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The effects of changes in snow structures on the population of tundra voles (*Microtus oeconomus)*

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Abstract

Global warming induces climate change that affects every ecosystem on Earth. The Arctic ecosystem appears to be more vulnerable in the face of climate change than ecosystems in other regions of the world. Between 1982 and 2011, the warming in the Eurasian Arctic region was faster during winter than in the North American region. Such a change has concrete effects on the small rodent community living under the snow during winter. For instance, the population of Norwegian lemming (*Lemmus lemmus*) has been strongly decreasing during the last decades and has recently missed its cycle peak in 2015 in northern Norway. At this moment, few studies are published on the effect of ice formation on the vole population dynamics. Thus, my aim in this study is to assess the effect of changes in snow structures on the population of tundra vole (*Microtus oeconomus*) from 2006 to 2019 in northern Norway.

The study has been conducted in a meadow habitat around three watershed areas: Ifjordfellet, Komagdalen, and Vestre Jakobselv. I used time-series data on the small rodent and snow quality from Climate-Ecological Observatory for Arctic Tundra (COAT). To answer my research questions, I tested the effects of the presence of ice on the bottom on the spring abundance, on the summer growth rate and the winter growth rate of the population of tundra voles.

As predicted, I found that the formation of ice impacted the winter growth rate of the tundra vole. Interestingly, the melt-freeze events did not seem to affect the spring abundance and the summer growth rate of the species. The population of tundra voles displayed cyclic peaks during the study period.

I conclude that ice crust formation has an impact on the tundra voles. The icy winter seems to affect the winter growth rate of the species which results in a low population abundance in spring. However, if I did not observe an increase in ground ice, milder winters are likely to be more frequent with climate change. If icing events increases, the effects on tundra voles that have been described in this study may become more pronounced.

1 | Introduction

Global warming induces climate change, and human activities influence global warming (Brunet and Van Etten, 2019; Christensen et al., n.d.). Indeed, we are now in the "Anthropocene", the first geological time where the climate and the ecosystems are influenced by humans instead of the natural process (Dirzo et al., 2014). The Arctic is more likely to be exposed to global warming than the other parts of the world (Christensen et al., 2007). Northern areas will become warmer and climate-tracking species will arrive from the warmer regions (Urban, 2020; Pecl et al., 2017). Climate change has the strongest effects on the Eurasian Arctic region than in North America. For example, the snow-covered period decreased by 12.6 days between 1982 and 2011, against 6.2 days in the American continent (Barichivich et al., 2013; Bokhorst et al., 2016). This expanding snow-free period boosts the growing season for vegetation, and thus the "Arctic greening" whose main process underlying is the expansion of tall shrubs throughout the tundra (Ims et al., 2013). In the high latitudes, there will be more rain-on-snow events, ice and sea-ice-melting (which will decrease the albedo and thus the absorption of the heat by ocean and land), unseasonal thaws, and changes of the seasons (longer summer, shorter winter) (Bokhorst, 2016; Liston and Hiemstra, 2011). However, the winter temperatures increase more than those during summer (Bokhorst et al., 2016; Christensen et al., n.d.; Walsh, 2014). Therefore, the major consequences of climate change in the Arctic can be expected to happen during winter.

Arctic winter is a tough time for the northern species. Winter is defined as the total number of months with snowfall, in our study from September to June/July (Ims and Fuglei, 2005). Snowy winter is the period where animals and plants have to survive. Indeed, herbivores and carnivores have to find their food, often hidden under the snow and the snowpack (Cooper, 2014). Small mammals live under the snow during winter. The subnivean spaces protect animals from most of their predators (Ims and Fuglei, 2005). While the wind gets the temperature very low above the snow, the subnivean space maintains a warmer temperature (insulation) for individuals living beneath it (Aars and Ims, 2002). Besides, the snow is a solid but brittle material. Hence, animals can easily move under the subnivean space and keep feeding (hunting small mammals or graze on the ground) (Aars and Ims, 2002; Kausrud et al., 2008). For instance, the lemmings choose to dig tunnels in the soft depth hoar layer, which has a lower abundance than the hard snow layers around (Poirier et al., 2019). Winter survival will shape the next spring population of northern species.

Northern ecosystems are shaped by the winter season (short vegetation growing season) and are adapted to it. Thus, arctic ecosystems will be typically touched by the shorter and warmer winter. Since the last decades, a lot of studies showed that the temperature became higher during winter (Barichivich et al., 2013; Bokhorst et al., 2016). Therefore, winter began later and ended earlier in the year. The onset of winter begins with snowfalls and low temperatures. However, when comes wintertime, temperatures rise above zero and bring mild weather, melting snow and rain can create icy layers in the snowpack or along the ground. This formation of ice crust encapsulates the vegetation on the ground (Hansen et al., 2013). Such an ice crust deprives herbivores of access to the low-lying plants. Ice formations will thus reduce both food accessibility and thermal insulation (Hansen et al., 2013; Ims et al., 2008a; Korslund and Steen, 2006).

Northern small rodents are a community of small mammals, mostly herbivorous, and a key component of the Arctic food web (Krebs, 2011). A keystone component is defined by the number and the importance of interactions with other components of its habitat (Ims and Fuglei, 2005). As herbivores, they transfer the energy from the plants into organic energy that can be assimilated by the carnivorous species, higher in the food web (Krebs, 2011). Being at the lower level of this food web, after the producers (i.e. plants) any change that could happen within the small rodent population will have a cascading effect on the whole trophic food web (Schmidt et al., 2012).

A high abundance of small rodents during their peak year influences the structure of tundra's vegetation (Olofsson, 2012). Rodents remove large quantities of plant biomass (Olofsson, 2012) and modify several aspects of vegetation dynamics, such as plant community composition (Ravolainen et al., 2011), seedling establishment (Nystuen et al., 2014), and plant-soil feedbacks (Tuomi et al., 2019). Small rodents may even counteract the climate-driven shrub expansion to the tundra by feeding on tall (Ravolainen et al., 2014).

Small rodent population cycles also influence predators’ dynamics. Indeed, when there is a high-abundance peak of small rodents, the population of the top predators like the arctic fox (*Vulpes lagopus),* the snowy owl (*Bubo scandiacus*)*,* as some others, increased in the same way (Ims et al., 2005). The effect of the small rodent population decreasing will be stronger on the specialist predators (snowy owl) (Ims et al., 2013). Whilst the generalist predators (golden eagle (*Aquila chrysaetos*) or the opportunist specialist predators (arctic fox) can still feed on other prey (Ims *et al*., 2013).

Cyclic peaks characterized the abundance of the small rodent population (Ims and Fuglei, 2005). Every 3 or 5 years there is a high peak of abundance. The different species tend to cycle in synchrony (Batzli and Jung, 1980). Nonetheless, the cycle rhythm depends on the species, on the latitude, and other events like climate events (Korpela et al., 2013). The reason(s) for these sudden peaks in the population is not yet known (Kausrud et al., 2008) but there are three dominating assumptions about mechanisms that might control small rodent cycles. The first model is the *bottom-up* model in which small rodent dynamic is controlled by the availability of food supply (Krebs, 2011). The second model is the *top-down* model in which small mammals cycle are shaped by the predation pressure or the diseases (Krebs, 2011). The third model is about social behavior, in which social interaction interspecific or intraspecific as territoriality or infanticide can change the population abundance (Krebs, 2011). However, in this study, I won’t look at the reasons that create cycles but how snow conditions modify the cycles.

It has been shown, in the last few decades, that the frequency of these peaks was decreasing (Cornulier et al., 2013; Ims et al., 2013). Warmer temperatures in the North conducts to a dampening of vole’s cycles (Cornulier et al., 2013). Declines in the population are most marked in spring (Cornulier et al., 2013). Currently, this dampening pattern is generalized to vole populations throughout Europe (Cornulier et al., 2013).

