Faculty of Technology, Natural Sciences and Maritime Sciences

Master in Ecology and Environmental Management

Spring 2024

Irene García Cuesta (258844) and María Elena Díaz Gómez (258840)

Exploring gastropod presence along an altitudinal gradient in reindeer habitat: implications for infection with brainworm disease.

University of South-Eastern Norway
Faculty of Technology, Natural Sciences and Maritime Sciences
Department of Natural Sciences and Environmental Health
PO Box 4
3199 Borre
http://www.usn.no

This thesis is worth 60 study points.

ABSTRACT

The emergence of diseases, such as cerebrospinal elaphostrongylosis caused by brain worms or Chronic Wasting Disease (CWD), as a critical threat to wildlife has accentuated the necessity of understanding disease dynamics within ecosystems. This evolving perspective in wildlife conservation accounts for the complex relationship between human activities, climate change and diseases prevalence in wildlife. This master thesis focuses on the host-parasite relationship between the parasitic nematode *Elaphostrongylus rangiferi,* which causes brainworm disease, and the tundra reindeer (*Rangifer tarandus tarandus*), which serves as the end host of this nematode. Gastropods act as intermediate host. Ultimately, brainworm disease is lethal for the end host. Norway hosts some of the last European populations of the tundra reindeer and thus has special responsibility for the conservation of this red listed species. The impacts of climate change, such as rising temperatures, influence the distribution patterns of the tundra reindeer and gastropods, resulting in their increased overlap in mountainous regions, which in turn may lead to an increase in brainworm infections. We investigated the spatial distribution and abundance of gastropods, i.e. snails and slugs, in plots along an altitudinal gradient in reindeer habitat in Hardangervidda National Park, Norway. We used two methods to find gastropods in the vegetation plots, i.e. visual search and traps, and evaluated the abundance of gastropods in relation to environmental characteristics of the plots. The results showed that the most important factors affecting the abundance of gastropods in reindeer habitats were elevation, soil moisture, and tree cover. Gastropod abundance was higher at lower elevations and in areas with dense tree cover along with high soil moisture levels. Our results suggest that future climate change may lead to an increase of gastropods at higher elevations, which may intensify the prevalence of brainworm infection in wild reindeer.

INTRODUCTION

Historically, wildlife conservation efforts have prioritized the study of the emergence of infectious diseases with zoonotic potential (Thompson et al., 2010). This research has mainly focused on diseases affecting wild species only when a disease greatly affected a hunted species or posed a threat to livestock (Cunningham et al., 2017). Over time, this has notably changed and today there is an increasing acknowledgment of the importance of pathogens in wildlife management (Cunningham et al., 2017). The effect of diseases on wildlife likely have increased over time due to human-induced factors, including human population growth, shifts in economic dynamics, climate change, habitat loss and changes in land use (Rizzoli et al., 2019). These factors have resulted in adverse effects on ecosystems and wildlife, including a more intense presence of host-parasite interactions and zoonotic diseases in wild populations (Dantas-Torres, 2015). Disease outbreaks can play a major role in the decline and extinction of isolated wildlife populations (Viggers et al., 1993).

The Eurasian tundra reindeer *(Rangifer tarandus tarandus)* is a migratory keystone species in northern Europe (Russell et al., 2018). However, wild reindeer herds have strongly declined in their historical range in Europe, and wild populations can now only be found in Norway and Finland (Gunn et al., 2009). In Norway, both semi-domesticated and wild reindeer exist, however, wild reindeer populations can only be found in mountain areas in southern Norway, i.e. south of the traditional grazing areas of semi-domestic reindeer herds (Thomson, 1978). Current estimates indicate that there are between 20,000–25,000 wild reindeer in Norway and they are part of a metapopulation divided into 24 different management areas (Lukacs et al., 2023; Figure 1).

These populations are generally isolated due to habitat fragmentation, human infrastructure developments, and human disturbances (Gundersen et al., 2022). Fragmented populations at low densities generally have less contact between individuals and the spread of diseases can decrease (McCallum & Dobson, 2007). However, reindeer are a gregarious species (Skarin et al., 2008) and the spread of diseases and parasites is thus highly relevant because of their social dynamics (Vander Wal et al., 2014; Webber & Vander Wal, 2020).

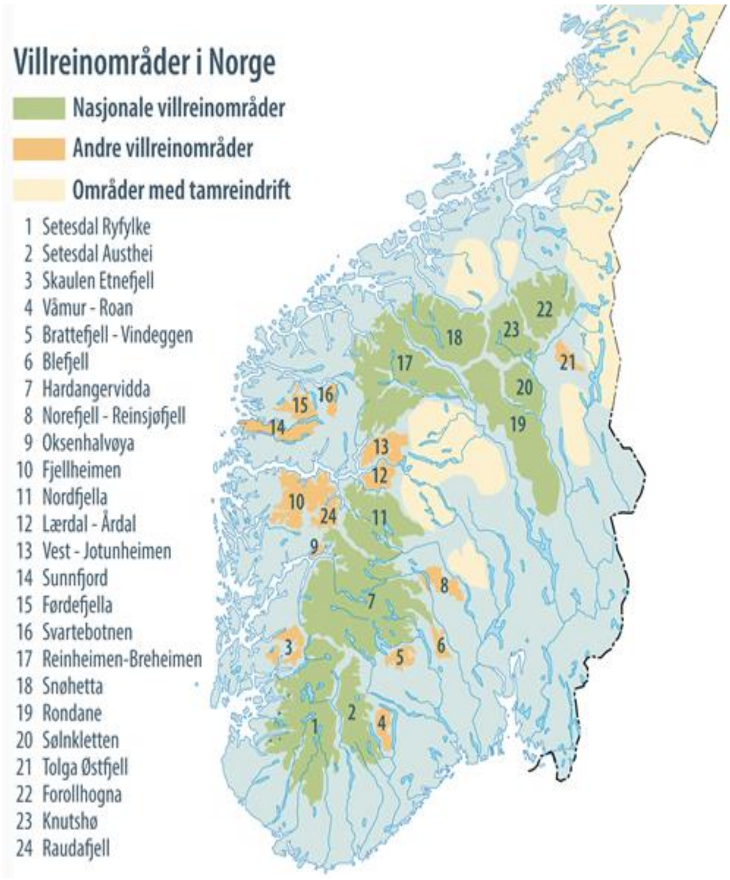


Figure 1. Distribution of wild reindeer populations in Norway (Norsk villreinsenter, 2024).

Diseases play a major role in the management of wild reindeer populations, especially the outbreak of Chronic Wasting Disease in 2016 (Mysterud et al., 2022). Reindeer are also commonly infected by various parasites, such as nematodes. Among these parasites, infection by the brainworm (*Elaphostrongylus rangiferi*) can cause cerebrospinal elaphostrongylosis (Handeland & Slettbakk, 1994). This parasite infects the central nervous system (CNS) and can produce symptoms such as malacia and axon degeneration in brain areas (Handeland & Norberg, 1992), as well as ataxia and hind leg paresis causing weakness (Davidson et al., 2020). It is believed that the majority of infections are asymptomatic or under-detected (Davidson et al., 2020), however, an infection ultimately results in an infected animals' death (Steen, 2022; Stuut, 2021). Gastropods serve as the intermediary host of *Elaphostrongylus rangiferi* (Ciezarek, 2022; Mørk et al., 2024; Rose Vineer et al., 2021), and reindeer are infected by consuming infected gastropods while feeding (Davidson et al., 2020).

Previous research has shown that *Elaphostrongylus rangiferi* development inside gastropods is highly temperature-dependent, with a faster development at high temperatures (Closset, 2021; Rose Vineer et al., 2021). This suggests that the effect of brainworm on wild reindeer populations may increase in the future due to climate change, which furthermore increases the geographic distribution of this parasite and its intermediate hosts (Hoberg et al., 2008; Okulewicz, 2017). Extreme weather conditions can affect disease outbreaks events (Ciezarek, 2022), and milder temperatures and increased precipitation may result in more parasite epidemics (Horstkotte et al., 2022), especially parasitic worms (Hoberg et al., 2008). Climate change may also result in trees, bushes and shrubs extending their distribution ranges to higher elevations and further north (Horstkotte et al., 2022; Tryland & Kutz, 2018), consequently resulting in an upward migration of the tree line (Closset, 2021). Reindeer exhibit a different diet throughout the year depending on the season. In spring and summer, they mainly feed on grasses, sedges, and willows (Turunen et al., 2009), while they feed primarily on lichens in winter (Bjerke, 2011). Climate change will likely result in a change of forage available to reindeer and a shift in the spatio-temporal feeding and migration patterns of reindeer between winter and summer feeding areas (Mallory & Boyce, 2018; Turunen et al., 2009; Vuojala-Magga, 2010), as well as creating more favorable conditions for the proliferation of parasites. These changes will likely also be associated with a quicker spread of diseases (Witter et al., 2012).

The distribution of terrestrial gastropods, which are the intermediate hosts of brainworm (Davidson et al., 2020), will also be significantly influenced by climate (Closset, 2021). Shifts and increases in gastropod distribution ranges have become evident over time, with certain species increasing their upper elevational limit (Baur & Baur, 2013), i.e., gastropods are expected to spread higher and further into mountain ranges (Solomon 2007; Rose Vineer et al., 2021). In general, the species richness and densities of gastropods decreases with elevation and increases as the habitat becomes more forested at lower latitudes (Baur et al., 2014) with shelter from solar radiation, higher humidity, high concentrations of plant-available nutrients, and high levels of pH (Closset, 2021). Soil pH decreases along the elevational gradient (Praeg et al., 2020). With the prolonged growing season for vegetation in mountainous regions, the activity period of gastropods is also extended, which also increases the time window during which reindeer can get infected (Vanneste et al., 2017).

Brainworms are an important parasite affecting reindeer in Norway (Davidson et al., 2020; Mørk et al. 2024; Tryland et al., 2022), however, little information is available about the overlap in the distribution of reindeer and snails and slugs as the intermediate hosts of the brainworm (Rose Vineer et al., 2021). The aim of this thesis is to evaluate how biotic and abiotic factors affect the spatial distribution and abundance of gastropods along an altitudinal gradient in reindeer habitat. We hypothesize that:

1) the distribution and abundance of gastropods decreases with increasing elevation (Baur & Baur, 2013),

2) the abundance of gastropods is higher in

    a) vegetation types with high plant cover and high presence of trees (Kappes et al., 2006; Kralka, 1986),

    b) humid areas (Martin & Sommer, 2004; Rizzoli et al., 2019) with high abundance of mosses, since their metabolic activity is intricately tied to the availability of water (Busby et al, 1978),

    c) areas with higher pH values (Closset, 2021; Godan, 1983; Walden, 1981).

