal nematodes (Fox et al., 2013). A major benefit to these models is that they can be used to model interventions which affect the definitive host such as vaccination. Although theoretically these models could be used for *Elaphostrongylus* if adapted to the differing lifecycle compared to GINs, the data are currently not available in order to do this, and the differing lifecycle means obtaining data for the parameterisation is more difficult experimentally. There is also potential for these models to be used with climate-dependent parameters, but these intra-host stages are more robust in the face of changing climate.

There are also models of the extra-mammalian lifecycle stages which are more sensitive to environmental changes. The GLOWORM-FL model (Rose et al., 2015) is a model such as this, which models the free-living stages of gastrointestinal nematodes of sheep and cattle and the rates of development, mortality and movement in relation to temperature and moisture levels. A different modelling method but similar

framework was used by Leathwick et al., (2015) to model the development and survival of the free-living stages of equine cyathostomins in relation to temperature and moisture. These models can then be used to make predictions about the effect of changing climatic conditions on parasites.

Models of different stages of the lifecycle can also be used for the intermediate host species. Individual-based models incorporating environmental stochasticity have been used to predict the distribution of gastropods as pest species, for example Willis *et al.* (2006) and Choi *et al.* (2006) forecasted the population dynamics of *Deroceras reticulatum* in the UK under different climatic conditions and predict times of high abundance and high risk to crops. The details regarding individual responses to different conditions, and physiological data required for mechanistic models is rarely available however, especially where multiple species are being considered. Therefore, empirical species distribution models, also known as habitat suitability models or ecological niche models, are more commonly used. These relate environmental conditions with species locations and can predict occurrence based on areas which have similar conditions.

1.5 AIMS

The aim of the present study was to develop models that can be used as decision support tools to support Sami herders in management of their herds to reduce incidence of clinical elaphostrongylosis. Mechanistic modelling frameworks were developed incorporating parasite biology and host interactions that can be applied over different geographic areas.

The specific objectives for this these are:

1. Predict where intermediate and definitive hosts co-occur under current and future climate
2. Predict the potential transmission of *E. rangiferi* under current and future climates
3. Evaluate the potential use of a simple degree-day model as a parasite control decision support tool

4. Explore the current potential to develop a model of *E. rangiferi* population dynamics to simulate more complex intervention measures

CHAPTER 2 – THE SPATIAL DISTRIBUTION OF POTENTIAL INTERMEDIATE HOST SPECIES OF *ELAPHOSTRONGYLUS RANGIFERI* AND THE THERMAL SUITABILITY FOR LARVAL DEVELOPMENT

2.1 INTRODUCTION

Transmission of *Elaphostrongylus rangiferi* relies on the presence of both intermediate and definitive host species in combination with environmental conditions suitable for parasite development. Many species of gastropod have been identified as potential intermediate hosts for *E. rangiferi* (Skorping, 1985a; Skorping and Halvorsen, 1980). Hansen and Halvorsen (1976) state that *"there will always be a danger of infection of reindeer on pasture containing snails and contaminated faeces"* but knowledge of the areas in which the intermediate host species are present will help determine the areas in which reindeer are at risk of infection with the parasite. Previously conducted field surveys have identified a lack of or very few gastropods being found above the treeline in Norway (Andersen and Halvorsen, 1984; Halvorsen et al., 1976), but thus far the potential distribution of species across the whole country has not been determined and there is a paucity of gastropod studies in this region. Ecological niche models can be developed to help predict the potential range of gastropods, and therefore aid in in predicting the areas with potential for transmission of *E. rangiferi*.

The distributions of gastropod species will depend on many different topographical as well as climatic and environmental factors. Lee et al. (2009) found a relationship between abundance of *Deroceras panormitanum* slugs and elevation. An upper elevational limit in *Arianta arbustorum* habitat was identified by Baur and Baur (2013) and it was found that this has shifted upwards over recent decades, in line with increasing average temperatures.

Poikilotherms are particularly sensitive to temperature changes. Increases in winter temperature and reduction of snow cover could change the phenology of gastropods by altering their winter dormancy periods. This can have knock-on effects on

reproduction as spermatogenesis is lower after shorter periods of hibernation (Gomot and Gomot, 1991). Terrestrial gastropods are especially susceptible to desiccation, therefore the combination of high temperature and drought can prove deadly, especially if it is above the level to which they are able to move into a suitable microclimate (Nicolai and Ansart, 2017). Water availability has been found to be the major limiting factor of terrestrial invertebrate species richness (Horsak and Chytry, 2014). Temperature and rainfall have been shown to be key factors in the population dynamics of the slug *Deroceras reticulatum* (Choi et al., 2004). There are species differences in ecology and physiology, even within the same genus. *D. reticulatum* slugs (used hereafter to refer to adults and juveniles) do not have a high cold tolerance and in extreme conditions can only overwinter during the egg stage of the lifecycle. In contrast, *D. laeve* slugs have been found to survive temperatures as low as -28^{O}C. *D. laeve* overwinter as slugs, but the eggs have been found to have poor cold tolerance (Berman et al., 2011). This highlights the importance of species differences in ecology and responses to climate change. It can therefore be predicted that different species will respond to changing climates differently, and that not only the overall number of individual gastropods, but also the species composition in an area may change.

Maximum entropy modelling (Maxent) is a method that has been extensively used for species distribution modelling (Phillips et al., 2006), including for modelling snail species as intermediate hosts of parasitic helminths. This has mainly been done for trematodes infecting humans, for example the distributions of *Biomphalaria* spp. snails as intermediate hosts for *Schistosoma* spp. have been modelled using Maxent on local (Manyangadze *et al.*, 2016), national (Manyangadze et al., 2016; Pedersen et al., 2014), and regional scales (Stensgaard et al., 2013) in Africa, and other countries including China (Habib et al., 2016). Few studies have focused on species distribution modelling of intermediate hosts for either nematode parasites of humans or animals, or even trematode parasites of animals, with some studies generally focusing on modelling the parasite itself. For example, York, Butler, and Lord (2014) modelled the potential distribution of *Angiostrongylus cantonensis* worldwide based on reports of disease in humans; and Kantzoura et al. (2011) modelled the distribution of different *Fasciola hepatica* genotypes in south eastern Europe using the locations of livestock found to be infected. It has also been considered for *Angiostrongylus vasorum* in the UK that the number of potential intermediate host species and the wide ranging

distribution means that species distribution models of intermediate hosts will not be informative (Morgan et al., 2009). However, Pickles et al. (2013) show that modelling the range and distribution of the parasite and its host separately can reveal ecological niche mismatches which could be of key importance for predicting range shifts in response to altered environmental conditions as compared to predicting parasite distribution alone, therefore combining models pertaining to different aspects of the parasite lifecycle can be a useful tool to encompass a wider variety of potential epidemiological changes. This has been exemplified by Stensgaard et al. (2013) who combined a species distribution model for the intermediate host *Biomphalaria* spp. snails developed using Maxent with a growing degree-day model for the parasite *Schistosoma mansoni* across the entire African continent.

Growing degree-day models were developed initially to represent plant growth within the growing season, but have also been used to predict the emergence of insects (e.g. Park et al., 2014) and have found many other applications including use for parasite development. For example, predicting egg hatching in the plant parasitic nematode *Criconemella xenoplax* (Westcott and Burrows, 1991) and the development of *Dirofilaria* spp. in mosquitos (Genchi et al., 2011, 2009). These models can then be applied to new areas, for example Yang et al. (2006) modelled thermal suitability for *Schistosoma japonicum* transmission in different regions of China, or to novel climatic scenarios such as a study by Ogden et al. (2006) where they used a degree-day model for *Ixodes scapularis* to predict whether range expansion into Canada would occur in the face of climate change. Degree-day models have been developed and used in multiple ways for protostrongylid nematodes of ruminants in the Canadian Arctic for example *Umingmakstrongylus pallikuukensis* (Kutz et al., 2002), *Parelaphostrongylus odocoilei* (Jenkins et al., 2005), and *Varestrongylus eleguneniensis* (Kafle et al., 2018). A preliminary model was also made for *Elaphostrongylus rangiferi* by Kutz, Hoberg, and Polley (2001) who took data from Halvorsen and Skorping (1982) for development of *E. rangiferi* in *Euconulus fulvus* and *Arianta arbustorum* and calculated the degree-days in both of these species individually, with different development rates and minimum threshold temperatures, using only the linear portion of the development curves, as 250 degree-days (DD) in each. Rose Vineer et al. (2021) expanded on this and further developed a degree-day model for *Elaphostrongylus rangiferi* in Norway, using it to determine how thermal

suitability for larval development has changed over the past 70 years across Fennoscandia. However, this model did not consider the distribution of the hosts.

In this present study Maxent modelling was used to determine areas within the reindeer range in Norway in which environmental and climatic conditions are suitable for gastropod habitation and to predict whether these species' distributions will shift in the face of climate change. This was combined with predictions of thermal suitability for larval development within the gastropod host made using the degree-day model developed by Rose Vineer et al. (2021) in order to determine in which areas there may be changes in parasite dynamics and increased risk of transmission.

2.2 METHODS

2.2.1 Data Sources

2.2.1.1 Species Occurrence data

Multiple terrestrial pulmonate gastropod species (Order Stylommatophora) were selected for distribution modelling. *Arianta arbustorum* (family Helicidae) was selected based on having a widespread distribution across Europe with increasing range (Bondareva et al., 2020), and its use as a model organism in *E. rangiferi* experimental studies (e.g. Skorping, 1988). The other species were selected based on their detection during field surveys in Norway (Closset, N and Stuut, M; unpublished data) and the availability of location data in the Global Biodiversity Information Facility (GBIF). They consist of three terrestrial snail species: *Punctum pygmaeum* (Family Punctidae), *Vitrina pellucida* (Family Vitrinidae), *Euconulus fulvus* (Family Euconulidae); and two terrestrial slugs *Deroceras laeve* (Family Agriolimacidae) and *Arion subfuscus* (Family Arionidae), all of which had been identified as potential intermediate host species (Skorping and Halvorsen, 1980).

Point occurrence data was taken from GBIF (GBIF, 2021) and was combined with data from gastropod surveys in the Rondane and Meråker regions of Norway (Closset, N and Stuut, M; unpublished data) (Figure 2.1). GBIF data includes museum and preserved specimens, and specimens dating back to the 19th century. However the reliability of these data may not be high as georeferencing of museum samples is known to be poor (Anderson, 2012), and the global climate has changed over this time.

Therefore, the data was included according to the following criteria: only data from human observations; excluded uncertainty >5000m; removal of data recorded before 1950. Although there were occurrence data available from outside of Europe, *A. arbustorum* is known to be an invasive species in North America (McAlpine et al., 2009) and therefore may not be at an equilibrium with its environment there, and as this violates an assumption of species distribution modelling it was necessary to exclude these regions from the model, and only European data were considered. This also reduced the computational time required for production of the models. The samples are assumed to be independent of each other; due to the small size of the species it is unlikely that repeated observations were recorded of the same individuals, however there may be potential for pseudo-replication with several collections in close proximity to each other.

Reindeer ranges were provided by the Norwegian Institute for Nature Research (NINA) as shapefiles for the wild and semi-domesticated herds. These were joined using the merge function in QGIS (QGIS.org, 2021).

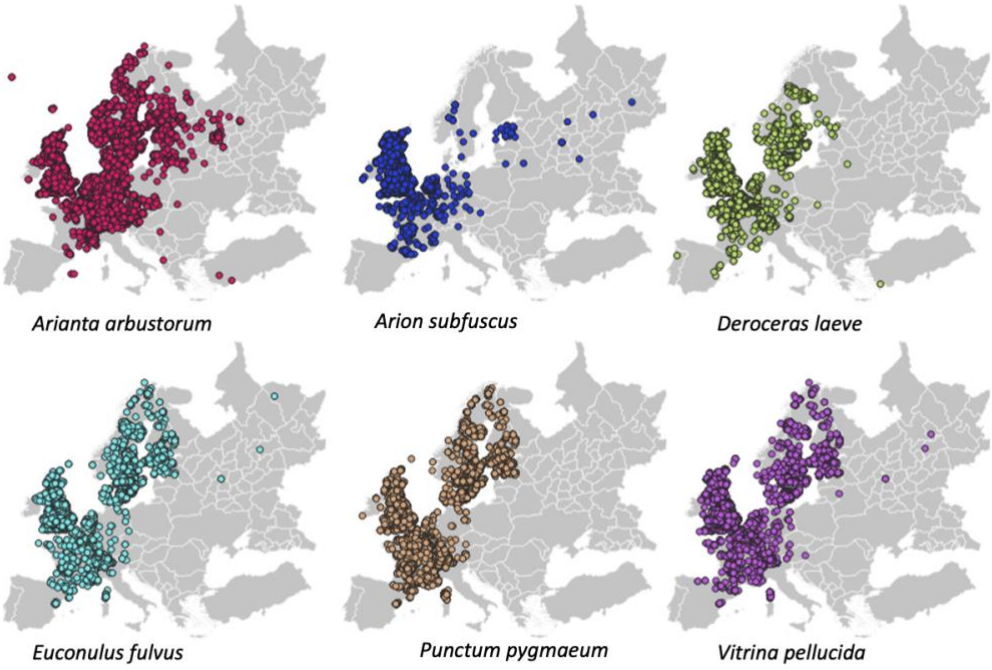


Figure 2.1 Species occurrence data used for Maxent model development including data from field surveys conducted in two regions of Norway, and data from GBIF after removal of data based on the exclusion criteria

2.2.1.2 Environmental data for present conditions

Bioclimatic variables from the World Clim version 2 database (Fick and Hijmans, 2017) are a set of 19 biologically meaningful seasonal temperature and rainfall measures which have been extensively used in species distribution modelling. The variables corresponding to the baseline or present-day climate are the average over the period from 1970 – 2000. These were obtained at the 30 second scale as global GeoTiff files. Elevation data was also obtained from the same database at the same scale.

Land cover data was obtained from the Corine Land Cover database (2018 v.2020_20u1; EEA Copernicus, 2018) as a GeoTiff file at a 100m x100m resolution for all EEA39 countries. This is a categorical dataset providing information about the biophysical characteristics of the earth using satellite imagery and divides land cover into multiple different categories. Due to the complexity of this and the previous finding that no gastropods were located above the treeline (Andersen and Halvorsen, 1984; Halvorsen et al., 1976), a different measure of forest cover was also included in the model; the FOR_2000 data obtained from the FAO Harmonised world soil database represents percentage forest cover of 5' by 5' grid squares across the world (Fischer et al., 2008). From this same database measures of soil quality were obtained. The variables considered to have biological relevance to gastropods were SQ1 representing nutrient availability, which included data on soil texture, carbon content and pH, and SQ4 representing oxygen availability to roots using data on soil drainage.

2.2.1.3 Environmental data for future projections

The use of climate variables as predictors for these models allows for predictions to be made of future species distributions in relation to climate change. Due to the lack of future predictions available for any of the soil or land cover parameters these were excluded from the future prediction models. The models run without these variables for the present day were compared to those including them. This contrasts to the methods used in some other studies where it was simply assumed that there was no change in the variables (e.g. Stensgaard et al., 2013). However due to the high rate of climate change at high latitudes including in Fennoscandia this scenario is unlikely, particularly with regards to greening and land cover (Polar Research Board, 2011). Elevation remained included due to this not changing over the period in question.

Future predictions were available for the bioclimatic variables previously selected. Two CMIP6 general circulation models (GCMs) were selected; CNRM-ESM2 and IPSL-CM6A-LR. Due to the recent release of the CMIP6 complement of climate models there are currently no comparisons of model performance over Europe, with comparison methods only evaluated for certain areas e.g. Japan (Shiogama et al., 2021). In the absence of other selection criteria, the models were chosen based on them having been developed in Europe. Data were available at a 2.5-minute resolution as averages for four 20-year periods (2021-2040, 2041-2060, 2061-2080, 2081-2100), and four different shared socioeconomic pathway (ssp) scenarios (ssp126, ssp245, ssp370, ssp585) representing different emissions scenarios, with the top three being selected for projections in this study. The ssp245, ssp370 and 585 represent intermediate, high and very high emissions respectively. The full complement of 19 bioclimatic variables were available for download as a single raster file (Fick and Hijmans, 2017) and were separated into individual bands using the writeRaster function (Hijmans, 2020) in R (R Core Team, 2013). The two GCMs were compared using the projections for the ssp585 high emissions scenario then the model selected for further use was chosen based on the results.

Future temperature data from the same source for the chosen GCM was accessed for input into the degree-day model and was available as monthly average maximum and minimum temperatures for the same time periods. These were available as raster files and were also separated into individual bands using the same method.

2.2.1.4 Data processing

A shape file was created for the European area by amalgamating individual country files from DIVA GIS (diva-gis.org). The raster files for the environmental variables were clipped to this area only, then checked for collinearity by calculating the variance inflation factor (VIF) using the vif function in the usdm package in R (Naimi et al., 2014). Variables with a VIF greater than 10 were removed. The remaining variables were then checked using the vifcor function with the correlation coefficient set to 0.8 (Menard, 2002) to remove any remaining correlated variables.

The remaining rasters were then aligned using the align raster function in QGIS version 3.16.2-Hannover (QGIS.org, 2021) to ensure equal scaling and matching boundaries. They were then converted to the ascii files required by Maxent using the writeRaster function in the raster package in R (Hijmans, 2020).

The same processing was completed for the raster files representing both current and future conditions for use in the species distribution models. The resulting resolutions were 0.008333 decimal degrees for the present day rasters and 0.041666 for the future rasters due to the larger scale of data available.

2.2.2 Model

2.2.2.1 The Species Distribution model

Presence only modelling is more commonly used than presence/absence due to the lack of readily available and reliable absence data such as is required for the latter. It uses pseudo-absences where comparison data is taken from the study area at random, and compares these with the environmental variables at the areas where the species occurrence data is provided (Phillips et al., 2006). MaxEnt is an open source software using this method, with 10,000 pseudo-absences being taken from across the whole study area at random (Phillips et al., 2017), and has been shown to perform well when compared to other presence-only modelling techniques (Elith et al. 2006).

The model was run using the MaxEnt program version 3.4.4 (Phillips et al., 2021). The standard settings were used in the Maxent software as these are designed to prevent over-fitting and were found to be suitable for most applications (Phillips and Dudík, 2008). The present-day models were run in Maxent using the ClogLog method. They were run 20 times with 75% of the data subset for training the model and the remaining 25% for testing. This was done using the random seed method to allow different subsets to be used each time.

In order to turn the scale of probabilities produced by the model into binary presence/absence predictions a threshold limit was selected. Maxent software produces a variety of threshold limits but the one selected for use in this model was the maximum training sensitivity and specificity as that has the most consistency

between different modelling methods (Liu et al., 2016, 2013). This threshold has also been used for many species distribution models (e.g. Pascoe et al., 2019).

Model performance was assessed using the area under the receiver operating curve (AUC), with an AUC of 0.5 representing a predicted distribution no better than chance, and values above 0.75 representing a useful model (Elith, 2000). Jackknife plots allowed visualisation of the importance of individual variables.

The model projections were compared using comparisons of the proportion of pixels above the threshold value selected, as done by Thuiller et al. (2005), Peterson et al. (2002), Wiens et al. (2009) and Stensgaard et al. (2013). This was done both to compare the different emissions scenarios between years, and to compare the two different GCMs for the high emissions scenario (ssp585).

2.2.2.2 The degree-day model

The degree-day model developed by Rose Vineer et al. (2021) was used in this study to predict changes to the thermal suitability index for larval development in the face of climate change. The number of degree days (DD) was calculated from multiple point estimates where the number of days post infection the L3 were observed (d.p.i) was multiplied by the number of degrees the ambient temperature (T) was above the minimum threshold temperature for development (T_{min}) (Equation 1).

$$DD = d.p.i \times (T - T_{min}) \quad (1)$$

This model calculated the required number of degree-days for development of first to third stage larvae within a range of gastropod hosts as 245, with a standard deviation of 39. In order to provide average daily temperatures for input into the model the mean of maximum and minimum was taken, and each day of the month was assigned the same value. The accumulated degree-days were then calculated using the minimum temperature threshold of 8°C and maximum of 21°C. The annual thermal suitability index was calculated by dividing the number of degree-days accumulated within the year by the number required for development. The model was run using functions

within the raster package in R (Hijmans, 2020). The model was run in areas of Norway that were within both the reindeer habitat and the predicted gastropod habitat.

2.3 RESULTS

2.3.1 Variable Selection

After removal of the variables exhibiting high levels of collinearity the remaining bioclimatic variables were: Bio8 – mean temperature of the wettest quarter; Bio9 – mean temperature of the driest quarter, Bio10 – mean temperature of the warmest quarter and Bio14 – precipitation of the driest month. SQ1 (the soil nutrient availability) was removed but the other variables all remained.

2.3.2 Present Day Distribution Models

After removal of the collinear variables a single run of the model for each species was done and the jackknife plots showed none of the variables negatively affected the AUC of the model, therefore all variables were included in the final models.

The AUC for all models (Table 2.1) are above the 0.75 required for a useful model (Elith, 2000). Although AUC for all species was found to be high, it is only possible to make comparisons between the different models within species, and not to make between species comparisons as AUC is strongly affected by the prevalence of the species (Lobo et al., 2008). For *Arianta arbustorum* the AUC value is higher for the full model but for all the other species AUC increased with the exclusion of the non-bioclimatic data. This suggested that the use of the bioclimatic-only model was acceptable and could be used for the future projections. The standard deviations are also extremely low, likely due to the large sample size for each species.

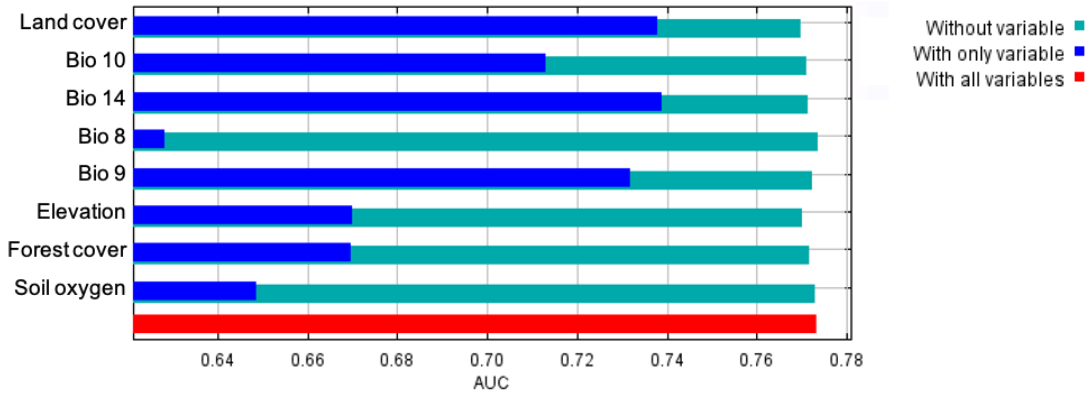
Jackknife plots are shown in Figure 2.2 (a-f) for the full model; in the bioclimatic model the relative contributions of each variable were the same as in these. In the full model landcover type, Bio9 (mean temperature of the driest quarter) and Bio14 (precipitation of the driest month) were consistently identified as the top three predictors of gastropod distribution. The levels of importance of most of the remaining variables was variable between species but SQ4 was consistently low. SQ4 represents

oxygen availability in the soil and soil drainage. This implies that either these parameters are not as important in determining gastropod distribution, or that they were simply not captured at the right scale to be of use. However, as removal did not increase the AUC of the models they were retained in the full model.

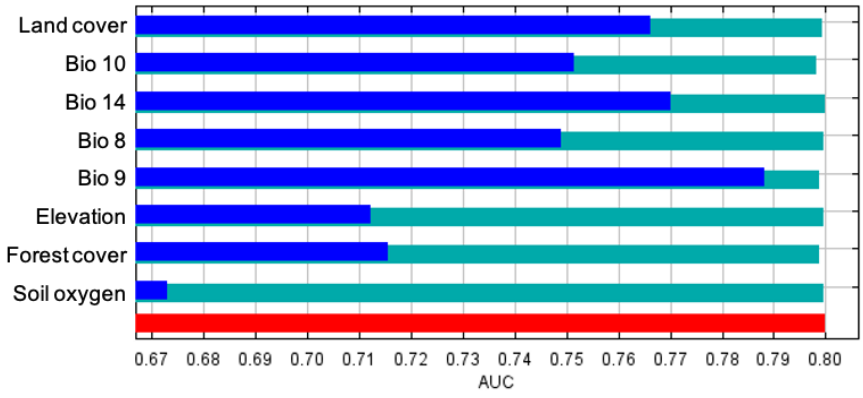
Table 2.1 Area under curve (AUC) and standard deviations obtained after running both the model including all variables, and the bioclimatic variables only for each species. These are the means (and standard deviation) from 20 runs of each model. The AUC values in every model are above the 0.75 threshold for a model to be considered good.

	A. arbustorum	***A. subfuscus***	***D. laeve***	***E. fulvus***	***P. pygmaeum***	***V. pellucida***
All variables	0.773 (0.003)	0.8 (0.003)	0.844 (0.003)	0.794 (0.003)	0.775 (0.002)	0.779 (0.004)
Bioclim only	0.766 (0.003)	0.840 (0.004)	0.865 (0.002)	0.820 (0.003)	0.817 (0.001)	0.808 (0.002)

A) Arianta arbustorum



B) Arion subfuscus



C) Deroceras laeve

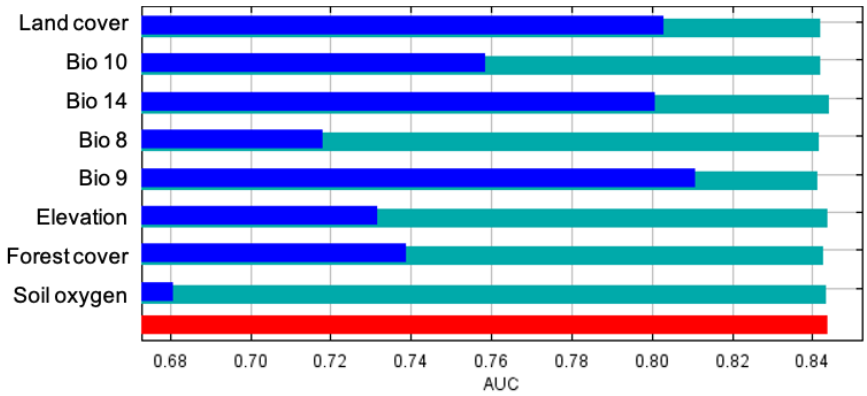
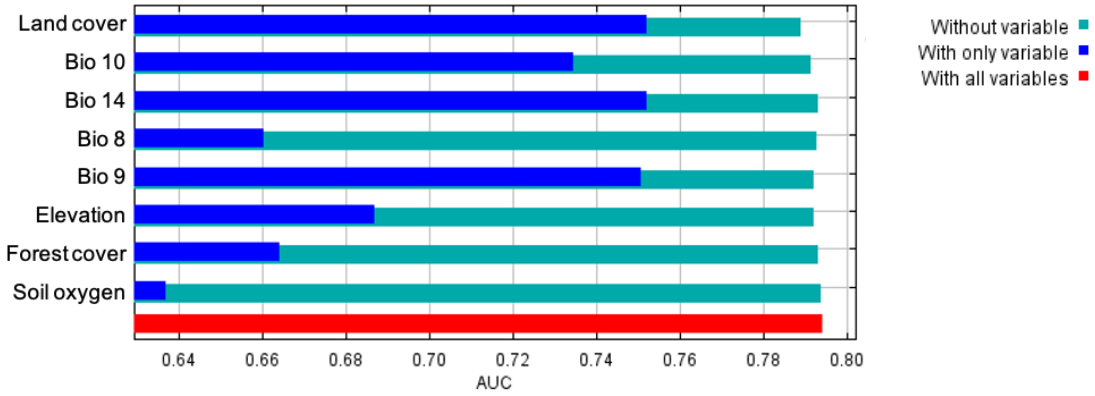
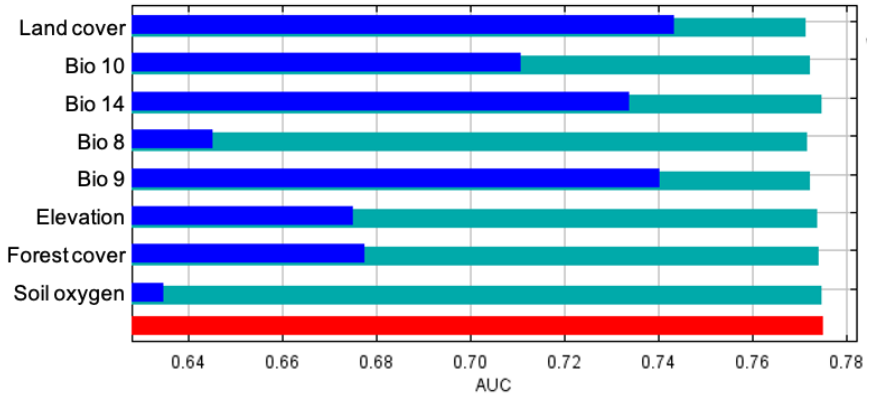


Figure 2.2 (A-C) Jackknife plots for each individual species showing the relative contributions of the variables to Area Under Curve (AUC; model performance). The green bar represents the model without that variable included, the blue bar the model with just that variable and the red bar with all variables included.

D) Euconulus fulvus



E) Punctum pygmaeum



F) Vitrina pellucida

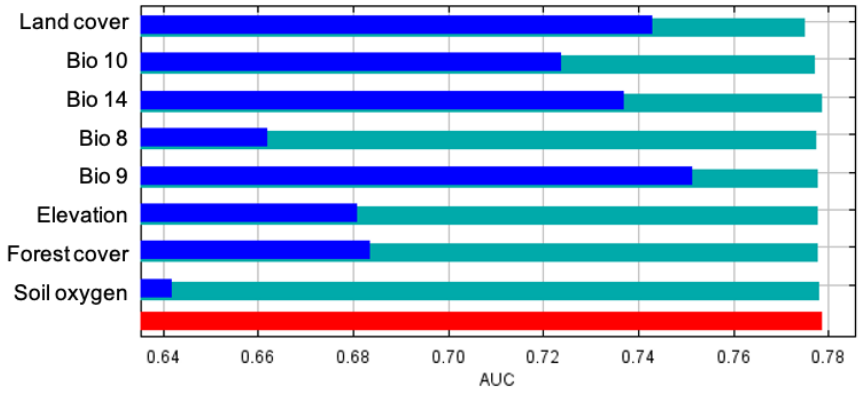


Figure 2.2 (D-F) Jackknife plots for each individual species showing the relative contributions of the variables to Area Under Curve (AUC; model performance). The green bar represents the model without that variable included, the blue bar the model with just that variable and the red bar with all variables included.

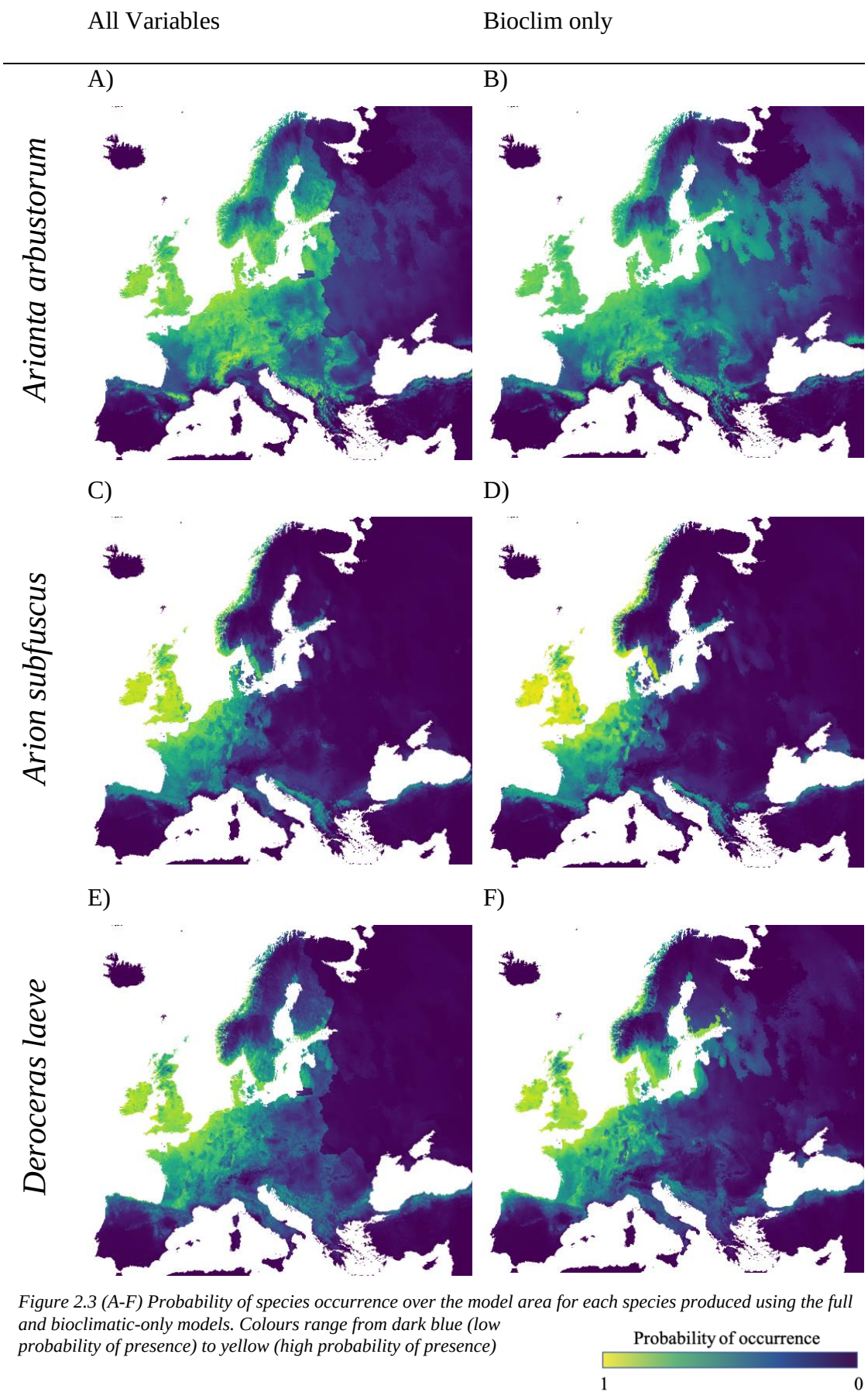


Figure 2.3 (A-F) Probability of species occurrence over the model area for each species produced using the full and bioclimatic-only models. Colours range from dark blue (low probability of presence) to yellow (high probability of presence)

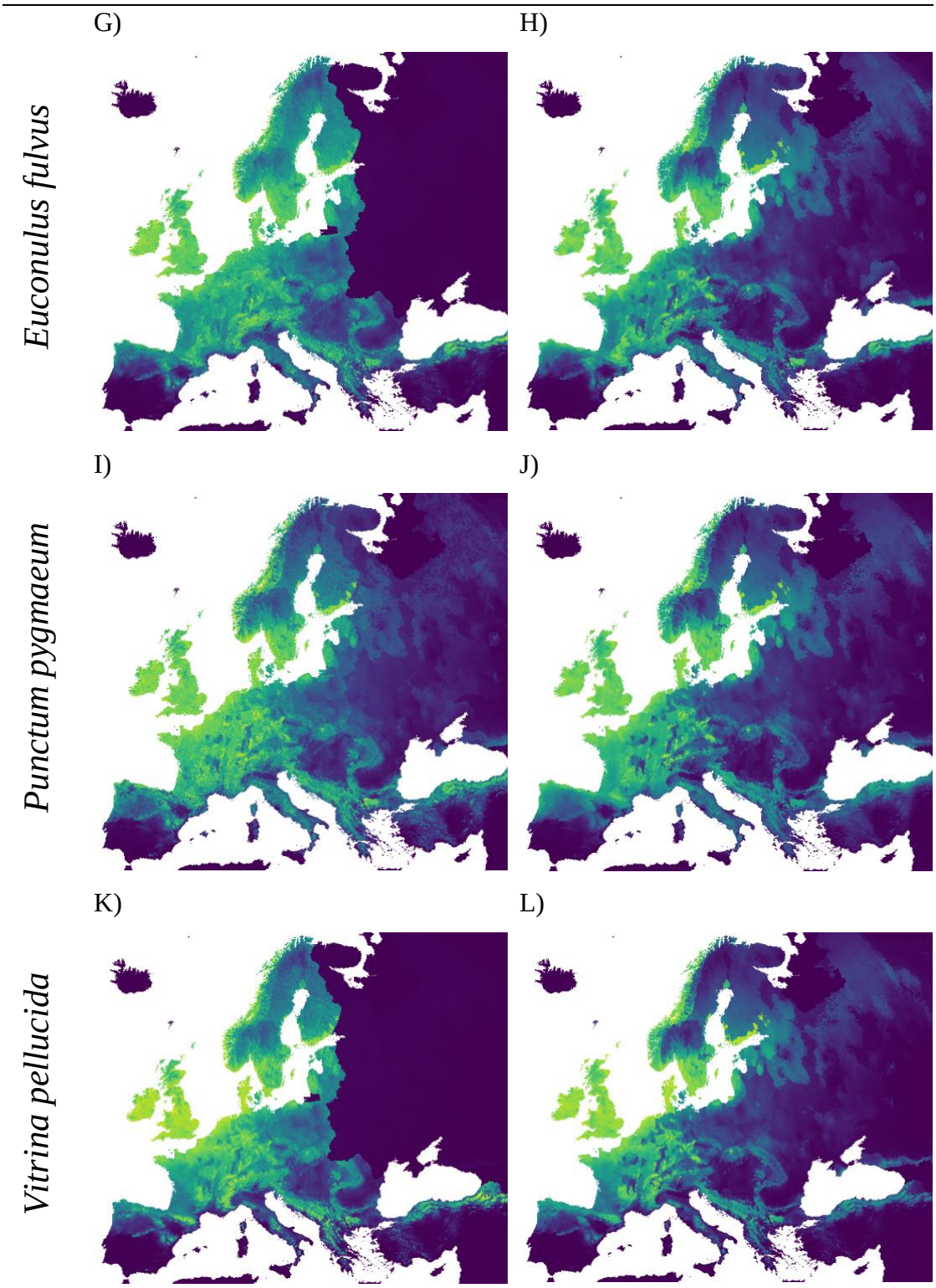


Figure 2.3 (G-L) Probability of species occurrence over the model area for each species produced using the full and bioclimatic-only models. Colours range from dark blue (low probability of presence) to yellow (high probability of presence)

Although all models performed well (AUC > 0.75, Table 2.1), there were visible differences in some regions between the distribution maps produced using the all-variables (full model) and bioclimatic variables-only models (Figure 2.3 *a-l*), with the full model producing a higher probability of occurrence over many of the areas, including areas of interest within Norway. Therefore, models using the bioclimatic data only are more conservative than the full models.

