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ARTICLE

Using subnivean camera traps to study Arctic small mammal community dynamics during winter

Jonas P. Mölle, Eivind F. Kleiven, Rolf A. Ims, and Eeva M. Soininen

Abstract: Small rodents are a key indicator to understand the effect of rapidly changing winter climate on Arctic tundra ecosystems. However, monitoring rodent populations through the long Arctic winter by means of conventional traps has, until now, been hampered by snow cover and harsh ambient conditions. Here, we conduct the first extensive assessment of the utility of a newly developed camera trap to study the winter dynamics of small mammals in the Low Arctic tundra of northern Norway. Forty functional cameras were motion-triggered 20 172 times between September 2014 and July 2015, mainly by grey-sided voles (*Myodes rufocanus* (Sundevall, 1846)), tundra voles (*Microtus oeconomus* (Pallas, 1776)), Norwegian lemmings (*Lemmus lemmus* (Linnaeus, 1758)) and shrews (*Sorex* spp.). These data proved to be suitable for dynamical modelling of species-specific site occupancy rates. The occupancy rates of all recorded species declined sharply and synchronously at the onset of the winter. This decline happened concurrently with changes in the ambient conditions recorded by time-lapse images of snow and water. Our study demonstrates the potential of subnivean camera traps for elucidating novel aspects of year-round dynamics of Arctic small mammal communities.

Key words: lemmings, voles, occupancy modelling, snow, winter ecology.

Résumé : Les petits rongeurs constituent un indicateur clé pour comprendre l'effet du changement rapide du climat hivernal sur les écosystèmes de la toundra arctique. Cependant, le suivi des populations de rongeurs pendant le long hiver arctique au moyen de pièges conventionnels a jusqu'à présent été entravé par la couverture neigeuse et les conditions ambiantes difficiles. Les auteurs réalisent ici la première évaluation approfondie de l'utilité d'un nouveau piège photographique pour étudier la dynamique hivernale des petits mammifères dans la toundra du bas-arctique au nord de la Norvège. Quarante appareils photo fonctionnels ont été déclenchés par le mouvement 20 172 fois entre septembre 2014 et juillet 2015, principalement par des campagnols de Sundevall (*Myodes rufocanus* (Sundevall, 1846)), des campagnols nordiques (*Microtus oeconomus* (Pallas, 1776)), des lemmings norvégiens (*Lemmus lemmus* (Linnaeus, 1758)) et des musaraignes (*Sorex* spp.). Ces données se sont avérées appropriées pour la modélisation dynamique des taux d'occupation des sites spécifiques aux espèces. Les taux d'occupation de toutes les espèces enregistrées diminuaient abruptement et de façon synchrone au début de l'hiver. Ce déclin se produisait en même temps que les changements des conditions ambiantes enregistrés par les images de neige et d'eau prises à intervalles. Cette étude démontre le potentiel des pièges

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photographiques subnivaux pour élucider de nouveaux aspects de la dynamique des communautés de petits mammifères de l'Arctique tout au long de l'année. [Traduit par la Rédaction]

Mots-clés : lemmings, campagnols, modélisation de l'occupation, neige, écologie hivernale.
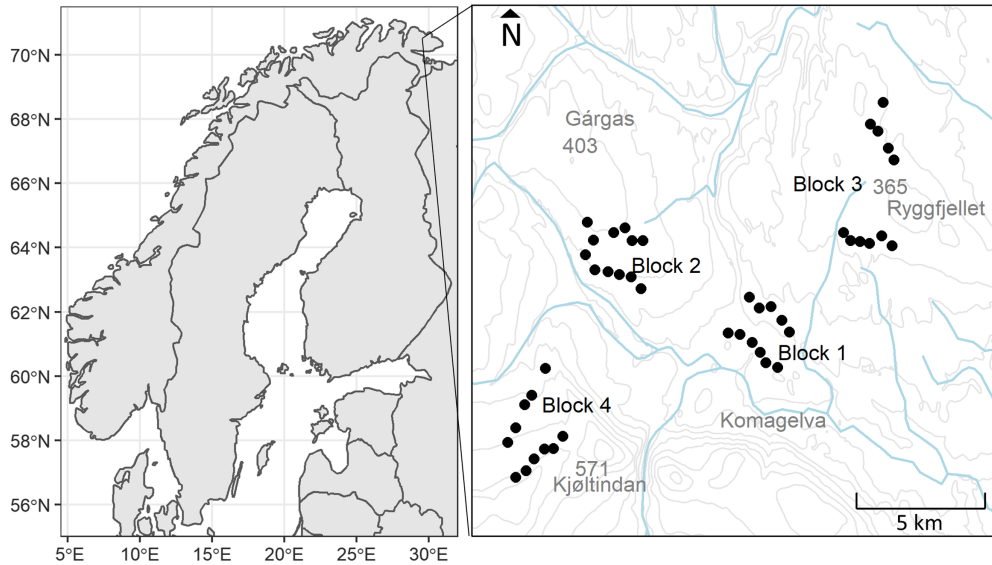
Introduction

