Master's Thesis Environmental Management

Using subnivean cameras to compare winter habitat occupancy of lemmings and voles in an arctic small rodent community

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Abstract

To understand the effect of rapidly changing winter climate on arctic tundra ecosystems, small rodents constitute a key indicator. Their population density cycles are very sensitive to changing winter climate and affect the entire food web. Monitoring arctic rodent populations through the long winter has until now been impeded by the snow cover. However, below-snow camera traps provide a potential solution to this impediment. Here, I conduct the first extensive assessment of the utility of such camera traps to analyse the dynamics of a rodent community during the Arctic winter. The study was conducted over winter 2014-2015 (9 ½ months) with 44 camera traps in a landscape-scale design on Varanger Peninsula, northern Norway. I investigated whether the functionality of the camera traps was compromised by the harsh environmental conditions in the tundra and assessed the applicability of the recorded data for modelling occupancy dynamics of the focal rodent community. For modelling purpose, environmental variables were gathered both from the camera trap images and from *in situ* habitat measurements at the trap sites. Of the 44 camera traps, 19 had technical failures, mostly caused by spring melt flooding, while 14 were temporarily filled with drifting snow during the winter. In total, the cameras were motion-triggered 16445 times by three small rodent species (Norwegian lemming (*Lemmus lemmus*), grey-sided vole (*Myodes rufocanus*) and tundra voles (*Microtus oeconomus*)). The modelled weekly occupancy declined steeply for all three species at the onset of the winter but had a tendency for recovery for two of the species in spring. Occupancy probability was shown to be higher in habitats with rich ground-structure and vegetation and snow-free periods. However, the effect of environmental variables differed between species and remains uncertain due to data limitation. The detection probability for the three species was estimated to range between 0.49 and 0.62 per week. I conclude that, with some adaptations in the setup, the subnivean camera traps are well suited for long-term application in order to obtain robust inferences on the year-round occupancy dynamics of low arctic small rodent communities.

Introduction

The Arctic climate is changing with temperatures rising almost twice as fast as on the global average, and the weather is becoming more variable. Especially the long winter season is subject to profound changes. These changes alter the characteristics of the tundra ecosystems, and investigation of their ecological consequences requires more effort (Arctic Climate Impact Assessment 2004, Post et al. 2009).

To better understand the ecosystem impacts of changing winter climate, it is crucial to specifically monitor species with key functions in the food web that can be hypothesised to have a clear link to winter climate change (Christensen et al. 2013, Ims et al. 2013). In most arctic and boreal food-webs, a central role is played by lemmings (*Lemmus* and *Dicrostonyx* spp.) and voles (*Myodes* and *Microtus* spp.) due to their high-amplitude population cycles with recurrent high-density peak years at 3-5 year (Ims and Fuglei 2005). These small rodents constitute a major food source for predators and some specialised predators adapt their population dynamics to rodent density (Hanski et al. 1991). Moreover, the small rodents can have a considerable effect on the vegetation when they reach their high-amplitude population peaks (Moen et al. 1993, Ravolainen et al. 2011).

During the last decades, the functionally important boreal and arctic rodent cycles have been dampened or collapsed in several places (Ims et al. 2008, Cornulier et al. 2013) and this has been attributed to changing winter climate (Kausrud et al. 2008, Gilg et al. 2009, Stien et al. 2012, Berteaux et al. 2016, Domine et al. 2018). It has been assumed that winter warm spells and rain on snow events (ROS) have a considerable negative effect on rodent survival rates by disrupting the insulating snow layer and causing that ground ice blocks habitat and food sources (Korslund and Steen 2006, Kausrud et al. 2008, Ims et al. 2011, Berteaux et al. 2016). The Norwegian lemming (*Lemmus lemmus* LINNEUS) has been proposed to be more vulnerable to such impacts than sympatric vole species (Angerbjörn et al. 2001, Ims et al. 2011, Kleiven et al. 2018).

To understand how the environmental drivers affect the population dynamics of cyclic small rodents it is essential to acquire good monitoring data (Ims et al. 2008, Korpela et al. 2013). But detecting lemmings in years with low population densities is difficult with conventional rodent traps (Turchin et al. 2000) and it is generally problematic to observe winter dynamics of arctic and boreal small rodents is as they live under the snow (Krebs 2013, Berteaux et al. 2016). Therefore, the strength of the inferences on ecological mechanisms is limited by the temporal resolution of the data that can be generated (Krebs 2013). It is particularly essential to monitor small rodent dynamics with an adequate frequency (Ehrich et al. 2019) that matches the timing of mild spells in winter (Domine et al. 2018). To fully understand small rodent cycles and keep track of the changing dynamics, new approaches are needed (Ehrich et al. 2019).

In the last years, cheaper and more advanced camera technology has led to a wide-scale implementation of camera trapping studies (Steenweg et al. 2017), and methodological adaptations of camera traps to specific ecosystem conditions and questions have been made

(Nichols et al. 2011, Glen et al. 2013, Burton et al. 2015). Camera traps are useful tools that require low work effort while providing a high sampling resolution (Kucera and Barrett 2011, Soininen et al. 2015). While camera traps are already applied in monitoring of small mammals (Meek et al. 2012, Glen et al. 2013, Rendall et al. 2014, Villette et al. 2016), no cameras have been applied in boreal or arctic regions to estimate winter season dynamics of cyclically fluctuating rodent communities. As the winter dynamics of such communities may be subjected to rapid environmentally driven extinctions of local populations (e.g. Aars and Ims 2002), probabilistic models based on camera trap occupancy data may be particularly suitable for modelling such dynamics. Also, occupancy models are the established way to analyse camera trapping data when one cannot detect all individuals that are present (Nichols et al. 2011).

Soininen et. al (2015) developed a below-snow camera trap to study winter population dynamics of small rodents in tundra ecosystems. A camera was specifically tailored for taking images of fast moving small mammals at short ranges. It was placed in a box that rodents could integrate in their subnivean tunnel systems during winter. Soininen et al. (2015) conducted a small pilot study verifying that that the camera trap functioned technically very well and was able to effectively record the activity of tundra voles (*Microtus oeconomus*) under the snow over a winter in a sub-arctic meadow habitat. In the present study, I conduct the first extensive-scale assessment of camera traps as a method for investigating winter season dynamics of cyclically fluctuating small rodent populations.

I investigated how the functionality of the camera trap developed by Soininen et al. (2015) was affected by environmental conditions during winter in low arctic tundra and how information about the particular environmental conditions potentially affecting rodent winter dynamics could be gained from the data. A major aim of the study was also assess the utility of the camera trap data for state-of-the art statistical models (Nichols et al. 2011) to estimate species-specific site occupancy rates and extinction-colonization dynamics as functions of environmental drivers.

2 Methods

2.1 Study design

2.1.1 Study area

This study was conducted in a low-arctic tundra landscape in the inner part of Varanger Peninsula, north-east of Norway (70°N, 30°E) (Fig.1) (Walker et al. 2005). Hilly plains, carved by river valleys shape the study area that is located on an altitude between 165 and 489 m a.s.l. The plains are characterised by dwarf-shrub dominated heaths (*Empetrum nigrum*, *Vaccinium* spp., *Betula nana*), occasionally interspersed by mesic areas with mires and graminoid or moss dominated snow bed habitats. Upland areas are covered with boulder fields above the alpine limit of vascular plants, whereas lowland valleys have rivers lined by wet meadows and willow thickets (*Salix* spp.) (Ravolainen et al. 2011).