2.3.3 Future Projections

2.3.3.1 Comparison of two climate models

The percentage of each study area above the threshold limit varied according to the general circulation models used throughout Europe (Figure 2.4) and within the reindeer herd ranges (Figure 2.5).

The CNRM-ESM2 model consistently predicted a larger range for all species in all time periods than the IPSL-CM6A-LR model. When this comparison was restricted to the reindeer ranges however the difference was much less pronounced for most species, with the differences being particularly small for the mid-century predictions. This comparison was performed for the highest emissions scenario, and we can predict that the differences would be smaller for the lower emissions scenarios. The CNRM-ESM2 model was selected for further use as it predicted larger areas with likely gastropod presence and therefore was more compatible with the aim of the study as it would be less likely to underestimate the risk of parasitic disease in an area.

2.3.3.2 Different emissions scenarios

Projections were run for three emission scenarios for four periods of 20 years using the CNRM-ESM2 GCM. The threshold limit was applied to create binary presence/absence data, and from these the proportion of the map in which the environment was suitable for habitation could be calculated. The predicted area of suitable habitat varied by species over Europe (Figure 2.6), within the range of the reindeer hosts (Figure 2.7) and across emission scenarios (ssps) (Figure 2.8 a-c and 2.9 a-c). A large proportion of the reindeer habitat is predicted to have suitable intermediate hosts for *E. rangiferi*, with estimates of the current distribution reaching

over 30% of the area for *E. fulvus*, and future projections reaching over 50% for *A. arbustorum*. All species except *A. arbustorum* show a clear decrease in predicted range compared with the current distribution at each timestep, even in the lowest emission scenario (ssp245) for the time period of 2021-2040, and overall there is seen to be a reduction in probability of occurrence over Europe. *A. arbustorum* shows a less clear pattern but with an overall decrease towards the end of the century (Figure 2.7). The distribution can be seen to shift Northwards across Europe, with only smaller changes in range seen at Northern latitudes (Figure 2.8). This is demonstrated within the reindeer ranges in Norway (Figure 2.7); there is an initial increase in the area with high probability of occurrence for all species in all emissions scenarios, with a gradual decrease in area seen by the end of the century in the snail species. In the two slug species (*A. subfuscus* and *D. laeve*) however, there is an overall increase in the area which remains even at the end of the century in the highest emissions scenario, although this range is still smaller than for several of the snail species. The areas of increase in probability of gastropod occurrence are particularly prominent in the south within the wild reindeer range, and in the north in Finnmark county where there is a particularly high concentration of semi-domesticated reindeer (Figure 2.9). Visual inspection of the individual species binary maps revealed that in all projections the distributions of the two slug species models were entirely within the distributions of the snails, and were of a much smaller land area.

2.3.3.3 The degree-day model projections

The degree-day model was run for the future emissions scenarios (GCM: CNRM-ESM2) for areas in which both the definitive and intermediate host species were predicted to be present. There is a visible increase in thermal suitability index in all emissions scenarios (Figure 2.10), with a particular increase in suitability towards mid-Norway, which represents the range of the southern herds of semi-domesticated reindeer. This is apparent even with the lower emissions scenario. In some areas such as in the north of Norway there is both an increase in thermal suitability and an increase in predicted gastropod habitat range, representing a potentially large increase in the risk of transmission for herds in these areas. In all scenarios the entire semi-domesticated reindeer area is suitable for the lifecycle of *E. rangiferi* to be completed within one year by the 2061-2080 time period. In the wild reindeer habitat however,

in the low emissions scenario some areas remain only suitable for the lifecycle to be completed in two years, and it is only towards the end of the century in the ssp585 high emissions scenario that the majority of the habitat is suitable for a one-year lifecycle.

2.4 DISCUSSION

The predictions made for habitat suitability for multiple gastropod species under climate change were combined with predictions of the thermal suitability for development of larvae within the gastropod host to determine areas in which there is predicted to be an increase in thermal suitability for development and an increase in risk of transmission. Although this does not appear to be uniform across the country it is predicted to occur in all areas, with the majority of the habitats occupied by both gastropods and reindeer being suitable for the full *Elaphostrongylus rangiferi* lifecycle to be completed in one year by the end of the century. However, species distribution models developed in this study for gastropod distributions across Norway predict that there are areas within the reindeer ranges that are not suitable for parasite development due to a lack of gastropod host species being present, and in the face of climate change these areas which are not suitable for gastropod habitation are predicted to expand. However, this is not consistent across the country with some areas, particularly in the north of Norway, predicted to become suitable for gastropod habitation where they were not previously. Overall although there is likely to be an increased risk of parasite transmission in areas with both intermediate and definitive hosts present, the areas where the intermediate hosts are likely to be present are predicted to decrease, but this will not be uniform across the country and some areas are predicted to be at risk of infection where they were not previously.

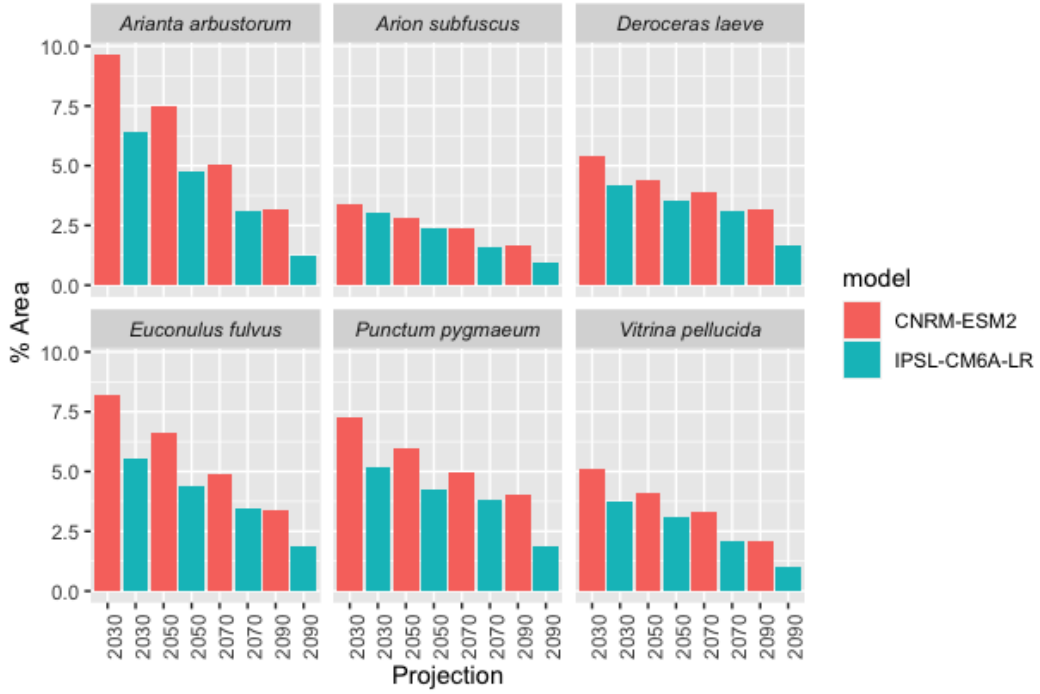


Figure 2.4 The percentage of Europe above the maximum sensitivity plus specificity threshold for each species for models run using two GCMs for ssp585 by decade. The red bars represent the model CNRM-ESM2, and the green bars IPSL-CM6A-LR

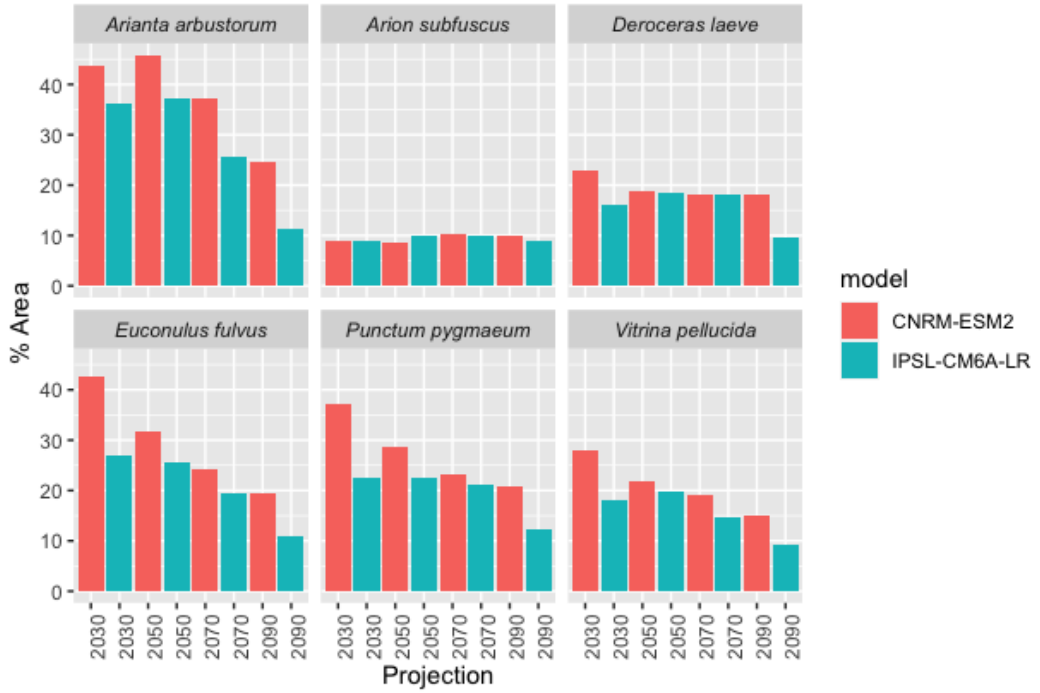


Figure 2.5 The percentage of the Norwegian reindeer range above the maximum sensitivity plus specificity threshold for each species for models run using two GCMs for ssp585 by decade. The red bars represent the model CNRM-ESM2, and the green bars IPSL-CM6A-LR

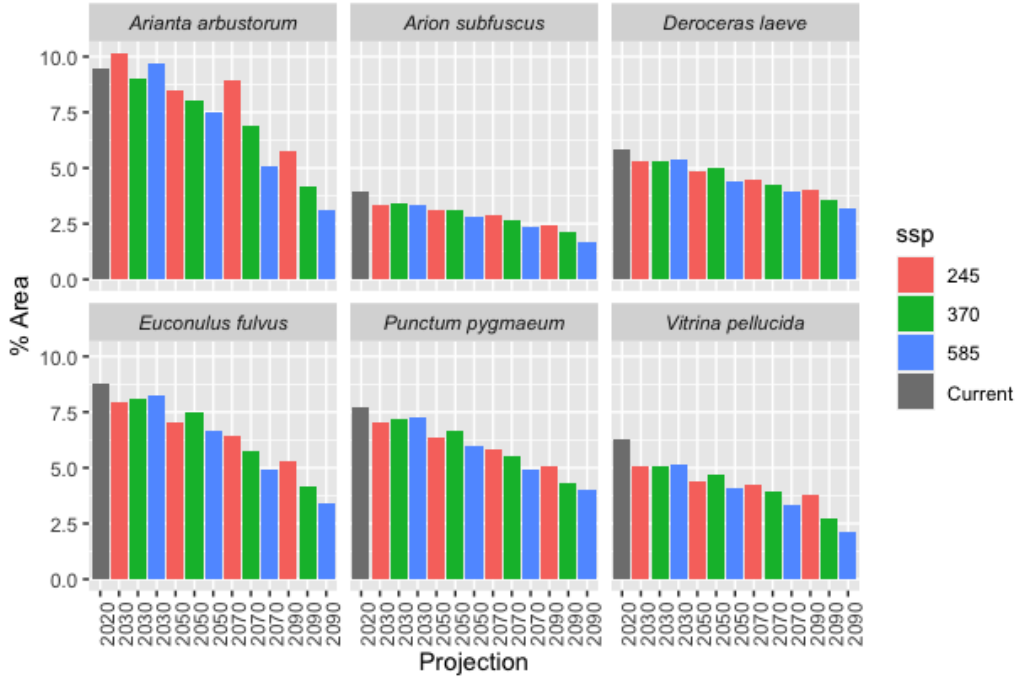


Figure 2.6 The percentage of Europe above the maximum sensitivity plus specificity threshold for each species by decade with projection using the CNRM-ESM-2 circulation model. The grey bar represents the present distribution, red bars ssp245, green bars ssp370 and blue bars ssp585

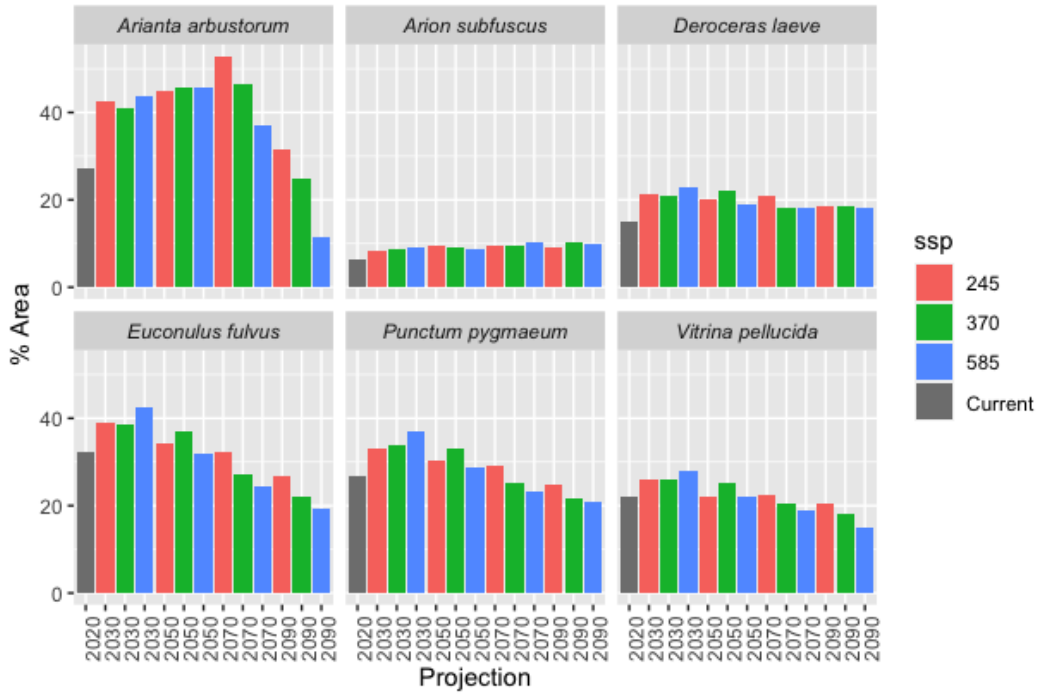


Figure 2.7 The percentage of the Norwegian reindeer range above the maximum sensitivity plus specificity threshold for each species by decade with projection using the CNRM-ESM-2 circulation model. The grey bar represents the present distribution, red bars ssp245, green bars ssp370 and blue bars ssp585

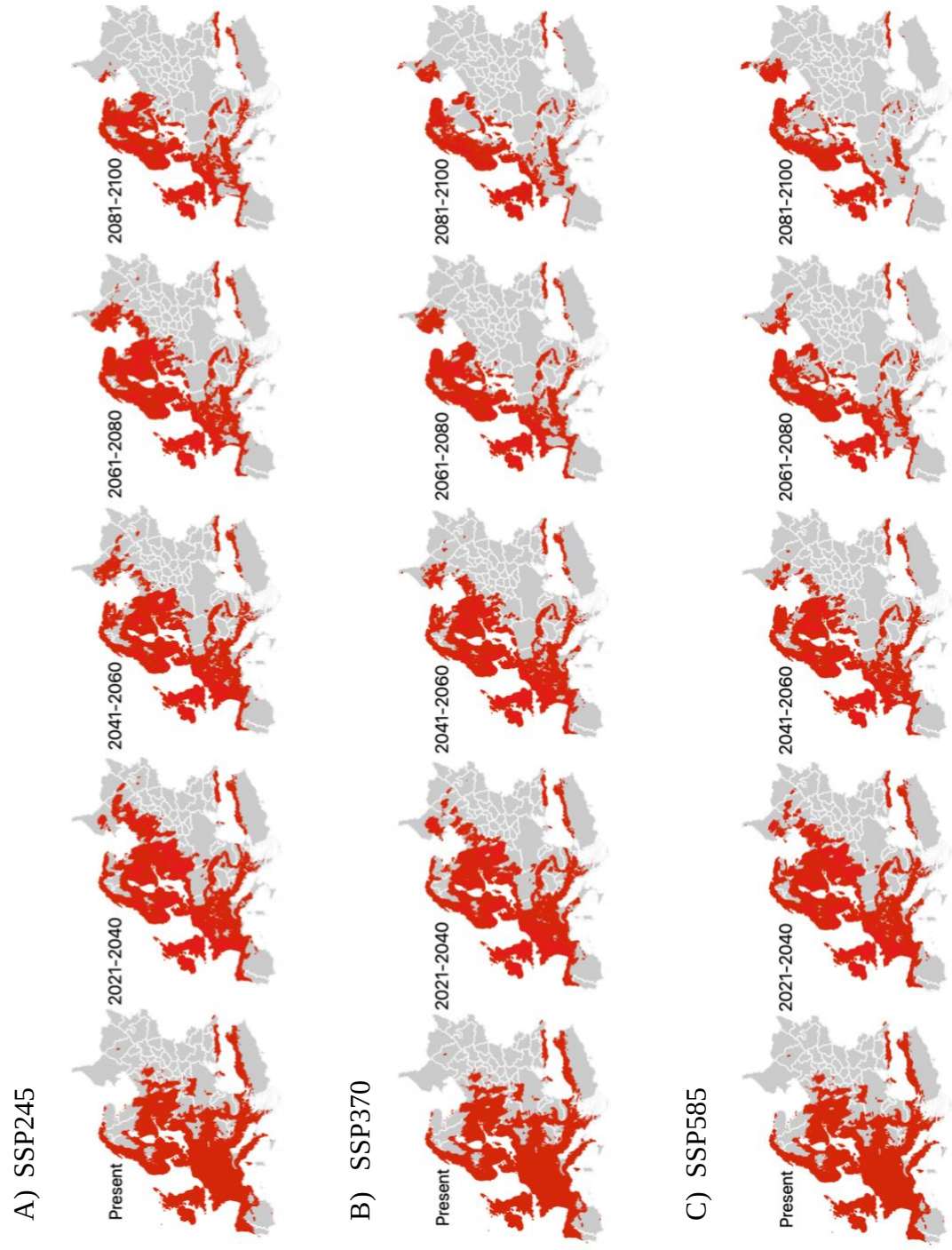


Figure 2.8 (A-C) Combined predicted range of all studied gastropods within Europe across a range of time periods and emissions scenarios. Red areas indicate predicted range based on a model developed using Bioclimatic variables only, the CNRM-ESM2 GCM and a threshold probability of presence based on the maximum sensitivity plus specificity. Grey areas indicate environmental conditions not meeting this threshold. The present predicted distribution is presented in each scenario for comparison

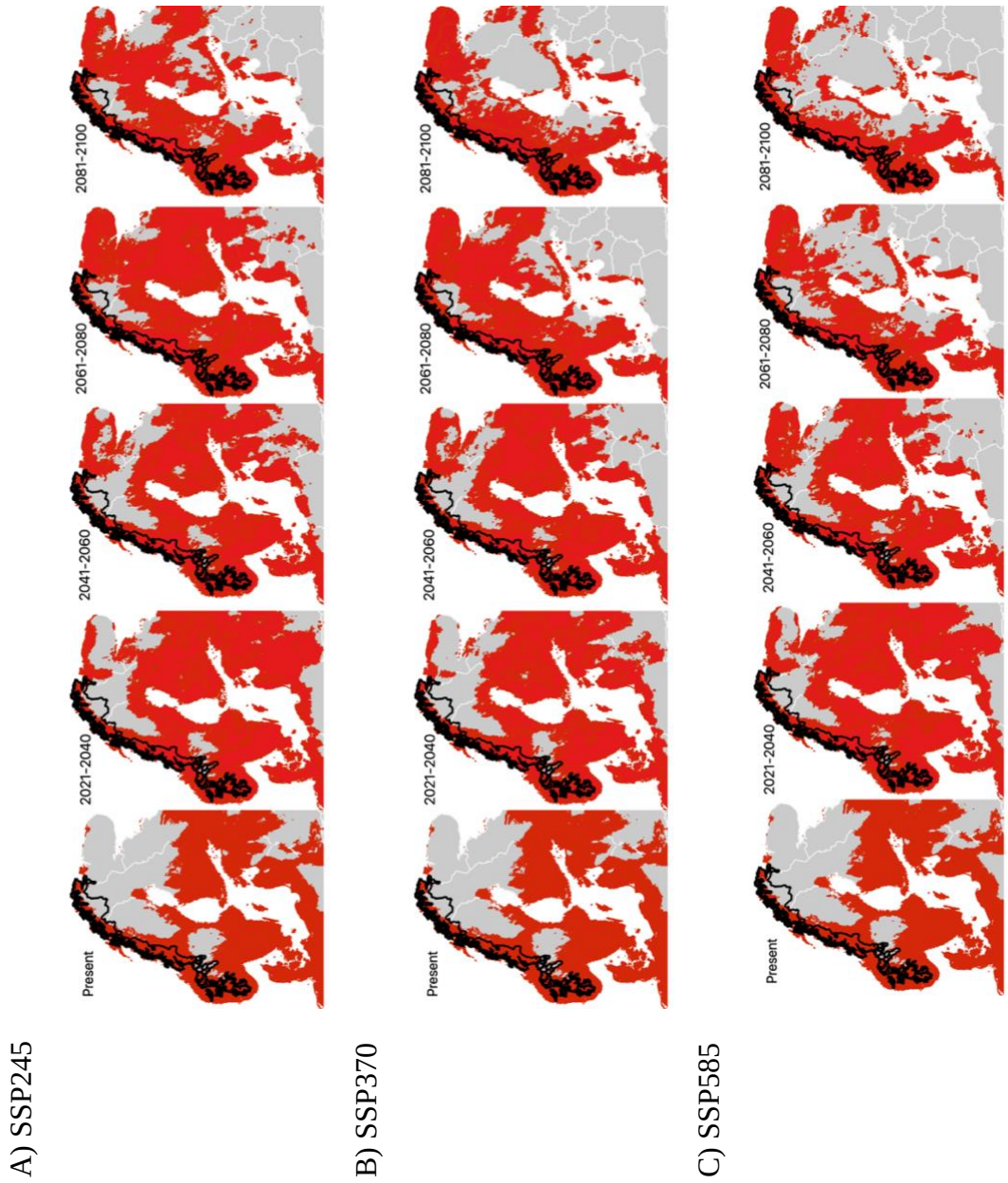
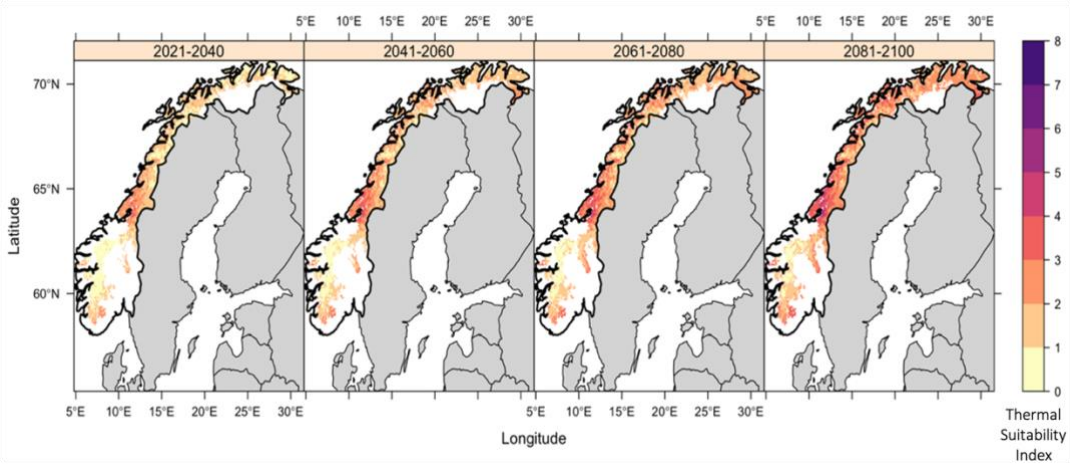
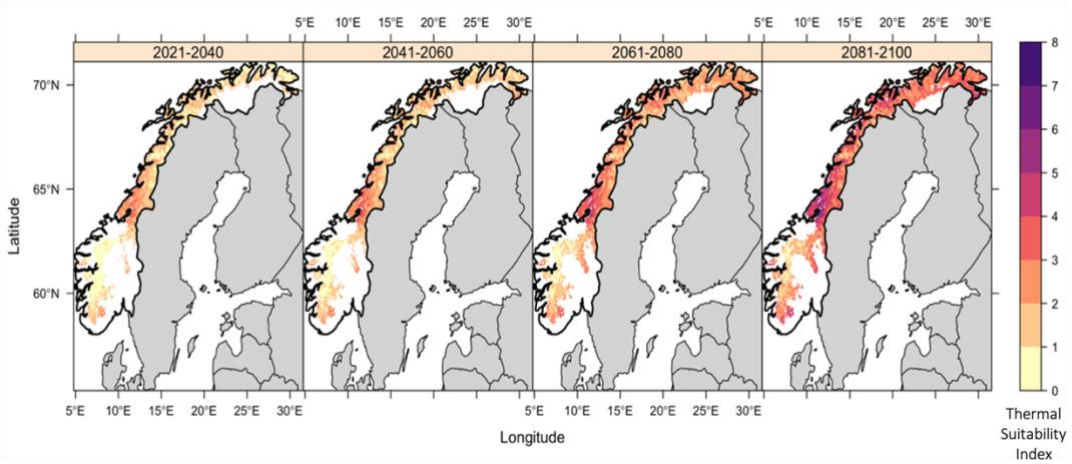


Figure 2.9 (A-C) Combined predicted range for all studied gastropods within Fennoscandia across a range of time periods and emissions scenarios. Red areas indicate predicted range based on a model developed using Bioclimatic variables only, the CNRM-ESM2 GCM and a threshold probability of presence based on the maximum sensitivity plus specificity. Grey areas indicate environmental conditions not meeting this threshold. The black outline indicates the extent of the reindeer ranges within Norway. The present predicted distribution is presented in each scenario for comparison

A) SSP245



B) SSP375



C) SSP585

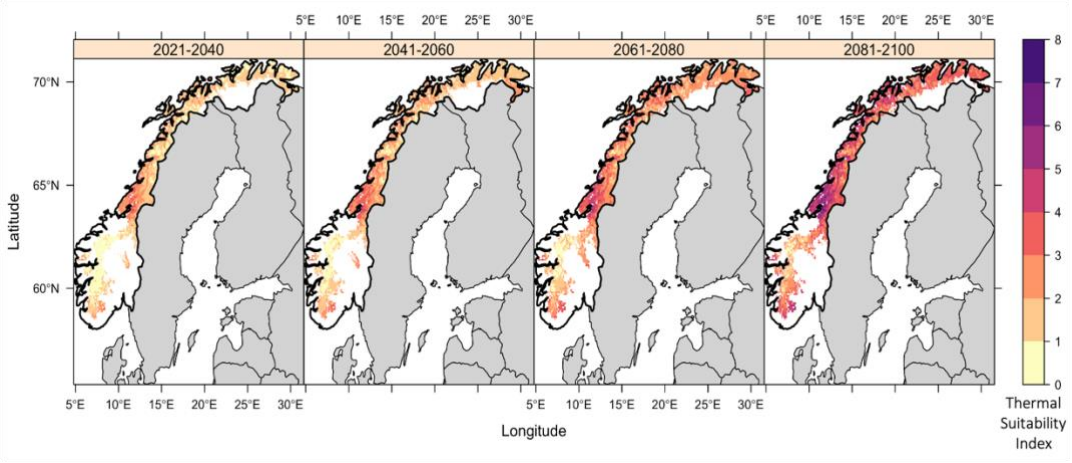


Figure 2.10 The degree-day model applied to three different emissions scenarios using the CNRM-ESM2 model in the areas with both definitive and intermediate host species at each time point. White areas indicate areas of Norway where one or both intermediate and definitive hosts are absent. Grey areas indicate other countries not included in the model. The 0-8 scale represents the number of times the development from L1-L3 could be completed within a year.

The high AUC values, the small standard deviations and the consistency between the results from the test and training runs show that the species distribution models produced for all species are good. The results found here also match the patterns and responses to climate change seen in other similar studies. Contraction of the range of snail species in the face of climate change was predicted by Stensgaard et al. (2013) who modelled the distribution of *Biomphalaria spp.* freshwater snails in Africa, and Willis et al. (2006) who found high extinction rates of *Deroceras reticulatum* in the south east of England by the 2080s in both high and low emissions scenarios. Hof (2011) found a high level of species richness along the coast of Norway which fits the prediction in this study that habitat suitability in that area will remain more stable than that found in Europe overall. Heterogeneity between the areas with high probability of occurrence for different species was seen as expected, and matches what was reported by Stensgaard et al. (2013), with the most significant differences here being seen between the two slug species and the four snail species.

Comparing the variables of importance for gastropod distributions across studies is not easy due to different parameters exhibiting collinearity in different regions depending on multiple factors. For example Pratumchart et al. (2019) modelled the distribution of *Bithynia siamensis goniomphalos* snails as an intermediate host species in Thailand and also found Bio14 (precipitation of the driest month), elevation and land cover, amongst other variables, to be important predictors of spatial distribution, but Bio14 was the only bioclimatic variable included in their model so it is not possible to conclude that this variable is of higher importance to the distribution than the others. Additionally some studies do not check for collinearity and instead include the full complement of bioclimatic variables, for example Bondareva, Genelt–Yanovskiy, and Abramson (2020) found that the most important variables for predicting *Arianta arbustorum* distribution in Europe were Bio7 (annual temperature range), Bio9 (mean temperature of the driest quarter), Bio10 (mean temperature of the wettest quarter) and Bio14, with Bio8 (mean temperature of the wettest quarter) being only the 7th highest contributor. This fits with the observation in the present study that Bio9 and Bio14 were important in all the models. However, Bio7 represents the annual temperature range and therefore exhibits a high level of collinearity with other temperature related variables, and thus cannot be interpreted as independent from them, hence its exclusion from the current study.

The majority of the gastropod species occurrence data which was available for use in this study was from the UK which has a very moderate temperate climate. Therefore, it is unlikely to represent or encompass the upper or lower threshold limits for any of the variables for the gastropod species. The downside of the Maxent method of generating pseudo-absences is that pseudo-absences may be taken from areas where the species is actually present but unrecorded. This may particularly occur over areas where sampling is difficult, such as across most of Fennoscandia, and for animals such as terrestrial gastropods which have not been extensively studied. As both the species occurrence data and the "current" climatic variables used in this study cover an extended time period (1950-2020 and 1970-2000 respectively) it may be that they do not represent the actual conditions in which the species were living. It also does not take into account any declining populations where the species is currently found but cannot be sustained. The exclusion of data from areas where certain species are known to be invasive (McAlpine et al., 2009) removes some of the uncertainty from the model.