The Arctic climate is changing with temperatures rising more than twice as fast as the global average (Davy and Outten 2020). This change in temperature drives profound changes in snow conditions during the long Arctic winter season (AMAP 2017). The changing cryosphere alters the characteristics of the tundra ecosystems, and investigation of the ecological consequences requires more effort (ACIA 2004; Post et al. 2009; Ims et al. 2013a). 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 expected to have a clear link to changes in winter climate (Christensen et al. 2013; Ims et al. 2013b). In many Arctic food webs, lemmings (*Lemmus* and *Dicrostonyx* spp.) and voles (*Myodes* and *Microtus* spp.) have such roles. Their high-amplitude population cycles have repercussions for the entire food web (Ims and Fuglei 2005), and these dynamics appear to change as a result of changes in the duration and physical properties of the snow layer (Kausrud et al. 2008; Gilg et al. 2009; Stien et al. 2012; Berteaux et al. 2017; Domine et al. 2018). Winter warm spells and rain-on-snow events appear to 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. 2017). However, this understanding is mainly based on indirect inferences from data collected during the snow-free period, and no direct assessment of wintertime dynamics of rodent populations within the Arctic has been published.

To understand how the environmental drivers affect the dynamics of cyclic small rodent populations it is essential to acquire high-quality monitoring data (Ims et al. 2008; Korpela et al. 2013). However, it is problematic to observe winter dynamics of Arctic and boreal small rodents as they live under the snow (Krebs 2013; Berteaux et al. 2017). Generally, the strength of the inferences about 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. 2020) that matches the timing of abrupt climatic events (Domine et al. 2018). To fully understand small rodent cycles and keep track of their changing dynamics in Arctic ecosystems, new approaches are needed (Ehrich et al. 2020).

During the last few years, cheaper and more advanced camera technology has led to 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. 2010; Glen et al. 2013; Burton et al. 2015; Soininen et al. 2015). Camera traps require low fieldwork effort while providing a high sampling resolution (Kucera and Barrett 2011; Soininen et al. 2015). Camera traps are already applied in the monitoring of small mammals (Meek et al. 2012; Glen et al. 2013; Rendall et al. 2014; Villette et al. 2016), and a small-scale pilot study from the subarctic forest has presented a below-snow camera trap to study small rodents during winter (Soininen et al. 2015). Indeed, as the winter dynamics of small mammals may be subjected to rapid environmentally driven extinctions of local populations (e.g., Aars and Ims 2002), camera trap occupancy data may be particularly suitable for modelling such extinction–colonization dynamics at the landscape scale. Occupancy models are the established way to analyse

Fig. 1. Map of Fennoscandia (left panel) and zoom on the study area on Varanger Peninsula (right panel) with the 44 camera trap sites (black points) in four spatially segregated blocks arranged in an elevation gradient. Numbers denote the elevation (in metres) of the summits of the highest hills. Grey lines represent elevation contours and blue lines represent rivers. The base map was taken from https://kartkatalog.geonorge.no/metadata/n250-map-data/442cae64-b447-478d-b384-545bc1d9ab48 (Kartverket 2015).

camera trapping data when one cannot detect all individuals that are present (Nichols et al. 2010). Still, such methods for studying winter season dynamics of cyclically fluctuating rodent communities have not yet been published.

Here, we present the first extensive-scale assessment of camera traps as a method for investigating winter season dynamics of an Arctic small mammal community. We investigated how the camera trap developed by Soininen et al. (2015) performed both in terms of technical functionality under the harsh ambient winter conditions in Arctic tundra and in terms of animal detection rates under such conditions. Furthermore, we assessed how information about the particular environmental conditions potentially affecting rodent winter dynamics could be gained from the camera trapping data. Finally, a major aim of the study was also to assess the utility of the camera trap data for state-of-the-art statistical models (Nichols et al. 2010) to estimate species-specific occupancy rates.