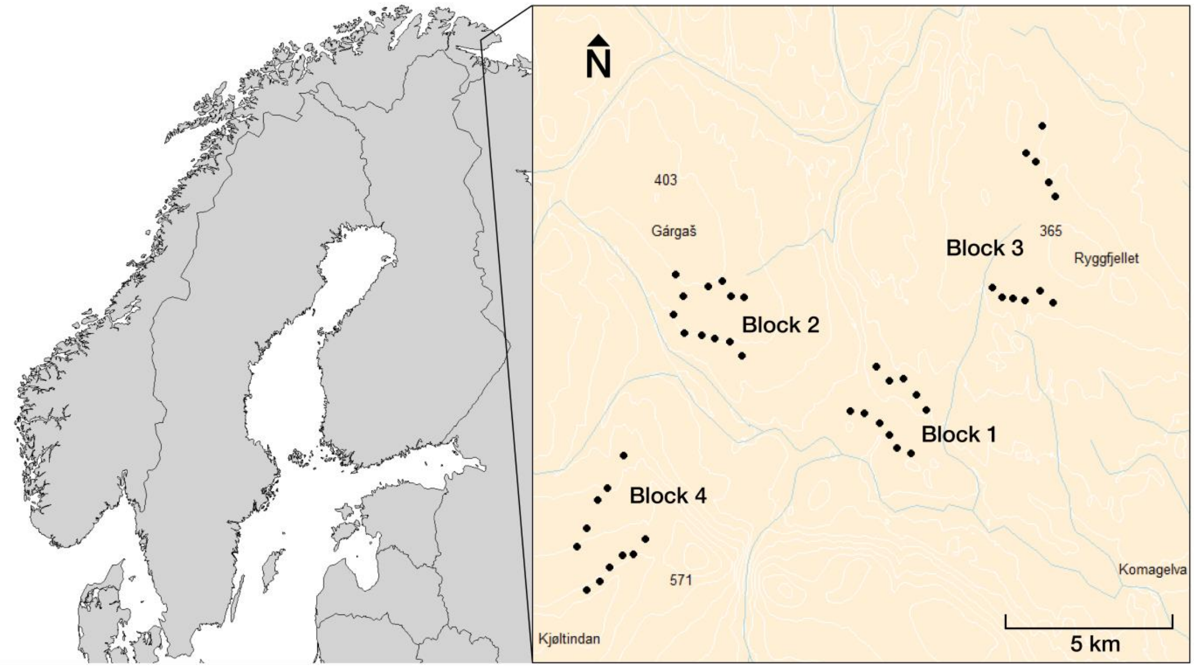

Fig. 1: Map of Norway and zoom on the camera trap sites on Varanger peninsula. The 44 camera traps are divided into four blocks of different lemming habitats.

Monthly mean temperatures (period 1961-1990), at the nearest weather station (Båtsfjord, at 150 m a.s.l. and 20 km from the nearest camera trap), range from -6.5°C in January to 11.0°C in July and the annual mean precipitation amounts 545mm (NMI 2020). The area is normally fully covered by snow at least from October to May (Malnes et al. 2016) with an average depth of 57cm (Virtanen et al. 1999). However, the snow cover is very heterogeneous, and snow beds can be covered by 4m of snow and persist until late July (Soininen et al. 2017).

2.1.2 Small rodent community

The study area is inhabited by three species of small rodents: Norwegian lemmings, grey-sided voles (*Myodes rufocanus* SUNDEVALL) and tundra voles (*Microtus oeconomus* PALLAS). Norwegian lemmings spend the summer in habitats with moist hummock tundra or mires and move to snow beds with dry ground in the winter (Kalela 1957). During summer, they co-occur with tundra voles that also tend to shift habitat between summer and winter seasons (Tast 1966). Grey-sided voles prefer dwarf shrub habitats (Viitala 1977). The three species exhibit an interspecifically synchronous, high-amplitude 4-year cycle on Varanger peninsula (Ims et al. 2011, Soininen et al. 2018, Kleiven et al. 2018). The population cycle of the Norwegian lemming has an amplitude that is typically more variable than the vole cycles and sometimes peaks of this species are missing in time series derived from snap trap monitoring (Ims et al. 2011). The present study covers a 9 ½ month period from fall 2014 to early summer 2015. This period is put into context of a whole vole cycle by data from a large-scale snap trap monitoring program on the Varanger Peninsula (Kleiven et al. 2018) (Fig. 2). The longer timeframe shows that the study period encompassed the typical seasonal winter decline of northern vole populations and included the phases of late increase (fall 2014) and early peak (spring 2015). During this cycle, the grey-sided vole was clearly the numerically dominant species, whereas the Norwegian lemming was almost absent (Fig. 2).

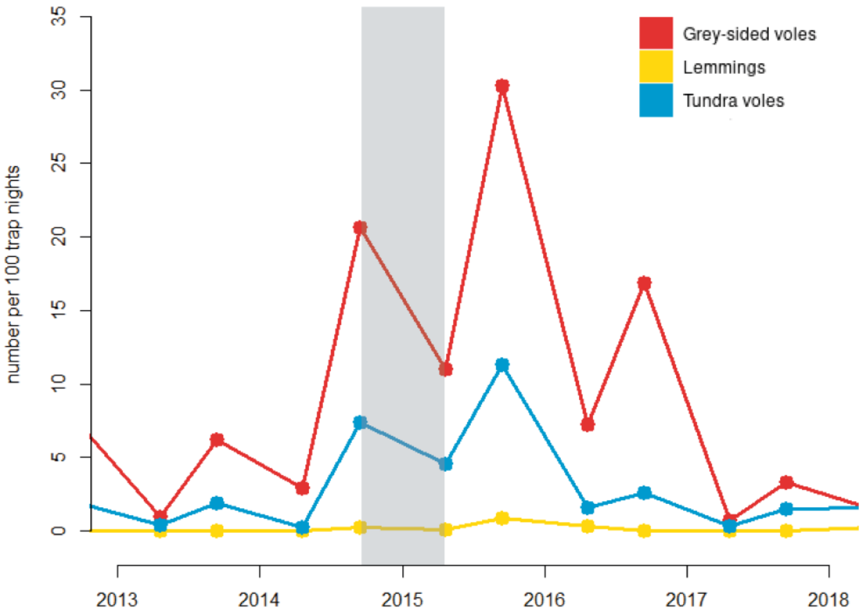

Fig. 2: Snap trapping data showing the dynamics of the small rodent community on the Varanger peninsula during the cycle that encompassed the present camera trap study. Number of trapped rodents per 100 trap nights in early July and September each year. The camera trap study period is highlighted by the bar.

2.1.3 Camera setup

The camera trap is described by Soininen et al. (2015). For my study, the wooden camera box was replaced with an aluminium box to improve durability. The cameras were programmed (Reconyx SM 750 Hyperfire) to take two pictures for each motion-triggered event and with one-minute quiet period (i.e. delay) after each event to avoid excessive amounts of photos. In addition, the cameras were programmed to take two pictures per day, at 01.00 hours AM and PM, to verify that the camera was functional and to obtain daily records of the ambient environmental conditions inside the camera trap (see below).