MATERIAL AND METHODS

Lifecycle of *Elaphostrongylus rangiferi*

The brainworm *Elaphostrongylus rangiferi* is a parasite with an indirect life cycle, i.e., it uses snails or slugs as an intermediate host (Figure 2). The process starts when reindeer ingest the intermediate host (snails/slugs) by accident while feeding. The following gastropod species have been demonstrated to be appropriate hosts in experimental settings: *Discus ruderatus*, *Arion silvaticus*, *Deroceras laeve* and *Deroceras reticulatum* (Davidson et al., 2020). The reindeer ingest worm larvae in infective stage 3(L3), afterward the larvae migrate through the blood from the gastrointestinal cavity to the central nervous system (Mitskevich, 1958). Within 40-90 days of arriving in the central nervous systems, the larvae mature to adults. The parasite can affect either the epidural (spinal cord) or subdural (brain) spaces of the host's central nervous system, where it develops to maturity (Hemmingsen et al., 1993). After 90-182 days, the parasites migrate to the skeletal muscle, where they produce eggs which are transported via the bloodstream to the host's lungs, where the new non-infective larvae (stage 1) hatch and enter the alveoli (Figure 2). These larvae are eventually coughed up by the reindeer, swallowed again by the same or other reindeer during feeding, and then passed through the digestive tract and get defecated. They can resist extremely low temperatures and survive for more than one year in feces on pasture (Davidson et al., 2020). The parasites in stage 1 of larvae (non-infective) complete their development process in around 3-4 months, then they infect gastropods either by attaching and penetrating their surface (Skorping, 1982) or by being ingested by them (Michigan Department of Natural Resources, 2024). Then, the parasites undergo development from the initial larvae stage to the third larvae stage and become infectious for the reindeer one more time (Hemmingsen et al., 1993) (Figure 2). The frequency of infection in snails naturally relies on the abundance of L1 larvae present in the environment and shows substantial variability across various species of gastropods (Skorping, 1988). The cycle starts again once a reindeer accidentally ingests a gastropod while grazing which has the parasite in larvae stage 3 (infective for reindeer) developed (Figure 2).

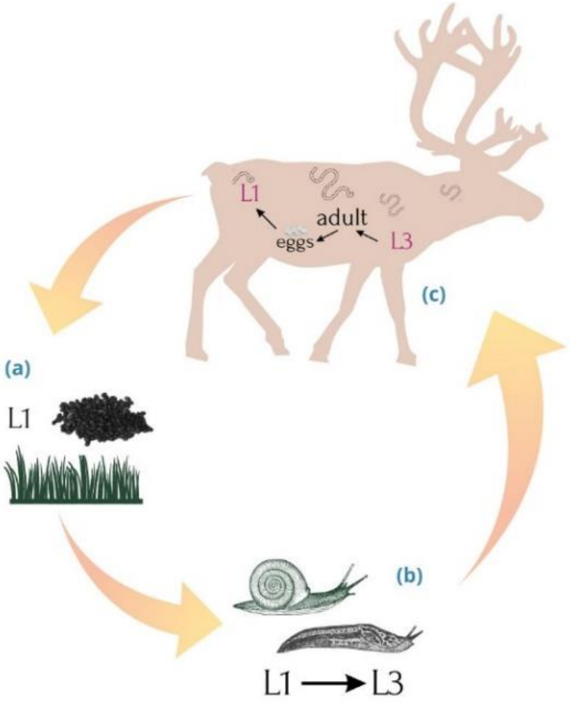


Figure 2. Life cycle of the brainworm *Elaphostrongylus rangiferi*. Produced by the authors based on Closset, 2021.

Study area and selection of transects

Our study was carried out in the area north-east of lake Bitdalsvatn (59º79'59.71"N, 007º86'27.78"E) and to the south-west of lake Møsvatn (59°51'59.99", N 8°04'60.00" E) in Vinje Municipality, Telemark, Norway. The area is a calving area for the Hardangervidda reindeer population (personal communication L. Romtveit, Norsk Villreinsenter Sør/Skinnarbu) and is located in Hardangervidda National Park. The area was selected based on the general distribution of the Hardangervidda reindeer population (red area in Figure 3), GPS-locations of radio-collared reindeer, and advice by L. Romtveit from Norsk Villreinsenter Sør/Skinnarbu.

Fieldwork was conducted from 21 August – 30 August 2023. We preselected 6 transects located in a reindeer calving area (personal communication L. Romtveit, Norsk Villreinsenter Skinnarbu; Figure 3). All transects were positioned along an elevational gradient to cover a wide range of vegetation types from the bottom of the valley into the alpine area inside of the wild reindeer habitat. To cover different terrain conditions, transects number 1, 2, and 3 were located in steep terrain, in contrast to transects 4,5, and 6 located in flatter terrain (Figure 3).

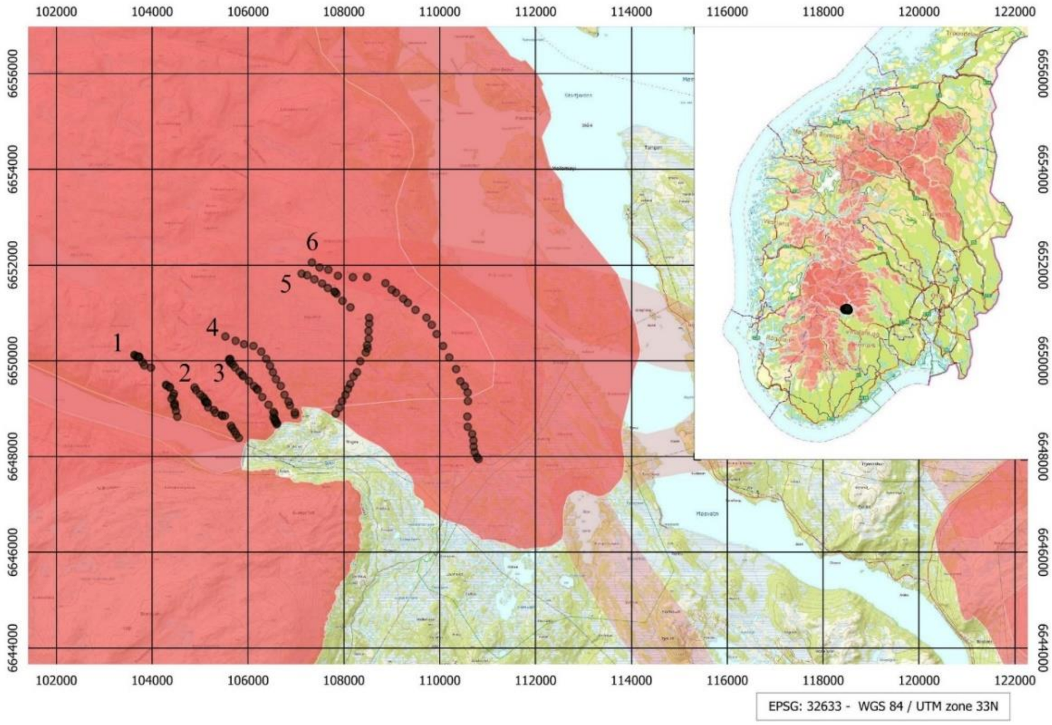


Figure 3: Map of the study area and location of 6 transects and plots (black dots) to evaluate the abundance of gastropods in wild reindeer habitat (red area) in Hardangervidda National Park, Norway, in August 2023. Produced using QGIS by the authors.

Field methods

As we progressed along each transect from the bottom to the top, our method for selecting plots (1 square meter quadrat) was guided by visual observation of the diverse vegetation types (Rekdal & Larsson, 2005). The minimum number of selected plots per vegetation type was 3. However, due to variations in the terrain characteristics and the length of each transect, the number of plots selected for each vegetation type could vary, allowing us to capture the full diversity of vegetation along each transect. The distance between consecutive plots was approximately 100 meters, providing an adequate coverage of the transect.

The data collection in the field consisted of two parts. The first part focused on the different characteristics of the habitats divided in abiotic and biotic factors that could be relevant for our study. Within the abiotic factors we focused on soil moisture, pH, weather conditions and plot terrain characteristics (location, soil type, and water). Vegetation type, its coverages percentages (trees, bushes, herbs/ferns, graminoids, mosses and lichens) and organic matter were assessed as the biotic factors. We also extracted the weather conditions during our study period (Appendix, Figures 1 and 2) to examine whether precipitation and temperature patterns might have an impact on our research. The second part consisted of the search of gastropods (snails and slugs) either by visual search in each plot or by placing traps which were left in place for 24 hours (traps were placed within certain plots, depending on the length of the transect and the variety of vegetation types encountered in them). All the data collected in the field were detailed in a protocol sheet for each plot (Appendix, Figure 3).

While the above description provides a baseline for our field methodology, further elaboration on abiotic and biotic conditions, as well as the gastropod search, can be found in the following sections.

Abiotic and biotic conditions

The abiotic conditions covered different variables, such as soil moisture, pH, weather, and plot terrain characteristics. Soil moisture within the topsoil (0 - 6 cm) was measured using Delta T's ML3 theta probe in combination with the HH2 moisture meter, providing an accuracy of +/- 1 vol-%. We took 5 measurements per plot (i.e., in the four corners and the center, which were averaged). Moreover, 3 teaspoons (equivalent to approximately 20 grams) of topsoil from 2 or 3 different locations within the quadrat were collected for pH analysis in the lab. In the field, we registered weather variables (i.e., sunny, partly sunny, overcast, partly overcast, rainy and foggy), topographical position of the plot (i.e., ridge, depression, slope or flat), moisture assessment (dry, partly dry, moist, bog), and water presence (none, puddles, creek) (see Appendix, Figure 3).

The biotic conditions focused on the organic matter, the vegetation type, and the assessment of vegetation coverage percentages (trees, bushes, herbs/ferns, graminoids, mosses and lichens). Organic matter was assessed as the absence (0) or presence (1) of decomposing leaves and branches. Along the transects, the occurring vegetation types were distinguished following the guideline of Rekdal and Larsson (2005) and used for placing the sampling sites. Each occurring vegetation type was covered by at least three (up to a variable number, depending on their spatial extent) sampling sites. Table 1 provides an overview of the occurring vegetation types, their main characteristics, and the sampling.

Table 1. Vegetation types and their characteristics in plots along an altitudinal gradient in reindeer habitat in Hardangervidda National Park, Norway, August 2023. N denotes the sample size.