The use of solely climate variables may limit the prediction of the ecological niche as they may fail to capture some of the species' individual requirements, as demonstrated by the smaller predicted distribution in the bioclimatic model compared to the full model, which included land cover and soil characteristics. However, creating a model using all possible requirements with limited physiological knowledge of the species is not possible and it is a known disadvantage of correlative models that this may occur (Zurell et al., 2020). None of the climatic variables included in the model represent low temperatures so no representation of the lower thermal limit of the species is seen in the model, except indirectly via collinearity with the other variables. However the lower thermal limit of ectotherms has been found to decrease with increasing latitude, showing a degree of adaptation or phenotypic plasticity (Aleuy et al., 2020, 2019; Aleuy and Kutz, 2020). In contrast, the upper thermal limit show much lower variability (Sunday et al., 2011), therefore upper thermal limits, and the variables included in this model, are more likely to prove limiting to the species' distributions. Although the bioclimatic variables are designed to have biological relevance, in gastropods it is likely to be microclimate that has more of an influence on distributions and this can be affected by a wide range of external factors. In addition, the

behavioural thermoregulation and movement capacity of gastropods may mean they are able to survive in a wider range of climates than is predicted in this model. This will also affect the predictions made using the degree-day model as the behavioural thermoregulation will affect the temperatures to which the gastropod, and thus the larvae, are exposed and this may not correlate with those estimated using air temperatures. This will also depend on many other factors, particularly including moisture availability. Small scale studies have found that surface temperatures rather than air or soil temperatures more closely predicted the development of the larvae when using a degree-day method, and that air temperatures often over-estimated the time needed for development, i.e. the larvae were developing faster than was predicted by this method (Kutz et al., 2002). Higher variability in surface temperatures compared to air temperatures has also been found, with a higher difference seen between them during winter months (Jenkins et al., 2005). Unfortunately, no large-scale data on more proximal factors such as soil surface temperatures is available for either current/historic time periods or future projections, therefore distal variables must be used as proxy.

The data used in the *E. rangiferi* degree-day model are based on experimental lab studies in which temperature was held at a constant. The model has yet to be tested under field conditions like the models for *Parelaphostrongylus odocoilei* (Jenkins et al., 2005), *U. pallikuukensis* (Kutz et al., 2002) and *Varestrongylus eleguneniensis* (Kafle et al., 2018) have, thus the effect of stochasticity is unknown. Saunders, Tompkins, and Hudson (2002) found that stochasticity in environmental temperatures accelerated egg development in *Heterakis gallinarum* above what was predicted from a degree-day model developed using constant mean temperature. This is one possible explanation for the apparent higher degree-day requirement for *E. rangiferi* as compared to the other species (245 compared to 163, 167 and 171 respectively in the aforementioned Arctic protostrongylids).

For all time periods and emissions scenarios modelled, the slug habitat areas were entirely encompassed by the snail distributions. However, the role of the slug habitats should not be discounted as it is not possible from these analyses to tell the relative importance they may have in transmitting the parasites within their range. Further field work is required to ascertain which gastropod species are infected in the wild and in

which species successful development from L1 to L3 is possible under field conditions. The microhabitats of the species may also be of key importance in bringing the intermediate and definitive hosts into contact. For example, in Russia, *D. laeve* is often found at the base of slopes in areas with lichen and moss cover (Berman et al., 2011) which comprise key food sources for reindeer (Turunen et al., 2016). It is also important to consider different development rates of larvae in shelled versus unshelled gastropods. When the data from the degree-day model developed by Rose Vineer et al. (2021) is divided into two classes for slug and snail species, very different results are seen; the number of degree-days required for development in snails increases slightly to 254 (SD 33), whereas for slugs it is just 198 days (SD 36). Although the sample size for the slug data is extremely small this is more similar to the rates of development seen in slugs by other Arctic protostrongylids. There are also physiological and life cycle differences between the gastropod species which may mean they respond to climate change in different ways which are not captured by this empirical model. For example, despite the similar distributions seen between the two slug species, they have very different life history traits, with *A. subfuscus* being long lived and *D. laeve* having a short lifecycle (reported in Berman, Meshcheryakova, and Leirikh, 2011) meaning the effect of climate change may affect the development of each species differently. There may also be effects of adaptation, as adaptation of populations of gastropods to different environmental conditions has already been observed; regional adaptations have been found in slug populations living in different climates within Russia (Zotin and Ozernyuk, 2002), and genetic differences have been found between different populations of *Arianta arbustorum* within Europe (Bondareva et al., 2020).

Gastropod prevalence is unlikely to be uniform across the predicted presence areas and it is likely to be the microclimate that has more of an effect at this scale. Indeed, Lee et al. (2009) found a “patches and gaps” pattern to slug density in an island ecosystem. There are also many other factors which can limit a species occurrence in an area such as human disturbance, use of chemicals, or geographic isolation preventing colonisation of suitable habitat. This can also mean that areas predicted to be suitable in the future will not be, due to factors such as habitat fragmentation and barriers to dispersal. Biotic interactions are also not generally considered in species distribution models even though they are known to affect species distributions (Araújo

and Luoto, 2007). Grazing reindeer have been shown to be associated with reduced gastropod abundance, presumed to be through engineering of the ecosystem and alteration of the microhabitats available (Suominen, 1999). It has also been predicted that species richness of gastropods in Fennoscandia will increase in response to climate change (Hof, 2011), therefore there may be new species colonising new areas, and the areas at risk of brainworm transmission may be larger than are predicted here. This will also change the biotic interactions within the ecosystem.

This study provides a key first insight into mapping areas of reindeer habitat where they are at risk of transmission of *Elaphostrongylus rangiferi* from gastropod intermediate hosts, how these areas may alter in response to climate change, and how the thermal suitability for larval development will also change. Overall, thermal suitability for larval development is expected to increase in all emissions scenarios and all time periods. In contrast habitat suitability of gastropods is predicted to show a reduction in overall area within the reindeer habitats, but with a change in distribution and species composition. This provides a step towards introducing control and management measures that can minimise infection by reducing exposure to the parasite.

CHAPTER 3: THE SPATIAL ECOLOGY OF REINDEER HERDS IN RELATION TO BRAINWORM TRANSMISSION

3.1 INTRODUCTION

For pathogens with limited dispersal ability the movement of the hosts is a key player in determining spatial disease transmission. In the case of protostrongylid parasites such as *Elaphostrongylus rangiferi* the gastropod intermediate hosts have limited capacity for long range movement therefore movement of the reindeer definitive host is the main determinant of potential contact with gastropods containing the infectious stages of the parasite, and the subsequent risk of infection. Models of parasite transmission to migratory ruminants have found that the interaction between the movement and climatic variables was pertinent to the transmission dynamics (Morgan et al., 2007).

In some disease systems, long distance movement or migration is an effective disease reduction strategy. There are two main theories as to how this occurs. Animals infected with pathogens have been shown not to survive long distance migration as well as their uninfected or less-infected counterparts; these highly infected individuals are more likely to perish and reduce the level of infection in the population. This is termed 'migratory culling' (Bradley and Altizer, 2005; Gils et al., 2007). In semi-domesticated populations even if infected individuals survive migration, the effect of slower migration and greater weight loss during migration may induce herders to remove these individuals from the population. The other method is termed 'migratory escape' (Bartel et al., 2011; Loehle, 1995) and occurs when animals move away from an area where infection is present thus reducing exposure to infection. Modelling has showed that in some disease scenarios migratory escape can greatly reduce the prevalence of a pathogen in the host population and proves beneficial to the herd population size even when the costs of migration are accounted for. Hall et al. (2014) modelled the effect of migration on disease transmission and population size of the Black-throated Blue Warbler (*Setophaga caerulescens*) and found moving away from the breeding grounds early is likely to be especially beneficial, as this was the peak

time of transmission in the disease system modelled. Data on this for the *E. rangiferi* transmission system could aid in management planning decisions. For *E. rangiferi*, however, the peak time of transmission will occur after the development of first to third stage larvae and will therefore occur later in the year than the breeding season. Additionally the model by Hall et al. (2014) assumes that there is no transmission at the wintering grounds, whereas there is evidence for over-winter transmission of gastrointestinal parasites of reindeer in the Arctic winter (Carlsson et al., 2012; Halvorsen et al., 1999). Additionally Lankester and Peterson (1996) found that wintering yards, particularly where animals were at a higher density and in areas without snow cover, provided greater potential for transmission of the protostrongylid *Parelaphostrongylus tenuis* to white-tailed deer and moose in Northern Minnesota compared to their summer grounds, as a higher prevalence of infection in gastropods was found there.

The concept of migratory escape has already been documented in reindeer. Abundance of warble fly (*Hypoderma tarandi*) larvae is negatively correlated with distance between calving grounds and main summer pasture in Finnmark county in northern Norway (Folstad and Andersen, 1991). Warbles exhibit a similar seasonal pattern to *E. rangiferi* in that the highest levels of larval shedding by the host into the environment are seen at calving time in the spring, and the highest risk of transmission is in the summer after development of the larvae on pasture. Evidence for migratory escape has also been seen in ticks on red deer in Norway; red deer migrating longer distances, and particularly moving to higher altitudes, have lower prevalences of ticks due to avoiding habitats most suitable for ticks for the majority of the questing season (Mysterud et al., 2016). In contrast however, evidence against migratory escape has been found for Elk (*Cervus canadensis*) endoparasites in western Canada; migratory elk were found to have the highest parasite species richness and the highest intensities of infection. They also had higher intensities of infection of *Fasciola magna* and this was thought to be related to movement to the summer grounds increasing exposure to the preferential environment for the intermediate host species (Normandeau et al., 2020). This concept has been termed environmental tracking and higher parasite diversity in migrant species has been found to occur across multiple ungulate species as it promotes year-round parasite transmission, however this pattern was not consistent for macroparasites (Teitelbaum et al., 2018). Overall, the impact of

migration on parasite transmission varies with parasite species and host-environment interactions and simple rules cannot be applied across parasite systems and the effect on each must be considered separately.

A study by Johns and Shaw (2016) suggests that both migratory escape and culling are effective in reducing disease prevalence in migratory populations, and that this alone may be a sufficient driver for the evolution of migration. However, the effects of migration and the role of parasitism in its evolution depends on the metric used to measure level of parasitism; measuring prevalence, intensity and species diversity separately can give very different results and show different effects in relation to migration and host fitness (Shaw et al., 2018). This present study assesses the effects of movement on the transmission potential of a single parasite species to determine if it affects intensity of infection. Species richness of parasites is not being considered. The aim of this work is to develop a preliminary model framework to apply a simple degree-day model as a decision support tool for brainworm risk management by reindeer herders.

3.2 METHODS

3.2.1 Data sources

3.2.1.1 Reindeer location data

GPS data were obtained from secondary datasets where satellite collars were placed on 14 individuals from one herd of wild reindeer and 54 individuals from one semi-domesticated herd. The wild reindeer were collared under licence from the Norwegian Food Safety Authority FOTS ID 15116. The semi-domesticated reindeer were collared by the Norwegian Veterinary Institute with permission of the herder for routine monitoring, and the data was shared with permission and approved under University of Liverpool research ethics approval number VREC945. The GPS locations were recorded at 4 hourly intervals and data were available from June 2018 to June 2021 for the semi-domesticated herd, and January 2017 to June 2021 for the wild herds, with variations in the amount of data available for each individual reindeer.

The locations of the reindeer were visualised in QGIS (QGIS.org, 2021) and checked for errors. Within the semi-domesticated herd there were multiple GPS locations

approximately 800km away from the main herd with no points in between; these were believed to be invalid, so the data from these collars were removed from the analysis.

The area in which each herd was located each month during the period of data availability was calculated using a minimum convex polygon method and data from all collared reindeer in that herd. This was done using the mcp function in the adehabitatHR package in R (Calenge, 2006), with the percentage set to 100% to not exclude any locations, as only a proportion of the herd were collared. The home ranges were calculated on a monthly basis using calendar months. If data were not available for a month in a year the missing data were duplicated from the same month in either the subsequent or preceding year depending on availability, as reindeer movements were assumed to vary only marginally from year to year.

3.2.1.2 Faecal larval counts

As part of ongoing veterinary surveillance, faecal samples had been collected by the Norwegian Veterinary Institute (NVI) from some individuals within the semi-domesticated herd in January or February and July of 2018, 2019 and 2020, and in March, June, August and October of 2020 in the wild herd. These were analysed by the NVI using a modified Baermann's technique on a mean weight of faeces of 8.6g. The larvae were morphologically identified, and the *E. rangiferi* larval count per gram calculated. Samples from the semi-domesticated herd were individually attributed to collared reindeer using their permanent identifying marks to allow individual analysis to occur, samples from the wild reindeer were not individually identifiable.

3.2.2 Degree-days

The degree-day model developed by Rose Vineer et al. (2021) was run using EOBS gridded mean daily temperature data on the 0.1 degree scale (Version 23.1; Cornes et al., 2018), resulting in a time series of daily degree-days for each grid cell. The number of degree-days was calculated from the number of degrees above the minimum developmental threshold temperature multiplied by the number of days post infection the L3 were detected. The first day that a grid cell fell within a reindeer range polygon was taken as the earliest date of larvae (L1) deposited in the environment. The cumulative sum of degree-days for each grid cell within the reindeer range polygon

was calculated daily and so the point at which the cell reached, or exceeded, the 245 degree-days required for larval development (Rose Vineer et al., 2021) could be determined, as well as the total cumulative degree-days for that location from the time of L1 deposition to 31st December each year. The date at which 245 degree-days was exceeded could then be used to determine when reindeer were at risk of reinfection, and the cumulative degree-days could be used to determine which parts of the range were highest risk, under the simplifying assumption that L1 were deposited on the first day any member of the reindeer herd was located in that area.

The cumulative degree-days were calculated for the end of each calendar month for each grid cell. These were converted to rasters using functions within the raster package in R (Hijmans, 2020) and were masked by the monthly polygon to show where the reindeer were located during that month and how many degree-days had accumulated in those grid cells up to that point.

Density of reindeer within the range and variation in density of larvae on pasture was not considered here as these data were not available. However, Ball et al. (2001) found no relationship between the density of a reindeer herd and abundance of *E. rangiferi* larvae in faecal samples.

3.2.3 Validation of the model

Individual faecal larval counts were compared with degree-day output for model validation, as higher cumulative exposure to areas with degree-days above 245 is expected to result in higher faecal larval counts. This could only be performed on data from the semi-domesticated herd as the samples from the wild herd were not individually identifiable. To provide a daily location for each collared individual where multiple latitudes and longitudes were recorded each day the mean of the values was taken. Daily locations were not available for all reindeer each year, but for several reindeer the missing locations occurred at the beginning of the year before any of the herd locations had accumulated degree-days above 245. The exact location of the reindeer during this period would not affect the results and therefore the reindeers' missing locations were assumed to be the same as the first available location.

The total number of days each reindeer was present in a grid cell in which the accumulated number of degree-days was above 245, and therefore they were potentially exposed to infectious third-stage larvae, was then summed. The overall value of the degree-days was not taken into account. The estimate of cumulative exposure was then compared to the larval count for the individual reindeer at the sampling date within January or February in both the following and subsequent year (e.g. Figure 3.1). The 4-4.5 month pre-patent period (Handeland, 1994) means that the 1st year sampling in January and February would represent infections acquired at the latest in September of the previous year. A linear regression of number of days potentially exposed against faecal larval count was performed on the collective samples for the 1st year and 2nd year sampling separately.

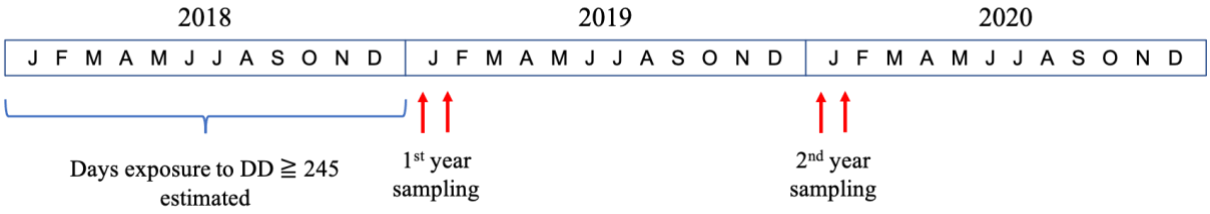


Figure 3.1 An example of the structuring of the data for validation. The number of days exposed to degree-days (DD) above or equal to 245 was summed for 2018, and this cumulative exposure was compared with faecal larval counts from the Jan/Feb of 2019 and 2020

3.3 RESULTS

3.3.1 Degree-days

Annual and spatial variations in areas with risk of transmission (cumulative degree-days from the date of first L1 deposition in an area) can be seen. The risk can be seen to increase throughout the year, with some areas of the reindeer ranges reaching 245 degree-days as early as July in both the studied herds (Figures 3.2 (*A-C*) and 3.3 (*A-D*)). Within the semi-domesticated herd some areas in which the reindeer are located later in the year are areas which they had not previously been located in that year and so the degree-days have not accumulated and are 0. This is particularly apparent in October-December 2020. Within the wild herd there is much less variation in herd location month-to-month.

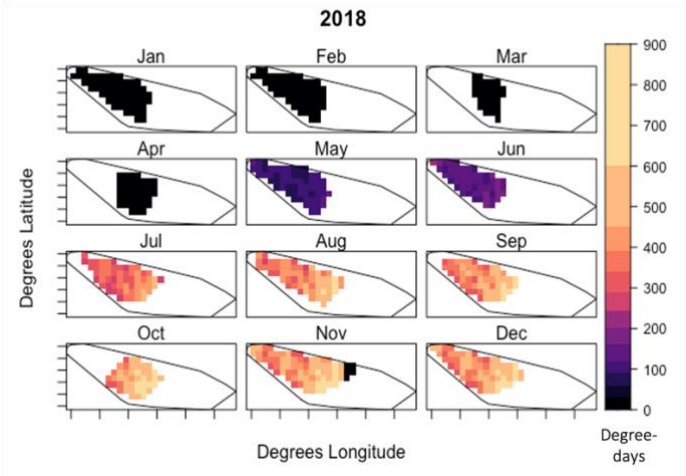
3.3.2 Faecal larval counts

Within the semi-domesticated herd, the faecal larval counts showed similar distribution patterns in the Spring (sampling between January and April) of each year. In the Autumn sampling (sampling between July and October) a higher proportion of the samples were found not to contain L1 (Figure 3.4). Within the wild reindeer herd, a similar pattern was seen in the Spring, and no reindeer were found to shed L1 during the Autumn sampling (Figure 3.5).

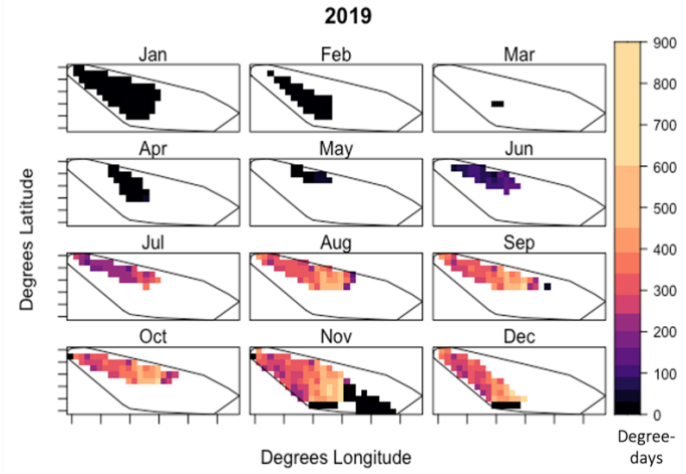
3.3.3 Model validation

With the addition of locations as described in 3.2.2 there were daily location data available for 30 reindeer in 2018, 11 in 2019 and 25 in 2020 within the semi-domesticated herd. There were faecal larval counts available for these reindeer in the January or February the following year in 28 cases and subsequent year (see Figure 3.1) in 14 cases. There were only 4 data points available at a 6-month interval therefore this was not included in the analysis. The linear model found no association between larval count and number of days in an area in which over 245 degree-days had accumulated in the previous year (R-squared = 0.04407, Adjusted R-squared = 0.007303, $F_{1,26} = 1.199$, p-value = 0.2836), nor 2 years previous (R-squared = 0.03126, Adjusted R-squared = -0.04947, $F_{1,12} = 0.3872$, p-value = 0.5454) (Appendix 3.2).

A)



B)



C)

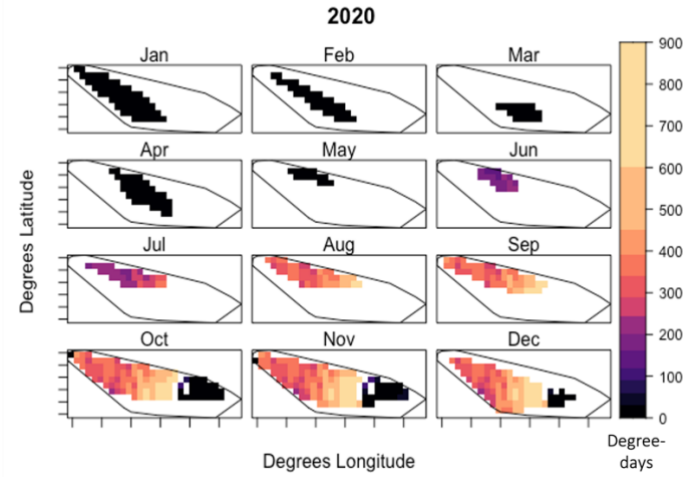


Figure 3.2 (A-C) The number of cumulative degree days (scale bar) predicted for L1 deposited within the range of the semi-domesticated reindeer herd for the years 2018-2020. The black outline shows the overall herd range with the coloured area showing the reindeer position for that month and therefore the predicted exposure to infection within that month. Colours range from black (0 degree-days) up to yellow (above 600 degree-days). The values on the x and y axes have been removed to preserve anonymity of the herd; the ticks on the x axis represent 0.5º longitude and y axis represent 0.2 º latitude.

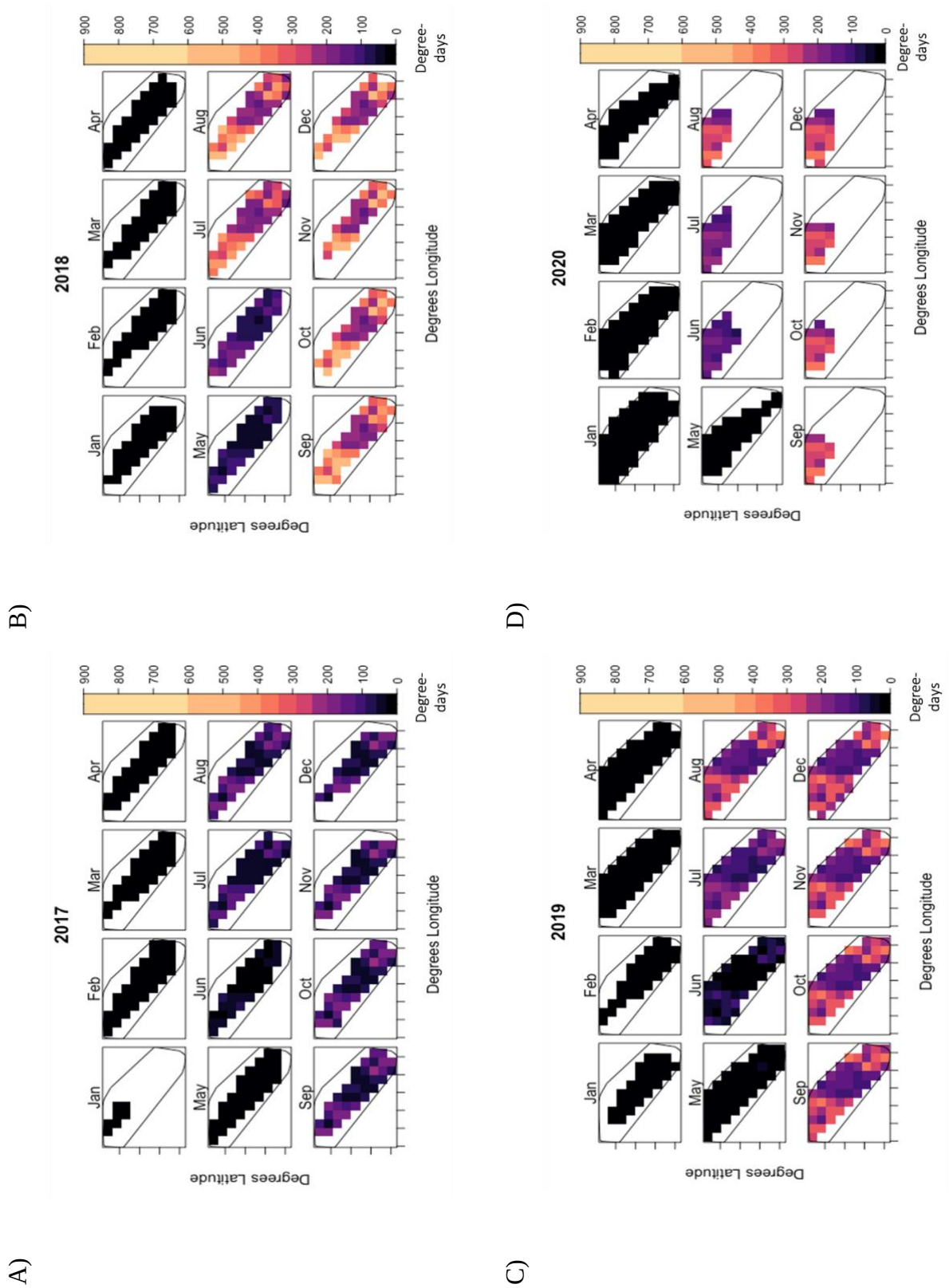


Figure 3.3 (A-D) The number of cumulative degree days (scale bar) predicted for L1 deposited within the range of the wild reindeer herd for the years 2017-2020. The black outline shows the overall herd range with the coloured area showing the reindeer position for that month and therefore the predicted exposure to infection within that month. Colours range from black (0 degree-days) up to yellow (above 600 degree-days). The values on the x and y axes have been removed to preserve anonymity of the herd; the ticks on both axes represent 0.2 º latitude and longitude

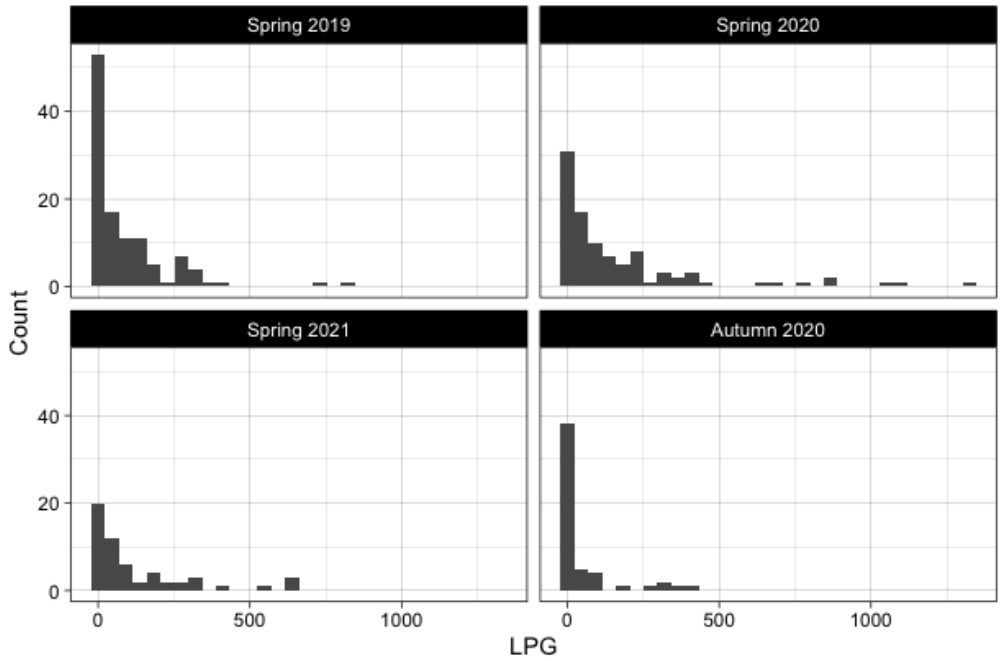


Figure 3.4 Histograms of the E. rangiferi larvae per gram in the semi-domesticated reindeer herd from the sampling periods between 2019 and 2021. Spring refers to sampling from January – April, and autumn July - October

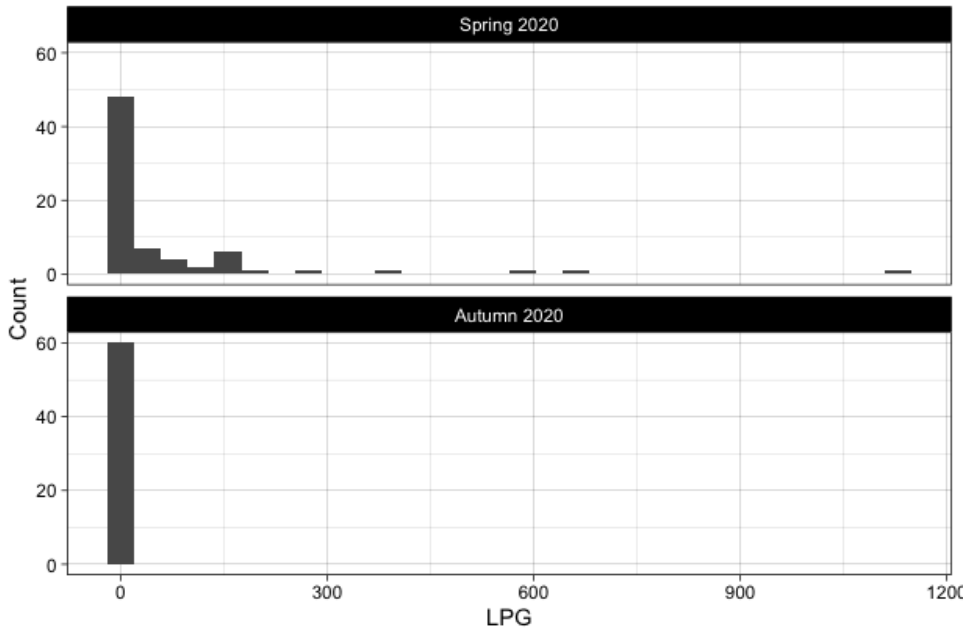


Figure 3.5 Histograms of the E. rangiferi larvae per gram in the wild reindeer herd from the sampling periods in the Spring and Autumn of 2020. Spring refers to sampling from January – April, and autumn July - October

3.4 DISCUSSION

The incorporation of animal movement data into infectious disease analysis is a relatively new field, with the majority of studies focusing on contact network or use of different land types (Dougherty et al., 2018). This study represents a novel combination of movement ecology with a degree-day model to predict areas of a species habitat at higher risk of parasite transmission.

Visualisation of the monthly cumulative degree-days reveals that L3 may be available for transmission from July, and there is little variation in this from year to year within the semi-domesticated herd. Within the wild herd the earliest availability is also seen in July, with L3 not being available in colder years until later or not at all. This represents the first potential measure of seasonal L3 development which could be used to predict the timing of disease emergence in reindeer herds. This information could then be used by Sami herders to plan intervention measures, and allow herders to move reindeer away from an area before the development of L1 to L3. The work here also demonstrates how host movement could be incorporated into a model of parasite development to track seasonal exposure to infection.

Although the degree-day model for *E. rangiferi* development itself has been loosely validated (Rose Vineer et al., 2021), and this modelling approach is promising, cumulative exposure to L3, measured as cumulative exposure to degree-days of >245, was not related to faecal larvae counts in the January of the following two years. However, particularly for the 2nd year sampling, there was only a very small data set and further data collection may yield a stronger relationship. In the single semi-domesticated herd used for validation, the model would not have generated useful predictions to inform veterinary treatment. However, with further data this could be developed into a tool to be used by reindeer herders to predict spatiotemporal risk of *E. rangiferi* transmission.

Ditmer et al. (2020) state that there may be greater importance than previously thought in the frequency of contacts between moose and high-risk environments in the transmission of *Parelaphostrongylus tenuis.* This fits with the observations that it may

not be density-dependent transmission driving rate of infection of reindeer with *E. rangiferi* (Ball et al., 2001; Halvorsen, 2012). The validation of the degree-day model here on an individual level did not show any relationships between frequency of contact between a reindeer and an at-risk area within a calendar year and the larval counts. However, with the limited data available for validation, how cumulative exposure to L3 relates to the intensity of infection is currently unclear. Furthermore, there are key areas where the degree-day model could be refined.

A limitation of this model is that mortality of larvae is not taken into account. It is likely that increased temperatures will lead to increased mortality of both the larvae and the intermediate hosts (Chapter 2), therefore there may not be infectious L3 within gastropods at the times predicted here. The lack of mortality in the model also necessitated each calendar year be considered as an independent entity with no transfer of larvae between years, however the roll-over of degree-days from one year to the next would represent development of larvae continuing in the spring once the minimum developmental temperature has been exceeded. It is possible that this does not occur in the field since Jenkins et al. (2005) found *Parelaphostrongylus odocoilei* larvae in *Deroceras leave* failed to resume development after overwintering within the IH. Additionally, Kutz et al. (2002) found infection intensity *of Umminmakstrongylus pallikukensis* in slugs that overwintered was lower than in those developing within the same year of infection, and also that slug mortality was high, particularly when larvae had developed to L3. They suggest that overwintering of free-living larvae is of greater importance than overwintering of larvae within intermediate hosts, therefore the annual cycles in this model may provide a fair representation of field scenarios.

In the reindeer herds modelled here there was no differentiation between the summer and winter grounds, with the herd range remaining relatively constant throughout the year in both the wild and semi-domesticated reindeer, but this is not the situation in all herds. In the far north of Norway reindeer have much greater differences in area between their winter, calving, and summer grounds than seen in the herds in the south, although there is overlap between the summer grounds of one herd and the calving grounds of another (Folstad and Andersen, 1991). This will therefore have an impact on parasite transmission and the duration of exposure to an at-risk area, with the herding strategy and timing of movement also being important factors. In Finnmark

county in the north, reindeer from multiple herds graze a common area before being separated for calving, some herds calve and summer on the same grounds, whereas some move later in the year and do not reach their final summer pastures until after calving. This leads to a separation between areas with the highest level of shedding and highest infection risk from *Hypoderma tarandi* (Folstad and Andersen, 1991). This interaction between reindeer movement and thermal suitability for parasite development is likely to be of great importance in determining infection rates of reindeer, and therefore incidence and severity of disease. *E. rangiferi* larval counts and GPS data from additional herds in different areas and with different migration strategies would help validate this model.