During September 15th -17th 2014, 44 camera traps were set up to cover lemming habitats at different altitudes in the study area. They were placed in four separate blocks (n=11 traps in each block) (Fig. 1). In two of the blocks cameras were placed primarily in snow bed sites

(Fig. 1, block 3 and 4), while the two other blocks had sites both in heath and mire habitats (1 and 2, Fig. 1). Within each block, the traps were placed in two lines with 5-6 traps. The minimum distance between traps was set to 300m to avoid that the same rodent individual included more than one camera trap within their home range (Ims 1987, Andreassen et al. 1998) and thus to assure that occupancy rates would be independent between the traps.

Criteria to choose the location of traps (Fig. 3) within blocks were that the vegetation should include food plants preferred by lemmings (mosses and graminoids) (Soininen et al. 2017). Placed among micro-topographic structures (between stones or hummocks), the camera traps were integrated with natural pathways that rodents normally use for movements in tundra habitats. Stones from the surrounding environment were put on the sides and top of the camera traps to secure them from strong winds.

Fig. 3: Camera trap placement in relation to topographic features. Rodent paths indicate usage (left), camera trap setting in snow bed habitat (centre) and risk of flooding (right).

Memory cards from all cameras were collected during July 1st -6th so that the entire study period covered approximately 290 days (42 weeks, rounded up). It was recorded which proportion of cameras had malfunctioned because of flooding and water damage or for other reasons (see below).

2.1.4 Sampling habitat data

Habitat variables were gathered to assess the effect of shelter, food plants and habitat specific snow conditions on camera functionality and small rodent occupancy. At each of the camera sites, micro-topography and vegetation were recorded in July 2019. For this purpose, four transects of 10m were measured originating at the camera and towards the cardinal directions (N, S, E, W). Then, a point intercept frame with three pins (Bråthen and Hagberg 2004) was applied to record the occurrence of vegetation categories in 12 frame plots per site (at 2, 6 and 10m of each transect) (Table 1). The micro-topography was measured by laying a chain on the ground, along each transect. The chain followed the ground structures and it was measured what distance it took to reach 10m of horizontal distance from the camera. For convenience, the measurement was done in five 2m sections.

Table 1: Vegetation identification at camera trap sites and PCA-transformed data as basis for constructing a *vegetation* covariate for modelling. Vegetation and ground categories that were recorded in 12 plots per camera trap site (37). Average number and standard deviation of plots per site were the respective category was present. Loadings of the categories in the first dimension of a PCA (see paragraph "Data preparation").

Categories	**No. plots with presence per site ± SD**	**Loading in PCA**
Empetrum nigrum	4.61 ± 3.30	0.05
Betula nana	3.00 ± 3.21	0.08
Vaccinum myrtillus	5.13 ± 3.39	0.06
Vaccinum uliginosum	0.55 ± 1.06	0.25
Salix spp.	0.11 ± 0.39	0.38
Salix herbacea	1.39 ± 1.78	-0.10
Juncaceae and *Eriophorum* spp.	0.08 ± 0.36	-0.34
other Cyperaceae	0.13 ± 0.58	0.32
Nardus stricta	4.03 ± 3.11	0.08
Deschampsia cespitos and *Calamagrostis phragmitoides*	1.45 ± 2.01	0.15
Rumex acetosa	0.05 ± 0.23	0.46
Legumes or Hemiparasites	1.29 ± 2.28	0.13
Juniperus communis	1.05 ± 1.43	0.11
Sphagnum spp.	0.42 ± 1.06	0.24
Acrocarpous mosses	2.63 ± 2.98	0.09
Pleuroicarpous mosses	1.89 ± 2.86	0.11
Dicranum spp.	6.13 ± 3.27	-0.05
Stones and rocks	4.42 ± 4.16	-0.08
Soil	5.37 ± 2.79	-0.02

2.2 Data analysis

2.2.1 Image data

Cameras with technical failure from the onset of the study were excluded from the analysis (n=5). For all other cameras, the recorded images were looked through with Reconyx MapView professional software (Reconyx Inc., Holmen, WI, USA), noting for each image whether it contained lemmings, tundra voles and grey-sided voles or "unknown vole" if the two vole species could not be distinguished. In addition to animal species, the following data on environmental conditions were recorded from the images: (1) Snow layer on the ground was recorded when snow was visible inside the trap or when the daylight did not penetrate the entrances of the trap, (2) snow potentially preventing detection of animals was recorded when there was so much snow in the trap that at least one entrance was fully covered, (3) melting snow (due to mild spells) was recorded when at least big drops of water or a general humidity was visible inside the trap, and (4) flooding due to large amounts of water covering the whole bottom of the traps. For the purpose of modelling, categories 1 and 2 (snow) and 3 and 4 (water) were combined to two binary variables (snow/no-snow and water/no-water). When the bad quality of an image impeded the inspection of images because a malfunctioning camera flash or snow on the lens, it was excluded from the dataset. Moreover, a sensor in the camera recorded the temperature inside the trap whenever an image was taken.

2.2.2 Environmental covariates

Environmental data were pre-processed with R-3.6.2 software (R Core Team 2019) to be able to use them as covariates (Table 2) in the occupancy models (see below). The binary variables *snow* and *water* were applied to evaluate how snow and water affect the accessibility of the camera trap and movement activity of small rodents. Moreover, the *snow* covariate was used to inform about the ecological effect of snow on food accessibility, shelter and other habitat conditions. I also calculated the weekly variance of the in-box temperature per site as a proxy for the thickness of the snow layer. While the insulation of a 30cm snow layer stabilises subnivean temperatures around 0°C (Pruitt 1970), more shallow or lacking snow cover should be indicated by more temperature variation. Therefore, the *temperature variance and snow* records were multiplied to one covariate that only has no effect (0) when snow is absent. It was assumed that this variable could account for melting events during the winter that potentially cause small rodent populations crashes. The *vegetation* covariate was based on a PCA of the vegetation data: I used the coordinates of each site in the first dimension. This dimension accounted for 29.86% of the total variation in the vegetation data set (Table 1). The *vegetation* variable was interpreted as to describe the habitat gradient from dry areas with low, sparse vegetation (stone, *S. herbacea*, *Dicranum* spp.) to wetter, more vegetated and diverse habitats (mosses incl. *Sphagnum* spp., *Vaccinium* spp. and grasses) (Table 1). From the measurements of topographic structure, the chain length was summed up per site and the horizontal distance was subtracted. The resulting variable was a measure of the *micro-topography* of a site and associated shelter availability and snow accumulation, which is dependent on wind exposure.

Table 2: Properties of environmental covariates for application in the occupancy model and binomial logistic models.

	Covariates				
	Species	**Temperature variance | snow**	**Snow**	**Vegetation**	**Micro-topography**
Binary/continous	binary	binary	continuous	continuous	continuous
Range	0/1	0/1	0-34,93	-2,93-4,7	1,42-9,78
Dimensions	site, week	site, week	site, week	site	site

2.2.3 Determinants of camera trap functionality

As substantial proportion of the camera traps were subjected to temporal or permanent malfunction (infiltration of water or snow) during the study period, binomial logistic models were used to analyse whether such failures were linked to habitat using *vegetation* and *micro-topography* as predictors.