Vegetation type	Characteristics	N of plots per transect and in total
1. Snowbed	Plots characterized by long lasting snow cover and short growing period	2(3 plots), 3(4 plots), 5(2 plots).
2. Alpine heathland	Plots dominated by dwarf shrubs and graminoids	1(16 plots), 2(6 plots), 3(9 plots), 4(2 plots), 5(9 plots), 6(15 plots)
3. Alpine meadow	Plots dominated by herbs, ferns and broad-leafed graminoids	3(1 plot).
4. Deciduous forest	Plots dominated by birch forest including heather, blueberry, grasses, herbs, and ferns	1(5 plots), 2(5 plots), 3(6 plots), 4(3 plots), 5(7 plots), 6(8 plots).
9. Mire & swamp	Plots in wetlands dominated by peat-forming plants (mires) or a broader vegetation range (swamps)	2(3 plots), 3(5 plots), 4(9 plots), 5(8 plots), 6(7 plots).

Gastropod data collection

We used two methods to estimate the abundance of gastropods in the plots because we wanted to compare which method was more useful and the most efficient for future field use. One method was based on visual search, and the other method consisted of setting up traps (Lucid et al., 2018; Clergeau et al., 2011).

In the visual search method, we thoroughly searched every 1m^2 plot for the presence of snails and slugs for a standardized time period, i.e., 15 minutes (Lucid et al., 2018). We collected all specimens and sorted them based on their observable characteristics, such as size, color, and body markings. Specimens displaying similar traits were placed into labeled tubes, each indicating the date, plot id, and transect id. We then sedated the snails and slugs in each tube with 5% ethanol to induce anesthesia and then euthanized them with a solution of 70% ethanol (Gilbertson & Wyatt, 2016). In addition to the visual search, we randomly selected at least one plot per different vegetation type along each transect to set up traps. A trap consisted of a petri dish filled with beer (as beer serves as an effective bait for attracting gastropods; Lucid et al., 2018) and covered with a cardboard roof. We placed 30 traps in vegetation plots along the transects. In the first transect we set four traps, three traps in the second transect, five traps in the third transect, three traps in the fourth transect, seven traps in the fifth transect, and eight traps in the sixth transect. All the data collected was in field protocol sheets (Appendix, Figure 3).

Laboratory methods

All snails and slugs collected in the field were identified at the species level by Rodrigo Bincalepe Salvador at The Arctic University Museum of Norway, Tromsø, Norway, in December 2023. We also conducted pH assessments of the soil samples collected at each plot. Soil samples were transferred to cardboard boxes and dried at 35-40 Celsius and adequate air circulation for up to 5 days until they were completely devoid of moisture. Afterwards, the dried soil samples were sifted through a 2-millimeter mesh sieve to isolate the fraction smaller than 2 millimeters containing clay, silt, and sand (Krogstad, 1992). Ten milliliters of soil were transferred to a graduated beaker and mixed with 25 milliliters of distilled water. After standing overnight and shaking, pH was measured following a 15 minutes waiting period. The electrode was positioned above the sediment in the suspension, and pH was recorded once stable (Krogstad, 1992). The pH values were recorded to one decimal point (Appendix, Table 1).

Statistical methods

We used descriptive statistics to present data on gastropods abundance (Figure 4 and Figure 5), species (Table 4) and laboratory results (Appendix, Table 1). We further followed the methods outlined by Zuur et al. (2009) to check for the presence of correlation and multicollinearity in our explanatory variables (Table 2) and afterwards the outliers to verify the accuracy of the model. The statistical analysis was conducted using R version 4.3.2 (R Core Team, 2022) and RStudio (RStudio Team, 2023). We used a significance level of $p \leq 0.05$. The adequacy of the models was assessed using the "DHARMa" package (Hartig, 2020), which was also employed to identify correlation, multicollinearity, outliers, and dispersion in and among predictor variables. The variables 'estimate coverage percentage of trees in a plot' and 'organic matter in a plot' had a correlation of $r = 0.77$, and we therefore removed the variable 'organic matter' from further analyses. The categorical variable 'vegetation type' was excluded because of its multicollinearity value > 6 (8.95), but also because the sample distribution was highly skewed, (i.e., only 1 plot for vegetation type 3, 57 plots for vegetation type 2, 34 plots for vegetation type 4, and 32 plots for vegetation type 9; Table 1).

Table 2. Explanatory variables used in the generalized linear model for assessing gastropod abundance. in both visual searches and using traps in 6 transects in reindeer habitat in Hardangervidda National Park, Norway, August 2023.

Explanatory variables	Type	Description	Units
Soil moisture	Numeric	Humidity level of the topsoil	Volume percentage
Elevation	Numeric	Vertical height above sea level	Meters above sea level
Mosses	Numeric	Coverage of mosses	Percentage
pH	Numeric	pH level of the topsoil	Dimensionless
Trees	Numeric	Coverage of trees	Percentage

After the exploratory data analysis, we used Generalized Linear Models (GLM) to analyze the data. Since the study area was not very large and there was a lack of variation in habitat among the different transects, we decided to not include a grouping effect for the transect, i.e. we did not use generalized linear mixed models, but only controlled for elevation in our analyses. We used a GLM with a Poisson data distribution to evaluate the factors affecting the number of visual observations of gastropods per vegetation plot (i.e., abundance). In addition, we used another GLM with a Poisson data distribution to evaluate the factors affecting the number of gastropods trapped per plot (i.e., abundance). In both models we used the response variable (number of gastropods found either by visual search or with traps) and the following explanatory variables: soil moisture, elevation (in meters above sea level), coverage percentage of mosses in the plots, coverage percentage of trees in the plots, and pH. In addition, we included the following interactions: trees*elevation, mosses*elevation, soil moisture*mosses, trees*soil moisture, pH*elevation and mosses*trees. These variables and interactions were chosen because of their biological meaning and supported by literature (Closset, 2021; Heiba et al., 2018; Praeg et al., 2020). We carried out a backwards selection procedure, in which all the variables are first included in the initial model, and then are removed one by one depending on their level of significance, until we got a final model containing only the significant variables ($p \leq 0.05$) (Pearce & Ferrier, 2000).

RESULTS

General results

Overall, we established 137 plots along the six transects (Table 3). A total number of 9 plots were characterized as snowbeds (vegetation type 1), 57 plots as alpine heathlands (vegetation type 2), just one plot was an alpine meadow (vegetation type 3), 34 plots were grouped into deciduous forest (vegetation type 4) and 32 plots were defined as mires and swamps (vegetation type 9).

Table 3. Number of vegetation plots (Plots) and vegetation types (Types) along altitudinal transects (Transects) evaluating the abundance of gastropods (Gastropods) in a transect, as well as the number of gastropods found with visual search (Visual) or in traps (Traps) along an altitudinal gradient in reindeer habitat in Hardangervidda National Park, Norway, August 2023.

Transect	# Plots	# Vegetation types	# Gastropods	Visual	Traps
1	21	2 (2 and 4)	18	12	6
2	20	5 (1, 2, 3, 4, 9)	2	2	0
3	24	4 (1, 2, 4, 9)	7	3	4
4	15	3 (2, 4, 9)	2	1	1
5	27	4 (1, 2, 4, 9)	6	2	4
6	30	3 (2, 4, 9)	9	4	5

We obtained a table with the pH values of each plot per transect after analyzing them in the lab (Appendix, Table 1). The values obtained correspond to a range between 3.88 and 6.3, which correspond to an acidic pH.

To obtain measures of soil moisture, we calculated the mean of the 5 measurements (top right, top left, center, bottom right and bottom left) taken in each plot of the study, and we did the mean between those 5, to get the final soil moisture values of a plot (Appendix, Table 2). The values vary between 13.70 and 112.36.

Gastropods species and measures of abundance

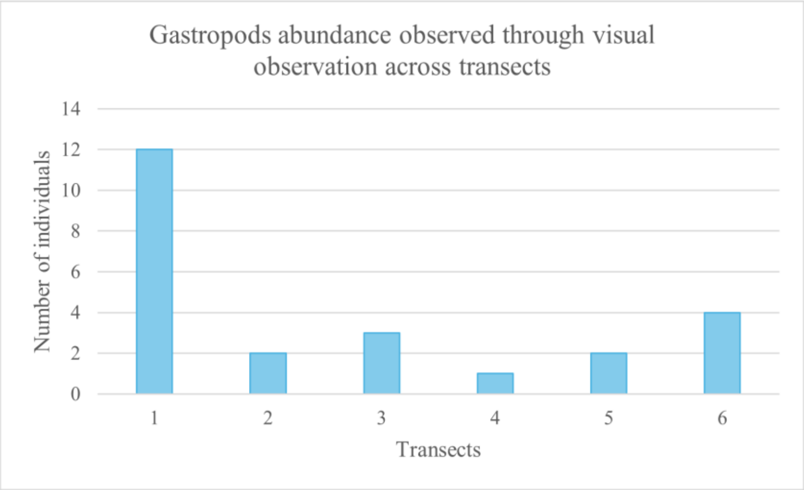
Overall, we found 44 gastropods (Table 4) of which 24 with visual search (1 snails and 23 slugs) and 20 in traps (2 snails and 18 slugs), (Table 3, Table 4). The individuals we found belonged to one species of snails, *Vitrina pellucida,* and nine species of slugs (Table 4) with the *Arion*-species being the most abundant. Among the *Arion*-species, there were 16 *Arion hortensis*, 7 *Arion silvaticus*, 6 *Arion ater* and 4 *Arion fasciatus*, a total of 33. We found 3 specimens of *Deroceras reticulatum* and 3 of *Vitrina pellucida*.

Table 4: Gastropod species and number of individuals per species found in plots along 6 altitudinal transects in reindeer habitat in Hardangervidda National Park, Norway, in August 2023.

Species	N
Arion ater	6
Arion fasciatus	4
Arion hortensis	16
Arion silvaticus	7
Arion subfuscus	1
Deroceras reticulatum	3
Deroceras sp.	2
Limax cinereoniger	1
Malacolimax tenellus	1
Vitrina pellucida	3

Gastropods density in relation to the vegetation type

Different numbers of individuals were observed across the different transects. With visual searching, the greatest number was found in transect 1 (12 individuals), with the lowest count on transect 4 (1 individual). Similarly, the use of traps revealed a higher abundance in transect 1 (6 individuals), contrasting with the smallest count in transect 4 (1 individual) (Figure 4). In relation to the vegetation type, with visual search, we found 23 gastropods (96%) in deciduous forest vegetation type and only one gastropod (4%) in alpine heathland vegetation type. Using traps, we caught 11 gastropods (55%) in deciduous forest vegetation type and 9 (45%) in mire and swamp vegetation type (Figure 5).