Mild-weather induced ice crust formation that will block the small mammals to feed on the ground (Ims et al., 2008a; Korslund and Steen, 2006). This deprivation might cause their death by starvation or make them too weak to reproduce for the next spring (or during winter for the Norwegian lemming (Lemmus lemmus) (Kausrud et al., 2008)). Thus, during winter with widespread ice formation combined with predation pressure, we can expect to see the small rodent population decreases dramatically (Aars and Ims, 2002; Ims et al., 2008). During a period with more frequent icy winters, we can expect rodent population dynamics to change, and in particular a reduced frequency and/or amplitude of the population peaks.

Norwegian lemming could be more vulnerable to the impact of global warming than the voles, as Kausrud et al. (2009) suggest. Unlike the vole cycles' that have maintained their regularity (Ims et al., 2011), Norwegian lemmings have lost the rhythm their cycle peak (Ims et al., 2008a, 2011). Moreover, Norwegian lemming does not have the same habits of life as the other rodent species. During winter, Norwegian lemmings live in snow bed habitat with the grey-sided vole (*Myodes rufocanus*) (Ims et al., 2013) while the tundra vole prefers to live in the meadow (*Microtus oeconomus*) (i.e. treeless habitats, with shrubs and monocotyledons as vegetation) (Ims et al., 2013). Norwegian lemming differs also by its food habits. The lemming feeds on mosses (Dicranum spp.) and on monocotyledons (*Avenella flexuosa*) (Kalela et al. 1961; Soininen et al., 2013), which grow very close to the ground. While grey-sided vole prefers dwarf shrubs in winter (Hansson 1969; Hansson and Larsson 1978) and the tundra vole feeds mostly on monocotyledons (in Finland (Tast 1974) and Alaska (Batzli and Henttonen, 1990; Batzli and Jung, 1980; Soininen, 2012), which grow higher than the mosses. Thus, scientists suggest that the lemmings could be more vulnerable because their food resources (mosses) are closer to the ground. Because mosses get easier locked into the ice than shrubs, lemmings have less available food (Ims et al., 2008; Korslund and Steen, 2006).

Besides, Norwegian lemming starts to reproduce under the snow in winter before the high predation pressure of summer, which make the population decrease (Ehrich et al., 2020). This early reproduction induces high peaks of rodent abundances from the onset of spring/summer (Ims and Fuglei, 2005). Winter breeding is essential for lemming outbreaks (Ims et al., 2011). Therefore, the winter population of lemmings shapes the spring population (Ims et al., 2011).. However, if there is an ice crust formation on the ground, the lemmings won't have enough energy to spend in reproduction. If they do have, lemmings might lose their offspring because of starvation. If lemmings have lost their offspring during winter, they might have less energy and food to reproduce in spring. Thus, their population won't even grow during summer. In contrast, voles start mainly to reproduce after snow melt, without any previous energy coast trying to breed in winter. Their offspring do not suffer from a lack of food during winter. Vole populations start to rise during summer and rely on their spring abundance. Thus, the peak of abundance appears in the autumn (Ims and Fuglei, 2005).

Since 1970-1980, several studies have shown that the population abundance of voles has decreased, and the cyclic peaks have diminished (Gliwicz and Jancewicz, 2016; Hörnfeldt, 2004; Ims et al., 2008b). In the study of Aars and Ims (2002) in southern Norway, the population of tundra vole continued to decline despite the addition of new rodents each spring in the field of the experiment. Even if this vole population decline was mainly explained the predation by birds, the more there were some days with temperatures above 0°C in winter (inducing winter with mild weather), the lower was the survival rate of the population. In a study from Sweden, Hörnfeldt (2004) caught the voles in a forest ecosystem touched by human activity. The peak of the grey-sided vole decreased, and the abundance of the population was close to zero from 1985. The main causes discussed were habitat fragmentation, pollution, and snow changes (faced to the ice crust formation and the increasing exposure to the predation). A study from Finland shows that there was a reduction in the amplitude of the vole's cycle in the coldest areas (Korpela et al. 2013). However, the cold and long winter was not associated with high amplitude in the rodent peaks, nor was the mild winter reducing the winter growth rate. Indeed, the cyclicity was weakened by increasing the growing season which improves the quantity of food available during the year.

Thus, some studies have been assessed how the changes in vole's population dynamics are linked to snow conditions. However, there is no study, or not any published yet, that combines snow structure measurements and population dynamics time-series on the evolution of the vole population, related to climate change.

Aims

In this study, I wanted to assess the effects of snow structure on population dynamics of tundra vole. I assumed the ice crust formation prevents rodents from feeding on the ground vegetation, and thus reduces the vole population during winter. To assess this, I combined data on the abundance of tundra vole in spring and in abundance with the presence of the ice on the bottom of the snowpack in March. Specifically, my first aim was to assess the effect of ice crust formation on the spring abundance of the tundra vole. I predicted that the population will be low after the winter with the presence of ice on the ground. Secondly, I aimed to define the impacts on the summer growth rate during the summer. I predicted that the presence of ice decreases the summer growth rate. My third aim was to evaluate the effect of ice on the winter growth rate of vole. I assumed that during icy winters the decrease of the population over winter would be more prominent than winter without mild weather.

2 | Material and methods

2.1 | Study area

The study has been done in three watershed areas in northeastern Finnmark, northern Norway. Two of the areas were at the Varanger peninsula (70-71°N and 28-31°E, Figure 1), Finnmark, north eastern Norway, and the third region were at Ifjordfjellet (71°N, 27°E) about 100km west of Varanger peninsula, in the low-arctic bordering sub-arctic forest from 2006 to 2019. The Varanger peninsula is at the southern fringe of the arctic tundra, the northernmost terrestrial biome (Ims et al., 2013). The annual mean temperature is about –3°C to 0°C. The variety in the bedrocks and in the topography lead to differences in local climate, nutrient levels, moisture run-off, and snow deposition over short distances that cause disparities in the vegetation (Ims et al., 2013).

In this area, there are two main types of habitats: dwarf shrub heaths and meadows with scattered willow thickets (i.e. tall shrub, *Salix spp*). The heath habitat is dominated by *Empetrum nigrum s. lat.*, *Betula nana* and *Vaccinium myrtillus*, which are the grey-sided vole food and habitat. The patches of meadows are heterogeneous in species with grasses (e.g. *Avenella flexuosa, Deschampsia cespitosa*), forbs (e.g. *Rumex acetosa, Trollius europaeus, Viola spp.*), vascular cryptogams (mainly *Equisetum spp*.), deciduous shrubs (mainly *Salix spp*.), sedges and rushes (e.g. *Carex bigelowii, Carex aquatilis coll*., *Juncus filiformis*), and mosses (Soininen et al., 2013).

In northern Norway, the ungulates and the rodent compose the functional group of the herbivores. The reindeer (*Rangifer tarandus*) and the moose (*Alces alces*) are some ungulates species of the tundra. The rodent community is composed of three species: the Norwegian lemming, the grey-sided vole, and the tundra vole. In this arctic ecosystem, the wolf is present as a predator of the reindeer and some important predators on the small rodents are also presents like the arctic fox, the least weasel, and the stoat (*Mustela erminea*) (Ims et al., 2013).

2.2 | Study species

My study will focus on the tundra vole. This species lives in a wet environment (like around creeks in the river) with meadow and willow thickets (*Salix spp.*) (Henden et al., 2011; Oksanen et al., 1999). In this kind of wet plains, the tundra vole is the dominant species among the small rodents (Henden et al., 2011). It mostly feeds on herbs and graminoids like monocotyledons during summer (*Eriophorum) (*Batzli and Henttonen, 1990; Batzli and Jung, 1980; Soininen, 2012; Tast, 1974). In winter, the tundra vole lives in the subnivean space. The rodent grazes on ramets of tall shrubs (under the snow) (Ravolainen et al., 2014). During summer, it keeps living under the vegetation to stay protected from its predators. However, it often moves outside on an open area where there are some more nutritious plants to feed on (like monocotyledon rich in proteins and vitamins) (Hovland et al., 1999, Henden et al., 2011).