2.2.4 Modelling of site occupancy

Of the 44 cameras, 37 were applied for occupancy modelling as five were excluded due to technical failures (see above) and additional two cameras were examined but not included due to missing environmental data.

The five environmental variables (Fig. 2) were integrated into a hierarchical dynamic occupancy model to estimate occupancy, colonisation, extinction and detection probability of the three small rodent species (MacKenzie et al. 2003). Applying this type of model was especially useful for my study as it enabled to investigate how environmental conditions affect detection probability. Thereby, the estimate of the species occupancy was also corrected for imperfect detection. Constructing a dynamic model over several "sampling seasons" allowed for analysing temporal dependence of the parameters on environmental predictors (MacKenzie et al. 2003). Here, one sampling season was defined as one week (primary occasion) with one survey each weekday (secondary occasion). I assumed that the local population at a given trap site would not change considerably during one week. As the camera traps recorded relatively few numbers of lemmings, the records of all three rodent species were combined in one dataset. The model was extended by a "species" dimension so that it could be assumed that some parameters were the same for all species (e.g. detection probability) while species-specific parameter estimates (e.g. colonisation and extinction probabilities) could also be estimated (White et al. 2013). The observations underlying the model were expressed in an array as

$$y_{i,t,j,s} | z_{i,t,s} \sim Bernoulli\ (z_{i,t,s} p_{i,t}),$$

where $y_{i,t,j,s}$ denotes the record of species s on site i, at season (week) t and survey (day) j. The observations have a Bernoulli distribution based on the latent occupancy (z) multiplied with the detection probability (p).

Detection probability (p): Through a logit link function detection probability was modelled jointly for the three species as a function of two environmental covariates. The equation for detection probability was thus:

$$logit(p_{i,t}) = a0 + \ a1 * snow + a2 * water,$$

where $a0$ is the intercept, $a1$ and $a2$ are the coefficients that describe the effect of the covariates.

Occupancy probability (Ψ): The initial occupancy probability ($\boldsymbol{\Psi_1}$=occupancy probability of small rodents in the first week) was modelled as:

$$logit(\Psi_{i,t=1,s}) = a3 + \ a4_s * snow_{i,t=1} + a5_s * vegetation_i + a6_s * micro - topography_i.$$

The effects $a4_s - a6_s$ were the species-specific coefficients of the covariates and $a3$ the intercept. The development of the occupancy changes over time ($\boldsymbol{\Psi_{t+1}}$, here $\boldsymbol{z}$**)** was modelled as a function of site colonization (*γ*) and extinction (*ε*) events:

$$z_{i,t,s} \sim Bernoulli\left(z_{i,t-1,s} \ * \ (1 - \varepsilon_{i,t-1,s}) + (1 - z_{i,t-1,s}) * \ \gamma_{i,t-1,s}\right)$$

Extinction (ε) and colonisation (γ) probability: Both were modelled similar to $\Psi_1$with a logit link but extended by t to describe seasonal changes and the temporal effect of the covariates.

$$logit(\gamma_{i,t,s}) = a7 + \ a8_s * temperature\ variance\ _{i,t} \ * snow_{i,t} + a9_s * snow_{i,t} + a10_s * vegetation_i + a11_s * micro - topography_i$$

$$logit(\varepsilon_{i,t,s}) = a12 + \ a13_s * temperature\ variance\ _{i,t} \ * snow_{i,t} + a14_s * snow_{i,t} + a15_s * vegetation_i + a16_s * micro - topography_i$$

The model of the four parameters ($\mathbf{p}, \mathbf{\Psi}, \boldsymbol{\gamma}$ $\mathbf{and}$ $\boldsymbol{\varepsilon}$) was implemented using the R software (R Core Team 2019). The estimation of the parameters was done in a Bayesian framework, running a Markov chain Monte Carlo (MCMC) with JAGS. For the model to converge, three chains with 250000 iterations were run and the first 40000 iterations were discarded as burn-in. The priors for the intercepts and coefficients $\mathbf{a1} - \mathbf{a16}$ were set to normal distributions between 0 and 0.1. The model was checked and indicated chain convergence as all $\hat{\mathrm{R}}$ values were below 1.1 (Gelman et al. 2013) and traceplots mixed well. Also, I ascertained that the model was fit for the dataset by performing a posterior predictive check (Kéry 2010). All resulting parameter estimates are given on logit scale and presented with 95% Bayesian credible interval [CI].

3 Results

3.1 Camera trap functionality

Of the 39 remaining camera traps that were examined, 14 (i.e. 35.9 %) were subjected to permanent failures later in the study period mainly due to flooding during the spring thaw period in May-June that damaged the camera electronics (Fig. 4). A binomial logistic model indicated that the probability of for such failures were significantly negative affected by the *micro-topography* covariate (-0.851: [-1.725:-0.245]).

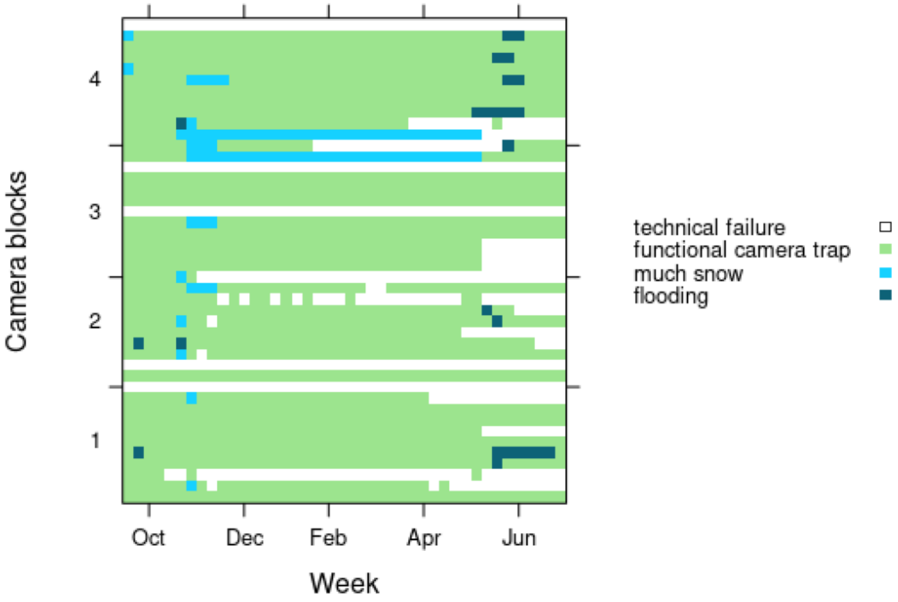

Fig. 4: Overview of the camera functioning at the 44 trap sites. Records per week and camera site (sorted by block). Categories are defined by the occurrence of at least one record per week. "Technical failure" includes records with bad quality and missing data. If none of the other categories was recorded for a week, it was categorised as "functional camera trap". "Much snow" and "flooding" means the trapping box was filled with snow or water to the extent that it would prevent entrance of rodents.

Moreover, 4.2% of the motion-triggered images were of such bad quality, that animals could easily be missed even if they were present (Table 3). At 14 sites, the traps were infiltrated by snow to the extent that it likely prohibited detection of animals (category 2 above) for shorter or longer periods during the winter (Fig. 4). A binomial logistic model showed a preventative effect of the covariates *vegetation* (-0.264 [-0.672:0.079]) and *micro-topography* (-0.378 [-0.954:0.049]) on large amounts of snow inside the camera trap.