Methods

Study area

This study was conducted in a Low Arctic tundra landscape in the inner part of Varanger Peninsula, northeast Norway (70°N, 30°E) (Fig. 1). Hilly plains carved by river valleys shape the study area that is located on an elevation between 165 and 489 m a.s.l. The plains are characterised by dwarf-shrub dominated heaths (*Empetrum nigrum* L., *Vaccinium* spp., *Betula nana* L.), 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.).

Monthly mean temperatures (period 1961–1990) at the nearest weather station (Båtsfjord, at 150 m a.s.l. and ca. 20 km from the nearest camera trap), range from −6.5 °C

Fig. 2. Seasonal and multi-annual dynamics of the three focal rodent species on the Varanger peninsula during the population cycle that encompassed the present camera trap study. Points denote the number of trapped rodents per 100 trap nights in early July and September each year. Solid lines denote changes over the 2-month summer periods (early July–early September), whereas broken lines denote changes over the 10-month periods (early September–early July) encompassing fall, winter, and spring. The light grey bar denotes the focal camera trap study period. The snap-trap data are from three sub-regions on Varanger Peninsula described by Ims et al. (2011). Each trapping period is based on 1176 trap-nights. The data are available from https://data.coat.no/dataset/ v_rodents_snaptrapping_abundance_regional_v1 (COAT 2018).
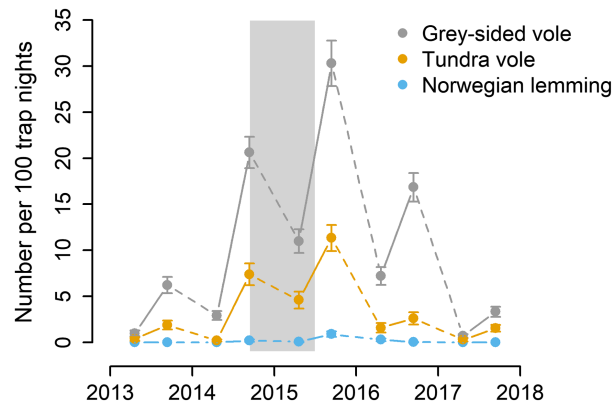
in January to 11.0 °C in July and the annual mean precipitation amount is 545 mm (NMI 2020). The area is normally fully covered by snow at least from October to May (Malnes et al. 2016) with an average depth of 57 cm (Virtanen et al. 1999). However, the snow cover is very heterogeneous, and snow beds can be covered by 4 m of snow and persist until late July (Soininen et al. 2017).

Small mammal community

The study area is inhabited by three species of small rodents: Norwegian lemming (*Lemmus lemmus* (Linnaeus, 1758)), grey-sided vole (*Myodes rufocanus* (Sundevall, 1846)) and tundra vole (*Microtus oeconomus* (Pallas, 1776)). Norwegian lemmings spend the summer in habitats with moist hummock tundra or mires and move to snow beds on 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 four year cycle on Varanger peninsula (Ims et al. 2011; Kleiven et al. 2018; Soininen et al. 2018). The population cycle of the Norwegian lemming has an amplitude that is typically more variable than the vole cycles and sometimes the peaks of this species are missing in time series derived from snap trap monitoring (Ims et al. 2011).

The present study covers a 9.5-month period from mid-September 2014 to early July 2015. As is evident from large-scale and long-term monitoring of the small rodent community on the Varanger Peninsula based on snap-trapping (Kleiven et al. 2018), our study period encompassed the winter season preceding the peak phase summer of the rodent cycle (Fig. 2). According to the snap-trapping data, the grey-sided vole was clearly the numerically dominant species during our study period, whereas the Norwegian lemming was almost absent (Fig. 2).

Other small mammals in the study area that so far have not been systematically monitored are insectivorous shrews (the common shrew, *Sorex araneus* Linnaeus, 1758, masked shrew, *Sorex caecutiens* Laxmann, 1788, and pygmy shrew, *Sorex minutus* Linnaeus, 1766) and

Fig. 3. Typical camera trap placements in different habitats and relations to micro-topographic features. Mesic hummock tundra with paths and grazing signs of rodents (left panel). Snow bed in early July (centre panel). Hummock tundra where the camera was damaged by flooding during the spring thaw (right panel).

carnivorous small mustelids (ermine, *Mustela erminea* Linnaeus, 1758, and least weasel, *Mustela nivalis* Linnaeus, 1766).