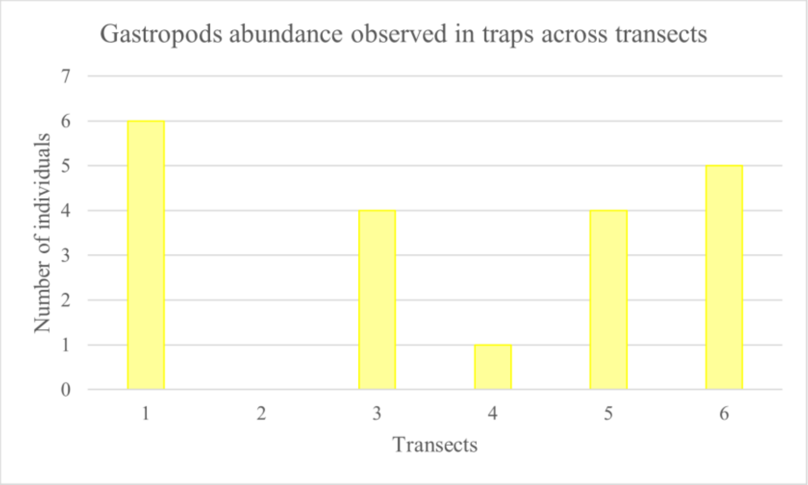
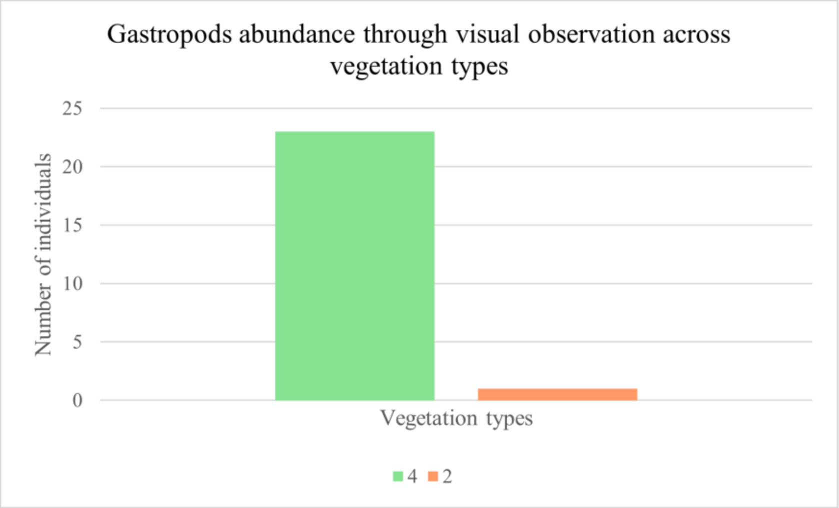


Figure 4. Number of gastropods found with visual observation (top) and traps (bottom) along 6 altitudinal transects in reindeer habitat in Hardangervidda National Park, Norway, in August 2023.



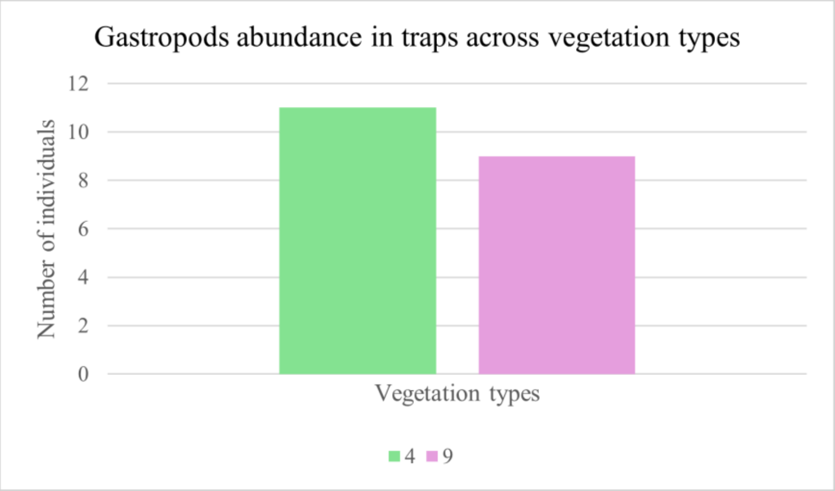


Figure 5. Gastropods found per vegetation type using visual search (top) and traps (bottom) along 6 altitudinal transects in reindeer habitat in Hardangervidda National Park, Norway, in August 2023.

Model results

We found that the abundance of gastropods based on visual search significantly decreased with increasing elevation and increasing proportion of trees inside a plot (Table 4). The significant interaction of the proportion of mosses and soil moisture suggests that there is a higher probability of finding gastropods in plots with low soil moisture if there is a high proportion of mosses (Table 5). The significant interaction of the proportion of trees and soil moisture suggests that there is a higher probability of finding gastropods in plots with a high proportion of trees if there are high levels of soil moisture (Table 5).

Table 5: Results of a generalized linear model evaluating the factors affecting the abundance of gastropods in visual searches in 6 transects in reindeer habitat in Hardangervidda National Park, Norway, August 2023.

Variables	Estimate	SE	Z	P
Intercept	10.95	7.024	1.559	0.118
Elevation	-0.017	0.006	-2.868	0.004
Trees	-0.205	0.101	-2.029	0.043
Mosses	0.024	0.016	1.496	0.142
Soil moisture	0.024	0.020	1.195	0.232
Mosses:soil moisture	-0.001	0.0003	-2.490	0.013
Trees: soil moisture	0.001	0.0003	2.414	0.016

We found that the abundance of gastropods based on trap catches significantly decreased with increasing elevation and increased with increasing soil moisture of a plot (Table 6). The significant interaction of elevation and proportion of mosses inside a plot suggests that there is a higher probability of finding gastropods at higher elevations in plots with a high proportion of mosses (Table 6). The significant interaction of the proportion of mosses and soil moisture suggests that there is a higher probability of finding gastropods in plots with low soil moisture if there is a high proportion of mosses (Table 6).

Table 6: Results of a generalized linear model evaluating the factors affecting the abundance of gastropods with traps in 6 transects in reindeer habitat in Hardangervidda National Park, Norway, August 2023.

Variables	Estimate	SE	Z	P
Intercept	64.422	34.569	1.864	0.062
Elevation	-0.077	0.035	-2.198	0.028
Soil moisture	0.159	0.052	3.019	0.003
Mosses	-0.670	0.3557	-1.885	0.059
Elevation:mosses	0.0008	0.0004	2.152	0.031
Mosses:soil moisture	- 0.001	0.001	-2.673	0.008

DISCUSSION

Overall, the results of this project support our hypothesis 1) “the abundance of gastropods decreases with increasing elevation”. We found only partial support for hypothesis 2a) “the abundance of gastropods is higher in the presence of trees”, as the importance of tree cover was connected to high ground moisture. We also found only partial support for hypothesis 2b) “higher abundance of gastropods in humid plots as well as plots with a high proportion of mosses”. We found no support for an effect of soil pH on gastropod abundance (hypothesis 2c).

Independent of the capture method, we found the abundance of gastropods to decrease with increasing elevation (Table 5 and Table 6), which fits well with previous findings (Baur & Baur, 2013; Davidson et al., 2020; Handeland et al., 2019; Stuut, 2021). Regions at higher elevations typically experience less land area, difficulting opportunities for life (Baur et al., 2014), as well as no shelter from solar radiation, colder temperatures, and less abundant vegetation in contrast to regions at lower elevations, making them more unlikely to host numerous gastropods (Closset, 2021). For both visual searching and trapping procedures, the results reveal that soil moisture and its interactions with mosses were significant variables that had better explain our results. The results suggest that there is a higher probability of finding gastropods in plots with low soil moisture if there is a high proportion of mosses (Table 5 and Table 6). However, our findings contradict existing literature, as habitats that are consistently moist tend to be dominated by moss vegetation (Migała et al., 2014). Moreover, some slugs feed on immature moss capsules but do not consume them once they are fully developed (Davidson et al., 1990). Gastropods sometimes use mosses as an emergency food (Boch et al., 2013) and some snail species lay down their eggs in mosses (Baur, 1994). In addition, mosses can serve as a shelter for gastropods, providing them with a humid terrestrial microenvironment (Božanić, 2011). On the other hand, Hettenbergerová et al. (2013) suggest that the preference of gastropods for higher or lower moisture depends on the species. Some species thrive in habitats with lower soil moisture values, while others prefer moderate levels, and still, others benefit from high moisture values (Hettenbergerová et al., 2013).

The influence that the other variables have in both procedures indicated distinct effects, so we will evaluate them separately for each procedure. For the visual search method (Table 5), the results indicate that in areas with an increasing proportion of trees, the probability of finding gastropods decreases. This outcome contrasts with what we expected and with literature, since gastropods find in forested areas more dead plant material to feed on (Closset, 2021) and these areas also offer increased vegetation cover, such as stems of tall plants that serves gastropods as estivation sites (Baur et al., 2014). We then focus on the interaction between trees and soil moisture, suggesting that there is a higher probability of finding gastropods in plots with a high proportion of trees if there are high levels of soil moisture. The general importance of both humidity levels and trees is supported by other studies (Closset, 2021; Heiba et al., 2018), which indicates that higher amounts of gastropods are found in calcium-rich areas with a higher presence of organic matter, typically covered by trees but also requiring high moisture values for decomposition and calcium availability (Juřičková et al., 2008; Seuffert & Martín, 2013).

For the trapping method (Table 6), soil moisture was statistically significant, suggesting that high levels of soil moisture are related to greater abundance of gastropods, which is supported by the literature because the distribution and abundance of gastropods generally is higher in humid areas (Martin & Sommer, 2004; Rizzoli et al., 2019). Based on the trap method, we observed a positive effect on the abundance of gastropods due to the interaction between elevation and mosses. While this interaction was not initially predicted to affect gastropod abundance, it coincides with findings in the literature. Bruun et al. (2006) reported that the highest moss richness is typically found in low-alpine areas. Considering the observation of gastropods above the tree line (Pearce & Örstan, 2006) and within mossy habitats (Božanić, 2011) our results suggest that the presence of gastropods may increase at higher elevations when mosses are present.

We also hypothesized higher pH to be related to the presence of gastropods (prediction 2c). Soil pH plays a crucial role in ecosystems and contributes to the distribution of the different vegetation types, which in turn are linked to gastropod abundance (Andersen & Halvorsen, 1984). We obtained acidic pH ranging from 3.8 to 6.3, yet pH did not emerge as a significant variable affecting gastropod densities in either search method. This could be explained because the pH range is too low to show an effect and because pH has not outcome as determinant factor in gastropods preferences. While certain gastropod species prefer alkaline soils, others are indifferent to pH changes (Ondina et al., 2004). In line with our results, Both Millar and Waite (1999) and Heiba et al., (2018), demonstrated that soil pH had no significant effect on gastropod abundance.