Climate change may affect multiple aspects of this system. With the relatively stationary nature of the wild reindeer herds and the southern semi-domesticated herds it is possible that in the face of climate change when the thermal suitability for development increases there will be a relatively greater increase in infection prevalence and intensity in the reindeer in these areas compared to the ones located further north, with greater levels of movement and migration between separate territories. There is also the possibility that under climate change 'migratory mismatches' will be induced as movement and lifecycle of the intermediate and definitive hosts respond at different rates or in relation to different factors, which may lead to either increased or decreased rates of infection in the definitive host (Hall et al., 2016). Climate change may also lead to the establishment of the parasite in areas where it is not currently found. Migration of caribou in Canada has been linked to establishment of new populations of *Varestronglylus* spp.; although this translocation may have been happening for a long time, only recently have climatic conditions been suitable for establishment of either the parasite or the intermediate host species (Kutz et al., 2013). Therefore, care must be taken if changing the migration of reindeer, to minimise risk of establishment of new parasite populations and resulting increases in the risk of transmission. There may also be small scale effects of climate change as warm summers affect reindeer activity patterns due to harassment by parasitic flies (Hagemoen and Reimers, 2002). This alteration to behaviour and movement on a small scale may alter the transmission dynamics as reindeer move to colder/ snowier sub-climates in order to avoid flies. These possibilities with currently unknown effects, highlight the need for the development of accurate models to determine where animals

are currently becoming infected, and with which predictions can be made for future scenarios.

This study demonstrates how spatially explicit animal movement and thus larval deposition patterns will affect the seasonal development of L3 on pasture and will therefore affect the potential risk of infection of reindeer. The use of the degree-day model in this study provides a useful framework which could be applied to different reindeer movement scenarios, and that with further validation may prove useful in aiding decision making by Sami reindeer herders regarding herding strategies and parasitic disease control.

CHAPTER 4 – A MECHANISTIC MODEL FRAMEWORK FOR WEATHER-DEPENDENT *E. RANGIFERI* POPULATION DYNAMICS

4.1 INTRODUCTION

The degree-day model for *Elaphostrongylus rangiferi* (Rose Vineer et al., 2021) only incorporates the effect of temperature on one process in the parasite lifecycle; the rate of development from first to third stage larvae within the intermediate host. It does not take into account the effect of temperature on other processes, particularly larval and gastropod mortality. It is important to know how each stage of the transmission cycle of a parasite will be affected by environmental changes in order to assimilate the intricacies of these changes together and accurately predict possible future alterations to parasite dynamics. In order to develop mechanistic models using these factors an understanding of the underlying mechanisms driving the relationships is necessary. The following describes the stages of the lifecycle of *Elaphostrongylus rangiferi* and how aspects of this may be affected by environmental factors.

4.1.1 Survival and Infectivity of Free-Living L1

Larvae deposited as L1 on the pasture must infect a gastropod intermediate host before they can begin their development. This may happen the same year as deposition or the L1 may survive over winter and infect gastropods the following year. Over-winter survival rates are high and larvae have been shown to survive >365 days at -80°C and -20°C (Lorentzen and Halvorsen, 1986). However, repeated cycles of freezing and thawing having been found to increase mortality (Lorentzen and Halvorsen, 1986), and with the predicted environmental changes in Fennoscandia (Jylhä et al., 2008) it is likely this will become more of a barrier to survival in the future.

Humidity also plays a role in accelerating the death of free-living L1; when kept at 22°C (a temperature which should be within the thermal tolerance range) at 20% humidity 100% of the L1 died within 10 days (Halvorsen et al., 1980), and half within

just 3.5 days (Lorentzen and Halvorsen, 1986). Although there are no experimental data regarding smaller changes in humidity and its effect on survival or infectivity rates, where stated, experiments are conducted at 80% humidity which is a fair representation of the current average humidity in Norway. However, whether humidity alters with climate change remains to be seen, and further empirical studies to investigate the impacts of smaller changes in humidity on *E. rangiferi* larvae may increase the predictive capacity of models.

Whether containment of larvae in faeces provides an advantage or disadvantage to survival at high temperatures compared to living on pasture is unclear (Cabaret et al., 1991), although at temperatures below freezing (-20°C) no difference was seen in survival rates (Lorentzen and Halvorsen, 1986). It has been hypothesised that larvae on pasture have lower survival but increased chances of infecting gastropod host species which are not attracted to faeces (Cabaret et al., 1991).

One factor that has not been considered experimentally is the migration, or release via faecal degradation, of L1 from faeces to the pasture. It is currently unknown how long *E. rangiferi* remain in faeces in the field, and whether this depends on environmental conditions such as moisture availability. Rainfall, relative humidity and faecal moisture content have been found to be important for migration from faeces onto pasture of arid-adapted protostrongylids (Solomon et al., 1997), trichostrongylid nematodes (Van Dijk and Morgan, 2011; Wang et al., 2014) and equine strongyles (Kuzmina et al., 2006). These studies were all performed in temperate climates and there are currently no data regarding the relative roles these factors play in *E. rangiferi* migration. However, the relative importance of this would depend on the bioecological characteristics of the intermediate host and whether they are herbivorous or coprophagic, and this is likely to vary depending on the species composition of the area.

4.1.2 Infection and Establishment in the Intermediate Hosts

A study of experimentally infected gastropods collected in northern Norway found that all species tested were susceptible to infection with *E. rangiferi* to some degree. During experimental infections there were significant differences in the proportion of

different species of gastropods becoming infected (on moist tissue paper/on moist faeces: 33.4-100%/9.1-100% of individuals of a species infected), the infection intensities (mean from infections on moist tissue paper/on moist faeces: 1.5-79.4 larvae/ 1.0-67.4 larvae), and the development rates of L1 to L3 (percentage of larvae developed to L3 after 24-27 days ranged from 0-100%) within different species of gastropod. Comparisons with other studies revealed that *Succinea* spp., *Deroceras reticulatum, Deroceras laeve, Discus ruderatus, Euconulus fulvus,* and *Trochulus hispida* were consistently identified as suitable intermediate hosts for protostrongylid parasites (Skorping and Halvorsen, 1980). The majority of experimental studies however have been performed using *Arianta arbustorum* in which the larvae may have different developmental rates and a minimum developmental temperature compared to other species (Halvorsen and Skorping, 1982; Skorping and Halvorsen, 1980).

As well as species of intermediate host, there are other factors determining the likelihood of L1 infecting a gastropod. This includes the concentration of larvae within the environment; in lab studies low densities of first stage larvae had a directly proportional relationship with instantaneous infection rate of gastropods but at higher densities of larvae gastropod infection rates were reduced (Skorping, 1988). The environmental conditions also play a role; the level of water in the environment is also known to be important as in experimental studies, significantly higher infection rates (measured as the number of larvae infecting snails within a 2-hour period) were seen in snails maintained in a water substrate compared to those kept on dry soil or lettuce. This is likely to be due to water being required for L1 movement (Skorping, 1982).

Although there are some examples of attraction to faeces and coprophagia being exhibited in intermediate hosts of *Angiostrongylus vasorum* (Valente et al., 2020) and *Parelaphostrongylus tenuis* (Garvon and Bird, 2011), these cases appear to be exceptions rather than normality. *Euconulus fulvus*, a potential intermediate host of *E. rangiferi*, and two other snail species have been found to be repelled by fresh sheep faeces but attracted to dried and weathered faeces (Boag, 1983), potentially reducing the exposure of the snail to parasites within faeces. Cabaret and Vendroux (2011) similarly found higher avoidance of fresh faeces than old faeces, with preferences seen in movement of gastropods towards plant extracts rather than faeces, with variation seen depending on both plant species and host species which produced the faeces

(sheep or goat). They also saw greater avoidance of faeces when there was dry weather, meaning that it is possible there may be an effect of climate change on exposure of gastropods to larvae. Additionally, Cabaret and Vendroux (2011) found close contact between gastropods and faeces to be positively associated with greater levels of infection with *Muelleris capillaris*, but that this was also associated with higher levels of gastropod mortality.

4.1.3 Development rates in the Intermediate Host

Environmental temperature has been identified as a key factor in determining development of the larvae from L1 to L3 within the intermediate host (IH), and there is a range of temperatures at which development can occur. There are differences seen between the gastropod species but the minimum required temperature for development is in the range of 8-10°C (Halvorsen and Skorping, 1982), and no development will occur at ambient temperatures below this. The high minimum development temperature required for *E. rangiferi* development in the gastropod IH is thought to be an adaptive characteristic as the over-winter survival rates of larvae are much higher in snails that are infected with L1 rather than those that have developed to L2 or L3 (Schjetlein and Skorping, 1995).

Significant levels of gastropod mortality are seen at ambient temperatures around 24-28°C (Halvorsen and Skorping, 1982), however behavioural thermoregulation by the IH will in most cases control for the excessively high environmental temperatures (Molnár et al., 2013a). Highest mortality of infected intermediate hosts has been found around the time of the first larval moult from L1 to L2 and could be caused by migration of the larvae through the gastropod leading to tissue damage (Skorping, 1985b).

4.1.4 Transmission to Reindeer

Although transmission to reindeer is unlikely to be directly affected by climate there will be changes to reindeer behaviour and feeding that may have impacts on parasite transmission, for example rain-on-snow events affecting foraging behaviour (Hansen et al., 2014), or increased snow melt leading to greater aggregation of reindeer (Anderson and Nilssen, 1998), both of which may affect access to infected gastropods.

In addition, there may be changes in reindeer and IH ranges which reduce or increase contact rates (Chapter 2).

4.1.5 Shedding by Reindeer

L1 are not passed in faeces until 4-4.5 months post infection (Handeland, 1994). In males, shedding is highest in the autumn months during the rut, and in females it is highest in the spring, likely a peri-parturient rise (Gaudernack et al., 1984; Halvorsen et al., 1985). Seasonal output of L1 therefore will be dependent on the population demography of the reindeer herd. A 2-year transmission cycle would reduce the impact of this seasonal pattern but in a 1-year cycle, as predicted in Chapter 2, the timing of L1 deposition on the pasture is of greater significance as this determines whether L3 will be available to infect the reindeer during the same year.

Serum antibody levels to *E. rangiferi* and faecal shedding of L1 are negatively associated; when reindeer are immunosuppressed, for example due to the increased circulating cortisol concentrations during the rut, shedding increases (Gaudernack et al., 1984). Therefore, other periods of immunosuppression and stress could lead not only to increased susceptibility to infection but to increased shedding of larvae as well.

The extra-mammalian stages of *E. rangiferi* are those that appear more sensitive to the effects of climate due to their close relationship with the environment, therefore a model focusing on these stages was developed. This study provides the first example of a population dynamic model for a protostrongylid nematode species.

4.2 METHODS

4.2.1 Model framework

A model framework was developed based on extra-mammalian stages of the parasite lifecycle, based on the GLOWORM-FL model framework (Rose et al., 2015) (Figure 4.1; equations 1-4). The state variables are represented by $L1_p$ (first stage larvae on pasture) and $L1_s$-$L3_s$ (first to third stage larvae within the gastropod). The parameters are i_1, the infection rate of the gastropod; μ_i, the stage-specific mortality rates where subscript *i* represents each different life cycle stage; and δ, development rate from L1 to L3. Because the development rate represents L1 to L3, when this process is divided

over two stages, the rate is doubled between each state variable, hence 2δ. $\mu_{2\text{-}4}$ represents the sum of snail ($\mu_{2\text{-}4s}$) and larvae ($\mu_{2\text{-}4l}$) mortality. New larvae will be deposited onto pasture daily ($L1p_{new}$) in the faeces of reindeer. These are differential equations with the dX/dt representing the amount of change (d) in the variable X over a set period of time (t).

$$\frac{dL1p}{dt} = -(i_1 + \mu_1)L1p + L1p_{new} \quad (1)$$

$$\frac{dL1s}{dt} = -(2\delta + \mu_2)L1s + i_1 L1p \quad (2)$$

$$\frac{dL2s}{dt} = -(2\delta + \mu_3)L2s + 2\delta L1s \quad (3)$$

$$\frac{dL3s}{dt} = -\mu_4 L3s + 2\delta L2s \quad (4)$$

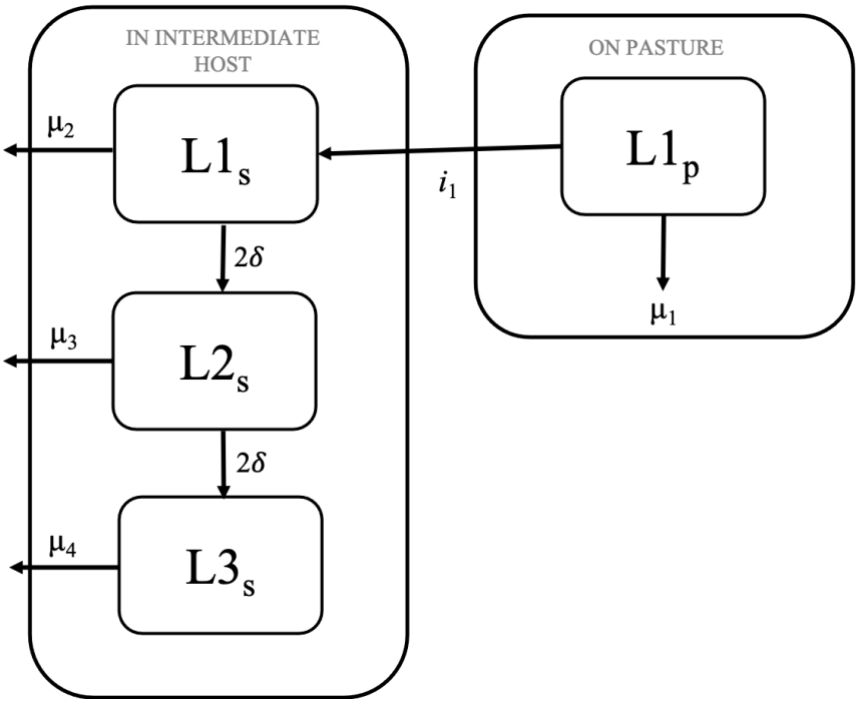


Figure 4.1 Model conceptual framework showing the different larval stages and the rates of change from which equations 1-4 were derived. i_1 = infection rate of snails with L1; μ_1 = mortality rate of L1 on pasture; δ = development rate L1 to L3; $\mu_{2\text{-}4}$ = mortality rate of larvae within IH

4.2.2 Parameter estimates

To estimate parameters, data were extracted from the literature. For parasite life-history parameters, data were extracted from papers pertaining to *Elaphostrongylus rangiferi* only. As no field data are currently available to determine which gastropods act as intermediate hosts, data regarding all potential intermediate hosts were included. Where raw data were not available in text or tables, values were estimated from graphs using Plot Digitizer version 2.6.9 (Huwaldt, 2020). All data analysis and modelling was performed in R (R Core Team, 2013).

4.2.2.1 Temperature-dependent larval mortality and development rates

The scientific literature was searched for studies tracking stages of development and mortality of larvae within gastropods over time at specified temperatures, as well as studies tracking mortality of free-living L1 at a range of temperatures to represent mortality of the larvae on pasture. To date no field studies have been performed therefore studies of experimental snail infections only were available. Point data were taken of the proportion of larvae either surviving, for mortality rates, or remaining as L1 or L2, for development rates, and the number of days since the last observation. For each point instantaneous daily rates were estimated (equation 5).

$$-\ln\left(proportion\ remaining\right)/days \qquad (5)$$

For example, from Halvorsen and Skorping (1982) the estimated proportion of larvae developed to L3 in *Arianta arbustorum* after 75 days at 12°C was 0.25, therefore the instantaneous daily rate was calculated as -ln(1-0.25)/75 = 0.0038 This was repeated for data from multiple sources, replicates and temperature treatments, with separate calculations performed using event-specific model parameters for mortality rates. Data were visualised and if a linear relationship was seen linear models were fitted to the data using the "lm" function in base R (R Core Team, 2013). The linear regression equation could then be used to estimate temperature-dependent development and mortality rates for simulations based on given time-series of ambient temperatures. If a linear relationship was not present and thus the assumptions of a linear model were not supported, then data was log-transformed and re-visualised to determine if that better met the assumptions of the model.

The data were also visually inspected to determine whether intensity of infection within the snail was related to development rate and could be a confounding factor in the temperature dependence.

4.2.2.2 Temperature-dependent gastropod mortality rates

The literature was searched for experimental infection studies reporting mortality of gastropods infected with *E. rangiferi.* The overall mortality rate was used rather than the excess deaths caused by infection as this provides a better representation of natural mortality rates in the field. Despite snail mortality rates being seen to vary depending on the stage of development of the larvae, with highest snail mortality being seen around the time of the first larval moult (Skorping, 1985b), in this case only overall mortality rates were taken, as variation in the dataset prevented estimation of mortality rates based on the life cycle stage of the larvae. Furthermore, the model simulates overlapping cohorts and therefore the overall mortality rate is needed regardless of stage of infection. The data were then visualised, and linear regressions were performed using the same method as for the larval development rates.

4.2.2.3 Gastropod infection rates

The literature was searched for experimental studies reporting infection rates of gastropods exposed to a known number of larvae for a set period of time. This was transformed into instantaneous hourly infection rates using the formula described in Skorping (1988) (Equation 6). This was converted into daily rates by multiplying by 24. The data were then visualised, and linear regressions were performed using the same method as for the larval development rates.

$$\frac{-\ln\left(1 - mean\ parasites\ per\ host * \frac{hosts}{exposure\ density}\right)}{hosts * exposure\ duration(hrs)} \quad (6)$$

As age of larvae is also known to have an effect on infectivity of L1 this was also considered in a multiple regression alongside temperature.

4.2.3 Model simulations

To test model performance, the model was run for an example herd over a three-year period with variation of the mortality rate parameter. Daily mean temperature data from 01-01-2018 – 31-12-2020 was obtained from the EOBS gridded dataset (version 23.1) at the 0.1 degree scale (Cornes et al., 2018). This was downloaded as a NetCDF file which was opened and data extracted in R using functions in the ncdf4 package (Pierce, 2019).

The model was then run over the entire Norwegian reindeer range encompassing both the semi-domesticated and wild reindeer using the EOBS data for a five-year period from 2016 – 2020. It was also run over a single semi-domesticated herd's geographic area using GPS data as described in Chapter 3 in order to demonstrate how this model could be used to provide spatial estimates of presence of infective L3 on a small scale.

In all model runs the larval input was kept at a constant of 100 larvae per gram faeces per day. As average daily faecal production of reindeer was not known and there is significant seasonal variation in faecal consistency (Ahman and White, 2019), the model was run using average daily faecal output of sheep (2000g) as presented in Rose et al. (2015) as proxy. Average reindeer density was also unknown so the density of sheep of 15 animals per hectare from Rose et al. (2015) was used. As these values were kept constant through the model runs they would only affect the number of larvae predicted to have developed, but not the temporal patterns, and therefore would not impact on the results in a meaningful way.

4.3 RESULTS

4.3.1 Parameter estimates

Parameter estimates are summarised in Table 4.1.

4.3.1.1 Temperature-dependent larval mortality

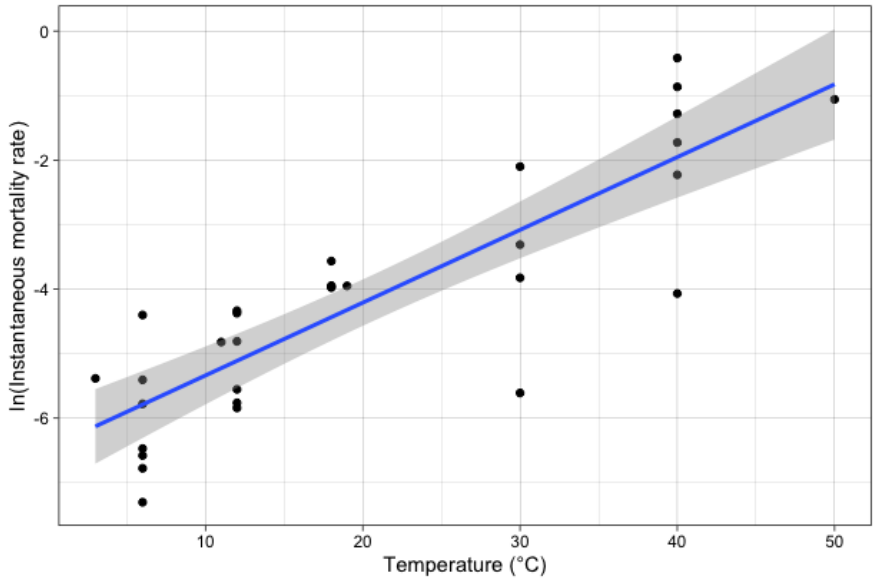
Free-living L1: A total of 40 data points were available for mortality of free-living L1 from two sources at temperatures ranging from 6 – 40°C (median 18°C) and a range of sampling periods from 2-210 days (median 45 days) (Table 4.1). Data visualisation revealed a non-linear relationship between the variables, but log transformation of the mortality rate revealed a linear relationship with a strong positive association between the variables. The linear model performed on the transformed data revealed the majority of the variation was explained by temperature (Adjusted R^2: 0.719, Figure 4.2a), thus the resulting regression equation was back transformed to provide the temperature-dependent instantaneous mortality rates within the model.

L1 – L3 in the IH: In the case of mortality of larvae within the gastropod intermediate host, rates were only available from one study at 3°C (Table 4.1), therefore no relationship between mortality and temperature could be determined. Similarly, data were not available for this parameter for any other Arctic protostrongylids due to the methodology used in the experiments requiring the larvae to be killed before assessing stage of development (Kutz et al., 2002; Kafle et al., 2018).

Table 4.1 Model parameters as defined in Figure 4.1, parameter estimates as equations which were used in the model, alongside the linear model statistics and data sources.

i – infection rate of snails with free-living L1 (instantaneous daily rate)	0.0153577 + 0.0017151 * temp	Multiple R^2: 0.2133, Adjusted R^2: 0.1901 $F_{1,34}$: 9.217, p: 0.004577	(Skorping, 1988, 1982)
μ_1 – mortality rate of free-living L1 (instantaneous daily rate)	exp(-6.46559 + 0.11278 * temp)	Multiple R^2: 0.7284, Adjusted R^2: 0.719 $F_{1,29}$: 77.76, p: 1.056e-09	(Halvorsen et al., 1980; Lorentzen and Halvorsen, 1986)
δ – development rate of L1 to L3 within IH (instantaneous daily rate)	-0.0134121 + 0.0015694 * temp	Multiple R^2: 0.4965, Adjusted R^2: 0.4125 $F_{1,6}$: 5.916 p: 0.05101	Halvorsen and Skorping 1982, *Arianta arbustorum* data only
μ_{2s}-μ_{4s} Gastropod mortality rate component	exp(-7.76093 + 0.13935 * temp)	Multiple R^2: 0.1897, Adjusted R^2: 0.1762 $F_{1,60}$: 14.05 p: 0.0004024	(Halvorsen and Skorping, 1982; Skorping, 1985b)

a)



b)

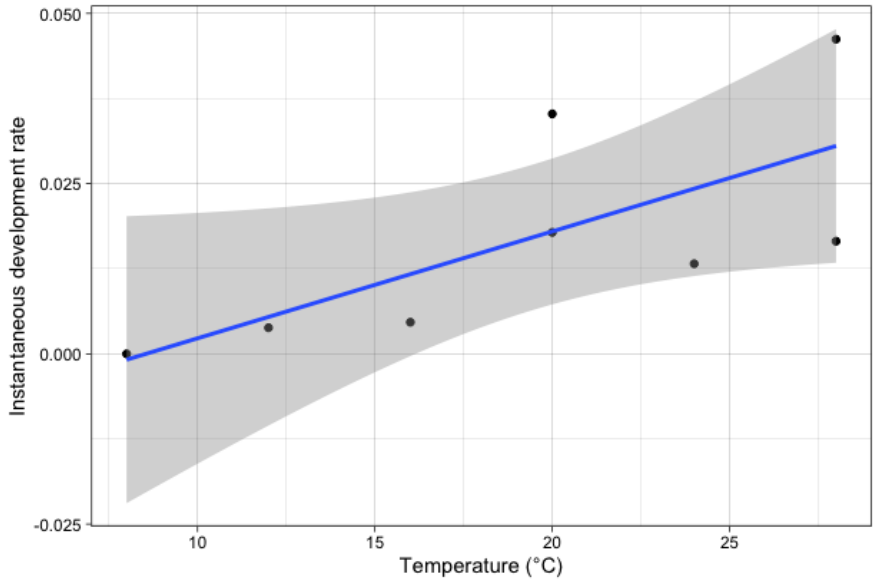
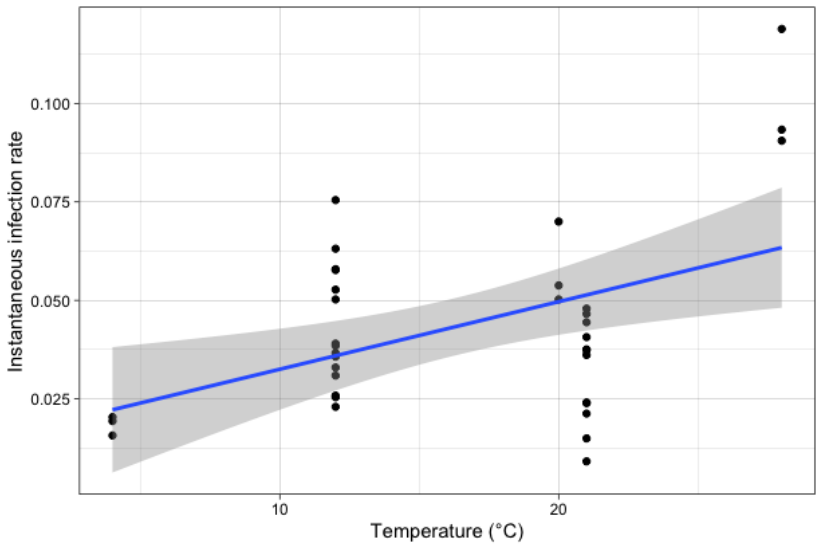


Figure 4.2 (A-B) Data (black points) and linear models (blue lines) with the 95% confidence interval (grey) used to parameterise the model a) The log transformed instantaneous daily mortality rate of free-living L1. Adjusted R^2= 0.719, p =1.056e-09; b) Instantaneous daily development rate from L1-L3. Adjusted R^2= 0.4125, p= 0.05101

c)



d)

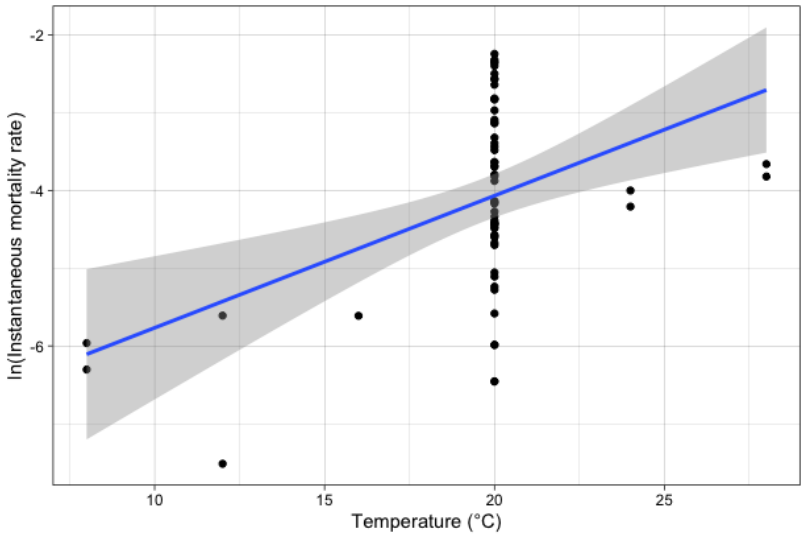


Figure 4.2 (C-D) Data (black points) and linear models (blue lines) with the 95% confidence interval (grey) used to parameterise the model c) Infection rate of gastropods with L1. Adjusted R^2= 0.1901, p= 0.004577; d) The log-transformed instantaneous daily gastropod mortality rate. Adjusted R^2= 0.1762, p= 0.0004024

4.3.1.2 Temperature-dependent larval development

Initially only overall development rate from L1 to L3 was considered, and a total of 53 data points were available from five sources at a range of temperatures from 8-28°C (median 20°C) and 12-180 days post infection (median 25.5 days) across 12 species of gastropod (Table 4.1). Infection intensity within the gastropod was known only for a limited number of these samples, and was variable where recorded. Due to the methodologies used in the sources requiring killing a sample of infected gastropods there are some cases where at a later sampling of gastropods within the same group a lower proportion of developed larvae were found than at an earlier sampling date, likely due to the balance between development and mortality at different time points and heterogeneity in infection intensity between individual gastropods. When these data were visualised, there was no clear relationship between instantaneous daily development rate and either temperature, larval density, or a combination of the two factors (Figures 4.3 and 4.4). A linear regression of development rate dependent on infection intensity was non-significant ($p=0.34$, Figure 4.3). A linear regression performed between development rate and temperature was also non-significant and also had extremely low R^2 values (Multiple $R^2= 0.01406$, Adjusted $R^2= -0.005271$, $F_{1,51}= 0.7273$, $p= 0.3977$ (Halvorsen et al., 1980; Halvorsen and Skorping, 1982; Skorping, 1985a, 1984; Skorping and Halvorsen, 1980). This lack of a clear pattern, and data which violate the assumptions of a linear model, meant it was not possible to fit a model with which to predict development rates at either a specified temperature or larval density.

In order to verify this, development rates from L1 to L2 were also extracted from the literature and plotted. Data were only collected where development had occurred solely to L2 and none had developed through to L3 thus the sample size was smaller than for the L1-L3 development and a total of 26 data points were available for development to L2 from three sources at a range of temperatures from 12-28 days (median 20 days) and 6-60 days post infection (median 14 days) across three species of gastropod, all of which were snails (Table 4.1). There was a considerable amount of variation between development rates calculated at different timepoints during the same experiment. The methods are the same as those above with the snails being killed

at each collection therefore the observations at each time point can be considered independent from each other. No clear relationship could be ascertained from this data (Figure 4.5).

In order to provide a putative equation for testing the model behaviour, the relationship between development rate and temperature was calculated based solely on data for *Arianta arbustorum* from Halvorsen and Skorping (1982) (Figure 4.2b), as a linear regression on this provided a better approximation for the relationship when compared to the relationship between development and temperature seen in other nematodes within gastropod hosts, for example *Angiostrongylus vasorum* (Ferdushy et al., 2010).

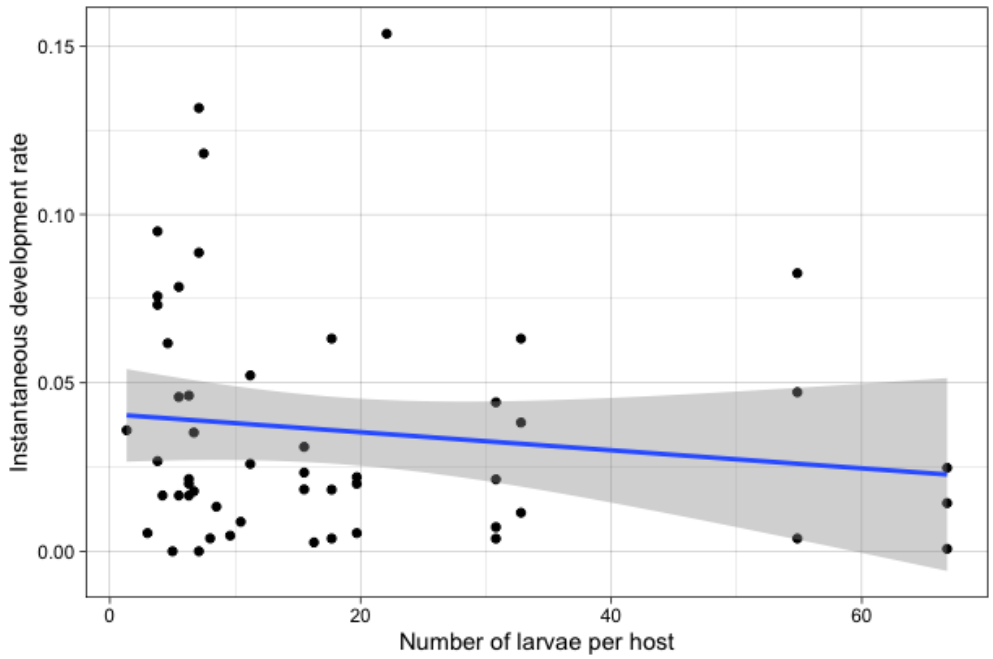


Figure 4.3 Relationship between number of larvae per host and instantaneous development rate. Regression line (blue) and 95% confidence interval (grey); Adjusted R^2= -0.001147, p-value= 0.3366

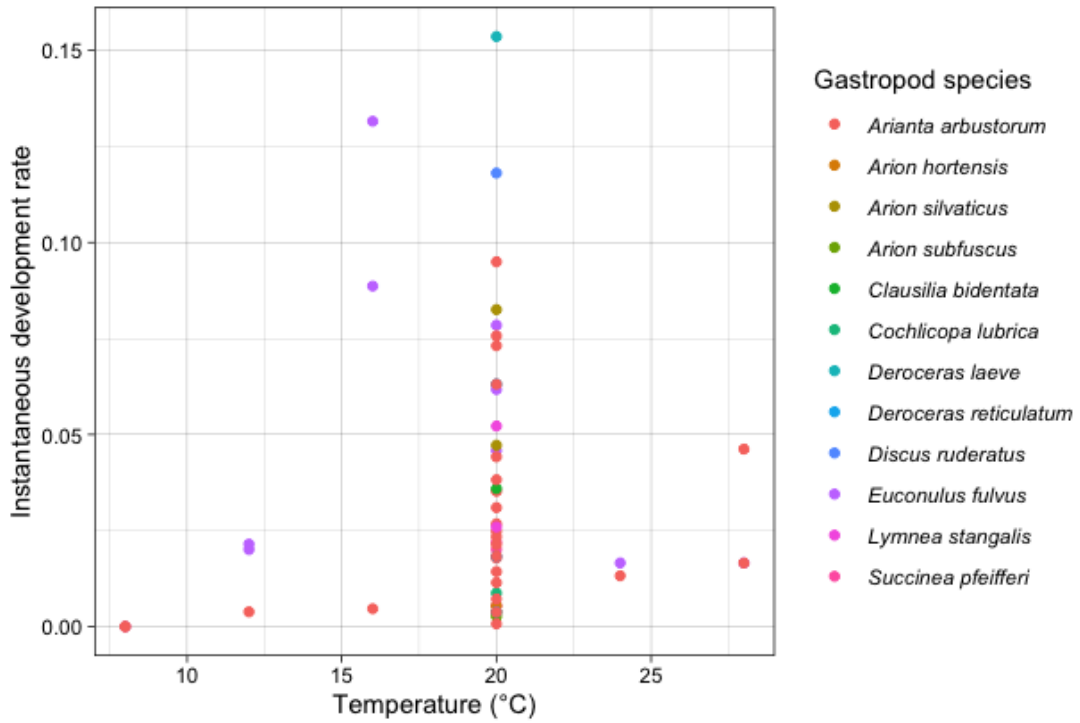


Figure 4.4 The instantaneous development rate of first- to third-stage larvae shows no clear relationship with temperature. The colours represent different gastropod species with the majority of the sampling being performed at 20°C

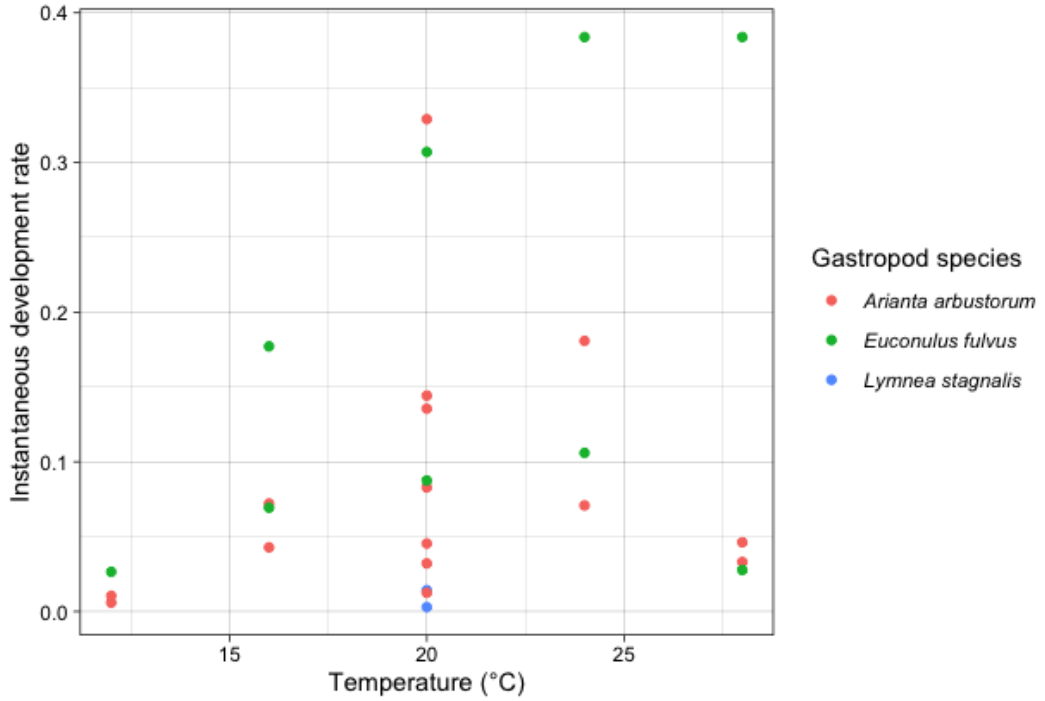


Figure 4.5 The instantaneous development rates of L1 to L2 for three gastropod species show no clear relationship with temperature, with high levels of variability between rates at the same temperature for different samples.