In total, the cameras recorded 60 438 images. The amount of motion-triggers per camera ranged from 14 to 4726 (mean=503 for cameras that functioned over the whole study period). Per week the whole sample of functional cameras were motion-triggered 479 times on average (range from 196 to 1332). High record numbers were mainly attributed to voles (Table 3). The different rodent species could be identified (Fig.5), with only a small proportion of records being classified as unknown voles and discarded from the analysis (Table 3). The cameras were motion-triggered 2098 times without any resulting images of animals in the trap.

Table 3: Summary statistics of number of camera traps and sum of weeks, days and triggering events with observation of the different rodent species and other categories of animal triggered observations.

Observation	No. traps	Weeks	Days	Triggers
Lemming	10	28	92	830
Grey-sided vole	26	314	1336	13019
Tundra vole	19	168	526	2596
Unknown vole	8	16	25	48
Other vertebrates	23	127	288	731
Bad quality	14	82	172	845
Total	39	500	2006	18069

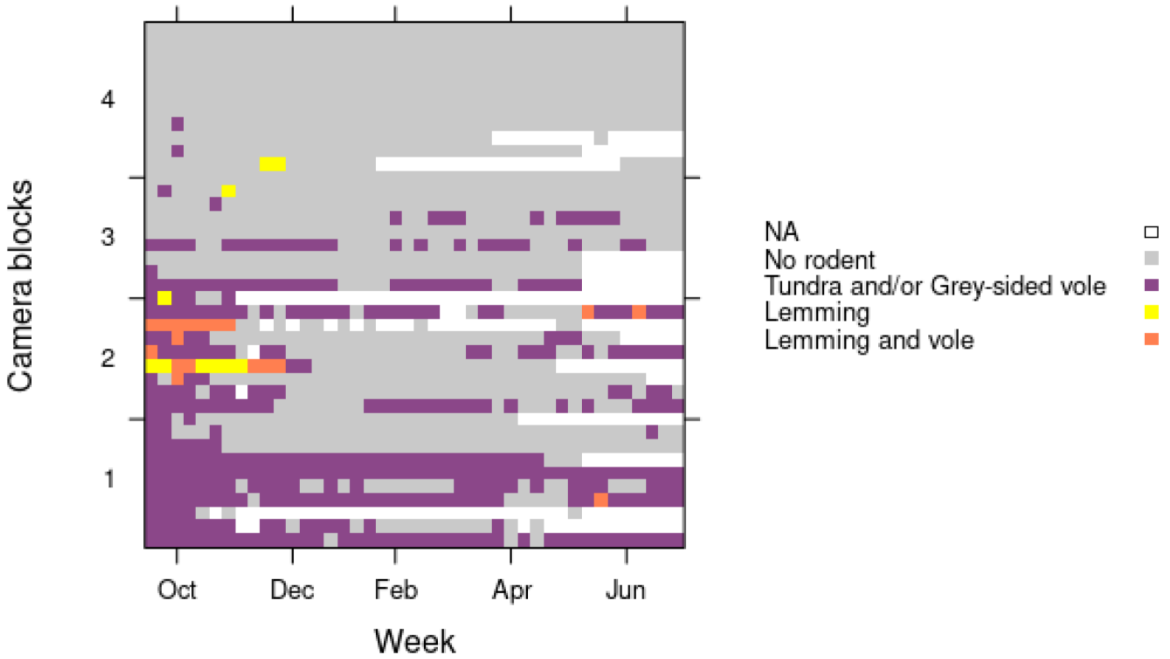

Fig. 5: Overview of small rodent records per week at the 39 functional camera traps (sorted by block). Occurrence of a small rodent is defined by at least one record per week. Similarly, when the camera was not recording images for at least one day, the whole week was assigned to NA. Snow or water, that infiltrated the camera trap (Figure 4) coincided with rodent records on some days and are thus not included.

3.2 Site occupancy dynamics

Occupancy: The estimated small rodent occupancy probability over time ($\boldsymbol{\Psi}$) showed a decrease in the early winter and an increase during the snow melt. Thereby the relative differences in occupancy probability between the species remained (Fig. 6). Grey-sided voles had the highest mean occupancy probability. But the population also had the strongest decline during the onset of winter and did not recover the high occupancy during the study period. Tundra voles also declined and were even absent for one week but strongly increased their occupancy probability from May on. The occupancy of lemmings was locally very restricted and they disappeared from December on, until the occupancy probability slightly increased in May. These small rodent occupancy patterns correspond to the appearance of water and the absence of snow (Fig. 6).