The distribution of gastropods in our study area was mainly influenced by the elevation but also by the presence of trees in high moisture areas. Forest ecosystems present in general the perfect conditions to develop gastropod populations (Kralka, 1986), and almost all our findings were in forests (Figure 5). The unexpected negative estimate for trees did not meet our expectations. Therefore, we interpreted this variable cautiously, emphasizing the need for future research to disentangle the effect of trees and how they interact with other variables and affect gastropods abundance. We also encountered 9 specimens in swampy areas (vegetation type 9), and this can be explained by the relationship previously mentioned between soil moisture and gastropods (Seuffert & Martín, 2013), but further research is needed in order to understand all the factors that best explain the findings of gastropods.

Previous studies had shown that *Discus ruderatus*, *Arion silvaticus, Deroceras laeve* and *Deroceras reticulatum*, species also found in this study, would seem to be particularly suited for the development of *Elaphostrongylus* larvae, based on recorded infection intensities and their development times (Davidson et al., 2020). We can, then, conclude that ten specimens from our samples were potential hosts for the brainworm disease of reindeer.

Climate change can influence *Elaphostrongylus* dynamics (Skorping & Halvorsen, 1980). The penetration of larvae in stage 1 (L1) in gastropods and their development times to infecting larvae stage 3 (L3) are increased under warm temperatures (Davidson et al., 2020). Temperatures close to 20°C result in the larvae needing a shorter time to reach L3 stage, since the thermal habitat range of *Elaphostrongylus* has expanded since 2000 (Rose Vineer et al., 2021). Elevated temperatures during summer season are related to an increased outbreak of *Elaphostrongylosis* in reindeer (Closset, 2021). Based on the historical weather records of the past 30 years in the study area (Yr.no, 2024), we observed that temperatures during summer have been over 20ºC in the past decades, which benefits the larvae development from stage 1 to stage 3 in less than 2 weeks (Rose Vineer et al., 2021; Davidson et al., 2020). The minimum temperatures in Hardangervidda during summer have increased from -5 to -1 °C in the last 5 years, to temperatures between 0-1ºC (Yr.no, 2024). The development of *Elaphostrongylosis* is halted at temperatures below freezing (Davidson et al., 2020). Overall, this suggests that the temperature increases during the last decades likely will result in more brainworm disease outbreaks (Rose Vineer et al., 2021, Davidson et al., 2020).

Regarding the habitat suitability for gastropods, there is an estimation in Fennoscandia that, due to increased temperatures above 20 degrees (Yr.no, 2024), gastropods are likely to move towards higher and more northern regions (Rose Vineer et al., 2021). There is another prediction in Norway about an increment of gastropod species' richness through the years as a result of alterations in their distribution patterns because of climate change (Hof, 2011), which favors the spread of brainworm disease, given the diverse range of gastropods identified as suitable intermediate hosts for *Elaphostrongylus* (Skorping & Halvorsen, 1980). These two findings should be considered in further research to investigate whether gastropods habitats have expanded over time and whether there is an increasing probability of overlap with reindeer habitats in Handangervidda National Park. Reindeer typically inhabit higher elevations, but their distribution patterns can shift due to various factors (Mallory & Boyce, 2018). In summer, they migrate north to avoid insect harassment and high temperatures (Closset, 2021; Gunn et al., 2009) and in winter they migrate south to access more vegetation and browse (Tyler et al., 2021). Studies suggest that climate change is causing significant amplification of *Elaphostrongylus rangiferi* development rates (Brooks & Hoberg, 2007; Davidson et al., 2020) and changes in vegetation especially in alpine regions, with alpine meadows and tundra ecosystems expected to transform into shrublands in the future (Kelly & Goulden 2008; Pearson et al., 2013; Wilson & Nilsson, 2009; Zhao et al., 2011). These changes in vegetation, including alterations in height, biomass, and plant cover (Alatalo et al., 2016; Virtanen et al., 2010), could affect the distribution patterns of both gastropods and reindeer (Mallory & Boyce, 2018), promoting an increased overlap of both species (Davidson, 2020), potentially raising the risk of reindeer infection (Closset, 2021).

Wild reindeer face increasing vulnerability to infections due to climate change (Rizzoli et al., 2019). They are a keystone species in Norway (Gundersen et al., 2022; NINA, 2024), and serve as an umbrella species promoting the conservation of a wide range of biodiversity and are listed as "Near Threatened" in the Norwegian Red List of Species (Mysterud et al., 2024), Norway carries a global responsibility to study wild Eurasian reindeer dynamics to understand how to manage them effectively, particularly to mitigate the risk of brainworm disease.

Limitations of the study and future directions

Information regarding the gastropod abundance and how their dynamics are shaped by temperatures in Norway is limited (Closset, 2021). Additional research and studies are required to gather more information about brainworm disease and its dynamics in wild reindeer herds (Tryland, 2012), as most of the studies have been carried out in semi-domesticated reindeer (Stunt, 2021; Tryland et al., 2022).

In future studies, we propose to increase the size of the study area to understand if and how changes in temperature affect the distribution of gastropods in Hardangervidda. We also believe that it would be helpful to obtain data on reindeer presence, like collecting pellets for DNA analysis to assess potential infections at crucial times. Additionally, investigating gastropod populations during the whole summer season will provide insights into their numbers and potential overlap areas with reindeer. This is because the development of the larvae to the infective L3 stage in the gastropods is strongly influenced by temperature, so we assume that reindeer mostly get infected during these months (Closset 2021; Davidson et al., 2020; Rose Vineer et al., 2021).

Setting up traps in plots likely is a more efficient method to collect data on gastropod abundance, however, we were not fully able to compare data collected by visual searches and traps. Nevertheless, a simple initial comparison of the proportions of the gastropod captured (visual search: 24 specimens in 137 plots; traps: 20 specimens in 30 plots) suggests that the trapping procedure demonstrates greater efficiency. Additionally, 1 specimen of *Arion Hortensis* was found in a trap above the treeline, which gives us insights into the presence of certain species in high-altitude ecosystems. Based on our observations in the field, prolonged rainfall combined with the attraction to the beer in the traps, could potentially encourage gastropods to emerge more frequently. Additional research is necessary to explore these findings and establish a uniform protocol for both approaches.

The soil moisture measurements were taken on the field based on one-time measurements, making them unlikely to provide a representative characterization of the habitat, as measurements were highly influenced by the precipitation from previous days (Appendix, Figure 1) As such, for future studies, continuous measurements should be considered, probably in combination with GIS-based assessments (like the calculation of the topographical wetness index or the vertical distance to water, based on digital elevation model)

CONCLUSIONS

Climate change modulates both gastropod distribution patterns and the increasing temperatures will likely result in increased distribution of *Elaphostrongylus rangiferi* as well as an increase in the spatial and altitudinal distribution of gastropod species that act as intermediate hosts. Although the distribution range of wild reindeer herds is decreasing in Norway due to climate change (Heggberget et al., 2002) and habitat fragmentation (Vistnes et al., 2004), the increases in the range and distribution of gastropods will results in an increased overlap of these species in alpine regions in the summer season. This thesis serves as a preliminary step and further research is needed to evaluate wild reindeer grazing patterns, and the potential of gastropods hosting the parasite *Elaphostrongylus rangiferi* in Hardangervidda National Park, which is an ideal setting for studying climate warming effects without human interference (Baur & Baur, 2013). Effective management strategies, including monitoring and control of gastropod populations, are crucial for mitigating the impact of brainworm disease in wild reindeer populations.

ACKNOWLEDGEMENTS

First, we would like to thank our supervisors Andreas and Roland for their constant support and guidance throughout the process of completing this thesis.

Thanks to Lena from the Norsk villreinsenter for providing us with information on collared reindeer which helped us create our reindeer area map and choose our transects within those reindeer areas. In addition, we want to thank Rebeca and Alina for helping us with the research line and Rodrigo from Arctic University Museum of Norway for his knowledge about snails and slugs that he generously shared with us.

Last but not least, thanks to our families who always support us no matter what, even if they do not understand our research questions very much, our friends and master's colleagues here in Bø (Amanda, Ana, Camilo, Edu, Emilio and Phong) for being always a refuge when needed and specially our friends back in Spain, always with words of encouragement and warmth.

BIBLIOGRAPHY

Alatalo, J. M., Jägerbrand, A. K., & Molau, U. (2016). Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. *Scientific Reports*, *6*(1), 21720.

Andersen, J., & Halvorsen, O. (1984). Species composition, abundance, habitat requirements and regional distribution of terrestrial gastropods in Arctic Norway. *Polar Biology*, *3*, 45-53.

Baur, B. (1994). Parental care in terrestrial gastropods. *Experientia*, *50*, 5-14.

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*(8), 596-599.

Baur, B., Meier, T., Baur, A., & Schmera, D. (2014). Terrestrial gastropod diversity in an alpine region: disentangling effects of elevation, area, geometric constraints, habitat type and land-use intensity. *Ecography*, *37*(4), 390-401.

Bjerke, J. W. (2011). Winter climate change: ice encapsulation at mild subfreezing temperatures kills freeze-tolerant lichens. *Environmental and Experimental Botany*, *72*(3), 404-408.

Boch, S., Berlinger, M., Fischer, M., Knop, E., Nentwig, W., Türke, M., & Prati, D. (2013). Fern and bryophyte endozoochory by slugs. *Oecologia*, *172*, 817-822.

Božanić, B. (2011). *Terrestrial mosses as living environment for invertebrates* (Doctoral dissertation, MS Thesis, Department of Ecology and Environmental Sciences, Faculty of Science, Palacky University in Olomouc, Czech Republic).

Brooks, D. R., & Hoberg, E. P. (2007). How will global climate change affect parasite–host assemblages?. *Trends in Parasitology*, *23*(12), 571-574.

Bruun, H. H., Moen, J., Virtanen, R., Grytnes, J. A., Oksanen, L., & Angerbjörn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*, *17*(1), 37-46.

Busby, J. R., Bliss, L. C., & Hamilton, C. D. (1978). Microclimate control of growth rates and habitats of the boreal forest mosses, Tomenthypnum nitens and Hylocomium splendens. *Ecological Monographs*, *48*(2), 95-110

Clergeau, P., Tapko, N., & Fontaine, B. (2011). A simplified method for conducting ecological studies of land snail communities in urban landscapes. *Ecological research*, *26*(3), 515-521.

Ciezarek, A. (2022). *Worms on the brain: Modelling parasitic disease transmission in reindeer* (Doctoral dissertation, University of Liverpool).

Closset, N. (2021). *Brainworm (Elaphostrongylus rangiferi) abundance in wild reindeer (Rangifer tarandus tarandus) in relation to gastropod densities* (Master's thesis).