4.3.1.3 Gastropod infection rates

Data were available from multiple sources regarding infection rates of snails when exposed to a known number of larvae for a set period of time (2 hours). A total of 36 data points were available from two sources for *Arianta arbustorum* at exposure densities between 1000 – 128,000 larvae (median 6000) with mean number of resulting infections ranging from 2.9-110.9 (mean 32.6) (Table 4.1). A linear regression revealed a weak but significant relationship between infection rate and temperature (Adjusted R^2= 0.1901, p= 0.004577; Figure 4.2c). As described, age of the larvae has been previously associated with reduced infectivity. Larval age data were available for a total 12 data points at 5, 20, 34 and 64 days (three samples at each) at 12°C in *Arianta arbustorum* and so this was included alongside temperature as an explanatory variable in a multiple regression. This produced an adjusted R^2 value of 0.3833 (p = 0.0188) leaving significant levels of the variation unexplained.

4.3.1.4 Gastropod mortality rate

A total of 61 data points were available for mortality rate of infected snails, from two sources and for two species, at temperatures ranging from 8-28°C (median 20) and 4-150 days (median 35) (Table 4.1). Snail mortality demonstrated a non-linear relationship with temperature and therefore was log transformed prior to linear regression. Gastropod mortality was significantly positively associated with temperature, but there was significant unexplained variation (Adjusted R^2= 0.19, p= 0.0004, Table 4.1, Figure 4.2d). When infection intensity was added to a multiple regression alongside temperature the adjusted R^2 value was 0.3866 (p = 2.044e-07) showing that although there was a significant relationship between infection intensity and mortality, there was still a large amount of variation in mortality rates unaccounted for.

4.3.2 Model simulations

Due to the lack of data on larval mortality within the gastropod the only measure of mortality incorporated into this model was gastropod mortality. It is assumed here that gastropod death also leads to mortality of the larvae, preventing onward transmission. Death of a single gastropod will lead to death of all larvae within it therefore overall larval mortality depends on the intensity of the infection within the gastropod.

Following the method as described in Kutz et al. (2005) the average infection intensity can be used to estimate larval mortality rates, however in the case of *Elaphostrongylus rangiferi* only infection intensities derived from lab infections are known and the average intensity collected here of 32.6 larvae is likely higher than would be seen in the field. Multiple simulations were therefore run using different infection intensity values to compare results (Figure 4.6 a-e). When run with intensities of 1 and 5 larvae/gastropod a clear annual increase in larval abundance can be seen which is likely to be an unrealistic scenario based on outbreak data. At intensities of 10 and above, aside from annual variation, there is no overall increase or decrease in larval numbers and the population appears relatively stable. A clear seasonal pattern is seen with sequential peaks of each of the larval developmental stages. As intensity is increased, the seasonality in L3 presence is reduced and the availability becomes more constant throughout the year, however based on infection rates of reindeer peaking in the autumn (Davidson et al., 2020) it is likely that there is a seasonal pattern to infections and therefore larval availability on pasture.

The value of 15 larvae per snail was used in the mortality parameter to run all further simulations based on the visible cessation of the build-up of larvae on pasture above an intensity of 10 larvae per gastropod (Figure 4.6) and to approximate the infection intensity of 13.6 used by Kutz et al. (2005). An example output of the model over the entire Norwegian reindeer habitat shows the annual cycle of L3 presence on pasture (Figure 4.7). This localises the peak in L3 availability to the summer months of June, July, and August, with spatial differences in the timing of the peak, and a gradual decline through the autumn and winter. When run for an individual reindeer herd (Figure 4.8) there is a clear heterogeneity in L3 abundance on a small scale, even when the sole variable altering is temperature, with no changes to input based on reindeer density or larval deposition. This represents a significant heterogeneity in parasite risk to the resident reindeer. There is also clear variation year-on-year in the timing of the peak L3 abundance and therefore the time period with the highest risk of infection for reindeer.

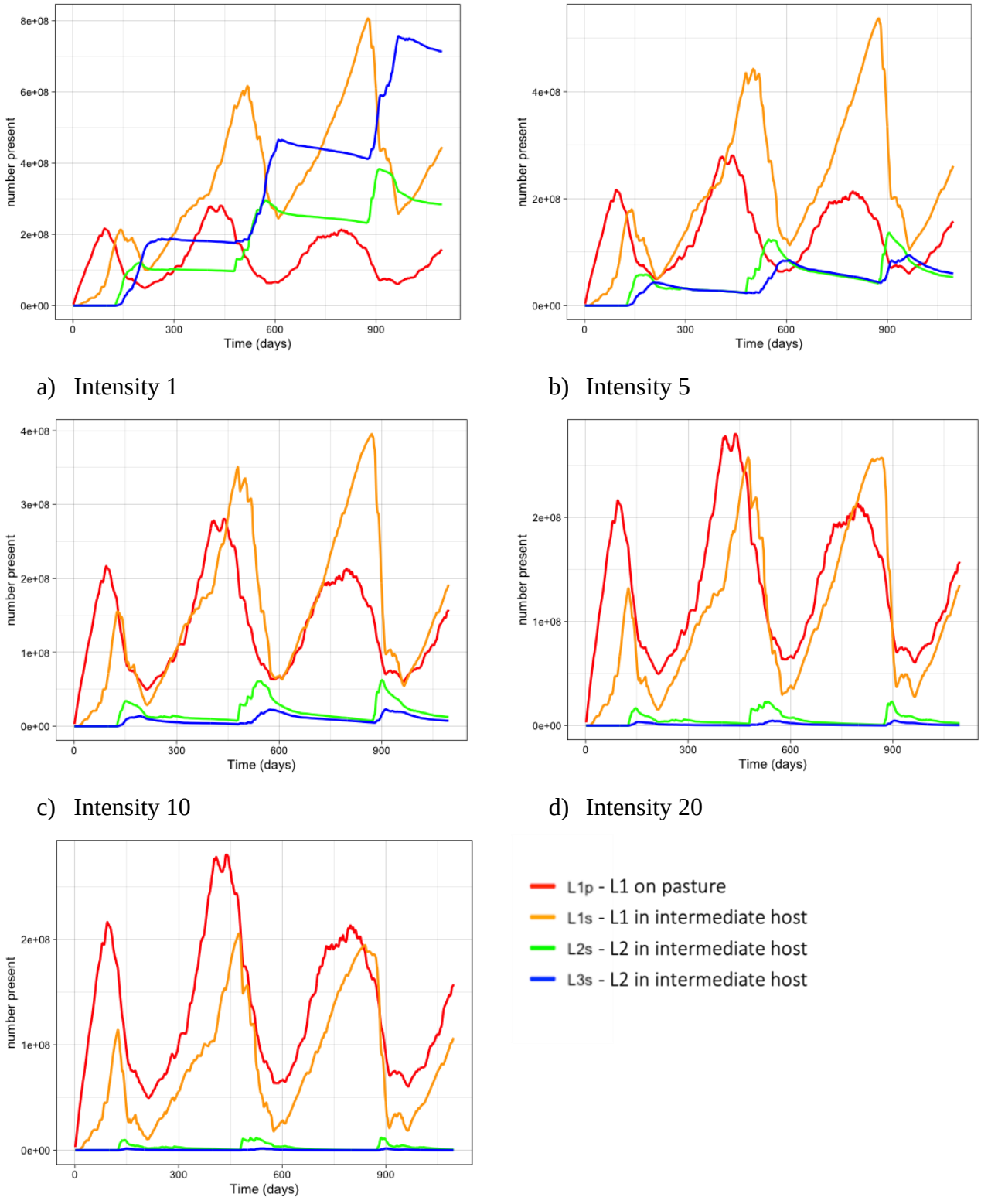


Figure 4.6 (A-E) The abundance of different stages of larvae over a three-year period run with daily input on 100 L1 per gram faeces deposited on pasture with different gastropod infection intensity-related mortality rates. Panels a-e represent different numbers of larvae within the intermediate host. The small fluctuations represent small daily changes in temperature with an overall clear seasonal pattern discernible. Red = L1p, Orange = L1s, Green = L2s, Blue = L3s

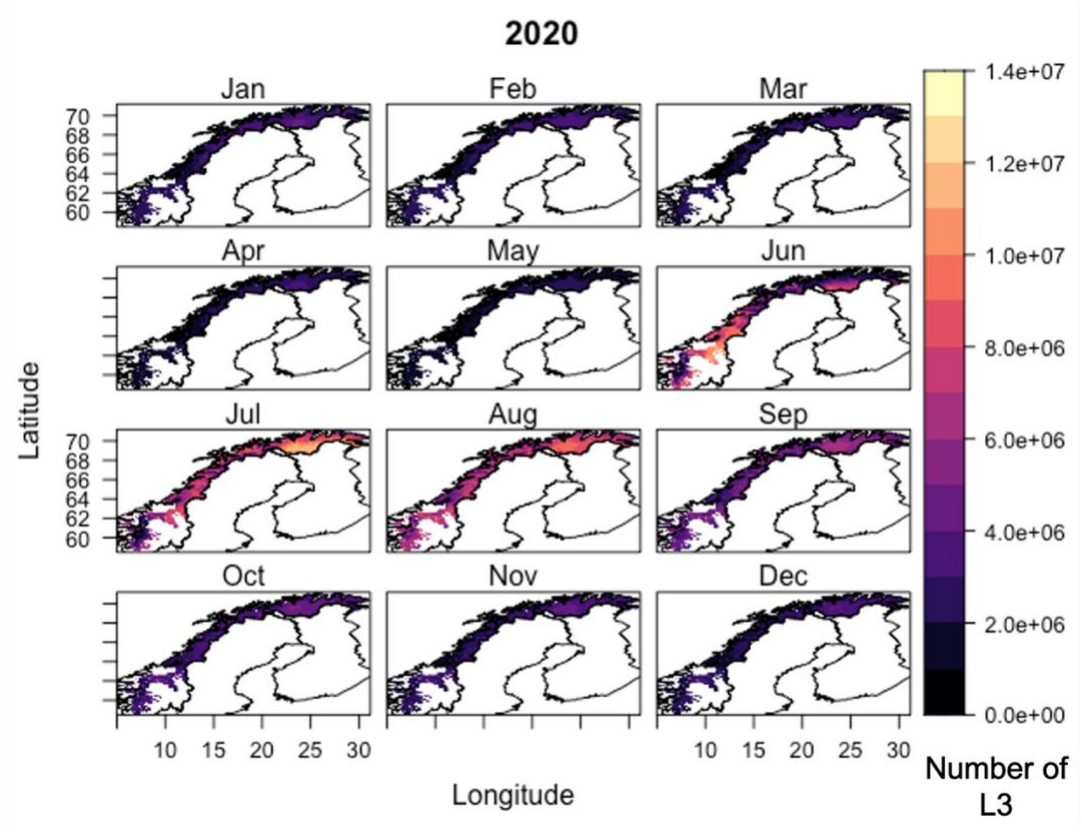
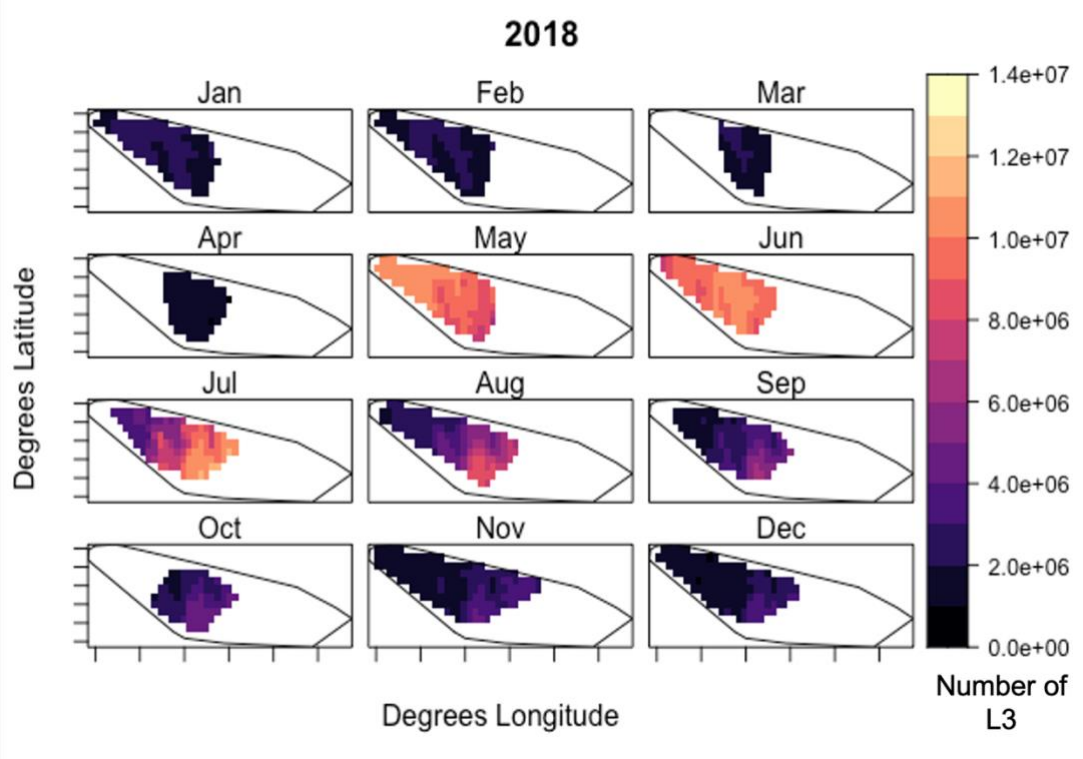


Figure 4.7 The model was run over the entire Norwegian reindeer habitat for 5 years from 2016-2020, the year 2020 is shown here as an example with the total number of L3 depicted by month (scale bar).

A)



B)

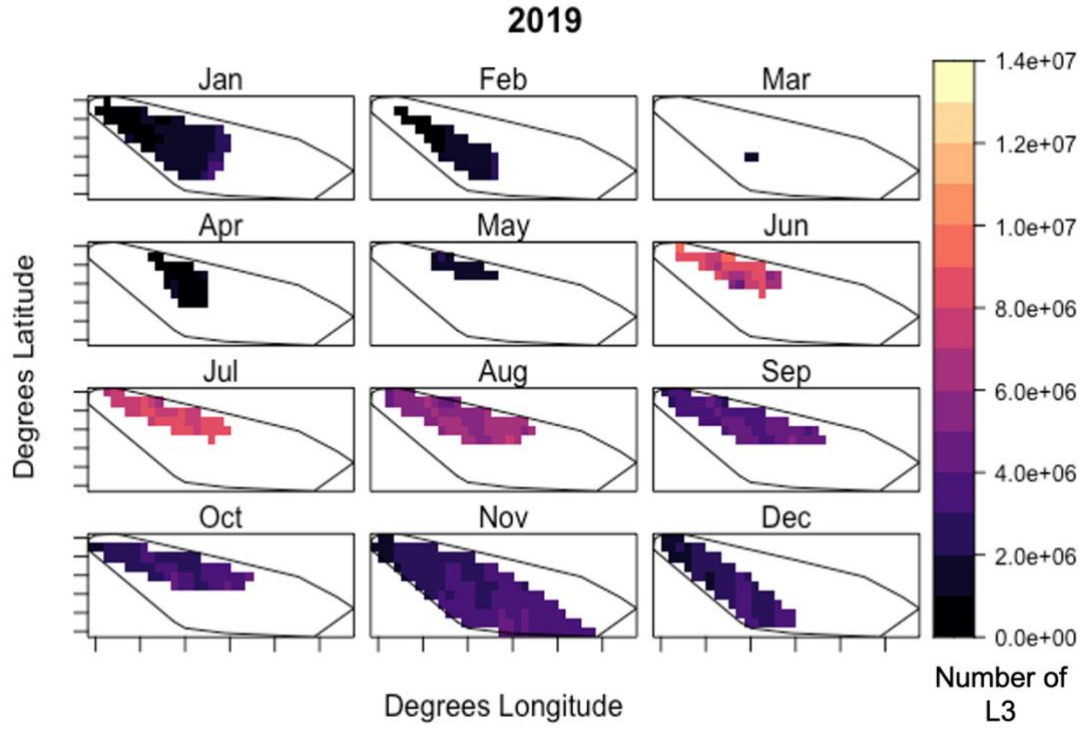


Figure 4.8 (A-B) An example of the spatial distribution of L3 abundance over the range of a reindeer herd by month, for the years 2018 and 2019. The outlined area represents the annual herd range, with the area coloured each month representing their current position. The values on the x and y axes have been removed to preserve anonymity of the herd; the ticks on the x axis represent 0.5º longitude and y axis represent 0.2 º latitude.

C)

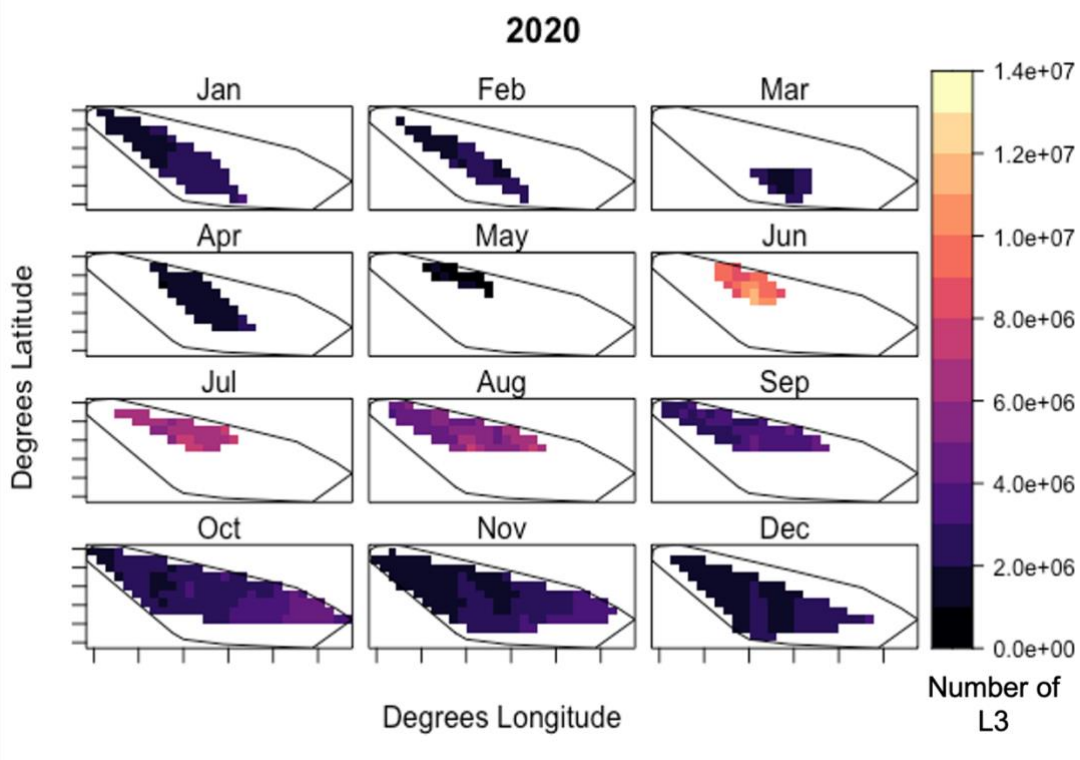


Figure 4.8 C An example of the spatial distribution of L3 abundance over the range of a reindeer herd by month, for the year 2020. The outlined area represents the annual herd range, with the area coloured each month representing their current position. The values on the x and y axes have been removed to preserve anonymity of the herd; the ticks on the x axis represent 0.5º longitude and y axis represent 0.2 º latitude.

4.4 DISCUSSION

As outbreaks of clinical elaphostrongylosis in Norwegian reindeer have previously been related to environmental conditions (Handeland and Slettbakk, 1994; Halvorsen, 2012) this model focuses on the extra-mammalian stages of the parasite lifecycle as it is these stages that are more affected by environmental conditions, and therefore show the greatest level of variation year on year. Although the model framework and structure can be seen to produce the expected patterns of larval development at certain input parameter values, there are currently several constraints to its use as a predictive tool to enable management decisions based on the timing and location of areas with high risk of reindeer infection.

As demonstrated, there is large variation created in the predictions by varying the infection intensity within the gastropod and its effects on the mortality rate within the model. Field data regarding natural infections with protostrongylids is lacking, however field surveys in Bulgaria found multiple protostrongylid species in 8 out of 14 gastropod species collected. There was a high level of variation in infection intensities between gastropod species, with the highest intensity of infection in three species of gastropod, reaching 43, 26 and 18 nematodes respectively. The remaining species had a maximum infection intensity in the range of 3-6 nematodes. There was also variation in intensity seen between the different nematode species (Georgiev et al., 2003). Kutz et al. (2002) found a slightly higher mean intensity of *Umingmakstrongylus pallikuukensis* larvae in *Deroceras laeve,* with a large degree of variation (mean 13.6 larvae/slug). These are however much lower than the maximum intensities found in lab studies, for example Skorping (1988) induced mean infection intensities of *E. rangiferi* in *A. arbustorum* of up to 100.9 larvae/snail. There is also a higher mortality rate of gastropods with increased densities of L1 within the IH (Skorping, 1984), which in the field may balance out the highest infection intensities seen experimentally. These relationships are not clearly defined as there is still a high level of overdispersion of parasite burden, even when each individual gastropod is exposed to larvae at the same dose. Therefore is it possible that the unequal exposure of gastropods to larvae in natural field situations will exacerbate this overdispersion (Skorping, 1985b). There may also be an effect of increasing infection intensity on decreasing development rates within the gastropod; although the relationship seen

here was non-statistically significant (Table 4.1), improved data on the development rates of larvae may reveal a stronger relationship. The relationship between temperature and development rate revealed no clear pattern even though it was hypothesised to be a strong relationship; this could be due to the high level of variation between experimental studies and the wide variety of gastropod species from which data were taken. Field surveys of infection could identify in which gastropod species *E. rangiferi* larvae are most commonly found, therefore focusing the input data for the model. This could also provide data on the average infection intensities within the host, further improving the predictions as previously stated. These two areas would provide the greatest improvement to parameterisation of the model and therefore should be prioritised in future research.

Larval mortality could not be explicitly incorporated into this model due to a lack of data. Experiments have been performed examining the death of larvae but in some cases it was difficult to determine whether larvae were alive or not (Lorentzen and Halvorsen, 1986; Schjetlein and Skorping, 1995). This lack of available and reliable data for parameterisation is a common problem in mechanistic epidemiological models of parasite systems so alternative methods are often employed to overcome this. Beltrame et al. (2018), for example, overcame a lack of applicable historical epidemiological data by applying 'expert-driven rules' to aid in evaluation of the model where data was lacking by reducing the number of parameter sets. This technique also used by Rose Vineer et al. (2020) to estimate the decline of immunity to gastrointestinal nematodes in cattle over the housing period for parameterisation of a mechanistic model of the intra-mammalian stages of the parasite lifecycle. Therefore, the methods used here to parameterise the model in areas where data were lacking was deemed appropriate.

A limitation of this model is that it sets no maximum for infection level, i.e. it assumes an unlimited population of gastropods to infect, with the infection rate parameter assuming a limitless intensity of infection within them. No data currently exist regarding the maximum level of infection permissive of gastropods and therefore no assumptions could be made. Additionally, as the gastropods themselves are not explicitly included in the model, inclusion of this measure would necessitate a large increase in model complexity.

The ability of the first stage larvae to infect the gastropod intermediate host declines with age of the larvae, and so L1 must infect a gastropod host within a short period after deposition for maximum establishment rates to be achieved. A reduction in establishment rates, seen as a reduction in infection intensity in the intermediate host, has been observed experimentally in L1 stored for just 3 weeks (Skorping, 1988). After 2 months a 50% reduction has been observed, with all larvae having died after 90 days storage at 12°C. At higher environmental temperatures this reduction in infectivity is accelerated (Skorping, 1982). The varying of parameters over time that would be necessary to incorporate the relationship between larval age and infectivity would also add an additional layer of complexity to the model.

Another aspect not considered in this model is the overwintering of the gastropods. The data included for gastropod mortality is solely for positive temperatures, but in winter when sub-zero temperatures are reached it is likely that gastropod mortality will increase. Additionally, no behavioural thermoregulation of the snails at low temperatures is accounted for in the model, but for that to be taken account the optimum temperature zones for each species must be known.

The output from the model shows that it can reveal temperature-induced heterogeneities in parasite abundance across a habitat even with equal parasite deposition; with the input of reindeer movement and varying density, and spatiotemporal deposition of larvae, this heterogeneity is likely to be increased. The development of an accurate population dynamics model would allow the prediction of development of the larvae, and thus the areas of the reindeer habitat that are likely to have higher risk of infection at certain times. This could lead to improved control by aiding in informing herder decisions regarding preventative measures including movement of the herd or timing of treatment.

The peak infectious L3 availability on pasture predicted in this model does not currently appear to coincide with the periods of the year when reindeer are immunosuppressed (in autumn during the rut and in the spring during calving for males and females respectively (Halvorsen et al., 1985)), however as this is due to the environmental conditions during that period, it is possible that this peak will shift with

climate change, and if it becomes earlier it may coincide with the suppression of immunity seen in peri-parturient females, and may also affect the development of disease in calves due to them being exposed to a higher infectious burden earlier in life, before immunity can develop.

Overall, the model represents the expected developmental pathway of the larval stages and can exhibit seasonal variations in infectious larvae abundance. With improvements to the accuracy of the parameter equations this model could be effectively applied over spatial areas to predict timing of high infection risk for reindeer.

CHAPTER 5: GENERAL DISCUSSION

5.1 KEY FINDINGS

Although brainworm disease has long been known about in Norway, many details regarding transmission remain unknown. The areas of the reindeer habitat in which they are becoming infected had not been determined. The species distribution models developed for potential gastropod intermediate host species (Chapter 2) provide a first insight into where these areas might be. They predict that the areas suitable for gastropod habitation, and thus the areas with potential for parasite transmission, may increase in certain areas of the Norwegian reindeer habitat in response to the changing climate. The degree-day model previously developed (Rose Vineer et al., 2021) was also applied to these climate change projections and revealed an increase in thermal suitability for larval development across all emissions scenarios and time periods modelled (Chapter 2). This increase was particularly prominent across the habitats of the semi-domesticated reindeer, but in the high emissions scenario the majority of the wild reindeer herd habitats also showed a switch from the currently predominating two-year lifecycle to the climate being suitable for development of L1 to infectious L3 within the gastropod host within the same year as deposition of L1 on pasture, leading to a potential increase in risk of infection of the reindeer.

The degree-day model was also used on a small scale to determine potential monthly risk of brainworm infection in a wild and a semi-domesticated reindeer herd by mapping areas of the reindeer herd's habitat in which the cumulative number of degree-days had reached or exceeded the number required for development of the larvae within the intermediate host (Chapter 3). This model, using daily weather data, revealed the earliest time period for transmission was July, with little variation year-on-year. This provided an estimate of the timing of peak infection risk and an initial indication of the timing of preventative management strategies. This work provides a useful framework which could be applied to any herd, including those with different movement strategies. With further validation incorporating intensities of infection this could be developed into a useful tool for reindeer herders to aid in management

decisions as it is relatively computationally inexpensive. However, the model is limited to a linear relationship between temperature and parasite development and therefore more refined models may be needed.

The development of more complex models containing more parameters, although computationally more expensive, can provide a better representation of the development and transmission system. The adaptation of the GLOWORM-FL model, originally developed for gastro-intestinal nematodes (Chapter 4), demonstrates the advantages of this. The incorporation of temperature dependent mortality of free-living larvae and larvae within gastropods, as well as the infection rate of gastropods as well as larval development rate means that this model can be run on multi-year cycles with no excessive build up of infection risk, closer approximating the true cycling of infectious larvae. This model also demonstrated a seasonal pattern in infectious L3 abundance with the peak appearing in the months of June, July and August in different areas of the reindeer habitat. In contrast to the degree-day model this model predicts different timings of the peak risk period for reindeer infections between different years. With further data collection for refinement of the parameters and clarifications on the temperature-dependent relationships this model too could be of use as a risk-forecasting tool.

5.2 THE USE OF MODELS IN PARASITE FORECASTING

Mechanistic parasite development and transmission models can be of great benefit for planning control measures such as the timing of drug treatments (e.g. Davis et al., 2018), predicting periods of heightened risk to optimise resource use (e.g. Babayani et al., 2016), to compare different control strategies (e.g. Berk et al., 2016) and for exploring the effect of control strategies on the development of anthelmintic resistance (e.g. Dobson et al., 2011; Nielsen et al., 2019). The aims of the models generated in this thesis are to aid in decision making regarding movement of reindeer herds and potentially the timing of anthelmintic treatment, in order to reduce incidence and severity of outbreaks of clinical elaphostrongylosis.

These models, as applied at a spatial level, can indicate in which areas there is likely to be a higher burden of infectious L3 within gastropods, based on the environmental

conditions in that area, and therefore an increased risk of transmission of the parasite. Knowledge of these areas could allow herders to move reindeer to new pastures that are at lower risk. There is a dose-response relationship between infective dose and onset and severity of clinical signs (Handeland et al., 1994). Therefore, management to reduce level of exposure and level of infection, although not avoiding disease completely, could limit the morbidity and mortality seen.

Several forecasting systems for ruminant parasites based on climatic data are already in use. The SCOPS (Sustainable Control Of Parasites in Sheep) *Nematodirus battus* forecast (scops.org.uk) uses data from 140 weather stations across the UK to produce a colour coded warning of the likelihood of parasite emergence in that area on a daily basis based on a model by Gethings et al., (2015). The National Animal Disease Information Service (NADIS) produces forecasts for parasitic gastroenteritis (based on Thomas and Starr, 1978) and *Fasciola hepatica* (based on Ollerenshaw and Rowlands, 1959) in ruminants, and blowfly strike in sheep (based on Wall et al., 2000) using weather data from the met office on a $40km^2$ grid on a monthly basis (nadis.org.uk). These forecasts are used by both farmers and vets to advise on and enact preventative control measures and it is hoped that the production of a comparable tool for *E. rangiferi* could similarly be useful in control, however there may be added challenges in ensuring the information was readily accessible to Sami herders. In addition, a forecasting tool could be of benefit to keepers of small ruminants which may co-graze with reindeer or make use of the same pasture at different times of year.

5.3 LIMITATIONS TO THE MODELS AND DATA

No model can be a perfect representation of a disease system, and modelling necessitates assumptions which result in the omission of potentially important factors and relationships. Each type of model therefore comes with its own set of assumptions and limitations. Although the models developed here have potential for future development into predictive forecasting tools, there are currently several limitations to their capacity.

An issue with the application of degree-day models is the large changes that can be induced in the model with even a small change in the value of the minimum developmental temperature, and the data on time taken for development to occur, which has a great dependence on sampling interval. These types of models are most accurate when applied in the same temperature ranges as used in the experimental studies that defined the parameters, but any uncertainty in these parameters can severely limit the applicability of the model, and especially when using them to predict future distributions under different climates, and to aid in the timing of intervention measures (Moore et al., 2012). The areas where this uncertainty is going to be most apparent are the areas in which it is most necessary, for example at the borderline between predicting a one-year development cycle and overwintering of the parasites being predicted. Although this is unlikely to affect the climate change projections to a great extent (Chapter 2), it will have a relatively bigger effect when used over a smaller time scale such as in Chapter 3.

A major current limitation is the lack of data on which species of gastropods act as intermediate hosts for *E. rangiferi* in the wild. The species distribution models in Chapter 2 demonstrate significant differences between the distribution of slug and snail species' ecological requirements, and the development of the degree-day model reveals different development rates within them. It is also likely that they will have different minimum developmental thresholds (Halvorsen and Skorping, 1982), affecting the degree-day model. Field surveys to detect infection in different gastropod species would provide valuable data that would help refine both these models as well as the population dynamics model (Chapter 4) as the data for parameterisation could be restricted to just the relevant species, and further experimental work could be focused on these. Data on the intensity of infection in the relevant species would also be of great benefit. As shown in the population dynamics model, the intensity of infection even when applied just to the mortality parameter has a significant impact on model predictions. Additionally, this can be used in the degree-day model to incorporate mortality as was done by Kutz et al. (2005). That would introduce the potential for the model to be run over a multi-year cycle rather than each year being run separately, which would improve the quality of the predictions.