Tundra vole is prey for several species. For instance, different birds like the long-tailed skua (*Stercorarius longicaudus)* and the rough-legged buzzard (*Buteo lagopus)* catch the rodent when it is out of its hiding. Some very generalist predators like foxes (red fox (*Vulpes vulpes*) and arctic fox) hunt the vole from above the snow by smelling its odor before to jump in the snow cover and catch it in its galleries. Some mustelids like the least weasel and the stoat hunt rodents through tunnels, under the snow, during winter. (Ims et al., 2013). Thus, predators hunt the tundra vole from the air to the subnivean space.

Cyclic rodent population peaks in this study area occur every 3-5 years. The breeding occurs in summer (snow-free period), and the peak in population abundance arrives in autumn (Soininen et al., 2018).

2.3 | Study design

This study was designed to assess the effects of snow changes on the population of tundra voles. I wasn't personally on the field to collect the data. Therefore, I use the long-term monitoring data collected by "the small rodent module" of Climate-Ecological Observatory for Arctic Tundra (COAT). Integrated ecosystem monitoring related to COAT has been conducted since 2005, in

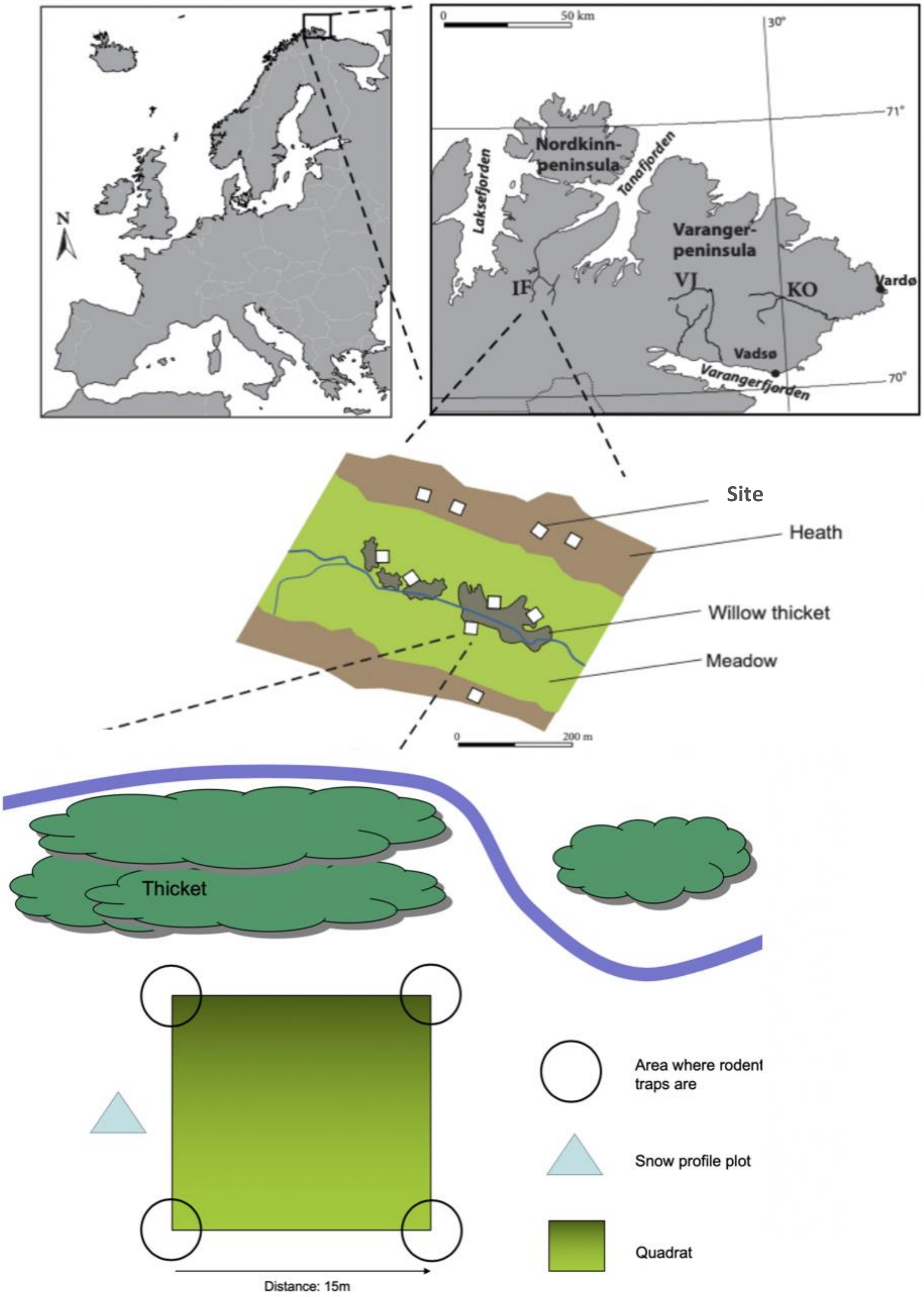

Figure 1 Map giving the location of the three watershed areas (IF (Ifjordfjellet), VJ (Vestre Jakobselv) and KO (Komagdalen)), in eastern Finnmark and Northern Norway, in the Varanger peninsula. And a representation of a meadow site which contains a quadrat (15m x 15m) with the positions of the snap traps and the snow profile plot.

three watershed areas (Figure 1). Two of these areas, Komagdalen and Vestre Jakobselv, are at the Varanger peninsula, at an approximate distance of 40 km from each other, while the third one, Ifjordfjellet, is ca. 100 km further west (Soininen et al., 2018). Since 2017, there was no more data from Ifjordjellet. Indeed, a road has been built through the study area, which made it difficult to differentiate the effects of climate change from the human impact's effects.

Each watershed area has two to four river valley sections i.e. shorter segments of the river valley, being separated by two to five km from each other. Each section has 4-6 sampling sites in the meadow habitat. The sites are at least at a 160m distance from each other. Both rodent trapping and snow structure measurements were done at each site (Figure 1).

2.4 | Tundra vole abundance

To cover the summer growth rate of the tundra vole (after early summer breeding), the trapping is conducted twice a year, in spring and autumn. The first session is from the 2nd to the 4th of July (to count the spring abundance). The second session is from the 31st of August to the 2nd of September (to count the autumn abundance). The animals were collected at each site in 15*15m sampling quadrats according to the widely used snap-trapping procedure (Myllymäki et al., 1971).

The traps are placed along natural runways for rodents or in front of holes and baited with raisins and oats. Three snap traps are placed within a radius of 2 meters from each corner of the sampling quadrats (i.e. 12 snap traps per sampling quadrat, Figure 1). The distance between neighboring grids had a range of 160–2200 m.

The number of quadrats included in the analysis of snow-tundra vole interaction varied over the years from 19 to 52.

2.5 | Snow profile analysis

In winter, snow profiles had been done to assess the snow changes (measure the depth and the structure of the snow with the presence of ice on the bottom and its thickness). To evaluate the effects of change in snow structure, the measurements of snow profiles were done around the same sampling sites as the snap trapping. All data from each site were used to plot ice proportion over the year (Figure 4).

To determine the impact of ice crust formation on the tundra vole population in the further statistic models, I only used the data from the deepest layer of snow in the site where the abundance of tundra vole was recorded.

2.6 | Statistical analysis

The variables that I used in my study was the locality (with three levels: “Ifjordfellet”, “Komagdalen”, “Vestre Jakoblsev”), the identity of the sampling site (with xx levels), the years (as a continuous variable), the presence of ice on the bottom (with two levels: “yes” or “no”), the abundance of tundra voles in spring, the abundance of tundra voles in autumn, the phase of the cycle where the population was, the summer growth rate and the winter growth rate.

In the data, the raw number of individuals represented trapping per 24 trap nights. In the analysis, I turned them into the number of individuals per 100 trap nights (n*100/24).

The cycle of the vole is divided into four phases: increasing (the year before peak year), peak (the year with the highest abundance, if two years had as high autumn abundance the latter year was defined as peak), decreasing (year after peak year), low (year(s) with very low abundance, in between peaks).