Cunningham, A. A., Daszak, P., & Wood, J. L. (2017). One Health, emerging infectious diseases and wildlife: two decades of progress?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1725), 20160167.

Dantas-Torres, F. (2015). Climate change, biodiversity, ticks and tick-borne diseases: The butterfly effect. *International Journal for Parasitology: Parasites and Wildlife, 4*(3), 452–461.

Davidson, A. J., Harborne, J. B., & Longton, R. E. (1990). The acceptability of mosses as food for generalist herbivores, slugs in the Arionidae. *Botanical Journal of the Linnean Society*, *104*(1-3), 99-113.

Davidson, R. K., Mørk, T., Holmgren, K. E., & Oksanen, A. (2020). Infection with brainworm (Elaphostrongylus rangiferi) in reindeer (Rangifer tarandus ssp.) in Fennoscandia. *Acta Veterinaria Scandinavica*, *62*, 1-15.

Gilbertson, C. R., & Wyatt, J. D. (2016). Evaluation of euthanasia techniques for an invertebrate species, land snails (Succinea putris). *Journal of the American Association for Laboratory Animal Science*, *55*(5), 577-581.

Godan, D. (1983). Pest slugs and snails. Biology and control. Berlin: Springer Verlag.

Gundersen, V., Myrvold, K. M., Kaltenborn, B. P., Strand, O., & Kofinas, G. (2022). A review of reindeer (Rangifer tarandus tarandus) disturbance research in Northern Europe: towards a social-ecological framework? *Landscape Research*, *47*(8), 1100–1116.

Gunn, A., Russell, D., White, R. G., & Kofinas, G. (2009). Facing a future of change: wild migratory caribou and reindeer. *Arctic*, *62*(3), iii-vi.

Handeland, K., & Norberg, H. S. (1992). Lethal cerebrospinal elaphostrongylosis in a reindeer calf. *Journal of Veterinary Medicine, Series B*, *39*(1-10), 668-671.

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*, *41*(1-10), 407-410.

Handeland, K., Davidson, R. K., Viljugrein, H., Mossing, A., Meisingset, E. L., Heum, M., ... & 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.

Hartig, F. (2020). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.2. Retrieved from: https://CRAN.R-project.org/package=DHARMa

Heggberget, T. M., Gaare, E., & Ball, J. P. (2002). Reindeer (Rangifer tarandus) and climate change: importance of winter forage. *Rangifer*, *22*(1), 13-31.

Heiba, F. N., Mortada, M. M., Geassa, S. N., Atlam, A. I., El-Wahed, A., & Sahar, I. (2018). Terrestrial gastropods: Survey and relationships between land snail assemblage and soil properties. *Journal of Plant Protection and Pathology*, *9*(3), 219-224.

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). *The Journal of parasitology*, *79*(5), 728-732.

Hettenbergerová, E., Horsák, M., Chandran, R., Hájek, M., Zelený, D., & Dvořáková, J. (2013). Patterns of land snail assemblages along a fine-scale moisture gradient. *Malacologia, 56*(1&2), 31-42.

Hoberg, E. P., Polley, L. Y. D. D. E. N., Jenkins, E. J., & Kutz, S. J. (2008). Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America.

Hof, A. R. (2011). European terrestrial gastropod distribution: How may climate change affect their diversity and current distribution. In A. M. Bianchi & J. N. Fields (Eds.), Gastropods: Diversity, Habitat and Genetics. Umeå: Nova Science Publishers, Inc., 2011.

Horstkotte, T., Holand, Ø., Kumpula, J., & Moen, J. (Eds.). (2022). *Reindeer husbandry and global environmental change: Pastoralism in Fennoscandia*. Taylor & Francis.

Juřičková, L., Horsák, M., Cameron, R., Hylander, K., Míkovcová, A., Hlaváč, J. Č., & Rohovec, J. (2008). Land snail distribution patterns within a site: the role of different calcium sources. *European Journal of Soil Biology*, *44*(2), 172-179

Kappes, H., Topp, W., Zach, P., & Kulfan, J. (2006). Coarse woody debris, soil properties and snails (Mollusca: Gastropoda) in European primeval forests of different environmental conditions. *European Journal of Soil Biology*, *42*(3), 139-146.

Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the national academy of sciences*, *105*(33), 11823-11826.

Kralka, R. A. (1986). Population characteristics of terrestrial gastropods in boreal forest habitats. *American Midland Naturalist*, 156-164.

Krogstad, T. (1992). Methods for soil analysis. Report 6/92. Institute for Soil Science. Ås-NHL.

Lukacs, M., Nymo, I. H., Madslien, K., Våge, J., Veiberg, V., Rolandsen, C. M., Bøe, C. A., Sundaram, A. Y. M., & Grimholt, U. (2023). Functional immune diversity in reindeer reveals a high Arctic population at risk. *Frontiers in Ecology and Evolution*, *10*, 1058674.

Lucid, M. K., Ehlers, S., Robinson, L., & Cushman, S. A. (2018). Beer, brains, and brawn as tools to describe terrestrial gastropod species richness on a montane landscape. *Ecosphere*, *9*(12), e02535.

Mallory, C. D., & Boyce, M. S. (2018). Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental Reviews*, *26*(1), 13-25.

Martin, K., & Sommer, M. (2004). Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *Journal of Biogeography*, *31*(4), 531-545.

McCallum, H. I., and A. Dobson. "Disease and connectivity." (2007).

Michigan Department of Natural Resources. (2024). Brainworm. Retrieved from https://www.michigan.gov/dnr/managing-resources/Wildlife/Wildlife-disease/WDM/brainworm.

Mitskevich, V. Y. (1958). The elucidation of the life-cycle of the nematode Elaphostrongylus rangiferi sp. nov. from reindeer. In *Dokl. Akad. Nauk SSSR* (Vol. 119, pp. 621-624).

Migała, K., Wojtuń, B., Szymański, W., & Muskała, P. (2014). Soil moisture and temperature variation under different types of tundra vegetation during the growing season: A case study from the Fuglebekken catchment, SW Spitsbergen. *Catena*, *116*, 10-18.

Millar, A. J., & Waite, S. (1999). Molluscs in coppice woodland.

Mørk, T., Eira, H. I., Rødven, R., Nymo, I. H., Blomstrand, B. M., Guttormsen, S., ... & Davidson, R. K. (2024). Necropsy findings, meat control pathology and causes of loss in semi-domesticated reindeer (Rangifer tarandus tarandus) in northern Norway. *Acta Veterinaria Scandinavica*, *66*(1), 1.

Mysterud, A., Flagstad, Ø., & Strand, O. (2024). Feralization: A threat to conservation of wild reindeer. *Conservation Science and Practice*, *6*(4), e13105

Mysterud, A., Rød-Eriksen, L., Hildebrand, A., Meås, R., Gudmundsson, A. F., & Rolandsen, C. M. (2022). The efficacy of wildlife fences for keeping reindeer outside a chronic wasting disease risk area. *Ecological Solutions and Evidence*, *3*(3), e12174.

Norwegian Institute for Nature Research (NINA), (2024). Renewable Reindeer. Retrieved from: https://www.nina.no/english/Fields-of-research/Projects/RenewableReindeer_new

Norwegian Wild Reindeer Center (Norsk villreinsenter), (2024). Retrieved from: https://villrein.no/villreinomrader/hardangervidda/

Ondina, P., Hermida, J., Outeiro, A., & Mato, S. (2004). Relationships between terrestrial gastropod distribution and soil properties in Galicia (NW Spain). *Applied soil ecology*, *26*(1), 1-9.

Okulewicz, A. (2017). The impact of global climate change on the spread of parasitic nematodes. Annals of Parasitology, 63(1), 15–20. doi: 10.17420/ap6301.79.

Pearce, J., & Ferrier, S. (2000). An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological modelling*, *128*(2-3), 127-147.

Pearce, T. A., & Örstan, A. (2006). Terrestrial gastropoda. *The mollusks: A guide to their study, collection, and preservation*, 261-285.

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature climate change, 3*(7), 673-677.

Praeg, N., Seeber, J., Leitinger, G., Tasser, E., Newesely, C., Tappeiner, U., & Illmer, P. (2020). The role of land management and elevation in shaping soil microbial communities: Insights from the Central European Alps. *Soil Biology and Biochemistry*, *150*, 107951.

QGIS Development Team. (2024). QGIS Desktop Version 3.26.3 "Buenos Aires". Open Source Geospatial Foundation Project. Code revision 65e4edfdada. URL https://qgis.org

R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RStudio Team. (2023). RStudio: Integrated Development Environment for R (Version 2023.12.1 Build 402). RStudio, PBC, Boston, MA. URL http://www.rstudio.com/.

Rekdal, Y., & Larsson, J. Y. (2005). Veiledning i vegetasjonskartlegging-M 1: 20 000–50 000. *NIJOS-rapport*.

Rizzoli, A., Tagliapietra, V., Cagnacci, F., Marini, G., Arnoldi, D., Rosso, F., & Rosà, R. (2019). Parasites and wildlife in a changing world: The vector-host- pathogen interaction as a learning case. *International Journal for Parasitology: Parasites and Wildlife*, *9*, 394–401.

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*, 603990.

Russell, D. E., Gunn, A., & Kutz, S. (2018). Migratory tundra caribou and wild reindeer. *Arctic report card 2018*, 67.

Seamless national Elevation model (SENORGE). (2024). Temperature- mean monthly temperature (Hardangervidda Nasjonalpark). Retrieved from: SeNorge - Snow maps and climate maps in Norway

Seuffert, M. E., & Martín, P. R. (2013). Distribution of the apple snail Pomacea canaliculata in Pampean streams (Argentina) at different spatial scales. *Limnologica*, *43*(2), 91-99.

Skarin, A., Danell, Ö., Bergström, R., & Moen, J. (2008). Summer habitat preferences of GPS-collared reindeer Rangifer tarandus tarandus. *Wildlife Biology*, *14*(1), 1-15.

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.

Skorping, A. (1982). Elaphostrongylus rangiferi: Influence of temperature, substrate, and larval age on the infection rate in the intermediate snail host, Aarianta arbustorum. *Experimental parasitology*, *54*(2), 222-228.

Skorping, A. (1988). The effect of density of first-stage larvae of Elaphostrongylus rangiferi on the infection rate in the snail intermediate host. *Parasitology, 96*(3), 487-492.

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. (2022). Experimental infection of moose (Alces alces) with Elaphostrongylus spp.(Nematoda, protostrongylidae) originating from reindeer (Rangifer tarandus) and moose, with special emphasis on clinical signs, gross-and microscopic lesions, and predilection sites. *Alces: A Journal Devoted to the Biology and Management of Moose*, *58*, 113-127.