For many Arctic parasites, including *Elaphostrongylus* spp., there can be a lack of surveillance data with which to train and validate models, and this often has to be based on anecdotally reported outbreaks rather than any quantitative measure. Due to the cost and logistics of carcass submission for investigations, together with awareness of the disease, meaning definitive diagnosis is often unnecessary, there are only low numbers of submissions to the Norwegian Veterinary Institute resulting in only small amounts of data being collected on incidence of *E. rangiferi* infection in any species (Davidson et al., 2020). Difficulties accessing remote areas grazed by reindeer, especially during winter, can limit the possibilities of collecting sequential faecal samples to monitor prevalence over time. However, the high freeze-tolerance of *E. rangiferi* (Lorentzen and Halvorsen, 1986) means that samples will not be affected by being frozen on the ground prior collection and they can also be stored for long periods of time. Therefore, this method of surveillance may be more feasible for long term monitoring, to provide data for validation of models.

"Community-based monitoring" and local/traditional ecological knowledge are key factors in the management of wildlife populations, especially in remote areas such as the Arctic where traditional scientific monitoring methods are harder to implement and achieve, as is giving the reindeer herders more autonomy over their own herd management (Peacock et al., 2020). Local knowledge and monitoring could be applied in this instance, for example by observations of the presence or absence of *Elaphostrongylus* spp. at slaughter. Although faecal samples provide a quantitative and non-invasive measure, they need to be sent to a lab and examined which can be difficult logistically and will result in a time delay, whereas observations of adult *Elaphostrongylus* spp. in the musculature can provide a more immediate idea of whether the management measures have been effective and whether they need to be altered in subsequent years. Additionally adult worms will be visible before larvae are detectable in the faeces (Handeland et al., 1994; Hemmingsen et al., 1993). This type of feedback with confirmation of cases is already in use to help develop the SCOPS *Nematodirus* forecast and to provide additional information to aid in decision support for farmers and vets.

In addition to experimental or field data relating to the parasite and transmission itself, there is also a high data requirement for climatic variables. Temperature is routinely

recorded from weather stations, for example by the Norwegian Meteorological Institute (met.no), however there have been issues found using data from the nearest weather stations as there can be significant differences between weather conditions recorded at neighbouring weather stations less than 10km apart (Dabbs, 2010). Surface temperature provides a better prediction of development rates than air temperature as it is a proximal variable rather than a distal one, as it is a measure of the environment that the L1 and intermediate hosts occupy. The use of air temperatures tends to overestimate the time required for development because they are generally lower than surface temperatures (Jenkins et al., 2005; Kutz et al., 2002). However, surface (or soil) temperature data are rarely available long term and only air temperatures are routinely recorded. There are other factors that can influence the soil temperature as well, including rain-on-snow events which have been found to increase soil temperatures (Putkonen and Roe, 2003). A combination a variables may be needed, however these were not available in the format required therefore could not be used in the models developed here. The importance of considering the microclimate on parasite development is shown in an experiment by O'Connor et al. (2008) where the interaction between rainfall and level of evaporation showed a stronger relationship with development of *Haemonchus contortus* than level of rainfall alone.

There can also be indirect effects of climate by its influence on other biotic relationships and there is evidence that the inclusion of these can improve a model (Araújo and Luoto, 2007). For example, there is an interesting relationship between *Deroceras reticulatum* and its parasitizing nematode *Phasmarhabditis hermaphrodita*. Although both the host and parasite have similar optimal thermal zones, slugs are more tolerant of temperatures above their optimum and at increases in environmental temperature the decreased activity of the parasite leads to less inhibition of slug activity and therefore an increase in slug fitness. A decrease in *P. hermaphrodita* prevalence was also seen at the higher temperatures (Wilson et al., 2015). However, under the conditions of winter warming *P. hermaphrodita* inhibition of slug feeding activity is increased (El-Danasoury and Iglesias-Pineiro, 2017). This shows the importance of separating out the physiological requirements of host and parasite in order to fully understand the interactions involved. However, there are extreme challenges involved in including all these biotic factors within a model, particularly due to a lack of data and understanding of the entire process and countless

interactions, and the complexity of lab studies needed to maintain and infect snail colonies to test these interactions.

5.4 DISEASE MITIGATION

In semi-domesticated herds there are limited opportunities for disease mitigation. The reindeer are generally only rounded up twice a year – once in the spring around calving, and in the autumn to sort the reindeer for sale, therefore even if a highly accurate predictive tool were developed and the ideal timing of anthelmintic treatment could be predicted it would not necessarily coincide with a period where it could feasibly be implemented. Any decision support tool developed would need to take into account current herding and management practices in order to provide practical solutions for the reindeer herders. The intended use of a tool would also need to be considered in its development. For example, a tool to aid in herding decisions may need to include forecasted weather in order to predict the development of larvae before it occurs, to allow reindeer to be moved before this. The trade-off would be a resulting decrease in accuracy of the model predictions. On the other hand, a tool to determine the timing of treatment after infection could utilise just recorded data.

Shifts in the timing of the peak larval load in relation to climate change could also alter the practicality of treatment. The optimal timing of treatment depends not only on larval availability on pasture, but also development within the reindeer. Determining the optimum timing cannot be based on faecal samples, as experimental studies have found neurological signs progressively appear from 4-5 weeks post infection, and there is a pre-patent period of 4-4.5 months. However the duration of the pre-patent period is based on data from two reindeer only therefore further validation is required (Handeland et al., 1994).

There are also only limited treatment options available. Currently the only licenced anthelmintics for reindeer in Fennoscandia are ivermectin and doramectin (Davidson et al., 2020) but there is only limited evidence for efficacy of ivermectin against *E. rangiferi*. In experimental infections ivermectin used to treat animals currently shedding larvae was found to reduce faecal shedding in some of the calves by 94%, but in others it did not appear effective at all, and larvae were found in the lungs in 5/6

of the treated calves (Nordkvist et al., 1983). These findings were supported by Oksanen et al. (1992) who found neither oral or subcutaneous ivermectin administration effectively reduced *E. rangiferi* larval shedding in naturally infected reindeer. It is thought that the routine autumn treatment of reindeer in Sweden is enough to control the parasite, but there is very little information available on the status of the disease in that country and so it is not possible to tell whether there is support for this assumption (reported in Davidson et al., 2020). However, as a relationship between infective dose and severity of clinical signs has been described in experimentally infected animals (Handeland et al., 1994), even a partial reduction may be enough to limit severity of outbreaks, and also may lead to a lower infectious burden on pasture and thus lower levels of infection the subsequent year.

Efficacy of other anthelmintics has been shown in small experimental trials, with mebendazole found to stop shedding by 50 days post treatment and fenbendazole by 15 days. One calf treated with fenbendazole was found to have a live worm within the central nervous system (CNS) but in animals treated with both benzimidazoles, granulomas containing dead worm remnants were seen, showing the efficacy of the anthelmintic at killing adults worms within the CNS (Nordkvist et al., 1983). Although these treatments are not currently licenced so cannot be recommended for treatment of reindeer, fenbendazole in particular is a widely used treatment licenced for many food producing animals so there may be potential for its use in the future.

5.5 WIDER CONTEXT

The production of an *Elaphostrongylus* spp. warning system will provide reindeer herders with a useful tool that can advise on management, but this must be interpreted in a wider context alongside a number of other intrinsic and extrinsic factors that will determine the best herding practices to be used at that time, based on a range of indicators of animal health as well as economic considerations. The management of risk of brainworm is just one aspect of reindeer management that fits into larger scope of reindeer herding decision making.

The impacts on other parasites must also be considered. In an elk population, migration was associated with increased parasite diversity and intensity of parasitism

as compared to non-migratory herds. Differing levels of intensity of infection with *Fasciola magna* between migratory herds was thought to be associated with timings of the movement, i.e. arrival at summer pasture coinciding with higher levels of infective larvae availability. There was no relationship with herd size or population density (Normandeau et al., 2020). However a significant negative association has been found between distance of summer grounds and calving grounds, and the level of warble fly infection in Norwegian reindeer (Folstad and Andersen, 1991). Therefore, any management measures introduced to mitigate the risk of *Elaphostongylus rangiferi* infection may have an impact on intensity of infection with other parasites.

Parasitism within the herd can also affect the reindeer population dynamics. In Svalbard reindeer (*Rangifer tarandus platyrhynchus*) it has been shown that high abundance of infection with *Ostertagia gruehneri* reduced the incidence of successful reproduction in female reindeer and that abundance of this parasite was related to host density the preceding year, meaning that parasite infection effectively regulated the size of the population. Treatment with anthelmintics in the Autumn was found to increase reproductive success in females the following spring (Albon et al., 2002). In the case of *E. rangiferi*, it is often young reindeer in better condition that have higher burdens of infection (Halvorsen, 1986). Interestingly, the infection and subsequent reduction in condition of the larger reindeer calves has been proposed as a mechanism via which inbreeding is reduced, as these larger calves are likely to be produced by dominant dams (Halvorsen, 1986).

Migrant animals are particularly sensitive to environmental changes, both climate and land use, due to their reliance on multiple different sites having optimal conditions. Alterations in just one of these may have large knock-on effects on the population (Robinson et al., 2009). There are many ways in which the climate can have an impact on both reindeer herders and reindeer health, including changes to winter grazing conditions. There are many factors that will impact on this and a model has been developed to try an incorporate multiple different environmental variables into predicting difficult conditions for reindeer (Vikhamar-Schuler et al., 2013). Although the model was successful at predicting bad years, it also predicted problems when herders reported there not being any. It is possible this is due to data limitations, but it

is also possible that the multifactorial nature of the climate and growing season means that there were mitigating factors in the falsely predicted years meaning they were not as harsh as was expected. The prediction of poor grazing conditions could also feedback into helping parasite management due to the relationship between level of parasitism and poor nutrition (Coop and Kyriazakis, 1999). Changes in level of snow cover will also impact on the herders themselves as it may increase difficulties in access to different areas (Peacock et al., 2020). Climate has also been found to have different effects on population abundance in coastal and inland reindeer herds in Svalbard (Hansen et al., 2019). Whether effects such as this occur in mainland Norwegian herds is unknown but as many of the northern herds migrate between inland and coastal areas (Suominen and Olofsson, 2000) this effect could affect the population in either way depending on the timing of the migration, and this is another factor that many have to be taken into account when making herding decisions.

The increased levels of infection seen in larger calves may simply be because they are able to outcompete the smaller reindeer for access to prime food sources such as forbs, which are also a preferred food source for many gastropods (Halvorsen, 1986). Alternatively the cause of this could be due to grazing decisions made by the individual reindeer in a 'parasitism vs nutrition trade-off' as has been demonstrated in faecal avoidance impacting directly transmitted gastrointestinal nematode infection (Fox et al., 2013). The smaller, and possibly weaker reindeer may be showing avoidance behaviour of this contaminated feed source as they will be unable to amount an effective immune response, whereas the reindeer in better condition will be more immunocompetent and have larger reserves so may not suffer the ill effects of parasitism so greatly, and so have less need for avoidance. Changes to grazing conditions may therefore change these dynamics as well.

5.6 CONCLUSIONS

Overall, the models that have been developed provide a useful first step in the development of a forecasting system to aid in decision making with the aim of reducing transmission of *Elaphostrongylus rangiferi* within Norwegian reindeer herds. They demonstrate that it is possible to use climatic data to predict spatiotemporal risk of transmission which could be used to inform management

strategies and provide a framework for further development. The development of the models will also help target further data collection in order to improve the reliability of the predictions made. Further data collection regarding the species of intermediate host involved in transmission in the field, as well as the temperature dependent development rate within them have been identified as key areas of research which will be of great benefit in refinement of the models and, ultimately, improving potential disease control methods. Control methods proposed to reduce incidence or severity of brainworm infection based on these models must be considered within the wider context of reindeer health and population management.

REFERENCES

Ahman, B., White, R.G., 2019. Rangifer diet and nutritional needs, in: Reindeer and Caribou Health and Disease. CRC Press, pp. 107–134.

Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E., Halvorsen, O., 2002. The role of parasites in the dynamics of a reindeer population. Proceedings of the Royal Society of London. Series B: Biological Sciences 269, 1625–1632. https://doi.org/10.1098/rspb.2002.2064

Aleuy, O.A., Hoberg, E.P., Paquette, C., Ruckstuhl, K.E., Kutz, S., 2019. Adaptations and phenotypic plasticity in developmental traits of *Marshallagia marshalli.* International Journal for Parasitology 49, 789–796. https://doi.org/10.1016/j.ijpara.2019.05.007

Aleuy, O.A., Kutz, S., 2020. Adaptations, life-history traits and ecological mechanisms of parasites to survive extremes and environmental unpredictability in the face of climate change. International Journal for Parasitology: Parasites and Wildlife 12, 308–317. https://doi.org/10.1016/j.ijppaw.2020.07.006

Aleuy, O.A., Peacock, S., Hoberg, E.P., Ruckstuhl, K.E., Brooks, T., Aranas, M., Kutz, S., 2020. Phenotypic plasticity and local adaptation in freeze tolerance: Implications for parasite dynamics in a changing world. International Journal for Parasitology 50, 161–169. https://doi.org/10.1016/j.ijpara.2019.12.004

Andersen, J., Halvorsen, O., 1984. Species composition, abundance, habitat requirements and regional distribution of terrestrial gastropods in Arctic Norway. Polar Biology 3, 45–53. https://doi.org/10.1007/BF00265567

Anderson, J.R., Nilssen, A.C., 1998. Do reindeer aggregate on snow patches to reduce harassment by parasitic flies or to thermoregulate? Rangifer 18, 3–17. https://doi.org/10.7557/2.18.1.1369

Anderson, R.P., 2012. Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. Annals of the New York Academy of Sciences 1260, 66–80. https://doi.org/10.1111/j.1749-6632.2011.06440.x

Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16, 743–753. https://doi.org/10.1111/j.1466-8238.2007.00359.x

Babayani, N.D., van Wyk, J.A., Morgan, E.R., 2016. An elaborated SIR model for haemonchosis in sheep in South Africa under a targeted selective anthelmintic treatment regime. Preventive Veterinary Medicine 134, 160–169. https://doi.org/10.1016/j.prevetmed.2016.10.016

Ball, M.C., Lankester, M.W., Mahoney, S.P., 2001. Factors affecting the distribution and transmission of *Elaphostrongylus rangiferi* (Protostrongylidae) in caribou (*Rangifer tarandus caribou*) of Newfoundland, Canada. Canadian Journal of Zoology-Revue Canadienne De Zoologie 79, 1265–1277. https://doi.org/10.1139/cjz-79-7-1265

Bartel, R.A., Oberhauser, K.S., Roode, J.C. de, Altizer, S.M., 2011. Monarch butterfly migration and parasite transmission in eastern North America. Ecology 92, 342–351. https://doi.org/10.1890/10-0489.1

Baur, B., Baur, A., 2013. Snails keep the pace: shift in upper elevation limit on mountain slopes as a response to climate warming. Canadian Journal of Zoology 91, 596-599. https://doi.org/10.1139/cjz-2013-0036

Beltrame, L., Dunne, T., Vineer, H.R., Walker, J.G., Morgan, E.R., Vickerman, P., McCann, C.M., Williams, D.J.L., Wagener, T., 2018. A mechanistic hydro-epidemiological model of liver fluke risk. Journal of the Royal Society Interface 15, 14. https://doi.org/10.1098/rsif.2018.0072

Berk, Z., Laurenson, Y.C.S.M., Forbes, A.B., Kyriazakis, I., 2016. A stochastic model to investigate the effects of control strategies on calves exposed to *Ostertagia ostertagi.* Parasitology 143, 1755–1772. https://doi.org/10.1017/S0031182016001438

Berman, D.I., Meshcheryakova, E.N., Leirikh, A.N., 2011. Cold hardiness, adaptive strategies, and invasion of slugs of the genus *Deroceras* (Gastropoda, Pulmonata) in northeastern Asia. Biology Bulletin of the Russian Academy of Sciences 38, 765–778. https://doi.org/10.1134/S1062359011080012

Bintanja, R., van der Linden, E., 2013. The changing seasonal climate in the Arctic. Presented at the EGU General Assembly 2013.

Boag, D.A., 1983. The response of terrestrial snails to the presence of ungulate feces, a source of nematode larvae (Metastrongyloidea: Protostrongylidae). Canadian Journal of Zoology 61, 1852–1856. https://doi.org/10.1139/z83-238

Bondareva, O., Genelt–Yanovskiy, E., Abramson, N., 2020. Copse snail *Arianta arbustorum* (Linnaeus, 1758) (Gastropoda: Helicidae) in the Baltic Sea region: Invasion or range extension? Insights from phylogeographic analysis and climate niche modeling. Journal of Zoological Systematics and Evolutionary Research 58, 221–229. https://doi.org/10.1111/jzs.12350

Bradley, C.A., Altizer, S., 2005. Parasites hinder monarch butterfly flight: implications for disease spread in migratory hosts. Ecology Letters 8, 290–300. https://doi.org/10.1111/j.1461-0248.2005.00722.x

Brooks, D.R., Hoberg, E.P., 2007. How will global climate change affect parasite–host assemblages? Trends in Parasitology 23, 571–574. https://doi.org/10.1016/j.pt.2007.08.016

Cabaret, J., Riseani, S., Baeza, E., 1991. Survival of Sheep and Goat 1st Stage Protostrongylid Larvae in Experimental Conditions - Influence of Humidity and Temperature. Journal of Helminthology. 65, 201–207. https://doi.org/10.1017/S0022149X00010713

Cabaret, J., Vendroux, P., 2011. The response of four terrestrial molluscs to the presence of herbivore feces: its influence on infection by protostrongylids. Canadian Journal of Zoology 64, 850–854. https://doi.org/10.1139/z86-127

Calenge, C., 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Henttonen, H., 2004. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. AMBIO: A Journal of the Human Environment 33, 436–447. https://doi.org/10.1579/0044-7447-33.7.436

Caminade, C., van Dijk, J., Baylis, M., Williams, D., 2015. Modelling recent and future climatic suitability for fasciolosis in Europe. Geospatial Health 9, 301–308. https://doi.org/10.4081/gh.2015.352

Carlsson, A.M., Justin Irvine, R., Wilson, K., Piertney, S.B., Halvorsen, O., Coulson, S.J., Stien, A., Albon, S.D., 2012. Disease transmission in an extreme environment: Nematode parasites infect reindeer during the Arctic winter. International Journal for Parasitology 42, 789–795. https://doi.org/10.1016/j.ijpara.2012.05.007

Choi, Y.H., Bohan, D.A., Potting, R.P.J., Semenov, M.A., Glen, D.M., 2006. Individual based model of slug population and spatial dynamics. Ecological Modelling 190, 336–350. https://doi.org/10.1016/j.ecolmodel.2005.04.019

Choi, Y.H., Bohan, D.A., Powers, S.J., Wiltshire, C.W., Glen, D.M., Semenov, M.A., 2004. Modelling *Deroceras reticulatum (*Gastropoda) population dynamics based on daily temperature and rainfall. Agriculture, Ecosystems & Environment 103, 519–525. https://doi.org/10.1016/j.agee.2003.11.012

Cohen, J.M., Lajeunesse, M.J., Rohr, J.R., 2018. A global synthesis of animal phenological responses to climate change. Nature Climate Change 8, 224–228. https://doi.org/10.1038/s41558-018-0067-3

Coop, R.L., Kyriazakis, I., 1999. Nutrition–parasite interaction. Veterinary Parasitology 84, 187–204. https://doi.org/10.1016/S0304-4017(99)00070-9

Cornes, R.C., Schrier, G. van der, Besselaar, E.J.M. van den, Jones, P.D., 2018. An Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. Journal of Geophysical Research: Atmospheres 123, 9391–9409. https://doi.org/10.1029/2017JD028200

Dabbs, G.R., 2010. Caution! All data are not created equal: The hazards of using National Weather Service data for calculating accumulated degree days. Forensic Science International 202, 49–52. https://doi.org/10.1016/j.forsciint.2010.02.024

Davidson, R.K., Mork, T., Holmgren, K.E., Oksanen, A., 2020. Infection with brainworm (*Elaphostrongylus rangiferi)* in reindeer (*Rangifer tarandus* ssp.) in Fennoscandia. Acta Veterinaria Scandinavica 62, 15. https://doi.org/10.1186/s13028-020-00524-4

Davis, E.L., Danon, L., Prada, J.M., Gunawardena, S.A., Truscott, J.E., Vlaminck, J., Anderson, R.M., Levecke, B., Morgan, E.R., Hollingsworth, T.D., 2018. Seasonally timed treatment programs for *Ascaris lumbricoides* to increase impact-An investigation using mathematical models. Plos Neglected Tropical Diseases 12, e0006195. https://doi.org/10.1371/journal.pntd.0006195

Descamps, S., Aars, J., Fuglei, E., Kovacs, K.M., Lydersen, C., Pavlova, O., Pedersen, Å.Ø., Ravolainen, V., Strøm, H., 2017. Climate change impacts on wildlife in a High Arctic archipelago - Svalbard, Norway. Global Change Biology 23, 490–502. https://doi.org/10.1111/gcb.13381

Ditmer, M.A., McGraw, A.M., Cornicelli, L., Forester, J.D., Mahoney, P.J., Moen, R.A., Stapleton, S.P., St-Louis, V., VanderWaal, K., Carstensen, M., 2020. Using movement ecology to investigate meningeal worm risk in moose, *Alces alces.* Journal of Mammalogy 101, 589–603. https://doi.org/10.1093/jmammal/gyaa019

Dobson, R.J., Barnes, E.H., Tyrrell, K.L., Hosking, B.C., Larsen, J.W.A., Besier, R.B., Love, S., Rolfe, P.F., Bailey, J.N., 2011. A multi-species model to assess the effect of refugia on worm control and anthelmintic resistance in

sheep grazing systems. Australian Veterinary Journal 89, 200–208. https://doi.org/10.1111/j.1751-0813.2011.00719.x
Dougherty, E.R., Seidel, D.P., Carlson, C.J., Spiegel, O., Getz, W.M., 2018. Going through the motions: incorporating movement analyses into disease research. Ecology Letters 21, 588–604. https://doi.org/10.1111/ele.12917
Duval, L., Robert, V., Csorba, G., Hassanin, A., Randrianarivelojosia, M., Walston, J., Nhim, T., Goodman, S.M., Ariey, F., 2007. Multiple host-switching of *Haemosporidia* parasites in bats. Malaria Journal 6, 157. https://doi.org/10.1186/1475-2875-6-157
EEA Copernicus, 2018. Copernicus Land Monitoring Service, Corine Land Cover data.
Egizi, A., Bulaga-Seraphin, L., Alt, E., Bajwa, W.I., Bernick, J., Bickerton, M., Campbell, S.R., Connally, N., Doi, K., Falco, R.C., Gaines, D.N., Greay, T.L., Harper, V.L., Heath, A.C.G., Jiang, J., Klein, T.A., Maestas, L., Mather, T.N., Occi, J.L., Oskam, C.L., Pendleton, J., Teator, M., Thompson, A.T., Tufts, D.M., Umemiya-Shirafuji, R., VanAcker, M.C., Yabsley, M.J., Fonseca, D.M., 2020. First glimpse into the origin and spread of the Asian longhorned tick, *Haemaphysalis longicornis*, in the United States. Zoonoses Public Health 67, 637–650. https://doi.org/10.1111/zph.12743
El-Danasoury, H., Iglesias-Pineiro, J., 2017. Performance of the slug parasitic nematode *Phasmarhabditis hermaphrodita* under predicted conditions of winter warming. Journal of Pesticide Science 42, 62–66. https://doi.org/10.1584/jpestics.D16-097
Elith, J., 2000. Quantitative Methods for Modeling Species Habitat: Comparative Performance and an Application to Australian Plants, in: Ferson, S., Burgman, M. (Eds.), Quantitative Methods for Conservation Biology. Springer, New York, NY, pp. 39–58. https://doi.org/10.1007/0-387-22648-6_4
Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x
Emanuelsson, U., 1987. Human Influence on Vegetation in the Torneträsk Area during the Last Three Centuries. Ecological Bulletins 95–111.
Estrada-Peña, A., Fuente, J. de la, Latapia, T., Ortega, C., 2015. The Impact of Climate Trends on a Tick Affecting Public Health: A Retrospective Modeling Approach for *Hyalomma marginatum* (Ixodidae). PLOS ONE 10, e0125760. https://doi.org/10.1371/journal.pone.0125760
Ferdushy, T., Kapel, C.M.O., Webster, P., Al-Sabi, M.N.S., Grønvold, J.R., 2010. The effect of temperature and host age on the infectivity and development of *Angiostrongylus vasorum* in the slug *Arion lusitanicus*. Parasitology Research 107, 147–151. https://doi.org/10.1007/s00436-010-1850-x
Fernandez-Ruiz, N., Estrada-Pena, A., 2021. Towards New Horizons: Climate Trends in Europe Increase the Environmental Suitability for Permanent Populations of *Hyalomma marginatum* (Ixodidae). Pathogens 10, 95. https://doi.org/10.3390/pathogens10020095

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315. https://doi.org/10.1002/joc.5086

Fischer, G., Nachtergaele, F., Prieler, S., van Velthuizen, H.T., Verelst, L., Wiberg, D., 2008. Global Agro-ecological Zones Assessment for Agriculture (GAEZ 2008.

Folstad, I., Andersen, O., 1991. Parasite avoidance: the cause of post-calving migrations in Rangifer? 69, 2423-2429.

Fox, N.J., Marion, G., Davidson, R.S., White, P.C.L., Hutchings, M.R., 2015. Climate-driven tipping-points could lead to sudden, high-intensity parasite outbreaks. Royal Society Open Science 2, 140296. https://doi.org/10.1098/rsos.140296

Fox, N.J., Marion, G., Davidson, R.S., White, P.C.L., Hutchings, M.R., 2013. Modelling Parasite Transmission in a Grazing System: The Importance of Host Behaviour and Immunity. PLoS ONE 8, e77996. https://doi.org/10.1371/journal.pone.0077996

Fox, N.J., Marion, G., Davidson, R.S., White, P.C.L., Hutchings, M.R., 2012. Livestock Helminths in a Changing Climate: Approaches and Restrictions to Meaningful Predictions. Animals 2, 93–107. https://doi.org/10.3390/ani2010093

Garvon, J., Bird, J., 2011. Attraction of the land snail *Anguispira* alternate to fresh faeces of white-tailed deer: Implications in the transmission of *Parelaphostrongylus tenuis.* Canadian Journal of Zoology 83, 358–362. https://doi.org/10.1139/z05-017

Gaudernack, G., Halvorsen, O., Skorping, A., Stokkan, K.A., 1984. Humoral immunity and output of 1st-stage larvae of *Elaphostrongylus rangiferi* (nematoda, metastrongyloidea) by infected reindeer, *Rangifer tarandus tarandus.* Journal of Helminthology 58, 13–18. https://doi.org/10.1017/s0022149x0002798x

Genchi, C., Mortarino, M., Rinaldi, L., Cringoli, G., Traldi, G., Genchi, M., 2011. Changing climate and changing vector-borne disease distribution: The example of *Dirofilaria* in Europe. Veterinary Parasitology, Heartworm Disease: Challenges in a Changing World American Hearthworm Society's Selected Papers Presented at the 13th Triennial State Of The Heartworm Symposium 2010 176, 295–299. https://doi.org/10.1016/j.vetpar.2011.01.012

Genchi, C., Rinaldi, L., Mortarino, M., Genchi, M., Cringoli, G., 2009. Climate and D*irofilaria* infection in Europe. Veterinary Parasitology 163, 286–292. https://doi.org/10.1016/j.vetpar.2009.03.026

Georgiev, D.M., Kostadinova, A., Georgiev, B.B., 2003. Land snails in the transmission of protostrongylids on pastures in Southern Bulgaria: variability of infection levels related to environmental factors. Acta Parasitologica 48, 208–217.

Gethings, O.J., Rose, H., Mitchell, S., Van Dijk, J., Morgan, E.R., 2015. Asynchrony in host and parasite phenology may decrease disease risk in livestock under climate warming: *Nematodirus battus* in lambs as a case study. Parasitology 142, 1306–1317. https://doi.org/10.1017/s0031182015000633

Gibbons, L.M., Halvorsen, O., Stuve, G., 1991. Revision of the genus *Elaphostrongylus cameron* (nematoda, metastrongyloidea) with particular reference to species of the genus occurring in Norwegian cervids. Zoologica Scripta 20, 15–26. https://doi.org/10.1111/j.1463-6409.1991.tb00272.x

Gils, J.A. van, Munster, V.J., Radersma, R., Liefhebber, D., Fouchier, R.A.M., Klaassen, M., 2007. Hampered Foraging and Migratory Performance in Swans Infected with Low-Pathogenic Avian Influenza A Virus. PLOS ONE 2, e184. https://doi.org/10.1371/journal.pone.0000184

Gomot, P., Gomot, L., 1991. Length of hibernation and the brain's influence on temperature-induced spermatogenic DNA synthesis in *Helix aspersa*. Comparative Biochemistry and Physiology Part A: Physiology 100, 689–692. https://doi.org/10.1016/0300-9629(91)90390-X

Habib, M.R., Guo, Y.-H., Lv, S., Gu, W.-B., Li, X.-H., Zhou, X.-N., 2016. Predicting the spatial distribution of *Biomphalaria straminea*, a potential intermediate host for *Schistoma mansoni*, in china. Geospatial Health 11, 375–383. https://doi.org/10.4081/gh.2016.453

Hagemoen, R.I.M., Reimers, E., 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71, 883–892. https://doi.org/10.1046/j.1365-2656.2002.00654.x

Hall, R.J., Altizer, S., Bartel, R.A., 2014. Greater migratory propensity in hosts lowers pathogen transmission and impacts. Journal of Animal Ecology 83, 1068–1077. https://doi.org/10.1111/1365-2656.12204

Hall, R.J., Brown, L.M., Altizer, S., 2016. Modeling vector-borne disease risk in migratory animals under climate change. Integrative and Comparative Biology 56, 353–364. https://doi.org/10.1093/icb/icw049

Halvorsen, O., 2012. Reindeer parasites, weather and warming of the Arctic. Polar Biology 35, 1749–1752. https://doi.org/10.1007/s00300-012-1209-0

Halvorsen, O., 1986. On the Relationship between Social Status of Host and Risk of Parasitic Infection. Oikos 47, 71–74. https://doi.org/10.2307/3565921

Halvorsen, O., Andersen, J., Hjermundrud, I., Wissler, K., 1976. Studies on the epidemiology of *Elaphostrongylus rangiferi* (Nematoda, Metastrongyloidea), a parasite of reindeer. The occurrence and distribution of gastropods in a selected summer pasture. Norwegian Journal of Zoology, Proceedings of the Scandinavian Society for Parasitology 24, 461.

Halvorsen, O., Andersen, J., Skorping, A., Lorentzen, G., 1980. Infection in reindeer with the nematode *Elaphostrongylus rangiferi* Mitskevich in relation to climate and distribution of intermediate hosts. Proceedings of the Second International Reindeer/Caribou Symposium, 17th-21st September 1979, Roro, Norway, Part B 449–455.