I tested the correlation effect between the variables in my study. To do that, I made a panel with the function “pair” in R studio, containing the correlation coefficient on the upper panel, and the plot between two variables on the lower panels. I present the correlation effect between the ice and the other variables as well as the correlation effect between the phase and the other variables, to see whether the phases are dependents of the other variables (see Table 1). There was no information about the winter growth rate. There is no strong correlation, $r < 0.6$, except between the spring abundance and the autumn abundance, which is normal because the autumn abundance of tundra voles depends on the individuals present in spring and depends on their reproductivity. I did the same for the cycle’s phase and I obtained the same low correlations. These weak correlation coefficients between my variables mean that I can include all of my variables in my models.

Table 1. Correlation effect between the presence of ice on the bottom and the other variables, and between the phase of the cycle where are the tundra voles (*M. oeconomus*) and the other variables.

	Correlation effect					
	Locality	**Sites**	**Spring abundance**	**Autumn abundance**	**Summer growth rate**	**Phase of the cycle**
Ice on the bottom	0.22	0.13	0,026	0,048	0,098	0,035
Cyclic phase	<0,001	<0,001	0,20	0,15	0,11	

Correlation coefficients between the variables that I have chosen to present in my study.

Effects of the ice on the abundance of tundra voles

To have an overview of what happened in Varanger between 2006 and 2019, I did one plot of the tundra vole's abundance over the years and another plot on the proportion of ice on the bottom over the years. All the data from each site were used to plot the overall dynamics of the tundra vole from 2006 to 2019 (Figure 2). In further analyses, only the data in the sites where they were also the snow state recorded was used. Sample size ranging between 0 to 29 individuals per 100 trap nights in spring, and between 0 to 38 individuals per 100 trap nights in autumn.

I made a plot, in R (R Core Team, 2019), with an abundance of rodents per 100 trap nights, according to the three rivers (Figure 2). To make this plot clearer, I revalue the season "spring" by "1" and the "autumn" by "6", with the function revalue in R, which added one or six point(s) on the year axis. In this way, the seasons for the same year were distant on the curve, but still distinguishable from the other year's point. For the ice proportion, I took the state of the deepest layer in each site and I calculated the proportion of ice (in percentage) for each river per year (Figure 3) in an excel document. I put this new variable in R (R Core Team, 2019), to do my plot of the ice proportion in the y-axis, according to the years in the x-axis, since 2006, in each locality.

To test if the frequency of icing increased from 2005, I made a generalized mixed effect model, with the function glm. My response variable was the ice. The fixed predictor variable was the year. The random predictors were the sites nested in the locality. I did this model using the family "Binomial", with the r-package lme4 (Bates et al., 2015).

Finally, to test how ice affects tundra vole populations, I did three mixed-effect models in R studio.

Effects of the ice on the tundra vole spring abundance

The first model was a linear mixed effect model on the spring abundance with the function glmer in R (R Core Team, 2019). The response variable was the spring abundance. The fixed predictor variable was the presence of ice and the cycle phase as an additive variable. The random predictor variables were the sites nested in the locality. I did this model using the family "Poisson".

I tested another model with the variable of the cycle phase in interaction with the variable of the presence of ice, both as fixed predictor variables. This interaction model did not converge. Thus, I will present the additive model in my results (see Table 3) and the interaction model in the Appendix (Table 4). The outcomes between the additive models and the interactions models were quite the same.

The distribution of the predicted values for each phase is presented in the box plot Figure 4.

Effects of the ice on the tundra vole summer growth rate

To calculate the summer growth rate, I used the intrinsic rate of increase to obtain my summer growth rate variable with the autumn abundance and the spring abundance of vole of the same year (i):

$$Rt = \ln (N_{\text{autumn, i}} + 0.1 / N_{\text{spring, i}} + 0.1)$$

The second model was a mixed-effect model on my summer growth rate, with the lmer function. The summer growth rate was my response variable. The fixed predictor variables were both the presence of ice and the cycle phase, interacting with each other. The random predictor variables were the sites nested in the locality (see Table 3). This model converged well so the results are presented in Table 3.

The distribution of the predicted values for each phase is presented in the box plot Figure 5.

Effects of the ice on the tundra vole winter growth rate

To calculate the winter growth rate, I used the spring abundance (year i) and the abundance of vole of the previous autumn (year i-1). I did the same procedures with the intrinsic rate of increase as:

$$Rt = \ln (N_{spring, i} + 0.1 / N_{autumn, i-1} + 0.1)$$

The third model was a mixed-effect model on my winter growth rate, with the lmer function My response variable was the winter growth rate. The fixed predictor variables were both the presence of ice and the cycle phase, interacting with each other. The random predictor variables were the sites nested in the locality (see Table 3). This model did converge as well.

I did a box plot of the distribution about the effect of ice on the winter growth rate with the raw values (see Figure 6) and I made another box plot with the predicted values from the model (see Figure 7).

3 | Results

Effects of the ice on the abundance of tundra voles

The population of tundra vole peaked four times: 2006-2007 (hereafter first peak), 2010-2011 (hereafter second peak), 2014-2015 (hereafter third peak), and 2018-2019 (fourth peak) (Figure 2).

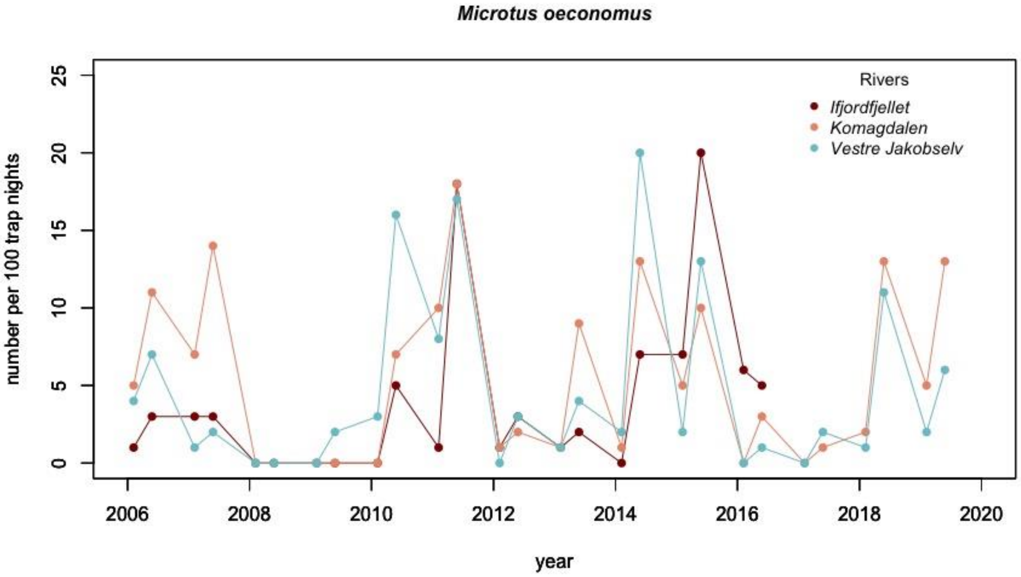

Figure 1 Tundra vole (*M. oeconomus*) abundance per 100 trap nights from 2006 to 2019. Data from the primary habitat (meadow) for tundra voles among three watershed areas (Ifjordfellet, Komagdalen, and Vestre Jakobselv). Lines go through season-specific mean abundances. Spring is defined as year.1 and autumn defined as year.6.