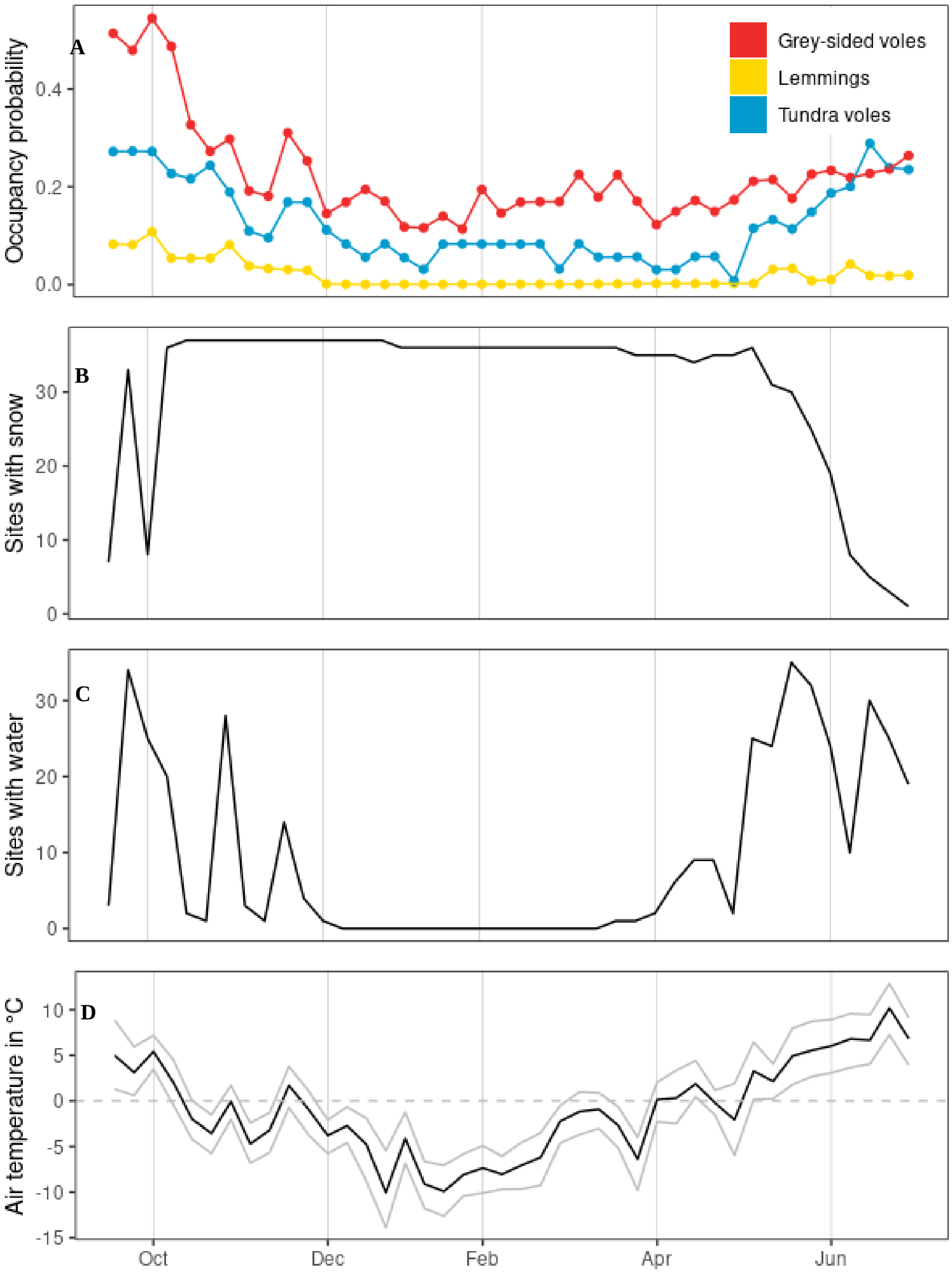

Fig. 6: Mean occupancy probability over time as estimated by a hierarchical dynamic occupancy model and comparison to abiotic measurements. The mean of the posterior distribution of the occupancy probability (Ψ), averaged over sites and given per week for the three small rodent species (A). Below is the number of sites per week with records of snow (B), water (C) and the weekly minimal and maximal air temperature at a near weather station (Båtsfjord) (D).

Some trends in the relationship between the covariates and parameters could not be identified by the model with the limited amount of data, but other relationships are apparent (Table 4). Due to wide credible intervals (CI of the coefficient clearly ranging from positive to negative), no conclusions could be made about the relationship between initial occupancy ($\boldsymbol{\Psi}_{i,t=1,s}$) and the covariates *snow* and *micro-topography* (Table 4). The *vegetation* covariate, however, showed that richly vegetated habitats positively influenced the initial occupancy probability of small rodents.

Table 4: Impact of environmental variables on initial occupancy, colonisation and extinction probability of three small rodents species, based on the estimates of a hierarchical dynamic occupancy model. Values are coefficient estimates on logit scale (95% Bayesian credible intervals). Confident estimates with meaningful credible intervals are highlighted in bold.

		Covariate			
Probability	**Species**	**Temperature variance | snow**	**Snow**	**Vegetation**	**Micro-topography**
Occupancy	Lemming		-0,326 [-6,388:5,680]	0,147 [-0,336:0,602]	0,006 [-6,169:6,194]
	Grey-sided vole		-3,037 [-8,234:1,761]	**1,153 [0,538:2,005]**	-0,002 [-6,178:6,196]
	Tundra vole		0,651 [-4,003:4,924]	**0,567 [0,189:1,025**	-0,010 [-6,189:6,212]
Colonisation	Lemming	0,026 [-0,102:0,114]	-0,320 [-2,924:1,602]	0,020 [-0,246:0,273]	-0,020 [-6,276:6,136]
	Grey-sided vole	**0,068 [0,007:0,123]**	**-1,398 [-3,112:-0,070]**	**0,229 [0,111:0,346]**	-0,033 [-6,255:6,201]
	Tundra vole	**0,067 [0,014:0,115]**	-0,609 [-2,051:0,543]	**0,423 [0,295:0,553]**	0,009 [-6,203:6,227]
Extinction	Lemming	0,111 [-0,030:0,262]	3,114 [-1,031:7,696]	0,425 [-0,184:1,054]	**-0,752 [-1,079:-0,460]**
	Grey-sided vole	-0,030 [-0,092:0,022]	**-1,480 [-2,864:-0,361]**	**-0,214 [-0,361:-0,072]**	-0,018 [-0,148:0,105]
	Tundra vole	0,043 [-0,019:0,102]	**3,998 [0,963:8,095]**	-0,128 [-0,301:0,040]	**-0,161 [-0,322:-0,012]**

Detection probability: Detection probability ($\boldsymbol{p_{i,t}}$) was estimated to be 0.615 in camera traps without *snow* and *water*, but dropped to 0.559 in the presence of *snow*, 0.544 in presence of *water* and to 0.486 when both *snow* and *water* was present during a week.

Colonisation probability: The estimated probability that a site was colonised by small rodents ($\gamma_{i,t,s}$) indicated to be positively affected by the *temperature variance|snow* covariate (Table 4). In contrast, *snow* had a negative effect on the colonisation of a site, especially by grey-sided voles (Table 4). Richer *vegetation* (i.e. higher score of the first PCA axis) had a positive effect on the colonisation probability of tundra voles and grey-sided voles but no effect on lemmings. The effect of *micro-topography* on colonisation was unclear.

Extinction probability: While *temperature variance|snow* had no effect on the extinction rate, the presence of *snow* made extinctions of grey-sided voles less likely but increased the extinction probability of lemmings and tundra voles. The *vegetation* covariate coincided with an increased extinction probability for lemmings but had the opposite effect on vole extinctions. Pronounced *micro-topography* decreased the probability of small rodent extinction in general.

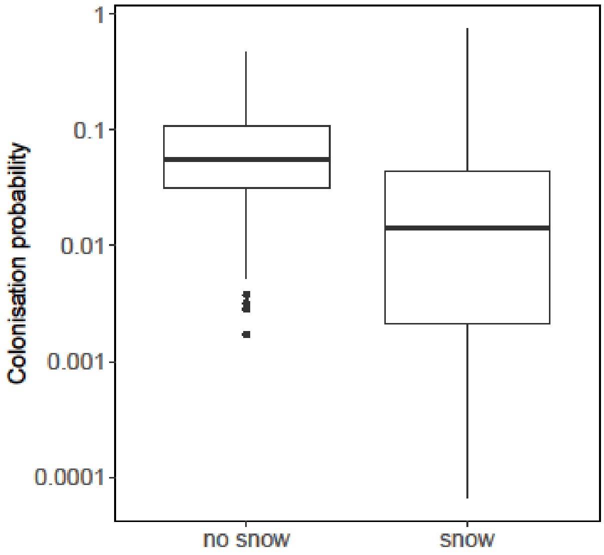

Fig. 7 Effect of the presence of snow, at all sites and weeks, on the estimated small rodent colonisation probability (γ), on logarithmic scale.

4 Discussion

For the first time, the camera traps collected data on the presence of the lemmings and voles with a high temporal and spatial resolution over the whole arctic winter (Fig. 5). The challenging tundra environment with drifting snow and spring floods caused quantitative data losses. Still, the gathered data were applicable for an occupancy model that could show the steep drop in small rodent numbers, from autumn to the next spring, that was apparent from the snap trapping data (Fig. 2). Additionally, the model estimates indicated that the main population decreases took place during a few weeks after the onset of snow in early winter. The effect estimates of covariates indicated that small rodent occupancy corresponded to habitats with micro-topographic structures and relatively dense vegetation as well as to the absence of snow. However, not all these preferences in environmental conditions were clear and consistent over species.