Halvorsen, O., Skorping, A., 1982. The influence of temperature on growth and development of the nematode *Elaphostrongylus rangiferi* in the gastropods *Arianta arbustorum* and *Euconulus fulvus*. Oikos 38, 285–290. https://doi.org/10.2307/3544666

Halvorsen, O., Skorping, A., Hansen, K., 1985. Seasonal cycles in the output of first stage larvae of the nematode *Elaphostrongylus rangiferi* from reindeer, *Rangifer tarandus tarandus.* Polar Biology 5, 49–54. https://doi.org/10.1007/bf00446045

Halvorsen, O., Stien, A., Irvine, J., Langvatn, R., Albon, S., 1999. Evidence for continued transmission of parasitic nematodes in reindeer during the Arctic winter. International Journal For Parasitology 29, 567–579. https://doi.org/10.1016/s0020-7519(99)00005-3

Handeland, K., 1994. Experimental studies of *Elaphostrongylus rangiferi i*n reindeer (*Rangifer tarandus tarandus)* - life-cycle, pathogenesis, and pathology. Journal of Veterinary Medicine Series B-Zentralblatt Fur Veterinarmedizin

Reihe B-Infectious Diseases and Veterinary Public Health 41, 351–365. https://doi.org/10.1111/j.1439-0450.1994.tb00238.x
Handeland, K., Davidson, R.K., Viljugrein, H., Mossing, A., Meisingset, E.L., Heum, M., Strand, O., Isaksen, K., 2019. *Elaphostrongylus* and *Dictyocaulus* infections in Norwegian wild reindeer and red deer populations in relation to summer pasture altitude and climate. International Journal for Parasitology - Parasites and Wildlife 10, 188–195. https://doi.org/10.1016/j.ijppaw.2019.09.003
Handeland, K., Norberg, H.S., 1992. Lethal cerebrospinal elaphostrongylosis in a reindeer calf. Journal of Veterinary Medicine Series B-Zentralblatt Fur Veterinarmedizin Reihe B-Infectious Diseases and Veterinary Public Health 39, 668–671. https://doi.org/10.1111/j.1439-0450.1992.tb01220.x
Handeland, K., Skorping, A., 1993. Experimental cerebrospinal elaphostrongylosis (*Elaphostrongylus rangiferi)* in goats .1. Clinical observations. Journal of Veterinary Medicine Series B-Zentralblatt Fur Veterinarmedizin Reihe B-Infectious Diseases and Veterinary Public Health 40, 141–147. https://doi.org/10.1111/j.1439-0450.1993.tb00121.x
Handeland, K., Skorping, A., 1992. Experimental Cerebrospinal Elaphostrongylosis (*Elaphostrongylus rangiferi)* in Goats. II. Pathological Findings. Journal of Veterinary Medicine, Series B 39, 713–722. https://doi.org/10.1111/j.1439-0450.1992.tb01226.x
Handeland, K., Skorping, A., Slettbakk, T., 1993. Experimental cerebrospinal elaphostrongylosis (*Elaphostrongylus rangiferi*) in sheep. Journal of Veterinary Medicine Series B-Zentralblatt Fur Veterinarmedizin Reihe B-Infectious Diseases and Veterinary Public Health 40, 181–189. https://doi.org/10.1111/j.1439-0450.1993.tb00126.x
Handeland, K., Skorping, A., Stuen, S., Slettbakk, T., 1994. Experimental studies of *Elaphostrongylus rangiferi* in reindeer (*Rangifer tarandus tarandus*): Clinical observations. Rangifer 14, 83–87.
Handeland, K., Slettbakk, T., 1995. Epidemiological Aspects of Cerebrospinal Elaphostrongylosis in Small Ruminants in Northern Norway. Journal of Veterinary Medicine, Series B 42, 110–117. https://doi.org/10.1111/j.1439-0450.1995.tb00689.x
Handeland, K., Slettbakk, T., 1994. Outbreaks of clinical cerebrospinal elaphostrongylosis in reindeer (Rangifer tarandus tarandus) in Finnmark, Norway, and their relation to climatic conditions. Journal of Veterinary Medicine Series B-Zentralblatt Fur Veterinarmedizin Reihe B-Infectious Diseases and Veterinary Public Health 41, 407–410. https://doi.org/10.1111/j.1439-0450.1994.tb00244.x
Handeland, K., Sparboe, O., 1991. Cerebrospinal elaphostrongylosis in dairy goats in northern Norway. Journal of Veterinary Medicine Series B-Infectious Diseases and Veterinary Public Health 38, 755–763. https://doi.org/10.1111/j.1439-0450.1991.tb00940.x
Hansen, B.B., Aanes, R., Herfindal, I., Kohler, J., Saether, B.-E., 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology 92, 1917–1923. https://doi.org/10.1890/11-0095.1
Hansen, B.B., Isaksen, K., Benestad, R.E., Kohler, J., Pedersen, A.O., Loe, L.E., Coulson, S.J., Larsen, J.O., Varpe, O., 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High

Arctic. Environmental Research Letters 9. https://doi.org/10.1088/1748-9326/9/11/114021
Hansen, B.B., Pedersen, A.O., Peeters, B., Le Moullec, M., Albon, S.D., Herfindal, I., Saether, B.-E., Grotan, V., Aanes, R., 2019. Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. Global Change Biology 25, 3656–3668. https://doi.org/10.1111/gcb.14761
Hansen, S.H., Halvorsen, O., 1976. *Elaphostrongylus rangiferi* (Nematoda, Metastrongyloidea) in the gastropod intermediate host. Norwegian Journal of Zoology, Proceedings of the Scandindavian Society for Parasitology 24, 462.
Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate Warming and Disease Risks for Terrestrial and Marine Biota. Science 296, 2158–2162. https://doi.org/10.1126/science.1063699
Hassol, S.J., 2004. Impacts of a warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, U.K. ; New York, N.Y.
Hausner, V.H., Fauchald, P., Tveraa, T., Pedersen, E., Jernsletten, J.-L., Ulvevadet, B., Ims, R.A., Yoccoz, N.G., Bråthen, K.A., 2011. The Ghost of Development Past: the Impact of Economic Security Policies on Saami Pastoral Ecosystems. Ecology and Society 16.
Haydock, L.A.J., Pomroy, W.E., Stevenson, M.A., Lawrence, K.E., 2016. A growing degree-day model for determination of *Fasciola hepatica* infection risk in New Zealand with future predictions using climate change models. Veterinary Parasitology 228, 52–59. https://doi.org/10.1016/j.vetpar.2016.05.033
Hemmingsen, W., Halvorsen, O., Skorping, A., 1993. Migration of adult *Elaphostrongylus rangiferi* (nematoda, protostrongylidae) from the spinal subdural space to the muscles of reindeer (*Rangifer tarandus*). Journal of Parasitology 79, 728–732. https://doi.org/10.2307/3283612
Hijmans, R.J., 2020. raster: Geographic Data Analysis and Modeling. R package.
Hoberg, E.P., Kutz, S.J., Nagy, J., Jenkins, E., Elkin, B., Branigan, M., Cooley, D., 2002. P*rotostrongylus stilesi* (Nematoda: Protostrongylidae): Ecological Isolation and Putative Host-Switching Between Dall's Sheep and Muskoxen in a Contact Zone. Comparative Parasitology 69, 1–9. https://doi.org/10.1654/1525-2647(2002)069[0001:PSNPEI]2.0.CO;2
Hof, A.R., 2011. European terrestrial gastropod distribution. How may climate change affect their diversity and current distribution, in: Gastropods: Diversity, Habitats and Genetics. Nove Science Publishers, Inc, p. 18.
Holt, G., Berg, C., Haugen, A., 1990. Nematode related spinal myelomeningitis and posterior ataxia in muskoxen (*Ovibos moschatus)*. Journal of Wildlife Diseases 26, 528–531. https://doi.org/10.7589/0090-3558-26.4.528
Horsak, M., Chytry, M., 2014. Unimodal Latitudinal Pattern of Land-Snail Species Richness across Northern Eurasian Lowlands. PLoS One 9(8), e104035. https://doi.org/10.1371/journal.pone.0104035
Huwaldt, J.A., 2020. Plot Digitizer.
Jenkins, E.J., Veitch, A.M., Kutz, S.J., Hoberg, E.P., Polley, L., 2005. Climate change and the epidemiology of protostrongylid nematodes in northern ecosystems: *Parelaphostrongylus odocoilei* and *Protostrongylus stilesi* in Dall's sheep (*Ovis d. dalli).* Parasitology 132, 387-401. https://doi.org/10.1017/s0031182005009145

Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLoS Biology 5, e157. https://doi.org/10.1371/journal.pbio.0050157

Johns, S., Shaw, A.K., 2016. Theoretical insight into three disease-related benefits of migration. Population Ecology 58, 213–221. https://doi.org/10.1007/s10144-015-0518-x

Jylhä, K., Fronzek, S., Tuomenvirta, H., Carter, T.R., Ruosteenoja, K., 2008. Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. Climatic Change 86, 441–462. https://doi.org/10.1007/s10584-007-9310-z

Kafle, P., Peacock, S.J., Grond, S., Orsel, K., Kutz, S., 2018. Temperature-dependent development and freezing survival of protostrongylid nematodes of Arctic ungulates: implications for transmission. Parasites & Vectors 11. https://doi.org/10.1186/s13071-018-2946-x

Kafle, P., Peller, P., Massolo, A., Hoberg, E., Leclerc, L.-M., Tomaselli, M., Kutz, S., 2020. Range expansion of muskox lungworms track rapid arctic warming: implications for geographic colonization under climate forcing. Scientific Reports 10. https://doi.org/10.1038/s41598-020-74358-5

Kantzoura, V., Kouam, M.K., Feidas, H., Teofanova, D., Theodoropoulos, G., 2011. Geographic distribution modelling for ruminant liver flukes (*Fasciola hepatica*) in south-eastern Europe. International Journal for Parasitology 41, 747–753. https://doi.org/10.1016/j.ijpara.2011.01.006

Kenyon, F., Sargison, N.D., Skuce, P.J., Jackson, F., 2009. Sheep helminth parasitic disease in south eastern Scotland arising as a possible consequence of climate change. Veterinary Parasitology, Special Section: EVPC 2008: Veterinary parasitology and climate change 163, 293–297. https://doi.org/10.1016/j.vetpar.2009.03.027

Kistler, W.M., Brown, J.D., Allison, A.B., Nemeth, N.M., Yabsley, M.J., 2014. First report of *Angiostrongylus vasorum* and *Hepatozoon* from a red fox (*Vulpes vulpes*) from West Virginia, USA. Veterinary Parasitology 200, 216–220. https://doi.org/10.1016/j.vetpar.2013.12.007

Kovats, R.S., Campbell-Lendrum, D.H., McMichel, A.J., Woodward, A., Cox, J.S.H., 2001. Early effects of climate change: do they include changes in vector-borne disease? Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 356, 1057–1068. https://doi.org/10.1098/rstb.2001.0894

Kutz, S.J., Checkley, S., Verocai, G.G., Dumond, M., Hoberg, E.P., Peacock, R., Wu, J.P., Orsel, K., Seegers, K., Warren, A.L., Abrams, A., 2013. Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic. Global Change Biology 19, 3254-3262. https://doi.org/10.1111/gcb.12315

Kutz, S.J., Hoberg, E.P., Nagy, J., Polley, L., Elkin, B., 2004. "Emerging" parasitic infections in arctic ungulates. Integrative and Comparative Biology 44, 109–118. https://doi.org/10.1093/icb/44.2.109

Kutz, S.J., Hoberg, E.P., Nishi, J., Polley, L., 2002. Development of the muskox lungworm, *Umingmakstrongylus pallikuukensis* (Protostrongylidae), in gastropods in the Arctic. Canadian Journal of Zoology-Revue Canadienne De Zoologie 80, 1977–1985. https://doi.org/10.1139/z02-197

Kutz, S.J., Hoberg, E.P., Polley, L., 2001. *Umingmakstrongylus pallikuukensis* (Nematoda : Protostrongylidae) in gastropods: Larval morphology,

morphometrics, and development rates. Journal of Parasitology 87, 527–535. https://doi.org/10.2307/3285088
Kutz, S.J., Hoberg, E.P., Polley, L., Jenkins, E.J., 2005. Global warming is changing the dynamics of Arctic host-parasite systems. Proceedings of the Royal Society B-Biological Sciences 272, 2571–2576. https://doi.org/10.1098/rspb.2005.3285
Kuzmina, T.A., Kuzmin, Y.I., Kharchenko, V.A., 2006. Field study on the survival, migration and overwintering of infective larvae of horse strongyles on pasture in central Ukraine. Veterinary Parasitology 141, 264–272. https://doi.org/10.1016/j.vetpar.2006.06.005
Laaksonen, S., Pusenius, J., Kumpula, J., Venäläinen, A., Kortet, R., Oksanen, A., Hoberg, E., 2010. Climate Change Promotes the Emergence of Serious Disease Outbreaks of Filarioid Nematodes. EcoHealth 7, 7–13. https://doi.org/10.1007/s10393-010-0308-z
Lafferty, K.D., 2009. The ecology of climate change and infectious diseases. Ecology 90, 888–900. https://doi.org/10.1890/08-0079.1
Lankester, M.W., Peterson, W.J., 1996. The possible importance of wintering yards in the transmission of *Parelaphostrongylus tenuis* to white-tailed deer and moose. Journal of Wildlife Diseases 32(1), 31–38. https://doi.org/10.7589/0090-3558-32.1.31
Lantto, P., 2010. Borders, citizenship and change: the case of the Sami people, 1751-2008. Citizenship Studies 14, 543–556. https://doi.org/10.1080/13621025.2010.506709
Leathwick, D.M., Donecker, J.M., Nielsen, M.K., 2015. A model for the dynamics of the free-living stages of equine cyathostomins. Veterinary Parasitology 209, 210–220. https://doi.org/10.1016/j.vetpar.2015.02.031
Lee, J.E., Janion, C., Marais, E., van Vuuren, B.J., Chown, S.L., 2009. Physiological tolerances account for range limits and abundance structure in an invasive slug. Proceedings of the Royal Society B - Biological Sciences 276, 1459–1468. https://doi.org/10.1098/rspb.2008.1240
Liu, C., Newell, G., White, M., 2016. On the selection of thresholds for predicting species occurrence with presence-only data. Ecology and Evolution 6(1), 337–348. https://doi.org/10.1002/ece3.1878
Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40, 778–789. https://doi.org/10.2307/23463638
Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17, 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x
Loehle, C., 1995. Social Barriers to Pathogen Transmission in Wild Animal Populations. Ecology 76, 326–335. https://doi.org/10.2307/1941192
Lorentzen, G., Halvorsen, O., 1986. Survival of the first stage larva of the metastrongyloid nematode *Elaphostrongylus rangiferi* under various conditions of temperature and humidity. Ecography 9, 301–304. https://doi.org/10.1111/j.1600-0587.1986.tb01223.x
Macova, A., Hoblikova, A., Hypsa, V., Stanko, M., Martinu, J., Kvicerova, J., 2018. Mysteries of host switching: Diversification and host specificity in rodent-coccidia associations. Molecular Phylogenetics and Evolution 127, 179–189. https://doi.org/10.1016/j.ympev.2018.05.009

Manyangadze, T., Chimbari, M.J., Gebreslasie, M., Ceccato, P., Mukaratirwa, S., 2016. Modelling the spatial and seasonal distribution of suitable habitats of schistosomiasis intermediate host snails using Maxent in Ndumo area, KwaZulu-Natal Province, South Africa. Parasites & Vectors 9, 572. https://doi.org/10.1186/s13071-016-1834-5

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B., 2021. IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.

McAlpine, D.F., Noseworthy, R.G., Schueler, F.W., Sollows, M.C., Maunder, J.E., 2009. Establishment and persistence of the copse snail, *Arianta arbustorum* (Linnaeus, 1758) (Gastropoda: Helicidae) in Canada. The Nautilus 123, 5.

McCann, C.M., Baylis, M., Williams, D.J.L., 2010. The development of linear regression models using environmental variables to explain the spatial distribution of *Fasciola hepatica* infection in dairy herds in England and Wales. International Journal for Parasitology 40, 1021–1028. https://doi.org/10.1016/j.ijpara.2010.02.009

Menard, S., 2002. Applied Logistic Regression Analysis. SAGE.

Moen, J., Danell, Ö., 2003. Reindeer in the Swedish Mountains: An Assessment of Grazing Impacts. Ambio 32, 397–402. https://doi.org/10.1579/0044-7447-32.6.397

Molnár, P.K., Dobson, A.P., Kutz, S.J., 2013a. Gimme shelter - the relative sensitivity of parasitic nematodes with direct and indirect life cycles to climate change. Global Change Biology 19, 3291-3305. https://doi.org/10.1111/gcb.12303

Molnár, P.K., Kutz, S.J., Hoar, B.M., Dobson, A.P., 2013b. Metabolic approaches to understanding climate change impacts on seasonal host-macroparasite dynamics. Ecology Letters 16, 9–21. https://doi.org/10.1111/ele.12022

Molnár, P.K., Sckrabulis, J.P., Altman, K.A., Raffel, T.R., 2017. Thermal Performance Curves and the Metabolic Theory of Ecology—A Practical Guide to Models and Experiments for Parasitologists. Journal of Parasitology 103, 423. https://doi.org/10.1645/16-148

Moore, J.L., Liang, S., Akullian, A., Remais, J.V., 2012. Cautioning the use of degree-day models for climate change projections in the presence of parametric uncertainty. Ecological Applications 22, 2237–2247. https://doi.org/10.1890/12-0127.1

Moore, J.L., Remais, J.V., 2014. Developmental models for estimating ecological responses to environmental variability: structural, parametric, and experimental issues. Acta Biotheoretica 62, 69–90. https://doi.org/10.1007/s10441-014-9209-9

Morgan, E.R., Jefferies, R., Krajewski, M., Ward, P., Shaw, S.E., 2009. Canine pulmonary angiostrongylosis: The influence of climate on parasite distribution. Parasitology International 58, 406–410. https://doi.org/10.1016/j.parint.2009.08.003

Morgan, E.R., Medley, G.F., Torgerson, P.R., Shaikenov, B.S., Milner-Gulland, E.J., 2007. Parasite transmission in a migratory multiple host system. Ecological Modelling 200, 511–520. https://doi.org/10.1016/j.ecolmodel.2006.09.002

Morley, N.J., 2010. Aquatic molluscs as auxiliary hosts for terrestrial nematode parasites : implications for pathogen transmission in a changing climate. Parasitology 137, 1041–1056. https://doi.org/10.1017/S0031182010000016
Mysterud, A., Qviller, L., Meisingset, E.L., Viljugrein, H., 2016. Parasite load and seasonal migration in red deer. Oecologia 180, 401–407. https://doi.org/10.1007/s00442-015-3465-5
Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37, 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x
Nicolai, A., Ansart, A., 2017. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. Conservation Physiology 5, 1–17. https://doi.org/10.1093/conphys/cox007
Niedringhaus, K.D., Brown, J.D., Ternent, M., Childress, W., Gettings, J.R., Yabsley, M.J., 2019. The emergence and expansion of sarcoptic mange in American black bears (*Ursus americanus)* in the United States. Veterinary Parasitology: Regional Studies and Reports 17, 100303. https://doi.org/10.1016/j.vprsr.2019.100303
Nielsen, M.K., Sauermann, C.W., Leathwick, D.M., 2019. The effect of climate, season, and treatment intensity on anthelmintic resistance in cyathostomins: A modelling exercise. Veterinary Parasitology 269, 7–12. https://doi.org/10.1016/j.vetpar.2019.04.003
Nordkvist, M., Rehbinder, C., Christensson, D., Rönnbäck, C., 1983. A comparative study on the efficacy of four anthelmintics on some important reindeer parasites. Rangifer 3, 19. https://doi.org/10.7557/2.3.2.477
Normandeau, J., Kutz, S.J., Hebblewhite, M., Merrill, E.H., 2020. Living with liver flukes: Does migration matter? International Journal for Parasitology: Parasites and Wildlife 12, 76–84. https://doi.org/10.1016/j.ijppaw.2020.05.002
O'Connor, L., Kahn, L., S.W, W.-B., 2008. Interaction between the effects of evaporation rate and amount of simulated rainfall on development of the free-living stages of *Haemonchus contortus*. Veterinary Parasitology 155, 223–34. https://doi.org/10.1016/j.vetpar.2008.05.010
Ogden, N.H., Maarouf, A., Barker, I.K., Bigras-Poulin, M., Lindsay, L.R., Morshed, M.G., O'Callaghan, C.J., Ramay, F., Waltner-Toews, D., Charron, D.F., 2006. Climate change and the potential for range expansion of the Lyme disease vector *Ixodes scapularis* in Canada. International Journal for Parasitology 36, 63–70. https://doi.org/10.1016/j.ijpara.2005.08.016
Oksanen, A., Nieminen, M., Soveri, T., Kumpula, K., 1992. Oral and parenteral administration of ivermectin to reindeer. Veterinary Parasitology 41, 241–247. https://doi.org/10.1016/0304-4017(92)90084-m
Ollerenshaw, C.B., 1966. The approach to forecasting the incidence of fascioliasis over England and Wales 1958–1962. Agricultural Meteorology 3, 35–53. https://doi.org/10.1016/0002-1571(66)90004-5
Ollerenshaw, C.B., Rowlands, W.T., 1959. A method of forecasting the incidence of fascioliasis in Anglesey. Veterinary Record 71, 591–598.
Park, C.G., Kim, D.S., Lee, S.M., Moon, Y.S., Chung, Y.J., Kim, D.-S., 2014. A forecasting model for the adult emergence of overwintered *Monochamus alternatus* (Coleoptera: Cerambycidae) larvae based on degree-days in Korea. Applied Entomology and Zoology 49, 35–42. https://doi.org/10.1007/s13355-013-0221-3

Pascoe, E.L., Marcantonio, M., Caminade, C., Foley, J.E., 2019. Modeling Potential Habitat for *Amblyomma* Tick Species in California. Insects 10, 201. https://doi.org/10.3390/insects10070201

Peacock, S.J., Mavrot, F., Tomaselli, M., Hanke, A., Fenton, H., Nathoo, R., Aleuy, O.A., Di Francesco, J., Aguilar, X.F., Jutha, N., Kafle, P., Mosbacher, J., Goose, A., Kutz, S.J., Ekaluktutiak Hunters Trappers, O., Kugluktuk Angoniatit, A., Olokhaktomiut Hunters Trappers, C., 2020. Linking co-monitoring to co-management: bringing together local, traditional, and scientific knowledge in a wildlife status assessment framework. Arctic Science 6, 247–266. https://doi.org/10.1139/as-2019-0019

Pedersen, U.B., Midzi, N., Mduluza, T., Soko, W., Stensgaard, A.-S., Vennervald, B.J., Mukaratirwa, S., Kristensen, T.K., 2014. Modelling spatial distribution of snails transmitting parasitic worms with importance to human and animal health and analysis of distributional changes in relation to climate. Geospatial Health 8, 335–343. https://doi.org/10.4081/gh.2014.23

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H., Stockwell, D.R.B., 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416, 626–629. https://doi.org/10.1038/416626a

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40, 887–893. https://doi.org/10.1111/ecog.03049

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips, S.J., Dudík, M., Schapire, R.E., 2021. Maxent software for modeling species niches and distributions.

Pickles, R.S.A., Thornton, D., Feldman, R., Marques, A., Murray, D.L., 2013. Predicting shifts in parasite distribution with climate change: a multitrophic level approach. Global Change Biology 19, 2645–2654. https://doi.org/10.1111/gcb.12255

Pierce, D., 2019. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files.

Polar Research Board, 2011. Frontiers in Understanding Climate Change and Polar Ecosystems Report of a Workshop. The National Academies Press.

Post, E., Forchhammer, M.C., 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B - Biological Sciences 363, 2369–2375. https://doi.org/10.1098/rstb.2007.2207

Pratumchart, K., Suwannatrai, K., Sereewong, C., Thinkhamrop, K., Chaiyos, J., Boonmars, T., Suwannatrai, A.T., 2019. Ecological Niche Model based on Maximum Entropy for mapping distribution of *Bithynia siamensis goniomphalos*, first intermediate host snail updates of *Opisthorchis viverrini* in Thailand. Acta Tropica 193, 183–191. https://doi.org/10.1016/j.actatropica.2019.03.004

Putkonen, J., Roe, G., 2003. Rain-on-snow events impact soil temperatures and affect ungulate survival. Geophysical Research Letters 30. https://doi.org/10.1029/2002gl016326
QGIS.org, 2021. QGIS Geographic Information System.
R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
Reinert, H., Benjaminsen, T.A., 2015. Conceptualising resilience in Norwegian Sámi reindeer pastoralism. Resilience 3, 95–112. https://doi.org/10.1080/21693293.2014.988916
Roberts, M., Heesterbeek, J.A.P., 1995. The dynamics of nematode infections of farmed ruminants. Parasitology 110 (Pt 4), 493–502. https://doi.org/10.1017/S0031182000064830
Robinson, R., Crick, H., Learmonth, J., Maclean, I., Thomas, C., Bairlein, F., Forchhammer, M., Francis, C., Gill, J., Godley, B., Harwood, J., Hays, G., Huntley, B., Hutson, A., Pierce, G., Rehfisch, M., Sims, D., Santos, B., Sparks, T., Stroud, D., Visser, M., 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7, 87–99. https://doi.org/10.3354/esr00095
Rose, H., Caminade, C., Bolajoko, M.B., Phelan, P., van Dijk, J., Baylis, M., Williams, D., Morgan, E.R., 2016. Climate-driven changes to the spatio-temporal distribution of the parasitic nematode, *Haemonchus contortus,* in sheep in Europe. Global Change Biology 22, 1271–1285. https://doi.org/10.1111/gcb.13132
Rose, H., Wang, T., Van Dijk, J., Morgan, E.R., 2015. GLOWORM-FL: A simulation model of the effects of climate and climate change on the free-living stages of gastro-intestinal nematode parasites of ruminants. Ecological Modelling 297, 232–245. https://doi.org/10.1016/j.ecolmodel.2014.11.033
Rose Vineer, Hannah, 2020. What Modeling Parasites, Transmission, and Resistance Can Teach Us. Veterinary Clinics of North America: Food Animal Practice 36, 145–158. https://doi.org/10.1016/j.cvfa.2019.11.002
Rose Vineer, H., Mørk, T., Williams, D.J., Davidson, R.K., 2021. Modeling Thermal Suitability for Reindeer (*Rangifer tarandus* ssp.) Brainworm (*Elaphostrongylus rangiferi)* Transmission in Fennoscandia. Frontiers in Veterinary Science 7. https://doi.org/10.3389/fvets.2020.603990
Rose Vineer, H., Verschave, S.H., Claerebout, E., Vercruysse, J., Shaw, D.J., Charlier, J., Morgan, E.R., 2020. GLOWORM-PARA: a flexible framework to simulate the population dynamics of the parasitic phase of gastrointestinal nematodes infecting grazing livestock. International Journal for Parasitology 50, 133–144. https://doi.org/10.1016/j.ijpara.2019.11.005
Saunders, L.M., Tompkins, D.M., Hudson, P.J., 2002. Stochasticity accelerates nematode egg development. Journal of Parasitology 88, 1271–1272. https://doi.org/10.1645/0022-3395(2002)088[1271:SANED]2.0.CO;2
Schjetlein, J., Skorping, A., 1995. The temperature threshold for development of *Elaphostrongylus rangiferi* in the intermediate host - an adaptation to winter survival. Parasitology 111, 103–110. https://doi.org/10.1017/s0031182000064659
Shaw, A.K., Sherman, J., Barker, F.K., Zuk, M., 2018. Metrics matter: the effect of parasite richness, intensity and prevalence on the evolution of host migration. Proceedings of the Royal Society B: Biological Sciences 285, 20182147. https://doi.org/10.1098/rspb.2018.2147

Shiogama, H., Ishizaki, N.N., Hanasaki, N., Takahashi, K., Emori, S., Ito, R., Nakaegawa, T., Takayabu, I., Hijioka, Y., Takayabu, Y.N., Shibuya, R., 2021. Selecting CMIP6-based future climate scenarios for impact and adaptation studies. SOLA 17 57-62. https://doi.org/10.2151/sola.2021-009

Skorping, A., 1988. The effect of density of 1st-stage larvae of *Elaphostrongylus rangiferi* on the infection-rate in the snail intermediate host. Parasitology 96, 487–492. https://doi.org/10.1017/s0031182000080124

Skorping, A., 1985a. *Lymnea stagnalis* as experimental intermediate host for the protostrongylid nematode *Elaphostrongylus rangiferi.* Zeitschrift für Parasitenkunde 71, 265–270. https://doi.org/10.1007/bf00926277

Skorping, A., 1985b. Parasite–induced reduction in host survival and fecundity: the effect of the nematode *Elaphostrongylus rangiferi* on the snail intermediate host. Parasitology 91, 555. https://doi.org/10.1017/s003118200006279x

Skorping, A., 1984. Density-Dependent Effects in a Parasitic Nematode, *Elaphostrongylus rangiferi,* in the Snail Intermediate Host. Oecologia 64, 34–40.

Skorping, A., 1982. *Elaphostrongylus rangiferi:* Influence of temperature, substrate, and larval age on the infection rate in the intermediate snail host, *Arianta arbustorum.* Experimental Parasitology 54, 222–228. https://doi.org/10.1016/0014-4894(82)90130-8

Skorping, A., Halvorsen, O., 1980. The susceptibility of terrestrial gastropods to experimental infection with *Elaphostrongylus rangiferi* Mitskevich (Nematoda: Metastrongyloidea). Zeitschrift für Parasitenkunde 62, 7–14. https://doi.org/10.1007/bf00925362

Smit, N.J., Malherbe, W., Hadfield, K.A., 2017. Alien freshwater fish parasites from South Africa: Diversity, distribution, status and the way forward. International Journal for Parasitology - Parasites and Wildlife 6, 386–401. https://doi.org/10.1016/j.ijppaw.2017.06.001

Solomon, A., Paperna, I., Glazer, I., Alkon, P.U., 1997. Migratory behaviour and desiccation tolerance of protostrongylid nematode first-stage larvae. International Journal for Parasitology 27, 1517–1522. https://doi.org/10.1016/S0020-7519(97)00143-4

Solomon, S., IPCC (Eds.), 2007. Climate change 2007: the physical science basis: contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge ; New York.

Steen, M., Blackmore, C.G.M., Skorping, A., 1997. Cross-infection of moose (*Alces alces*) and reindeer (*Rangifer tarandus*) with Elaphostrongylus alces and *Elaphostrongylus rangiferi (*Nematoda, Protostrongylidae): Effects on parasite morphology and prepatent period. Veterinary Parasitology 71, 27–38. https://doi.org/10.1016/s0304-4017(97)00013-7

Stensgaard, A.-S., Utzinger, J., Vounatsou, P., Hürlimann, E., Schur, N., Saarnak, C.F.L., Simoonga, C., Mubita, P., Kabatereine, N.B., Tchuem Tchuenté, L.-A., Rahbek, C., Kristensen, T.K., 2013. Large-scale determinants of intestinal schistosomiasis and intermediate host snail distribution across Africa: does climate matter? Acta Tropica, CONTRAST alliance: optimized surveillance and sustainable control of schistosomiasis 128, 378–390. https://doi.org/10.1016/j.actatropica.2011.11.010

Stuart, P., Paredis, L., Henttonen, H., Lawton, C., Torres, C.A.O., Holland, C., 2020. The hidden faces of a biological invasion: parasite dynamics of invaders and

natives. International Journal for Parasitology 50, 111–123. https://doi.org/10.1016/j.ijpara.2019.11.003
Sunday, J.M., Bates, A.E., Dulvy, N.K., 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proceedings of the Royal Society B: Biological Sciences 278, 1823–1830. https://doi.org/10.1098/rspb.2010.1295
Suominen, O., 1999. Impact of Cervid Browsing and Grazing on the Terrestrial Gastropod Fauna in the Boreal Forests of Fennoscandia. Ecography 22, 651–658. http://www.jstor.com/stable/3683319
Suominen, O., Olofsson, J., 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: A review. Annales Zoologici Fennici 37, 233-249. http://www.jstor.org/stable/23735717
Sutherst, R.W., 2001. The vulnerability of animal and human health to parasites under global change. International Journal for Parasitology 31, 933–948. https://doi.org/10.1016/s0020-7519(01)00203-x
Teitelbaum, C.S., Huang, S., Hall, R.J., Altizer, S., 2018. Migratory behaviour predicts greater parasite diversity in ungulates. Proceedings of the Royal Society B: Biological Sciences 285, 20180089. https://doi.org/10.1098/rspb.2018.0089
Thomas, R.J., Starr, J.R., 1978. Forecasting the peak of gastrointestinal nematode infection in lambs. Veterinary Record 103, 465–468. https://doi.org/10.1136/vr.103.21.465
Thompson, R.M., Beardall, J., Beringer, J., Grace, M., Sardina, P., 2013. Means and extremes: building variability into community-level climate change experiments. Ecology Letters 16, 799–806. https://doi.org/10.1111/ele.12095
Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. PNAS 102, 8245–8250. https://doi.org/10.1073/pnas.0409902102
Tomaselli, M., Kutz, S., Gerlach, C., Checkley, S., 2018. Local knowledge to enhance wildlife population health surveillance: Conserving muskoxen and caribou in the Canadian Arctic. Biological Conservation 217, 337–348. https://doi.org/10.1016/j.biocon.2017.11.010
Turunen, M., Vuojala-Magga, T., 2014. Past and Present Winter Feeding of Reindeer in Finland: Herders' Adaptive Learning of Feeding Practices. Arctic 67, 173-188-173–188. https://doi.org/10.14430/arctic4385
Turunen, M.T., Rasmus, S., Bavay, M., Ruosteenoja, K., Heiskanen, J., 2016. Coping with difficult weather and snow conditions: Reindeer herders' views on climate change impacts and coping strategies. Climate Risk Management 11, 15–36. https://doi.org/10.1016/j.crm.2016.01.002
Valente, R., Robles, M. del R., Diaz, J.I., 2020. Gastropods as intermediate hosts of *Angiostrongylus* spp. in the Americas: bioecological characteristics and geographical distribution. Memórias do Instituto Oswaldo Cruz 115, e200236. https://doi.org/10.1590/0074-02760200236
Van Dijk, J., Morgan, E.R., 2011. The influence of water on the migration of infective trichostrongyloid larvae onto grass. Parasitology 138, 780–788. https://doi.org/10.1017/S0031182011000308
Vikhamar-Schuler, D., Hanssen-Bauer, I., Schuler, T.V., Mathiesen, S.D., Lehning, M., 2013. Use of a multilayer snow model to assess grazing conditions for reindeer. Annals of Glaciology 54, 214–226. https://doi.org/10.3189/2013AoG62A306

Visser, M.E., Holleman, L.J.M., Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172. https://doi.org/10.1007/s00442-005-0299-6

Vors, L.S., Boyce, M.S., 2009. Global declines of caribou and reindeer. Global Change Biology 15, 2626–2633. https://doi.org/10.1111/j.1365-2486.2009.01974.x

Wall, R., French, N.P., Fenton, A., 2000. Sheep blowfly strike: a model approach. Research in Veterinary Science 69, 1–9. https://doi.org/10.1053/rvsc.2000.0383

Wang, T., van Wyk, J.A., Morrison, A., Morgan, E.R., 2014. Moisture requirements for the migration of *Haemonchus contortus* third stage larvae out of faeces. Veterinary Parasitology 204, 258–264. https://doi.org/10.1016/j.vetpar.2014.05.014

Westcott, S., Burrows, P., 1991. Degree-Day Models for Predicting Egg Hatch and Population Increase of *Criconemella xenoplax*. Journal of Nematology 23, 386–392.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. PNAS 106, 19729–19736. https://doi.org/10.1073/pnas.0901639106

Willis, J.C., Bohan, D.A., Choi, Y.H., Conrad, K.F., Semenov, M.A., 2006. Use of an individual-based model to forecast the effect of climate change on the dynamics, abundance and geographical range of the pest slug *Deroceras reticulatum* in the UK. Global Change Biology 12, 1643–1657. https://doi.org/10.1111/j.1365-2486.2006.01201.x

Wilson, M.J., Digweed, A.J., Brown, J., Ivanonva, E.S., Hapca, S.H., 2015. Invasive slug pests and their parasites-temperature responses and potential implications of climate change. Biology and Fertility of Soils 51, 739–748. https://doi.org/10.1007/s00374-015-1022-3

Woolhouse, M., 2011. How to make predictions about future infectious disease risks. Philosophical Transactions of the Royal Society B: Biological Sciences 366, 2045–2054. https://doi.org/10.1098/rstb.2010.0387

Yang, G.-J., Gemperli, A., Vounatsou, P., Tanner, M., Zhou, X.-N., Utzinger, J., 2006. A growing degree-days based time-series analysis for prediction of *Schistosoma japonicum* transmission in Jiangsu province, China The American Journal of Tropical Medicine and Hygiene 75, 549–555. https://doi.org/10.4269/ajtmh.2006.75.549

York, E.M., Butler, C.J., Lord, W.D., 2014. Global Decline in Suitable Habitat for *Angiostrongylus (= Parastrongylus) cantonensis*: The Role of Climate Change. PLoS One 9, e103831. https://doi.org/10.1371/journal.pone.0103831

Zotin, A.A., Ozernyuk, N.D., 2002. Thermal Compensation of Respiration in Pulmonate Snails (Pulmonata) of *Arion* and *Deroceras* Genera Living in Polar and Temperate Climatic Zone. Biology Bulletin of the Russian Academy of Sciences 29, 468-472. https://doi.org/10.1023/A:1020461709677

Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitão, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schröder, B., Serra-Diaz, J.M., Thuiller, W., Yates, K.L., Zimmermann, N.E., Merow,

C., 2020. A standard protocol for reporting species distribution models. Ecography 43, 1261–1277. https://doi.org/10.1111/ecog.04960