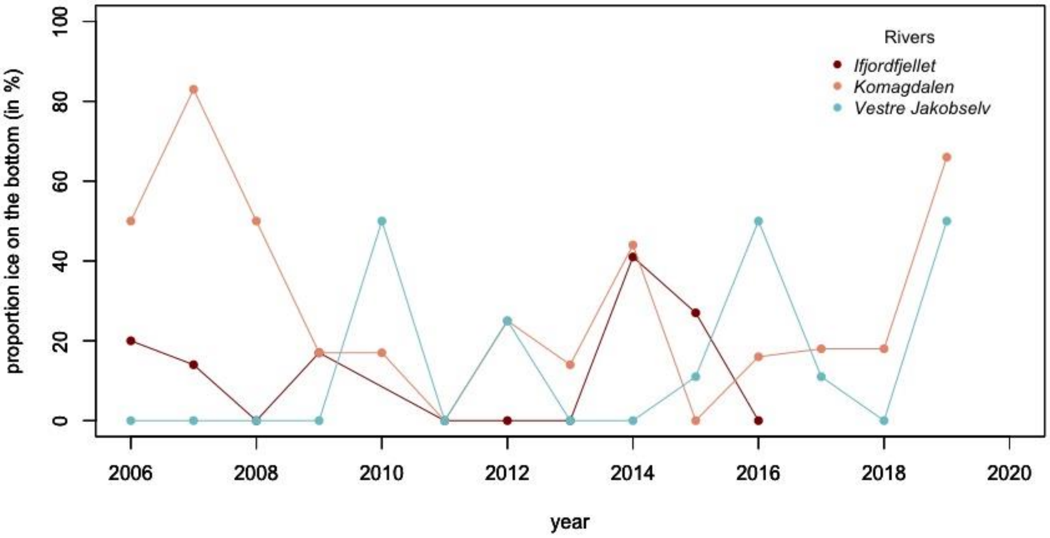

Figure 2 Proportion of ice (in percentage) on the bottom among all the sites per river over the years from 2006 to 2019. Data from the three watershed areas (Ifjordfellet, Komagdalen, and Vestre Jakobselv).

Overall, the tundra vole population declines the spring after an icy winter (Figures 3 and 4). In 2007, there were more than 80% of the sites in Komagdalen with ice formation. This icing event coincides with the decreasing spring abundance of tundra vole from the previous autumn (Figure 2). In 2011, it seems that the absence of ice let the rodents reached a great peak among the three rivers. In 2012, the formation of ice crust at Vestre Jakobselv coincided with the absence of tundra vole in spring. In 2014, the widespread ice crust formation in Komagdalen and Ifjordfellet, also coincided with the low spring abundance of tundra vole, compared to the increasing population in the previous year. The same coincidence appeared twice more. First time in 2015, at Ifjordfellet and Vestre Jakobselv, and the second time in 2019 at Vestre Jakobselv and Komagdalen. The abundance in Komagdalen was the same in both autumn 2018 and 2019, which makes it difficult to recognize the peak year among them. Nevertheless, the decrease phase of the fourth cycle has not yet arrived and conclusions about this last cycle are therefore somewhat uncertain.

Table 2 Effect of years on the frequency of ice from 2006 to 2019 in Varanger.

Predictors	**Response**
	Ice
	Estimate (Confidence Interval)
Fixed effects	
Intercept	-1.61 (-2.81; -0.48)
Year	*0,01 (-0.08; 0.09)*
Random effect	
Sites (nested in locality)	0.71 (0.51)
Locality	0.54 (0.29)

Parameter estimates of a generalized mixed effect model for the effect of the years on the formation of ice. Intercept is calculated for ice "no", locality "Komagdalen" and year "2006". Estimate refers to regression coefficients in the proportion of ice added or removed from a year to another. Within the parenthesis, it is the confidence interval of the estimations. Random effects are presented as standard deviation, within parentheses the proportion of the variance and the residuals for each random effect. Estimates with italics mean that 95% of the confidence interval includes zero at most 0.05.

The amount of ice evolved a lot throughout the years and there has not been the same proportion of ice from one river to another (Figure 3). Overall, Komagdalen was more prone to icing events than the two other watershed areas (as shows the Figure 3). I found that 2007, 2010,2014, and 2019 were the years highly touched by mild weather.

Based on my model, the ice does not become more frequent between 2005 and 2019 (Table 2). In Table 2, the confidence interval for ice "yes" is not significant, indicating no increase over time. However, the effect size is positive. The effect goes in the expected direction and corresponds to an annual increase of 1% in the probability of ground ice.

Effects of the ice on the tundra vole spring abundance

Table 3 presents the analysis of the effects of ice on the spring abundance of the tundra vole. I did not find a clear effect of ice on the spring abundance. The confidence interval for ice "yes" was not significant. I releveled each phase in the model to test if the ice could affect a phase more than another for the spring population. It appeared that the ice does not affect the spring population, no matter the phase of the cycle.

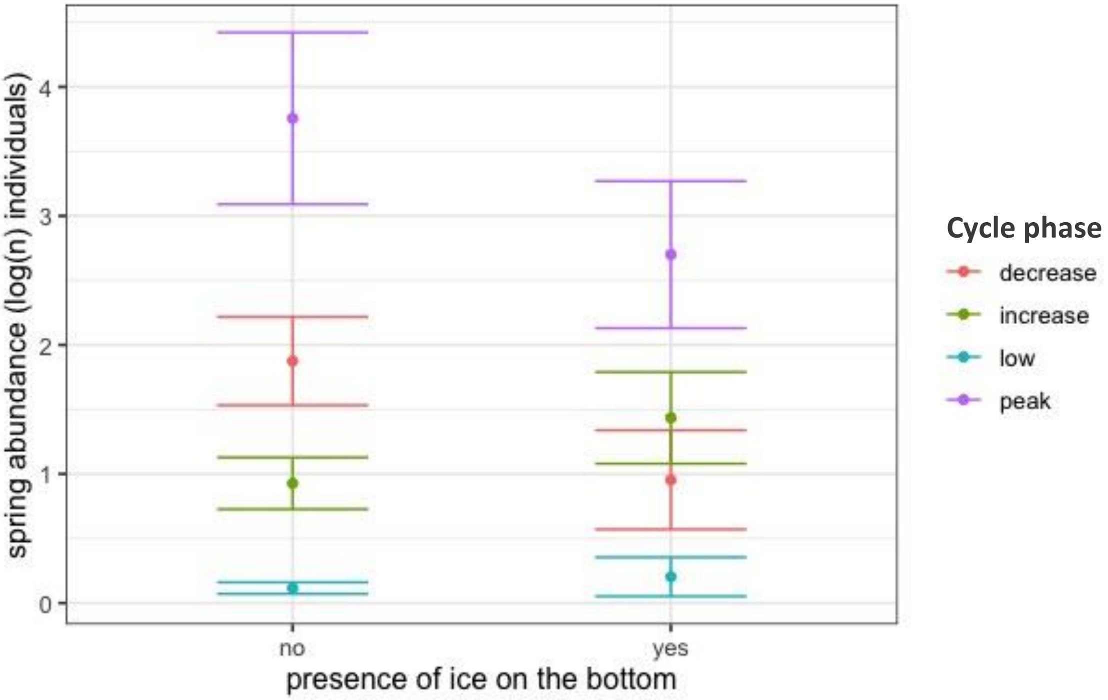

Figure 3 Box plot of the mean spring abundance of the tundra vole according to the absence of ice (no) or the presence of ice (yes) on the ground. The data came from the predicted value of the model between 2006 and 2019. The boxplots represent a mean of abundance in Varanger, all of the three rivers combined (Ifjordfellet, Komagdalen, and Vestre Jakobselv).

Figure 4 illustrates the response of the spring population to the ice for each phase. For each cycle phase, the mean spring abundance changes by one vole, more or less, between winter with ice and winter without ice. However, considering the large variability between the sites, these differences in the spring population are not significant.

Effects of the ice on the tundra vole summer growth rate

The summer growth rate of tundra vole was positive with or without icing events during winter. The model did not show any clear effect of the ice on the summer growth rate of the tundra vole (Table 3). I releveled each phase of the cycle in the model and, still, the presence of ice did not have any clear effect on the summer growth rate of the rodent.

However, Figure 5 shows that the summer population seems to thrive better after an icy winter. In every phase of the cycle, the summer population is growing more after an icy winter than after a winter without ice. Specifically, the low phase and the decrease phase increase by 2.5-fold their growth rate during summer after icing. Still, the variability between the sites was large (as shown in Figure 5). Therefore, the results are not significant.