4.1 Camera functioning and data quality

Applying the camera trapping method in a tundra ecosystem largely worked well. Data losses were related to camera site characteristics such as micro-topography (water damage to due flooding) and vegetation (infiltration of wind-drifting snow) that are likely to become diminished by slight adaptations of the camera setup. When positioning the camera traps it has to be considered that technical failures were negatively related to micro-topographic structures. This correlation mirrors the increased likelihood of flooding at relatively flat sites, especially in spring. The probability of snow infiltrating the camera traps also revealed a correlation to rather open sites with little vegetation cover. Associated strong winds and drifting snow could be repelled by covering the entrances of exposed traps with stones so that only gaps are left for the small rodents to pass. Moreover, traps should be further stabilised with additional stones to prevent dislocation which could be an issue as well. Other potential problems like humidity on the lens, numerous empty images, nest building or distinguishing between species (Soininen et al. 2015) were of no concern here. Kalhor et al. (2019) considered that permafrost in arctic environments could cause serious frosting of camera traps and impair their performance, as happened on Bylot Island. In my study, frost was not an issue, probably due to milder temperature and a thicker snow layer on Varanger peninsula, compared to some other arctic regions. Camera functioning may thus be more problematic in colder regions, while mild climate arctic regions allow for state-of-the-art camera traps to function during the whole winter.

4.2 Study limitation

The novel camera trapping approach performed well in generating frequent data throughout the year that were suitable for the construction of an informative occupancy model. However, the low quantity of data only allows for first indications as a basis for further, robust studies. Especially the sparse lemming observations limited the scope of analysis and ruled out the application of a species-specific model. By combining the records of different species in one model, with the assumptions made on the similarity of the parameters for lemmings and voles, the strength of inferences could be increased (White et al. 2013). Still, species-specific inferences are to be treated carefully as many parameters were estimated with high uncertainty. Other approaches, of analysing occupancy in a single species model (MacKenzie et al. 2003) or including multiple species in a multistate model (Nichols et al. 2007), can be applied to get more species-specific estimates but require better data (MacKenzie et al. 2017). Also, the robustness of covariate effect estimates is limited by the low quantity of data. Particularly the impact of the presence of snow is based on very few snow-absence data. In addition to the lack of robustness, the complete loss of camera traps due to environmental hazards is undesirable due to potential bias. To ameliorate data loss, the camera trap positioning could be improved and entrances covered with stones, as mentioned above. The estimated detection probabilities indicate that the approach of using the camera traps generates data that are representative of the local small rodent population. However, the estimates may be inaccurate as the applied covariates *snow* and *water* are too coarse to capture the different prerequisites for detection. To ensure better estimates it should be differentiated between a trap that is filled with snow or water and an almost empty trap.

4.3 Rodent dynamics and snow impact

Despite the data limitations, population dynamics could be estimated for all three species. It appears what happened before, in autumn, the vole species reached peak densities while the lemming population remained low (Fig. 2): The collapse of the lemming population was evident already during the early part of the pre-peak winter when lemming numbers typically increase (Ims et al. 2011). Potentially, the observed population decrease of lemmings and tundra voles was accelerated by seasonal habitat shifts of these species that may not have been covered well enough by the camera traps. Investigating potential additional winter habitats in the study area could ensure comprehensive records. Nonetheless, it is likely that the whole population decreased in the winter.

How these small rodent population dynamics were affected by environmental conditions could only partially be unravelled by the model. The presence of snow coincided with lower occupancy probabilities of lemmings and tundra voles and had a contradictory effect on grey-sided vole occupancy parameters (Table 4). In contrast, variable temperatures, associated with a thin snow layer, affected the occupancy probability of small rodents rather positively and did not have the expected detrimental effect on them (Korslund and Steen 2006, Berteaux et al. 2016). Considering that the study did not comprehensively represent vole habitats, inferences on the role of snow in vole population dynamics cannot be drawn here. Clearly, this particular snow season was fatal for the lemming population. Preceding studies assumed that lemmings are particularly sensitive to the physical condition of the snow layer (Ims et al. 2011). It can be an important shelter, allowing for reproduction (Oksanen et al. 2008) or turn into a barrier on the ground that exposes lemmings to the harsh weather and blocks the access to their food sources (Korslund and Steen 2006, Kausrud et al. 2008, Berteaux et al. 2016). In contrast, vole species that are more generalistic in their food and habitat choice (Angerbjörn et al. 2001, Ims et al. 2008) can be expected to be less affected by a freezing of the lower snow layer. The snap trapping data show that vole populations coped better with the winter decline. The mechanisms of how the condition of the snow layer affects the different small rodent populations can be further revealed by the camera traps. They provide local data on the snow cover and subnivean temperatures and additional information on snow properties could be obtained through local measurements (Domine et al. 2018) or remote sensing and snow modelling (Ehrich et al. 2019). Together with a higher quantity of data, this would allow for more solid estimates and a differentiated analysis on the effects of snow conditions.

In my study, the data material was also not sufficient to really assess questions related to habitat use. Nevertheless, the colonisation and extinction probabilities showed an affinity of both vole species to sites that were more vegetated which corresponds to previous descriptions (Tast 1966, Viitala 1977). Lemmings had a higher extinction rate at sites with lower micro-topographic structure (Table 4) and were hardly recorded by cameras in particular snow bed habitats (Fig. 4). Usually, rather flat snow beds are preferred lemming winter habitats (Kalela et al. 1961) but due to generally sparse records, interpretations are groundless.

4.4 Outlook

In conclusion, a slightly adapted study design is suitable to be applied for long-term monitoring. To ensure good quality and quantity of data, the camera traps need to be better prepared for windblown snow and meltwater. Then, based on records from several years and further specified information on snow properties, occupancy models can be applied to obtain a better understanding of which mechanisms in winter determine the growth or collapse of the local lemming population and unravel vole population dynamics. Moreover, the method has the potential for investigating further research questions. Habitat occupancy preferences and seasonal movement patterns can, for instance, be examined as the traps were able to detect lemmings despite low densities. Moreover, individual records of stoats and least weasels show that the camera trap can be used to study winter dynamics of the predator-prey relationship between mustelids and small rodents from a new perspective (Kleiven unpubl.). Similar approaches have been made by Kervola et al. (2019) who used camera traps to investigate the impact of mustelid odour on small rodent occurrence. Also, potential technical improvements in image processing techniques or remote photo gathering could further facilitate the method application and allow for data generation in higher quantities and more remote regions (Bjørndalen et al. 2016).

Ehrich et al. (2019) discuss how to approach lemming monitoring in the future and argue for a combination of different methods and the further development and application of subnivean camera traps. Their evident robustness against arctic climate and low-effort use makes the traps particularly valuable in remote regions with harsh conditions. As for now, a lack of resources limits the establishment of camera traps in some regions but it should be the aim to establish camera traps in the endeavour of standardised monitoring of the whole arctic (Christensen et al. 2013, Ehrich et al. 2019). As warm spells during the arctic winter are becoming more frequent (Putkonen and Roe 2003) this approach is critical to further understand the small rodent population cycles and how they are changing. This is crucial to understand the ongoing processes in the arctic ecosystems and the severe changes that are about to come.

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Appendix

Example images of environmental conditions that were scored from the images

Fig. 8: Snow layer on the ground was recorded when it was visible snow inside the trap or when the daylight did not penetrate the entrances of the trap (1).

Fig. 10: Snow potentially preventing detection of animals (2).

Fig. 11: melting snow (due to mild spells) was recorded when at least big drops of water or a general humidity was visible inside the trap (3).