Stuut, M. (2021). *Investigating the effect of herd and landscape factors on brainworm (Elaphostrongylus rangiferi) prevalence and infection intensity in a semi-domesticated reindeer (Rangifer tarandus tarandus) herd* (Master's thesis).

Thompson, R. C. A., Lymbery, A. J., & Smith, A. (2010). Parasites, emerging disease and wildlife conservation. *International Journal for Parasitology*, *40*(10), 1163–1170.

Thomson, B. R. (1978). The behaviour of wild reindeer in Norway. *University of Edinburgh. E-theses online service, British library.*
Tian, Q., Jiang, Y., Tang, Y., Wu, Y., Tang, Z., & Liu, F. (2021). Soil pH and organic carbon properties drive soil bacterial communities in surface and deep layers along an elevational gradient. *Frontiers in microbiology*, *12*, 646124.

Tryland, M. (2012). Are we facing new health challenges and diseases in reindeer in Fennoscandia?. *Rangifer*, *32*(1), 35-47.

Tryland, M., & Kutz, S. J. (Eds.). (2018). *Reindeer and Caribou: health and Disease*. CRC Press.

Tryland, M., Nymo, I. H., Sánchez Romano, J., & Riseth, J. Å. (2022). Husbandry and diseases of semi-domesticated Eurasian tundra reindeer in Fennoscandia. In *The Management of Enclosed and Domesticated Deer: International Husbandry Systems and Diseases* (pp. 413-447). Cham: Springer International Publishing.

Turunen, M., Soppela, P., Kinnunen, H., Sutinen, M. L., & Martz, F. (2009). Does climate change influence the availability and quality of reindeer forage plants?. *Polar Biology, 32,* 813-832.

Tyler, N. J., Hanssen-Bauer, I., Førland, E. J., & Nellemann, C. (2021). The shrinking resource base of pastoralism: Saami reindeer husbandry in a climate of change. *Frontiers in sustainable food systems*, *4*, 585685.

Vander Wal, E., Laforge, M. P., & McLoughlin, P. D. (2014). Density dependence in social behaviour: home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. *Behavioral ecology and sociobiology*, *68*, 383-390.

Vanneste, T., Michelsen, O., Graae, B. J., Kyrkjeeide, M. O., Holien, H., Hassel, K., … De Frenne, P. (2017). Impact of climate change on alpine vegetation of mountain summits in Norway. Ecological Research, 32(4), 579–593. doi: 10.1007/s11284-017-1472-1

Viggers, K. L., Lindenmayer, D. B., & Spratt, D. M. (1993). The Importance of Disease in Reintroduction Programmes. Wildlife Research, 20(5), 687–698.

Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J. A., & Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography*, *19*(6), 810-821.

Vistnes, I., Nellemann, C., Jordhøy, P., & Strand, O. (2004). Effects of infrastructure on migration and range use of wild reindeer. *The Journal of Wildlife Management*, *68*(1), 101-108.

Vuojala-Magga, T. (2010). Knowing, training, learning: The importance of reindeer character and temperament for individuals and communities of humans and animals. *Good to eat, good to live with: Nomads and animals in northern Eurasia and Africa. Northeast Asian Study Series*, *11*, 43-62.

Walden, H. (1981). Communities and diversity of land molluscs in Scandinavian woodlands. J Conch, 30, 351–372.

Webber, Q. M., & Vander Wal, E. (2020). Heterogeneity in social network connections is density-dependent: implications for disease dynamics in a gregarious ungulate. *Behavioral Ecology and Sociobiology*, *74*, 1-13.

Wilson, S. D., & Nilsson, C. (2009). Arctic alpine vegetation change over 20 years. *Global Change Biology*, *15*(7), 1676-1684.

Witter, L. A., Johnson, C. J., Croft, B., Gunn, A., & Poirier, L. M. (2012). Gauging climate change effects at local scales: weather-based indices to monitor insect harassment in caribou. *Ecological Applications*, *22*(6), 1838-1851.

Yr.no (served by Norwegian Meteorological Institute and the Norwegian Broadcasting). (2024). Retrieved from: Yr - Bitdalsvatnet - Statistics as a graph - Last 13 months.

Zhao, D., Wu, S., Yin, Y., & Yin, Z. Y. (2011). Vegetation distribution on Tibetan Plateau under climate change scenario. *Regional Environmental Change*, *11*, 905-915.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). Mixed Effects Models and Extensions in Ecology with R. Springer.

APPENDIX:

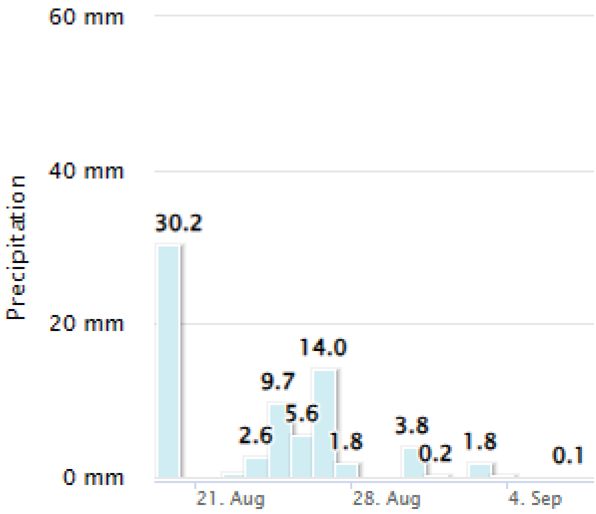


Figure 1: Precipitation at Bitdalsvatn between 21st of August and 1st of September. Source: SeNorge - Snow maps and climate maps in Norway

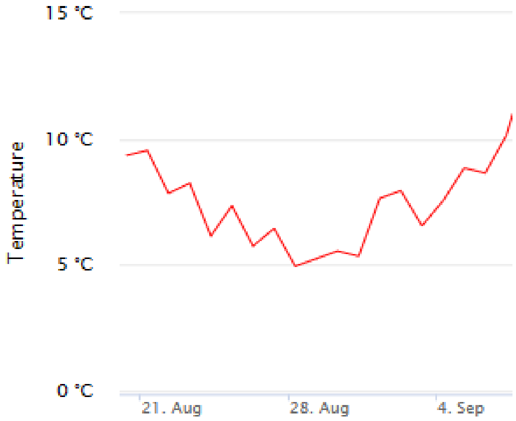
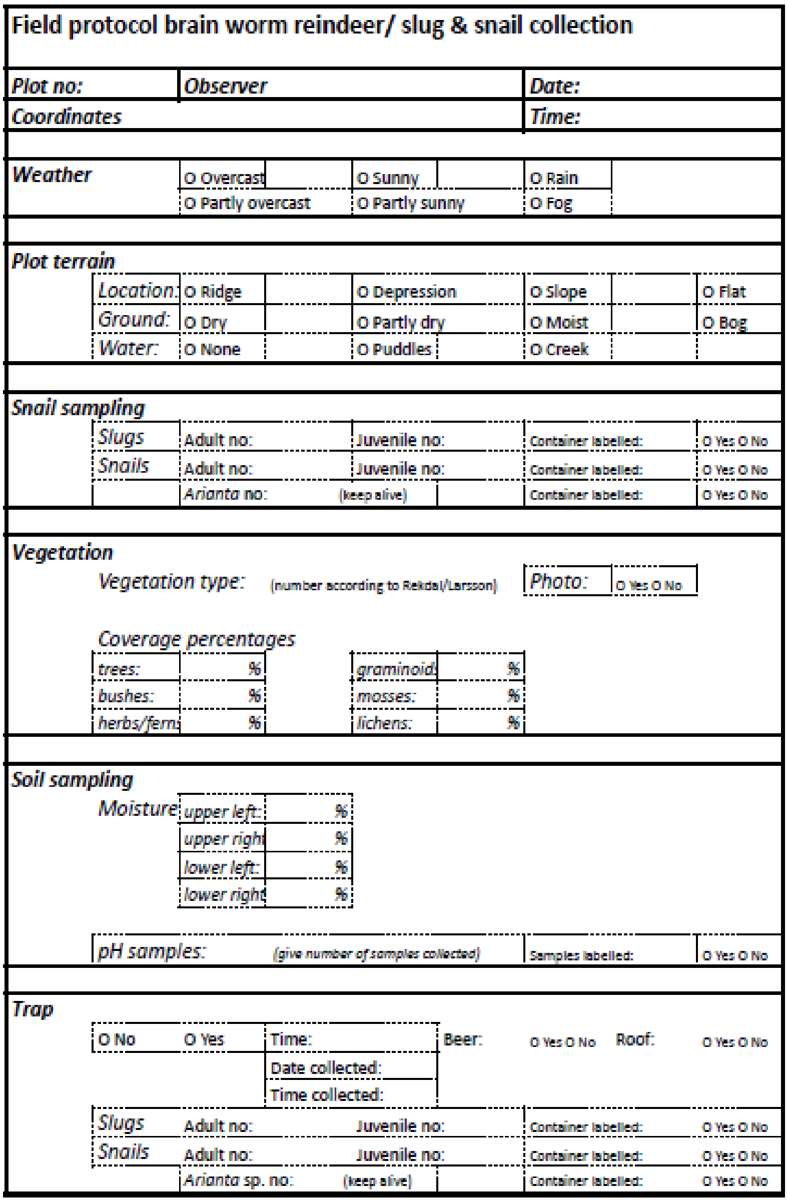


Figure 2: Temperature at Bitdalsvatn between 21st of August and 1st of September. Source: [SeNorge - Snow maps and climate maps in Norway.]()



Field protocol brain worm reindeer/ slug & snail collection

Plot no:	*Observer*	*Date:*
Coordinates		*Time:*

Weather

○ Overcast ○ Sunny ○ Rain

○ Partly overcast ○ Partly sunny ○ Fog

Plot terrain

Location: ○ Ridge ○ Depression ○ Slope ○ Flat

Ground: ○ Dry ○ Partly dry ○ Moist ○ Bog

Water: ○ None ○ Puddles ○ Creek

Snail sampling

Slugs Adult no: Juvenile no: Container labelled: ○ Yes ○ No

Snails Adult no: Juvenile no: Container labelled: ○ Yes ○ No

Arianta no: (keep alive) Container labelled: ○ Yes ○ No

Vegetation

Vegetation type: (number according to Rekdal/Larsson) *Photo:* ○ Yes ○ No

Coverage percentages

trees:	%	*graminoid:*	%
bushes:	%	*mosses:*	%
herbs/fern:	%	*lichens:*	%

Soil sampling

Moisture

upper left:	%
upper righ	%
lower left:	%
lower right	%

pH samples: *(give number of samples collected)* Samples labelled: ○ Yes ○ No

Trap

○ No ○ Yes Time: Beer: ○ Yes ○ No Roof: ○ Yes ○ No

Date collected:

Time collected:

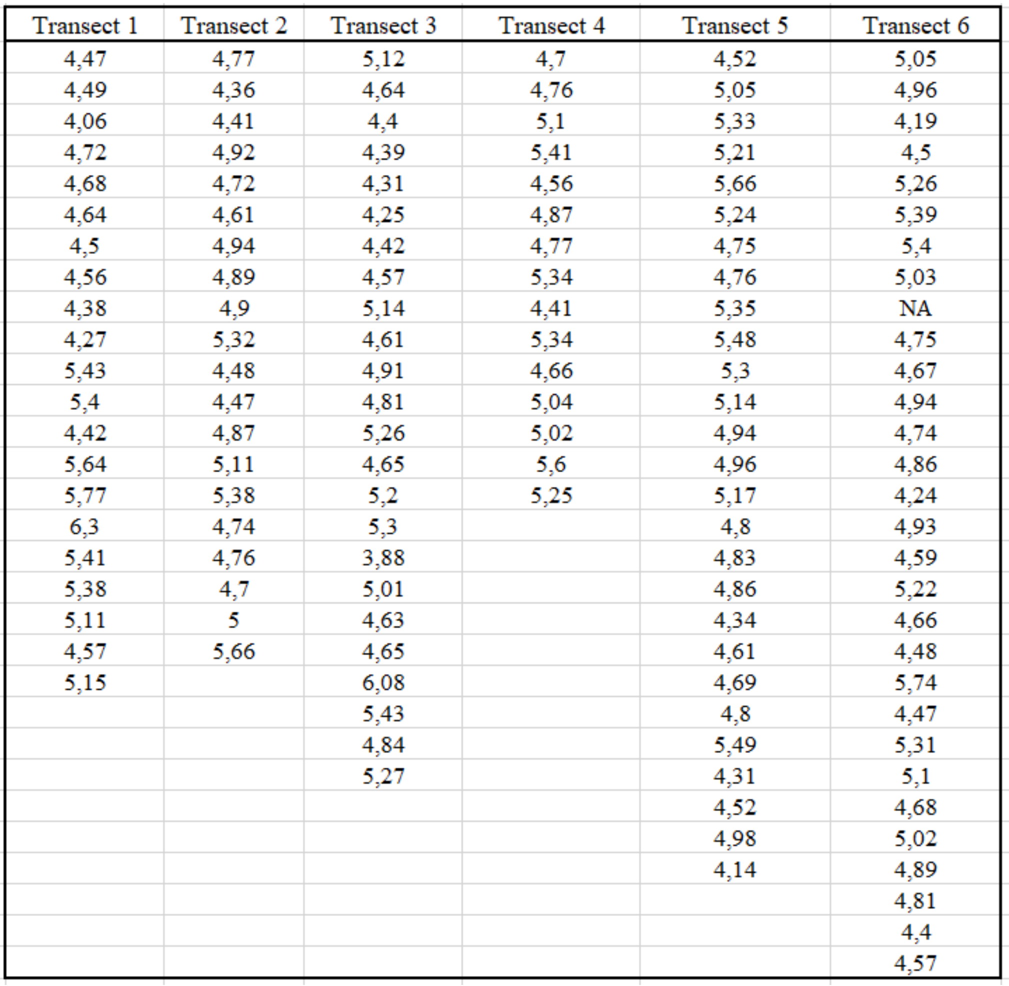
Slugs Adult no: Juvenile no: Container labelled: ○ Yes ○ No

Snails Adult no: Juvenile no: Container labelled: ○ Yes ○ No

Arianta sp. no: (keep alive) Container labelled: ○ Yes ○ No

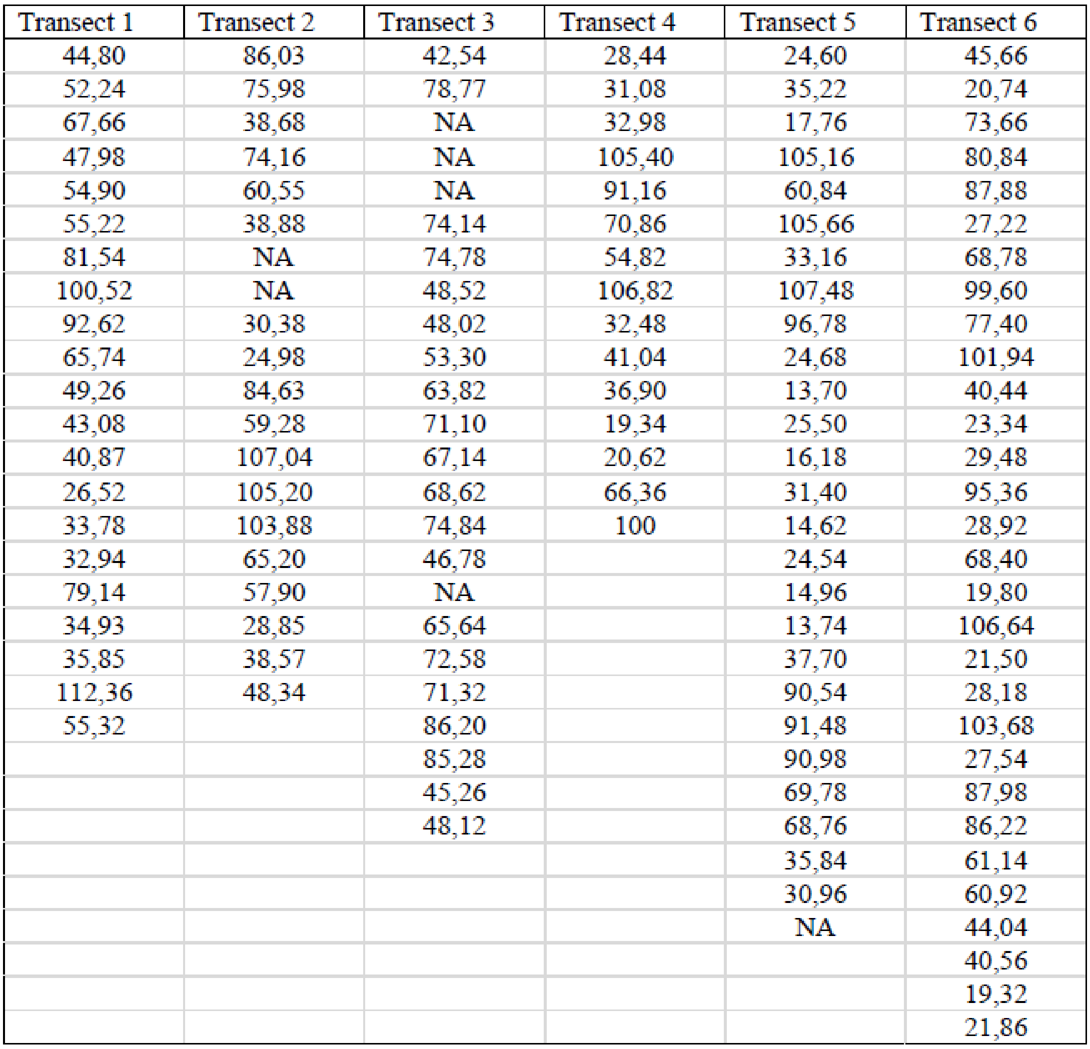
Figure 3: Field protocol used during the fieldwork. Noted down for the general information: the plot number, the GPS coordinates of the plot, the name of the observer, date and time. The weather: (overcast, sunny, rain, partly overcast, partly sunny, fog), plot terrain: (location, ground and water presence), snail sampling: (slugs, snails), vegetation: (vegetation type with coverage percentages: trees, bushes, herbs/form, graminoids, mosses, lichens), soil sampling: (moisture).

Table 1: pH values of each vegetation plot obtained after lab work.



Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
4,47	4,77	5,12	4,7	4,52	5,05
4,49	4,36	4,64	4,76	5,05	4,96
4,06	4,41	4,4	5,1	5,33	4,19
4,72	4,92	4,39	5,41	5,21	4,5
4,68	4,72	4,31	4,56	5,66	5,26
4,64	4,61	4,25	4,87	5,24	5,39
4,5	4,94	4,42	4,77	4,75	5,4
4,56	4,89	4,57	5,34	4,76	5,03
4,38	4,9	5,14	4,41	5,35	NA
4,27	5,32	4,61	5,34	5,48	4,75
5,43	4,48	4,91	4,66	5,3	4,67
5,4	4,47	4,81	5,04	5,14	4,94
4,42	4,87	5,26	5,02	4,94	4,74
5,64	5,11	4,65	5,6	4,96	4,86
5,77	5,38	5,2	5,25	5,17	4,24
6,3	4,74	5,3		4,8	4,93
5,41	4,76	3,88		4,83	4,59
5,38	4,7	5,01		4,86	5,22
5,11	5	4,63		4,34	4,66
4,57	5,66	4,65		4,61	4,48
5,15		6,08		4,69	5,74
		5,43		4,8	4,47
		4,84		5,49	5,31
		5,27		4,31	5,1
				4,52	4,68
				4,98	5,02
				4,14	4,89
					4,81
					4,4
					4,57

Table 2: Soil moisture values of each vegetation plot obtained after calculating the mean with the five moisture measurements taken in the field.



Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
44,80	86,03	42,54	28,44	24,60	45,66
52,24	75,98	78,77	31,08	35,22	20,74
67,66	38,68	NA	32,98	17,76	73,66
47,98	74,16	NA	105,40	105,16	80,84
54,90	60,55	NA	91,16	60,84	87,88
55,22	38,88	74,14	70,86	105,66	27,22
81,54	NA	74,78	54,82	33,16	68,78
100,52	NA	48,52	106,82	107,48	99,60
92,62	30,38	48,02	32,48	96,78	77,40
65,74	24,98	53,30	41,04	24,68	101,94
49,26	84,63	63,82	36,90	13,70	40,44
43,08	59,28	71,10	19,34	25,50	23,34
40,87	107,04	67,14	20,62	16,18	29,48
26,52	105,20	68,62	66,36	31,40	95,36
33,78	103,88	74,84	100	14,62	28,92
32,94	65,20	46,78		24,54	68,40
79,14	57,90	NA		14,96	19,80
34,93	28,85	65,64		13,74	106,64
35,85	38,57	72,58		37,70	21,50
112,36	48,34	71,32		90,54	28,18
55,32		86,20		91,48	103,68
		85,28		90,98	27,54
		45,26		69,78	87,98
		48,12		68,76	86,22
				35,84	61,14
				30,96	60,92
				NA	44,04
					40,56
					19,32
					21,86