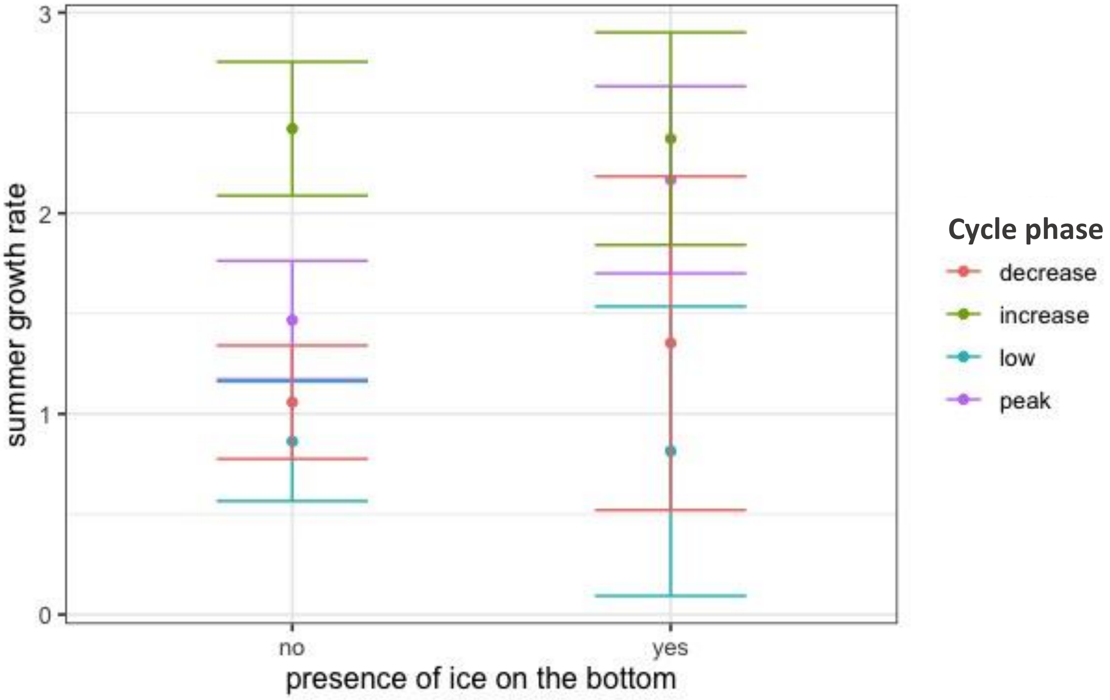

Figure 4 Box plot of the mean summer growth rate of the tundra vole according to the absence of ice (no) or the presence of ice (yes) on the ground. The data came from the predicted value of the model between 2006 and 2019. The boxplots represent a mean of the growth rate in Varanger, all of the three rivers combined (Ifjordfellet, Komagdalen, Vestre Jakobselv).

Table 3 Effects of ice on the tundra vole spring abundance and effects of ice and cycle phase on the tundra vole summer and winter growth rate.

Predictors	**Responses**		
	Spring abundance	**Summer growth rate**	**Winter growth rate**
	Estimate (log(n)) **(confidence interval (log(n))**	**Estimate (x)** **(confidence interval (x))**	**Estimate (x)** **(confidence interval (x))**
Fixed effects			
Intercept	1.28 (0.83; 1.71)	1.47 (0.92; 2.02)	-0.21 (-1.005; 0.58)
Year			
Ice bottom yes	*-0.16 (-0.44; 0.104)*	*0.70 (-0.35; 1.71)*	**-1.28 (-2.54; -0.001)**
Phase low	**-3.32 (-4.02; -2.73)**	-0.60 (-1.38; 0.16)	**-1.39 (-2.29; -0.52)**
Phase decrease	**-0.69 (-0.89; -0.49)**	-0.40 (-1.16; 0.33)	**-2.03 (-2.87; -1.19)**
Phase increase	**-1.16 (-1.41; -0.91)**	**0.95 (0.14; 1.78)**	0.02 ((-1.01; 1.01)
Ice bottom yes * phase low		*-0.74 (-2.54; 1.09)*	*-0.09 (-2.20; 1.98)*
Ice bottom yes * phase decrease		*-0.40 (-2.31; 1.62)*	*-1.10 (-3.47; 1.14)*
Ice bottom yes * phase increase		*-0.74 (-2.54; 1.09)*	*0.58 (-1.58; 2.72)*
Ice bottom yes * phase low		*-0.74 (-2.54; 1.09)*	*-0.09 (-2.20; 1.98)*
Ice bottom yes * phase decrease		*-0.40 (-2.31; 1.62)*	*-1.10 (-3.47; 1.14)*
Random effect			
Sites (nested in locality)	0.69 (0.47)	0.15 (0.49%)	0.41 (3.85%)
Locality	0.15 (0.02)	0.15 (0.49%)	0.39 (3.39%)
Residuals		2.01 (99,02%)	2.10 (92,76%)

Parameter estimates of two kind of models. First model is a linear mixed model for the effects of ice on the spring abundance of the tundra vole. Intercept is calculated for ice “no” and locality “Komagdalen”. Estimate refers to regression coefficients in logarithm scale of n individuals of tundra vole. The confidence interval for the estimations is present within the parenthesis in logarithm scale. Random effects are presented as standard deviation, and within parentheses are the proportion of the variance. Second kind of model is a generalized mixed effect model for the effect of the interaction of ice and the cycle phases on the summer growth and the winter growth of the tundra vole. Intercept is calculated for ice “no”, phase “peak” and locality “Komagdalen”. Estimate refers to regression coefficients in x multiplication factor of the abundance between the two seasons. Within the parenthesis, it is the confident interval of the estimations, the borders are represented in x multiplication factor. Random effects are presented as standard deviation, within parentheses are the proportion of the variance. The residuals are the distance between the raw values and the predicted values. Estimates with bold indicate that 95% of the confidence interval does not include 0, with italics that 95% of the confidence interval includes zero at most 0.05.

Effects of the ice on the tundra vole winter growth rate

During winter, population abundance was decreasing without ice (negatives number in estimation for each phase with the intercept "no ice" Table 3). Furthermore, the presence of ice resulted in a two-fold reduction of the predicted growth rate. However, the effect of ice was present only in the increase and decrease phase of the cycle, not during the low and the increase phase (based on releveling the model).

Figures 6 and 7 show the repartition of each cycle phase in the winter growth rate of the tundra vole, by the presence or absence of ice. Without ice, both box plots from Figures 6 and 7 look like the same. However, the model seems to widen the box plots for each phase if there is ice formation crust on the ground (Figure 7).