Fig. 9: flooding due to large amounts of water covering the whole bottom of the traps (4).

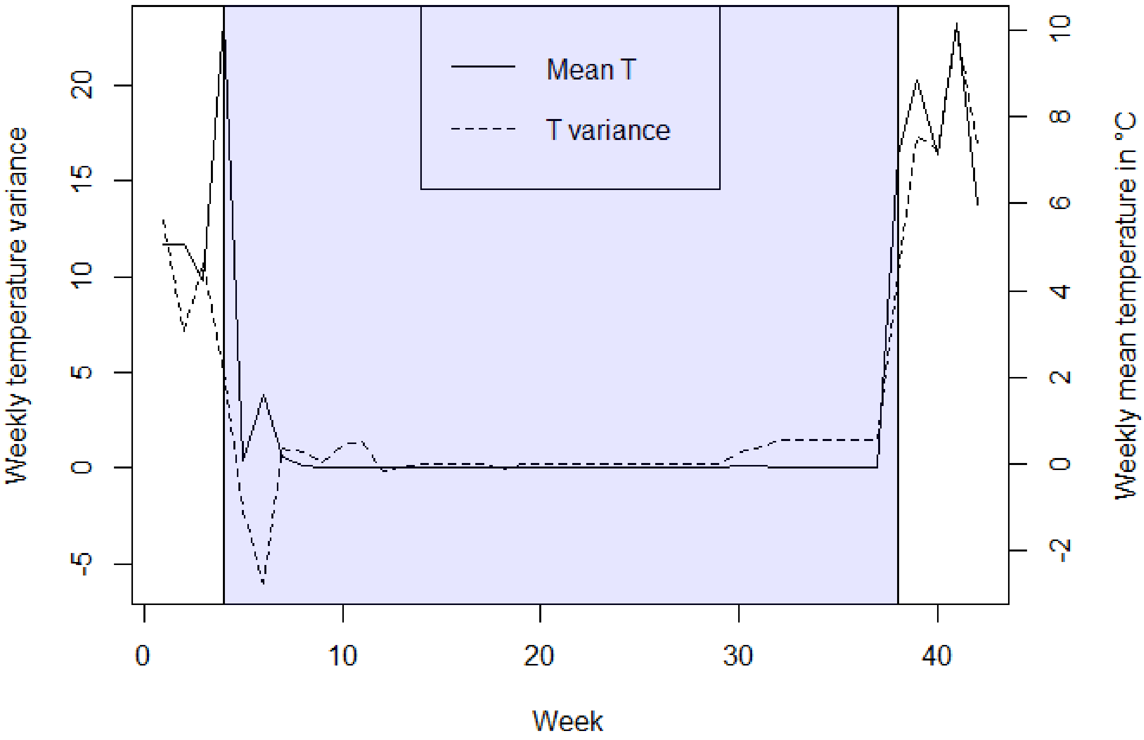

Fig. 12: Example temperatures measured in camera trap F7_3 (Block 3). Weekly mean and variance of temperature measured at 1am and 1pm. Grey background indicates the period when snow that was recorded on the images.

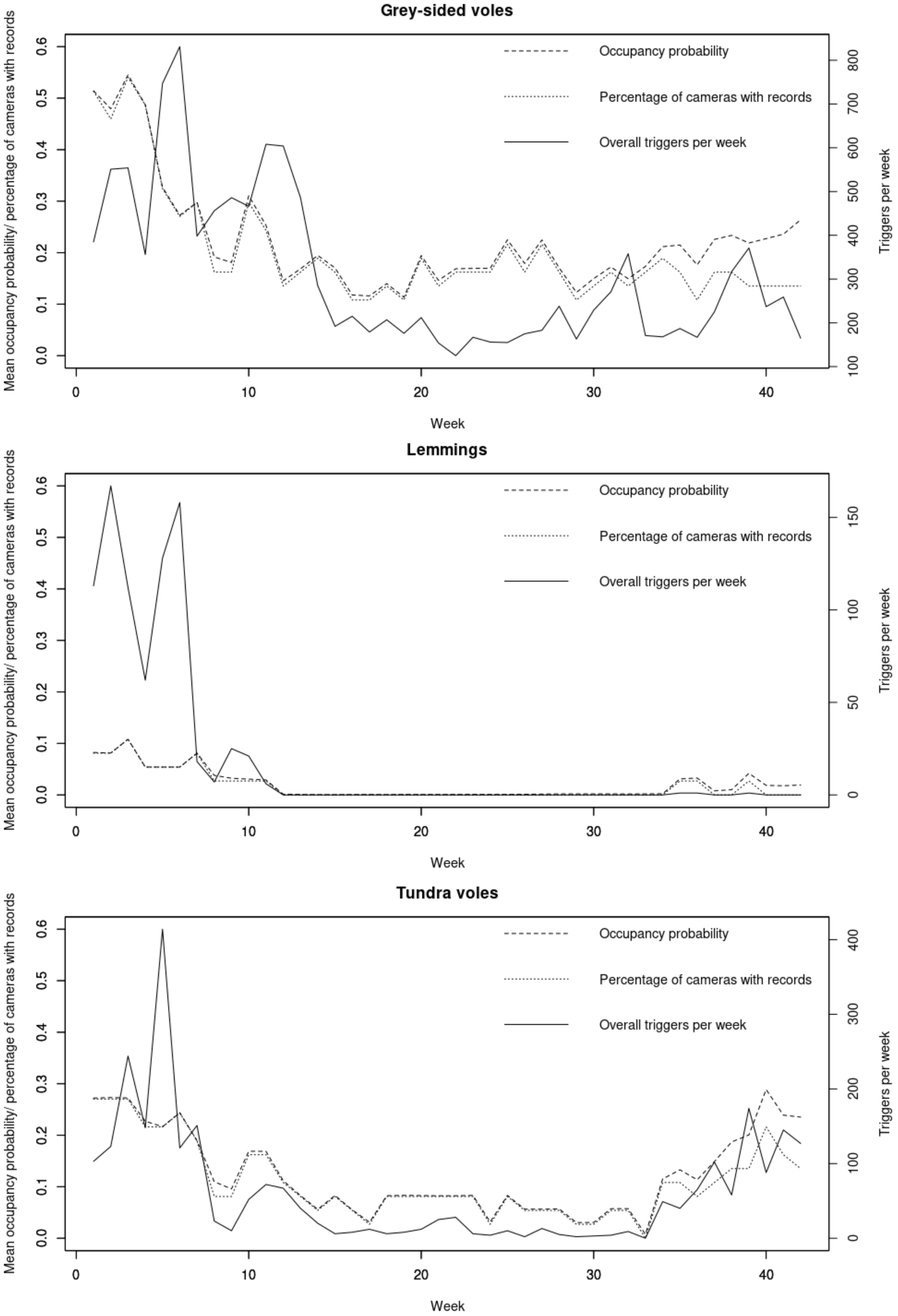

Fig. 13: For each of the three species, mean estimated occupancy per week, percentage of cameras with records and sum of triggers per week is plotted over the study period.

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Declaration

Herewith, I declare that this thesis has been completed independently and unaided and that no other sources other than the ones given here have been used. The submitted written version of this work is the same as the one electronically saved and submitted on CD. The written version is rating relevant. Furthermore, I declare that this work has never been submitted at any other time and anywhere else as a final thesis.

22.04.2020,