APPENDICES

APPENDIX 3.1 R Script for analysis of reindeer GPS and faecal larvae count data

```
library(ggplot2)
library(adehabitatHR)
library(data.table)
library(ncdf4)
library(raster)
library(cruts)
library(sp)
library(rasterVis)
library(viridis)
library(rgdal)
setwd("###")

#### Use the data created by the DD model ####
dd <- nc_open("Elaph_DD.nc")
lon = ncvar_get(nc = dd, varid = "longitude")
lat = ncvar_get(nc = dd, varid = "latitude")

time = ncvar_get(nc = dd, varid = "time")
tunits = ncatt_get(dd, "time", "units")
nt = dim(time)

tustr <- strsplit(tunits$value, " ") #Split the elements of a character vector x into substrings according to the matches to substring split within them
tdstr <- strsplit(unlist(tustr)[3], "/")
tmonth <- as.integer(unlist(tdstr)[2])
tday <- as.integer(unlist(tdstr)[1])
tyear <- as.integer(unlist(tdstr)[3])
thuman = seq(from = as.Date(paste(tyear, tmonth, tday, sep = "-")), length = nt, by = "day")
```

```
#### FUNCTION TO CALCULATE CUMULATIVE ANNUAL DEGREE-DAYS ####
annualdd = function (annualmcp, startdate, enddate) {
  annualminlon = annualmcp@bbox[1,1]
  annualminlat = annualmcp@bbox[2,1]
  annualmaxlon = annualmcp@bbox[1,2]
  annualmaxlat = annualmcp@bbox[2,2]
  annuallon_range = which(lon<annualmaxlon & lon>annualminlon)
  annuallat_range = which(lat<annualmaxlat & lat>annualminlat)
  annualdat_range = which(thuman<=as.Date(enddate) & thuman>=as.Date(startdate))
  annual.array <- array(dim = c(length(annuallat_range), length(annuallon_range), length(annualdat_range)))

  for (i in 1:length(annualmcp)) {
    minlon = annualmcp[i,]@bbox[1,1]
    minlat = annualmcp[i,]@bbox[2,1]
    maxlon = annualmcp[i,]@bbox[1,2]
    maxlat = annualmcp[i,]@bbox[2,2]

    lon_range = which(lon<maxlon & lon>minlon)
    lat_range = which(lat<maxlat & lat>minlat)
    if (length(lat_range) == 0) {lat_range = which(lat<(maxlat+0.1) & lat>minlat)} else {lat_range = which(lat<maxlat & lat>minlat)}

    start.date <- as.Date(annualmcp[i,]@data[["id"]], format = "%Y-%m-%d")
    end.date <- as.Date(enddate)
    dat_range = which(thuman<=end.date & thuman>=start.date)

    temp.dat = ncvar_get(nc = dd, varid = "DD", start = c(lat_range[1], lon_range[1], dat_range[1]),
                         count = c(length(lat_range), length(lon_range), length(dat_range)))
```

```
  temp.dat <- array(temp.dat, dim = c(length(lat_range), length(lon_range), length(dat_range)))

  annual.array[(length(annuallat_range) - (last(annuallat_range) - lat_range[1])):(length(temp.dat[,1,i])+(length(annuallat_range) - (last(annuallat_range) - lat_range[1])-1)),
           (length(annuallon_range) - (last(annuallon_range) - lon_range[1])):(length(temp.dat[1,,i])+(length(annuallon_range) - (last(annuallon_range) - lon_range[1])-1)),
           (length(annual.array[1,1,]) - (length(temp.dat[1,1,])-1)):length(annual.array[1,1,])] = temp.dat

 }


 annual.arraycs <- annual.array

 for (i in 1:length(annual.array[,1,1])){
  for (j in 1:length(annual.array[1,,1])){
   annual.arraycs[i,j,] <- cumsum(ifelse(is.na(annual.array[i,j,]), 0, annual.array[i,j,])) + annual.array[i,j,]*0
  }
 }
 return(annual.arraycs)
}

#### FUNCTION TO CALCULATE MONTHLY DEGREE-DAYS AS A RASTER ####
monthlydd <- function (annual.arraycs, annualmcp){
 annualminlon = annualmcp@bbox[1,1]
 annualminlat = annualmcp@bbox[2,1]
 annualmaxlon = annualmcp@bbox[1,2]
 annualmaxlat = annualmcp@bbox[2,2]
```

```
Jan <- annual.arraycs[,,31]
Feb <- annual.arraycs[,,(31+28)]
Mar <- annual.arraycs[,,(31+28+31)]
Apr <- annual.arraycs[,,(31+28+31+30)]
May <- annual.arraycs[,,(31+28+31+30+31)]
Jun <- annual.arraycs[,,(31+28+31+30+31+30)]
Jul <- annual.arraycs[,,(31+28+31+30+31+30+31)]
Aug <- annual.arraycs[,,(31+28+31+30+31+30+31+31)]
Sep <- annual.arraycs[,,(31+28+31+30+31+30+31+31+30)]
Oct <- annual.arraycs[,,(31+28+31+30+31+30+31+31+30+31)]
Nov <- annual.arraycs[,,(31+28+31+30+31+30+31+31+30+31+30)]
Dec <- annual.arraycs[,,(31+28+31+30+31+30+31+31+30+31+30+31)]

Jan.ras <- raster(Jan, xmn = annualminlon, xmx = annualmaxlon, ymn = annualminlat, ymx = annualmaxlat)
Jan.ras <- flip(Jan.ras, direction = "y")
Jan.ras <- mask(Jan.ras, annualmcp[1,])
Feb.ras <- raster(Feb, xmn = annualminlon, xmx = annualmaxlon, ymn = annualminlat, ymx = annualmaxlat)
Feb.ras <- flip(Feb.ras, direction = "y")
Feb.ras <- mask(Feb.ras, annualmcp[2,])
Mar.ras <- raster(Mar, xmn = annualminlon, xmx = annualmaxlon, ymn = annualminlat, ymx = annualmaxlat)
Mar.ras <- flip(Mar.ras, direction = "y")
Mar.ras <- mask(Mar.ras, annualmcp[3,])
Apr.ras <- raster(Apr, xmn = annualminlon, xmx = annualmaxlon, ymn = annualminlat, ymx = annualmaxlat)
Apr.ras <- flip(Apr.ras, direction = "y")
Apr.ras <- mask(Apr.ras, annualmcp[4,])
May.ras <- raster(May, xmn = annualminlon, xmx = annualmaxlon, ymn = annualminlat, ymx = annualmaxlat)
May.ras <- flip(May.ras, direction = "y")
May.ras <- mask(May.ras, annualmcp[5,])
```

```
  Jun.ras <- raster(Jun, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Jun.ras <- flip(Jun.ras, direction = "y")
  Jun.ras <- mask(Jun.ras, annualmcp[6,])
  Jul.ras <- raster(Jul, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Jul.ras <- flip(Jul.ras, direction = "y")
  Jul.ras <- mask(Jul.ras, annualmcp[7,])
  Aug.ras <- raster(Aug, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Aug.ras <- flip(Aug.ras, direction = "y")
  Aug.ras <- mask(Aug.ras, annualmcp[8,])
  Sep.ras <- raster(Sep, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Sep.ras <- flip(Sep.ras, direction = "y")
  Sep.ras <- mask(Sep.ras, annualmcp[9,])
  Oct.ras <- raster(Oct, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Oct.ras <- flip(Oct.ras, direction = "y")
  Oct.ras <- mask(Oct.ras, annualmcp[10,])
  Nov.ras <- raster(Nov, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Nov.ras <- flip(Nov.ras, direction = "y")
  Nov.ras <- mask(Nov.ras, annualmcp[11,])
  Dec.ras <- raster(Dec, xmn = annualminlon, xmx = annualmaxlon, ymn =
annualminlat, ymx = annualmaxlat)
  Dec.ras <- flip(Dec.ras, direction = "y")
  Dec.ras <- mask(Dec.ras, annualmcp[12,])

  annual.stack <- stack(Jan.ras, Feb.ras, Mar.ras, Apr.ras, May.ras, Jun.ras, Jul.ras,
Aug.ras, Sep.ras, Oct.ras, Nov.ras, Dec.ras)
  return(annual.stack)
}
```

```
#### EXAMPLE USE WITH HERD DATA ####
locs <- read.csv("gps_data.csv")
head(locs)
locs$tag <- as.factor(locs$tag)
locs$DateTime <- as.POSIXct(locs$DateTime, format = "%d/%m/%Y %H:%M")

# Whole herd annual area for plotting later
locsherd <- locs[,c(3:4, 7)]
locsherd$ProjectName <- as.factor(locsherd$ProjectName)
coordinates(locsherd) <- c("Longitude", "Latitude")

locsherdmcp <- mcp(locsherd, percent = 100)

# Annual locations #
locs2018 <- locs[which(locs$DateTime >= "2018-01-01" & locs$DateTime < "2019-
01-01"),]
locs2019 <- locs[which(locs$DateTime >= "2019-01-01" & locs$DateTime < "2020-
01-01"),]
locs2020 <- locs[which(locs$DateTime >= "2020-01-01" & locs$DateTime < "2021-
01-01"),]

# 2020 #
locs2020sp <- locs2020[,3:5]
locs2020sp$DateTime <- trunc(locs2020sp$DateTime, units = "months")
locs2020sp$DateTime <- as.factor(locs2020sp$DateTime)

coordinates(locs2020sp) <- c("Longitude", "Latitude")

locs2020mcp <- mcp(locs2020sp, percent = 100)

# 2019 #
locs2019sp <- locs2019[,3:5]
locs2019sp$DateTime <- trunc(locs2019sp$DateTime, units = "months")
locs2019sp$DateTime <- as.factor(locs2019sp$DateTime)
```

```
coordinates(locs2019sp) <- c("Longitude", "Latitude")

locs2019mcp <- mcp(locs2019sp, percent = 100)

# 2018 #
# 2018 gps data starts from jun so bind Jan-may from 2019 data (not using 2020 due to leapyear)
locs2018sp <- locs2018[,3:5]
locs2019add <- locs2019[,3:5]
locs2018sp$DateTime <- as.Date(locs2018sp$DateTime, format = "%Y-%m-%d")
locs2019add$DateTime <- as.Date(locs2019add$DateTime, format = "%Y-%m-%d") - 365
locs2018sp <- rbind(locs2019add[which(locs2019add$DateTime >= "2018-01-01" & locs2019add$DateTime <= "2018-05-31"),], locs2018sp)
locs2018sp$DateTime <- sort(locs2018sp$DateTime)

locs2018sp$DateTime <- as.POSIXct(locs2018sp$DateTime, format = "%Y-%m-%d")

locs2018sp$DateTime <- trunc(locs2018sp$DateTime, units = "months")
locs2018sp$DateTime <- as.factor(locs2018sp$DateTime)

coordinates(locs2018sp) <- c("Longitude", "Latitude")

locs2018mcp <- mcp(locs2018sp, percent = 100)

# Cumulative daily degree-days
dd2020 <- annualdd(locs2020mcp, "2020-01-01", "2020-12-31")
dd2019 <- annualdd(locs2019mcp, "2019-01-01", "2019-12-31")
dd2018 <- annualdd(locs2018mcp, "2018-01-01", "2018-12-31")

# Monthly sums of dd (for plotting)
mondd2020 <- monthlydd(dd2020, locs2020mcp)
```

```
mondd2019 <- monthlydd(dd2019, locs2019mcp)
mondd2018 <- monthlydd(dd2018, locs2018mcp)



locsminlon = locsherdmcp@bbox[1,1]
locsminlat = locsherdmcp@bbox[2,1]
locsmaxlon = locsherdmcp@bbox[1,2]
locsmaxlat = locsherdmcp@bbox[2,2]
breaks = c(0, 30, 60, 90, 120, 160, 200, 245, 290, 340, 390, 450, 600, 900)
xlim = c(locsminlon, locsmaxlon)
ylim = c(locsminlat, locsmaxlat)

levelplot(mondd2018, col.regions = magma(15)[c(1:7, 9:14)], at = breaks,
        xlim = xlim, ylim = ylim, main = "2018",
        xlab = "Degrees Longitude", ylab = "Degrees Latitude",
        scales = list(alternating=0),
        # scales = list(y=list(labels=c("","1","","","","","2")), x=list(labels = c("", "1",
"", "2", "", "3", ""))),
        colorkey = list(title = "dd", height = 0.9, space = "right"),
        names.attr = c("Jan", "Feb", "Mar", "Apr", "May", "Jun", "Jul", "Aug", "Sep",
"Oct", "Nov", "Dec")) + layer(sp.polygons(locsherdmcp))

levelplot(mondd2019, col.regions = magma(15)[c(1:7, 9:14)], at = breaks,
        xlim = xlim, ylim = ylim, main = "2019",
        xlab = "Degrees Longitude", ylab = "Degrees Latitude",
        scales = list(alternating=0),
        # scales = list(y=list(labels=c("","1","","","","","2")), x=list(labels = c("", "1",
"", "2", "", "3", ""))),
        names.attr = c("Jan", "Feb", "Mar", "Apr", "May", "Jun", "Jul", "Aug", "Sep",
"Oct", "Nov", "Dec")) + layer(sp.polygons(locsherdmcp))

levelplot(mondd2020, col.regions = magma(15)[c(1:7, 9:14)], at = breaks,
        xlim = xlim, ylim = ylim, main = "2020",
        xlab = "Degrees Longitude", ylab = "Degrees Latitude",
```

```
        scales = list(alternating=0),
        # scales = list(y=list(labels=c("","1","","","","","2")), x=list(labels = c("", "1", "", "2", "", "3", ""))),
        names.attr = c("Jan", "Feb", "Mar", "Apr", "May", "Jun", "Jul", "Aug", "Sep", "Oct", "Nov", "Dec")) + layer(sp.polygons(locsherdmcp))



#### VALIDATION ####
#### FUNCTION TO CALCULATE NUMBER OF AT RISK DAYS FOR EACH REINDEER ####
indivdd = function (dailylocs, annualmcp, annual.arraybin, startdate, enddate) {
  annualminlon = annualmcp@bbox[1,1]
  annualminlat = annualmcp@bbox[2,1]
  annualmaxlon = annualmcp@bbox[1,2]
  annualmaxlat = annualmcp@bbox[2,2]
  annuallon_range = which(lon<annualmaxlon & lon>annualminlon)
  annuallat_range = which(lat<annualmaxlat & lat>annualminlat)
  annualdat_range = which(thuman<=as.Date(enddate) & thuman>=as.Date(startdate))

  rein.array <- array(dim = c(length(annuallat_range), length(annuallon_range), length(annualdat_range)))

  for (j in 1:nrow(dailylocs)) {
    lon_to_plot = which.min(lon < dailylocs$Longitude[j]) -1
    lat_to_plot = which.min(lat < dailylocs$Latitude[j]) -1
    dat_to_plot = which(thuman == dailylocs$DateTime[j])
    rein.array[(lat_to_plot - first(annuallat_range) +1), (lon_to_plot - first(annuallon_range) +1), (dat_to_plot - first(annualdat_range)+ 1)] =
      paste(as.character(rein.array[(lat_to_plot - first(annuallat_range) +1), (lon_to_plot - first(annuallon_range) +1), (dat_to_plot - first(annualdat_range)+ 1)]),as.character(dailylocs$tag[j]))
  }
```

```
  # Combine the two arrays to show reindeer name only when dd >245
  # Change NA values to FALSE
  annual.arraybin[is.na(annual.arraybin)] <- FALSE
  anyNA(annual.arraybin, recursive = FALSE)

  inf.mat = matrix(nrow = length(rein.array[,,1]), ncol = length(rein.array[1,1,]))

  for (k in 1:length(rein.array)){
    if (annual.arraybin[k] == TRUE) inf.mat[k] = rein.array[k]
  }

  ind_dd <- matrix(ncol = 2, nrow = nlevels(dailylocs$tag))

  for (i in 1:nlevels(dailylocs$tag)){
    if (length(dailylocs$tag[dailylocs$tag==(levels(dailylocs$tag)[i])])>=365){
      x <- grepl(levels(dailylocs$tag)[i], inf.mat)
      ind_dd[i,1] <- levels(dailylocs$tag)[i]
      ind_dd[i,2] <- sum(x==TRUE)}
    else {
      ind_dd[i,1] <- levels(dailylocs$tag)[i]
      ind_dd[i,2] <- NA
    }
  }
  return(ind_dd)
}

# Binary daily cumulative sums
dd2018.bin <- dd2018 >= 245
dd2019.bin <- dd2019 >= 245
dd2020.bin <- dd2020 >= 245

# DAILY INDIVIDUAL LOCS #
# 2018
```

```
locs2018.daily <- locs2018[,c(3:5,9)]
locs2018.daily$DateTime <- as.Date(locs2018.daily$DateTime)
locs2018.daily <- aggregate(cbind(locs2018.daily$Latitude, locs2018.daily$Longitude), by = list(locs2018.daily$DateTime, locs2018.daily$tag), FUN = mean)
colnames(locs2018.daily) <- c("DateTime", "tag", "Latitude", "Longitude")

# Check how many days in the year there is data for each individual
for (i in 1:nlevels(locs2018$tag)) {
  print(paste(levels(locs2018$tag)[i],

(length(locs2018.daily$tag[locs2018.daily$tag==(levels(locs2018$tag)[i])]))))  }

# Find the first day of the year with dd >245
v <-  which(dd2018.bin, arr.ind = TRUE)
v[1,3]
locs2018.daily$tag <- as.character(locs2018.daily$tag)
locs2018.daily$tag <- as.factor(locs2018.daily$tag)

# ...Find first date of location data for each individual and if before the first day of risk, create values before it
for(i in 1:nlevels(locs2018.daily$tag)){
  re<-
yday(first(locs2018.daily[which(locs2018.daily$tag==(levels(locs2018.daily$tag)[i])),1]))
  if(re!=1){
    # ...If first date > first risk then rbind the reindeer loc for all days before that as the same
    tr <- data.frame(DateTime = seq(from = as.Date("2018-01-01", format = "%Y-%m-%d"), to = (as.Date("2018-01-01", format = "%Y-%m-%d") + re -2), by = 1),
                     tag = rep((levels(locs2018.daily$tag)[i]), times = re-1),
                     Latitude =
rep(first(locs2018.daily[which(locs2018.daily$tag==(levels(locs2018.daily$tag)[i])),3]), times = re-1),
```

```
                Longitude                                                =
rep(first(locs2018.daily[which(locs2018.daily$tag==(levels(locs2018.daily$tag)[i])),
4]), times = re-1))

   locs2018.daily <- rbind(locs2018.daily, tr)
  }
}

# 2019
locs2019.daily <- locs2019[,c(3:5,9)]
locs2019.daily$DateTime <- as.Date(locs2019.daily$DateTime)
locs2019.daily<-aggregate(cbind(locs2019.daily$Latitude,
locs2019.daily$Longitude), by = list(locs2019.daily$DateTime, locs2019.daily$tag),
FUN = mean)
colnames(locs2019.daily) <- c("DateTime", "tag", "Latitude", "Longitude")

v <-  which(dd2019.bin, arr.ind = TRUE)
v[1,3]
locs2019.daily$tag <- as.character(locs2019.daily$tag)
locs2019.daily$tag <- as.factor(locs2019.daily$tag)

# ...Find first date of location data for each individual, e.g. and the day of the year it is
for(i in 1:nlevels(locs2019.daily$tag)){
  re<-
yday(first(locs2019.daily[which(locs2019.daily$tag==(levels(locs2019.daily$tag)[i])
),1]))
  if(re!=1){
    # ...If first date > first risk then rbind(?) the reindeer loc for all days before that as
the same
    tr <- data.frame(DateTime = seq(from = as.Date("2019-01-01", format = "%Y-%m-
%d"), to = (as.Date("2019-01-01", format = "%Y-%m-%d") + re -2), by = 1),
                tag = rep((levels(locs2019.daily$tag)[i]), times = re-1),
```

```
                Latitude = rep(first(locs2019.daily[which(locs2019.daily$tag==(levels(locs2019.daily$tag)[i])), 3]), times = re-1),
                Longitude = rep(first(locs2019.daily[which(locs2019.daily$tag==(levels(locs2019.daily$tag)[i])), 4]), times = re-1))

   locs2019.daily <- rbind(locs2019.daily, tr)
  }
}

# 2020
locs2020.daily <- locs2020[,c(3:5,9)]
locs2020.daily$DateTime <- as.Date(locs2020.daily$DateTime)
locs2020.daily <- aggregate(cbind(locs2020.daily$Latitude, locs2020.daily$Longitude), by = list(locs2020.daily$DateTime, locs2020.daily$tag), FUN = mean)
colnames(locs2020.daily) <- c("DateTime", "tag", "Latitude", "Longitude")

v <-  which(dd2020.bin, arr.ind = TRUE)
v[1,3]
locs2020.daily$tag <- as.character(locs2020.daily$tag)
locs2020.daily$tag <- as.factor(locs2020.daily$tag)

# ...Find first date of location data for each individual, e.g. and the day of the year it is
for(i in 1:nlevels(locs2020.daily$tag)){
  re<-
yday(first(locs2020.daily[which(locs2020.daily$tag==(levels(locs2020.daily$tag)[i])),1]))
  if(re!=1){
    # ...If first date > first risk then rbind(?) the reindeer loc for all days before that as the same
    tr <- data.frame(DateTime = seq(from = as.Date("2020-01-01", format = "%Y-%m-%d"), to = (as.Date("2020-01-01", format = "%Y-%m-%d") + re -2), by = 1),
```

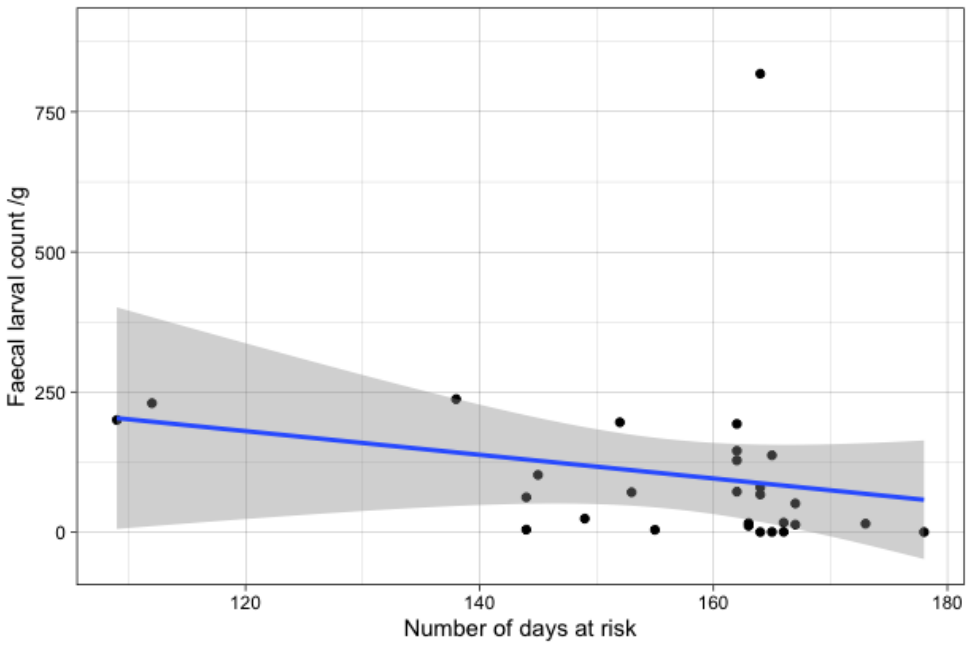
```
                tag = rep((levels(locs2020.daily$tag)[i]), times = re-1),
                Latitude = rep(first(locs2020.daily[which(locs2020.daily$tag==(levels(locs2020.daily$tag)[i])), 3]), times = re-1),
                Longitude = rep(first(locs2020.daily[which(locs2020.daily$tag==(levels(locs2020.daily$tag)[i])), 4]), times = re-1))

   locs2020.daily <- rbind(locs2020.daily, tr)
  }
}

indiv2018 <- indivdd(locs2018.daily, locs2018mcp, dd2018.bin, "2018-01-01", "2018-12-31")
indiv2019 <- indivdd(locs2019.daily, locs2019mcp, dd2019.bin, "2019-01-01", "2019-12-31")
indiv2020 <- indivdd(locs2020.daily, locs2020mcp, dd2020.bin, "2020-01-01", "2020-12-31")

#### MATCH EXPOSURE WITH LARVAL COUNTS THE FOLLOWING YEARS ####
flc <- read.csv("sampling_2019_2020_2021.csv")
flc <- flc[,c(2, 4, 5, 6, 7, 19, 20)]
flc$Sampling.date <- as.POSIXct(flc$Sampling.date, format = "%d/%m/%Y")
flc$Sex <- as.factor(flc$Sex)
# flc$ClipID <- as.factor(flc$ClipID)
flc$MonthYear <- as.factor(trunc(flc$Sampling.date, unit = "months"))

# Divide larval counts into 6 month periods
flc2019Spring <- flc[which(flc$Sampling.date >= "2019-01-01" & flc$Sampling.date <= "2019-06-30"),]
flc2019Autumn <- flc[which(flc$Sampling.date >= "2019-07-01" & flc$Sampling.date <= "2019-12-31"),]
```

```
flc2020Spring <- flc[which(flc$Sampling.date >= "2020-01-01" & flc$Sampling.date <= "2020-06-30"),]
flc2021Spring <- flc[which(flc$Sampling.date >= "2021-01-01" & flc$Sampling.date <= "2021-06-30"),]
flc2021Spring <- flc2021Spring[!is.na(flc2021Spring$ClipID),]
flc2020Autumn <- flc[which(flc$Sampling.date >= "2020-07-01" & flc$Sampling.date <= "2020-12-31"),]

#2018
indiv2018 <- as.data.frame(indiv2018)
i2018s1y <- merge(indiv2018, flc2019Spring[,c(4,6)], by.x = "V1", by.y = "ClipID")
i2018s2y <- merge(indiv2018, flc2020Spring[,c(4,6)], by.x = "V1", by.y = "ClipID")

#2019
indiv2019 <- as.data.frame(indiv2019)
i2019s1y <- merge(indiv2019, flc2020Spring[,c(4,6)], by.x = "V1", by.y = "ClipID")
i2019s2y <- merge(indiv2019, flc2021Spring[,c(4,6)], by.x = "V1", by.y = "ClipID")



# 2020
indiv2020 <- as.data.frame(indiv2020)
i2020s1y <- merge(indiv2020, flc2021Spring[,c(4,6)], by.x = "V1", by.y = "ClipID")

# Combine by time difference
spring1yr <- rbind(i2018s1y, i2019s1y, i2020s1y)
spring2yr <- rbind(i2018s2y, i2019s2y)

colnames(spring1yr)[colnames(spring1yr)=="V2"] <- "days.exposed"
colnames(spring2yr)[colnames(spring2yr)=="V2"] <- "days.exposed"

# Numeric models
spring1yr$days.exposed <- as.integer(spring1yr$days.exposed)
spring1yr$Elaphostrongylus.LPG <- as.numeric(spring1yr$Elaphostrongylus.LPG)
spring2yr$days.exposed <- as.integer(spring2yr$days.exposed)
```

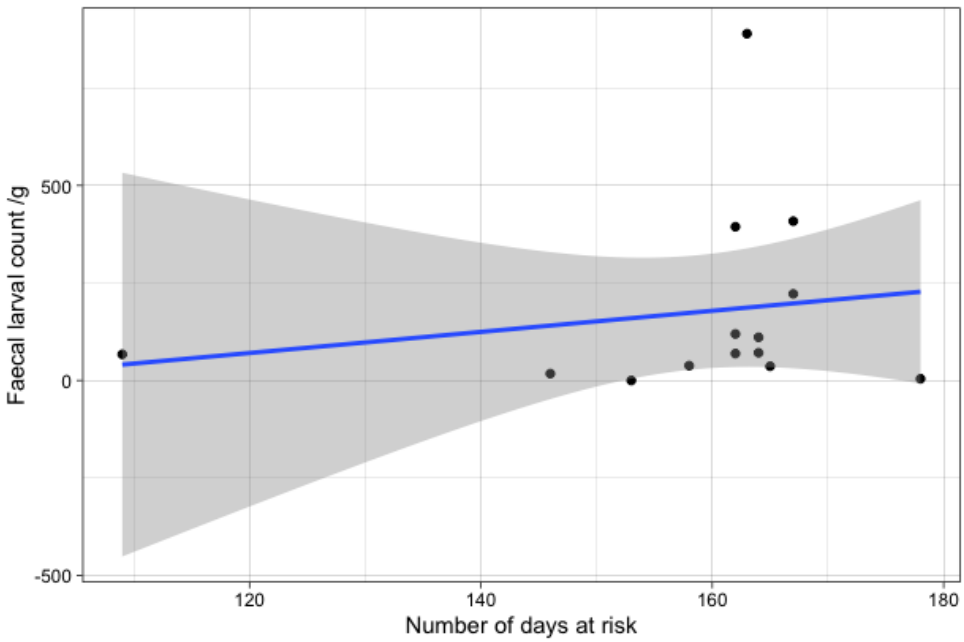
```
spring2yr$Elaphostrongylus.LPG <- as.numeric(spring2yr$Elaphostrongylus.LPG)

yr1mod <- lm(spring1yr$Elaphostrongylus.LPG~ spring1yr$days.exposed)
summary(yr1mod)

yr2mod <- lm(spring2yr$Elaphostrongylus.LPG~ spring2yr$days.exposed)
summary(yr2mod)
```

APPENDIX 3.2 Linear regressions for model validation

A)



B)



The number of days an individual reindeer is in an area with the accumulated degree-days greater than 245 within a calendar year compared to their faecal larval count 1 month *(A)* and 13 months *(B)* after. The regression line (blue) and 95% confidence interval (grey) show non-significant relationships. (**A**: R^2adj 0.007303, p-value 0.2836; **B**: R^2adj -0.04947, p-value 0.5454)

APPENDIX 4.1 R Script for ELAPHSIM model and simulations

```
library(data.table)
library(viridis)
library(ggplot2)
library(rgdal)
library(ncdf4)
library(raster)
library(rasterVis)
library(rnaturalearth)
library(deSolve)
setwd("###")

elaphsim = function (init, start, end, input, temp)
{
  date.range = seq(as.Date(start), as.Date(end), "days")
  if (length(date.range) != length(temp))
    stop("Error: length of climatic data and dates do not match. Ensure climatic data
correspond to the start and end dates (one entry per day)")
  global.t = seq(1, length(date.range))
  ints = 15 # average infection intensity in gastropod
  inf = pmax(0, (0.0153577 + 0.0017151 * temp)) #infection rate of L1p to L1s
  dev.1 = pmax(0, -0.0134121 + 0.0015694 * temp) #development rate from L1 to
L3
  dev.1 = pmin(1, dev.1)
  mu.1 = pmin(1, exp(-6.46559 + 0.11278 * temp)) #L1 mortality rate on pasture
  mu.2 = pmin(1, exp(-7.76093 + 0.13935 * temp)*ints) #L1s mortality rate (snail
mortality * infection intensity)
  mu.3 = pmin(1, exp(-7.76093 + 0.13935 * temp)*ints)  #L2s mortality rate (snail
mortality * infection intensity)
  mu.4 = pmin(1, exp(-7.76093 + 0.13935 * temp)*ints)  #L3s mortality rate (snail
mortality * infection intensity)

  infrate <- approxfun(x = inf, method = "linear", rule = 2)
```

```
 dev1rate <- approxfun(x = dev.1, method = "linear", rule = 2)
 mu1rate <- approxfun(x = mu.1, method = "linear", rule = 2)
 mu2rate <- approxfun(x = mu.2, method = "linear", rule = 2)
 mu3rate <- approxfun(x = mu.3, method = "linear", rule = 2)
 mu4rate <- approxfun(x = mu.4, method = "linear", rule = 2)
 print("parameters loaded successfully")

 event = data.frame(var = "L1p", time = global.t, value = input, method = "add")

 para.dyn = function(t, para.init, para.par) {
  with(as.list(c(para.init, para.par)), {
   dev1 = dev1rate(t)
   mu1 = mu1rate(t)
   mu2 = mu2rate(t)
   mu3 = mu3rate(t)
   mu4 = mu4rate(t)
   in1 = infrate(t)
   dL1p = -(in1 + mu1) * L1p
   dL1s = -(dev1 * 2 + mu2) * L1s + (in1 * L1p)
   dL2s = -(dev1 * 2 + mu3) * L2s + (dev1 * 2) * L1s
   dL3s = -(mu4) * L3s + (dev1 * 2) * L2s
   return(list(c(dL1p = dL1p, dL1s = dL1s, dL2s = dL2s, dL3s = dL3s)))
  })
 }
 print("model function loaded successfully")
 para.init = c(L1p = init[1], L1s = init[2], L2s = init[3], L3s = init[4])
 print("initial conditions for state variables loaded successfully")
 para.sol = lsoda(y = para.init, times = global.t, func = para.dyn,
                  parms = NULL, events = list(data = event))
 print("simulation finished - review any warning messages above this line")

 return(para.sol)
}
```

```
parainterp = function(para, dates, method="linear") {
  indices = which(seq(as.Date(dates[1]), as.Date(rev(dates)[1]), "days") %in%
as.Date(dates))
  days = seq(1, length(seq(as.Date(dates[1]), as.Date(rev(dates)[1]), "days")), 1)
  interpfun = approxfun(y = para, x = indices, method = method)
  return(interpfun(days))
}

# Load and prepare larval data
lpg_values <- read.csv("lpg_values.csv")
lpg_values$Date <- as.Date(lpg_values$Date, "%d/%m/%Y")
flcs = lpg_values$lpg*2000*15 # flc values* weight of faeces * reindeer density
flc.dates = lpg_values$Date
flc = parainterp(para = flcs, dates = flc.dates)

# Load and prepare temperature data
tg = nc_open("tg_ens_mean_0.1deg_reg_v23.1e.nc")

lon = ncvar_get(nc = tg, varid = "longitude")
lat = ncvar_get(nc = tg, varid = "latitude")

time = ncvar_get(nc = tg, varid = "time")
tunits = ncatt_get(tg, "time", "units")
nt = dim(time)

tustr <- strsplit(tunits$value, " ")
tdstr <- strsplit(unlist(tustr)[3], "-")
tmonth <- as.integer(unlist(tdstr)[2])
tday <- as.integer(unlist(tdstr)[3])
tyear <- as.integer(unlist(tdstr)[1])
thuman = seq(from = as.Date(paste(tyear, tmonth, tday, sep = "-")), length = nt, by =
"day")

# Set the bounds for the model
```

```
minlon = #Coordinate
minlat = #Coordinate
maxlon = #Coordinate
maxlat = #Coordinate
lon_range = which(lon<maxlon & lon>minlon)
lat_range = which(lat<maxlat & lat>minlat)

start.date <- as.Date("2016-01-01", format = "%Y-%m-%d")
end.date <- as.Date(last(thuman))
dat_range = which(thuman<=end.date & thuman>=start.date)

# Create an empty array to hold output
out.array <- array(dim = c(length(temp.dat[,1,1]), length(temp.dat[1,,1]),
length(temp.dat[1,1,])))

# Loop through each grid cell within the range and output number of developed L3
for(i in 1:length(temp.dat[,1,1])){
  for(j in 1:length(temp.dat[1,,1])){
    cell <- data.frame(as.Date(seq(from = start.date, to = end.date, by = 1)),
temp.dat[i,j,])
    colnames(cell) <- c("date", "temp")
    temp = cell$temp

    out = elaphsim(init = c(flcs[1], 0, 0, 0), start = "2016-01-01", end = "2020-12-31",
input = flc, temp = temp)
    out.df = as.data.frame(out)

    out.array[i,j,] <- out.df$L3s
  }
}

# Divide the output into individual years
L3.2016 <- out.array[,,1:366]
L3.2017 <- out.array[,,367:731]
```

```
L3.2018 <- out.array[,,732:1096]
L3.2019 <- out.array[,,1097:1461]
L3.2020 <- out.array[,,1462:1827]
```