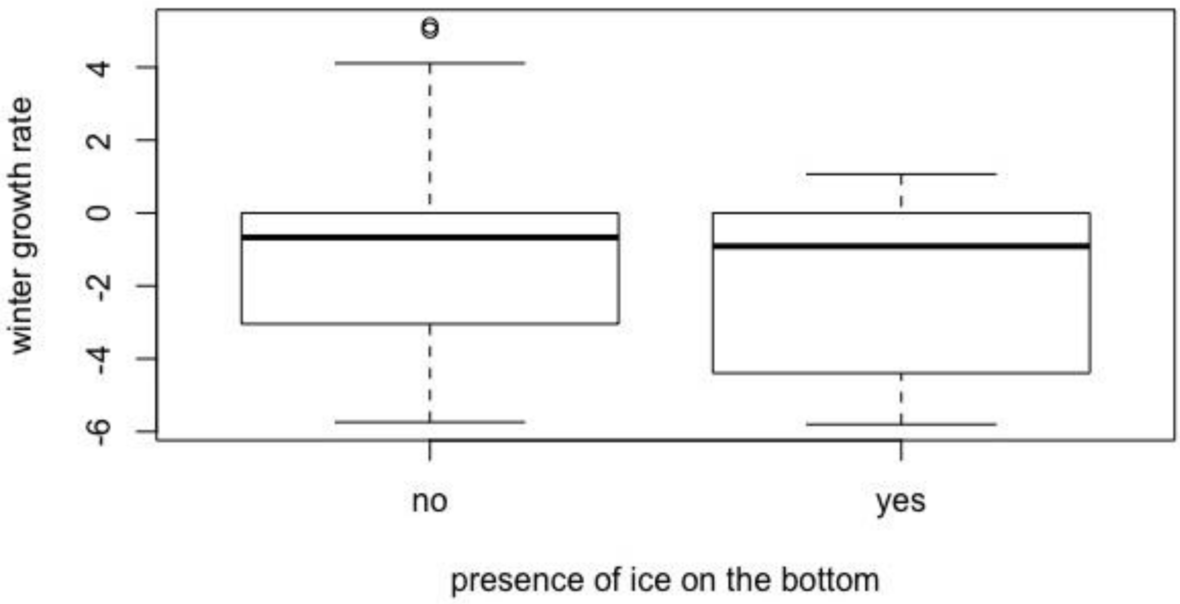

Figure 5 Box plot of the mean winter growth rate of the tundra vole from 2006 to 2019, according to the absence of ice (no) or the presence of ice (yes) on the ground. The data came from the raw data took on the field. The boxplots represent a mean of the growth rate in Varanger, all of the three rivers combined (Ifjordfellet, Komagdalen, Vestre Jakobselv). The vertical axis is given by the multiplication factor of the number of tundra voles gained or lost on average during winter. The whiskers refer to the smallest value and to the highest value of the timeseries. The outliers above the "no" boxplot defined the values numerically distant from the rest of the data.

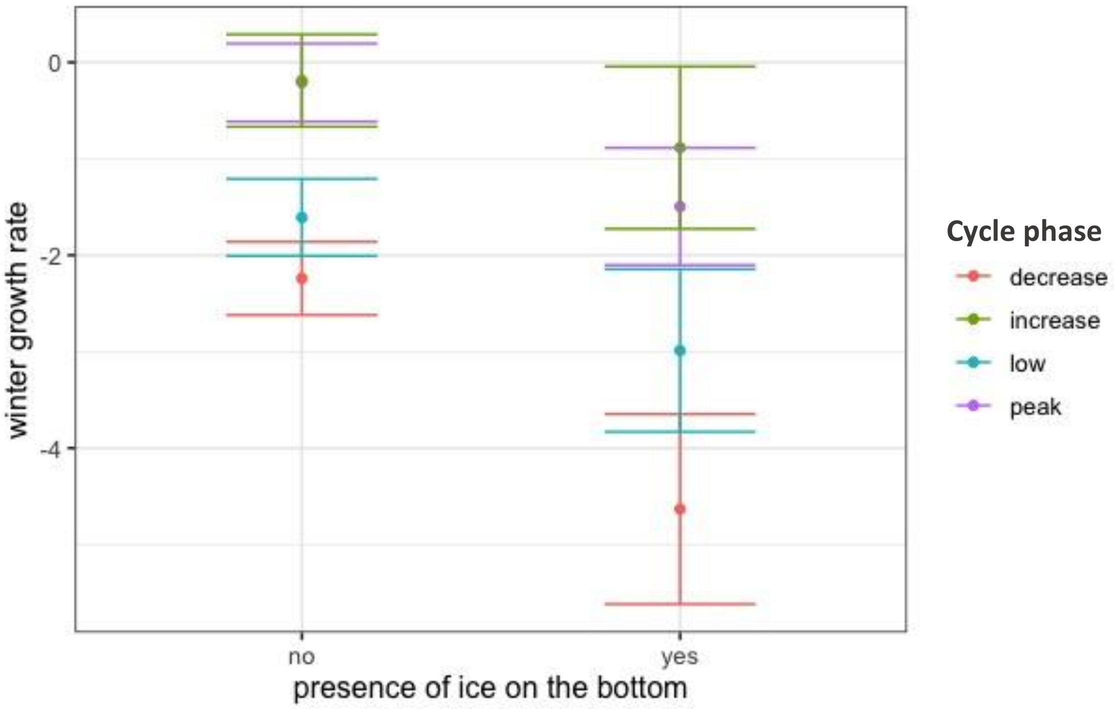

Figure 6 Box plot of the mean winter growth rate of the tundra vole according to the absence of ice (no) or the presence of ice (yes) on the ground. The data came from the predicted value of the model between 2006 and 2019. The boxplots represent a mean of the growth rate in Varanger, all of the three rivers combined (Ifjordfellet, Komagdalen, Vestre Jakobselv). The winter growth rate is given by the multiplication factor of the number of tundra voles gained or lost on average during winter according to the cycle phase where is the tundra vole (decrease, low, increase, and peak).

4 | Discussion

I found no support to my first hypothesis that ice affects the spring population of tundra vole. This indicates that the snow structure does not influence the population dynamics during the spring. My model did not show any clear effect of ice formation on the summer growth rate either which does not support my second hypothesis that ice was going to slow down the summer growing population. The snow structure in winter might not affect population dynamics during summer. However, I found a clear effect of ice on the winter growth rate confirming my third hypothesis that the winter growth rate was going to decrease. This indicates that the population growth is affected by ice formation during winter and could explain the low spring abundance after icy winter.

Ice and food are both factors that influence the cycle of voles (Korslund and Steen, 2006). The ice layer can reduce the population growth rate by one to two folds compared to a year without ice during a peak. These voles likely died by starvation due to the privation of food. Interestingly, it appears that the formation of ice crust has mostly an effect on the peak and the decrease phase. Whilst the ice does not influence the population during the increase and low phases. I assume the predation pressure might be stronger than the ice impact during these two phases of the cycle when there are already a few individuals from the last autumn. This study does support the results found before in Fennoscandia(Aars and Ims, 2002; Korslund and Steen, 2006). They had found that the ice cover prevented the tundra voles from feeding and thus reduced their winter survival rate.

Interestingly, I found no clear effect of ice on the spring abundance nor the summer growth rate of tundra vole. After an icy winter, the low and decrease phase are the years showing a higher growth rate in summer, than the two other cycle phases. No matter what happened with the snow structures during winter, or the number of survivors present in spring, the tundra vole population seemed to cover the loss during the summer. Thanks to their high ability to reproduce in a short term(Ims and Fuglei, 2005), they can go to one or two rodents (trapped) in spring to more than fifteen individuals (trapped) the next autumn (see Figure 2, the year 2011 at Ifjordfellet and the year 2014 at Vestre Jakobselv). However, this large change in the population abundance could be explained by the arrival of some new individuals from other sites, around the sampling grid. Although there are some patches of ice on the meadow, tundra voles can probably find some ice-free place where they can feed during winter. Besides, they feed on ramets of tall shrubs that are high enough to be available above the ice layer. The ice patches may also preserve some vegetation from winter grazing. Hence, the patches of ice can deliver some food in early spring when there is nothing left from winter grazing (Korslund and Steen, 2006).

Amount of ice gives the impression to appear in a higher proportion since 2010 (Figure 3). However, I did not find any clear increase in the frequency of icing, but I probably do not have enough data to assess this frequency. However, the effect size of the year corresponded to an annual increase of 1%. In fifty years, it would be 50% of a meadow covered by ice. In the long term, it could make a large difference for the winter survival of small rodents. Hence, some new patterns in the population cycle could emerge.

Since 2006, the synchronicity of the peaks between the different populations of tundra voles looks to disappear. Indeed, the first peak in 2006 in Vestre Jakobselv without ice on the bottom and it appeared in Komagdalen the next year while there were 80% of the sites covered by ice. For the third peak, the population in Komagdalen rose three consecutive years with ice on the bottom and peaked in 2014, as it did in Vestre Jakobselv but without ice. In Ifjordfellet, the voles peaked one year later in 2015 as strongly as before in Vestre Jakobselv, but with some ice on the bottom. This pattern seems to reappear in 2018-2019 in Komagdalen (if the time before the end of the study was a peak). Thus, the tundra vole population can peak in synchrony without sharing the same snow structures. As well as tundra vole can be unsynchronized by sharing the same snow conditions over the regions of Varanger. This study could not support what scientists said about climate events that synchronize the dynamics of voles over large distances, notably driven by heavy rain on snow (Hansen et al., 2013). In Varanger, the population of Tundra vole does not seem to be synchronized by icing.

Population of voles in Komagdalen might be more resistant faced to climate change, even if this locality is more prone to ice crust formation (see Figures 2 and 3 in 2006, 2007 and 2019). The population can peak in the highest abundance with ice on the bottom than other ice-free localities. The cycle tends to be damped in Komagdalen when the formation of ice crust is more prominent (see Figure 2 in 2007, 2014, and 2019). If the abundance during a peak year decrease, there is more food available during winter, allowing several consecutive years of high abundance in the population (Korslund and Steen, 2006). I can assume that these facts are linked to each other. Moreover, this could be explained by the edge habitats of thickets that provide food and cover from outside threats (Henden et al., 2011). However, the results from Henden do not include any data from my sites in Sandfjorddalen, where there is no thicket at all. Thus, the abundant edge habitats might explain the higher survival rate, but it is just an assumption.

Tundra vole does not react in the same way with climate events throughout Europe. In Poland and Eastern Germany, the tundra voles do not share the general pattern of cycle dampening (Cornulier et al., 2013). Except for these two cases, the population of tundra voles in Europe seems to be affected in the same way by icing events. In the European tundra vole populations, there is a decline in spring abundance and winter growth rate, while the summer growth rate increase without being impacted, and cycle pattern is dampening (Cornulier et al., 2013). There are also some tundra voles in the North American Arctic, but I did not find any study on the way that icing events could affect them. It may be possible that there are not many changes in the snow structures in North America because the winter is still colder than Eurasian Arctic (Barichivich et al., 2013; Bokhorst et al., 2016).

Tundra vole seems to be less affected by icy winter than other sympatric small rodent species. Indeed, the meadow rodents appear to keep their cyclic patterns with some great peak year. On the contrary, the population of Norwegian lemming became low in Fennoscandia since the past century (Ims et al., 2008b, 2011). From 2011 onward, the lemming did not show any strong peak and missed the last peak displayed by the grey-sided vole and the tundra vole in 2015 (COAT, 2020, n.d.; Ims and Fuglei, 2005; Kausrud et al., 2008; Soininen et al., 2018,). As for the grey-sided vole, their cycles tend to be damped (Ims and Fuglei, 2005; Ims et al., 2008, Soininen et al., 2018) and became several consecutive years at high abundances without a singular peak year. However, the tundra vole cycles tend to be damped like the grey-sided vole, as it happened in Komagdalen (Figure 2).

Reasons for error in this study could be the amount of data. The study may not cover enough years or enough sites to assess the effects of mild weather on the tundra vole in northern Norway. Some collected data on small rodents were useless because of the variable use of sites per year. Moreover, I might not define the cycle phase in the right way for this study as there are several ways to define this. Besides, my study comes from wildlife, then I have no control over the predation pressure, and on the vole migrations in and out of the trapping sites.

5 | Conclusion

I conclude that changes in snow structures affect the tundra vole. Winter growth rate during the peak and the decrease phase clearly decreased during years with ice formation. However, the melt-freeze events do not seem to touch the low phase and the increase phase of the population during the winter. As well, the spring abundance and the summer growth rate of tundra vole do not change very much from a year without ice to a year with ice. The summer population compensates for the loss from winter. Thus, the population might be affected by icing events during winter and be reestablished from the onset of spring.

Among other sympatric small rodent species in Fennoscandia, tundra vole remains a resilient species toward climate change. This species seems to keep its prominent cycle peak every 3 or 5 years, unlike the Norwegian lemming with an unstable cycle from several decades. However, the tundra vole may exhibit similar changes in its population dynamics as the grey-sided vole, i.e. dampening population cycles. These new patterns might be the first step to a more dramatic future for the population of tundra vole.

I might have not enough data to assess the effects of the changes in the snow structures. The period of study might be too short to assess the effect of climate change in northern eastern Norway. What should be done next is to have both data on voles trapping and snow profile for every site of the study. Also, it would be better to use snow profile data and climate data to make spatially explicit models of the snow structure to increase the number of sites with data on snow structures.

The dampening cycle pattern began to appear a few years ago. If the area covered by does increase by 1%, it could make some substantial changes in the population dynamics. Therefore, I want to encourage further study on the effect of icing events on tundra voles. As a keystone herbivore in the Arctic, we have to know how voles react to climate change. It would also be interesting to see if the climate does synchronize the tundra vole’s dynamics over time.

Acknowledgments

I thank my supervisor Eeva Marjatta Soininen for having accompanied me throughout my writing and for having helped me with the use of the software R. I also thank the team from the “small rodent module” of the program COAT (Climate-ecological Observatory for Arctic Tundra) for its work on the field, and the data they gave to me, that I could exploit in this dissertation.

Copy right:

Photography on the front cover: Geir Vie
Figure 1: combination of the map of Henden et al, (2011), and a sketch of Eeva Marjatta Soininen.

Appendix

Table 4 Effects of the interaction of ice and the phase of the cycle on the tundra vole spring abundance and on the growth rate during summer and winter.

Predictors	**Responses**		
	Spring abundance	**Summer growth rate**	**Winter growth rate**
	Estimate (log(n)) (confidence intervals (log(n))	**Estimate (n) (confidence intervals (n))**	**Estimate (n) (confidence intervals (n))**
Fixed effects			
Intercept	1.32 (0.85; 1.79)	1.47 (0.92; 2.02)	-0.21 (-1.005; 0.58)
Ice bottom yes	*-0.33 (-0.67; 0.01)*	*0.70 (-0.35; 1.71)*	**-1.28 (-2.54; -0.001)**
Phase low	**-3.48 (-4.28; -2.83)**	-0.60 (-1.38; 0.16)	**-1.39 (-2.29; -0.52)**
Phase decrease	**-0.69 (-0.91; -0.47)**	-0.40 (-1.16; 0.33)	**-2.03 (-2.87; -1.19)**
Phase increase	**-1.39 (-1.72; -1.08)**	**0.95 (0.14; 1.78)**	0.02 ((-1.01; 1.01)
Ice bottom yes * phase low	*0.05 (-1.06; 2.34)*	*-0.74 (-2.54; 1.09)*	*-0.09 (-2.20; 1.98)*
Ice bottom yes * phase decrease	*0.11 (-1.23; 0.42)*	*-0.40 (-2.31; 1.62)*	*-1.10 (-3.47; 1.14)*
Ice bottom yes * phase increase	**0.13 (0.20; 1.32)** (mistake likely due to the failure to converge)	*-0.74 (-2.54; 1.09)*	*0.58 (-1.58; 2.72)*
Random effect			
Sites (nested in locality)	0.69 (0.47)	0.15 (0.49%)	0.41 (3.85%)
Locality	0.18 (0.03)	0.15 (0.49%)	0.39 (3.39%)
Residuals		2.01 (99,02%)	2.10 (92,76%)

Parameter estimates of two kinds of models. The first model is a linear mixed model for the effect of the interaction of ice and cycle phase on the spring abundance of the tundra vole. Intercept is calculated for ice “no”, the phase “peak” and locality “Komagdalen”. Estimate refers to regression coefficients in logarithm scale of n individuals of tundra vole. The confidence interval for the estimations is present within the parenthesis in the logarithm scale. Random effects are presented as standard deviation, and within parentheses are the proportion of the variance. The second kind of model is a generalized mixed effect model for the effects of ice and the cycle phases on the summer growth and the winter growth of the tundra vole. Intercept is calculated for ice “no”, phase “peak” and locality “Komagdalen”. Estimate refers to regression coefficients in x multiplication factor of the abundance between the two seasons. Within the parenthesis, it is the confidence interval of the estimations, the borders are represented in x multiplication factor. Estimates with bold indicate that 95% of the confidence interval does not include 0, with italics that 95% of the confidence interval includes zero at most 0.05. Random effects are presented as standard deviation, within parentheses are the proportion of the variance. The residuals are the distance between the raw values and the predicted values.

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