Study design

The camera trap is described by Soininen et al. (2015). We replaced the wooden camera box, presented by Soininen et al. (2015), with an aluminium box to improve durability. We programmed the cameras (Reconyx SM 750 Hyperfire; Reconyx Inc., Holmen, Wisconsin, USA) to take two images for each motion-triggered event and to have a 1-min quiet period (i.e., delay) after each event to avoid an excessive number of photos. To verify whether the camera was functional and to monitor the ambient environmental conditions inside the camera trap, we programmed two additional time-lapse images per day (at 1:00 AM and PM). The cameras had a thermometer, and the temperature was recorded every time an image was taken.

During 15–17 September in 2014, 44 camera traps were set up to cover lemming habitats at different elevations in the study area. They were placed in four separate blocks ($n = 11$ trap sites in each block) (Fig. 1). Two of the blocks consisted primarily of snow bed sites (Fig. 1, blocks 3 and 4), whereas the two other blocks had heath, mesic hummock tundra, and mire sites (Fig. 1, blocks 1 and 2). Within each block, the traps were placed in two lines with 5–6 traps. The minimum distance between traps was 300 m to avoid the same rodent individual including more than one camera trap within its home range (Ims 1987; Andreassen et al. 1998) and, thus, to ensure that occupancy rates would be independent between the traps.

Criteria for the choice of location of traps 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).

Memory cards from all cameras were collected during 1–6 July in 2015 so that the entire study period covered approximately 290 days. Malfunctioning of cameras due to flooding and water damage or for other reasons was recorded.

Data analysis
Image data

Cameras with technical failure from the onset of the study were excluded from the analysis ($n = 4$). Images of all other cameras were classified using Reconyx MapView professional software (Reconyx Inc., Holmen, Wisconsin, USA). When a malfunctioning camera flash or snow/ice on the lens caused bad quality images and impeded their inspection, these images were excluded from the data set.

For the movement-sensor triggered images, we noted whether an image contained lemmings, tundra voles, and grey-sided voles, or "unknown vole" if the two vole species could not be distinguished. Mustelids and shrews were also recorded, but the latter without being able to distinguish the different species.

Based on the two time-lapse images per day, we recorded a daily score for the presence of snow and water (see Appendix A, Fig. 1A).

Snow was scored as:

(0) No snow present in the entrances of the camera traps,
(1) shallow snow present, but not sufficient to cover the trap entrances and, thus, not a closed snow layer that can harbour a rodent tunnel system,
(2) a closed snow layer that was higher than both of the 7 cm high entrances of the traps, or
(3) a lot of snow inside the trap to the extent that it potentially prevented the detection of animals tunnelling their way through the trap.

Water was scored as:

(0) No visible humidity inside the trap,
(1) big drops of water or generally wet surface of the floor of the trap,
(2) light flooding with water up to half the height of the trap entrances, or
(3) severe flooding with a water level more than half as high as the trap entrances or higher so that terrestrial animals were not able to enter the traps.

The scores with the value of 3 for both snow and water obstructed the observation of animals. To be able to include camera traps with such scores in the occupancy model, these covariate values were treated in the analysis as NAs.

In addition to images, the camera traps provide a temperature record for each image. Temperature recordings from time-lapse images provide site-level data that can be useful to estimate the length of the snow-covered season, or indicate insulating properties of the snow pack. However, as we recorded explicit data for snow and water within the camera boxes, we here provide temperature data only to illustrate its possible uses.

Occupancy modelling

Occupancy models determine the probability of a species presence, taking into account that some individuals may remain unobserved. This framework allows both occupancy probability and detection probability to be estimated as a function of covariates (MacKenzie et al. 2003). Here we used a dynamic (i.e., estimating changes over time) occupancy model over repeated sampling occasions to estimate occupancy of the three rodent species and shrews collectively over the entire study period (MacKenzie et al. 2003). Mustelids occurred too infrequently to be included. As our main interest here was to investigate the functionality of the camera traps, we modelled detection probability as a function of environmental covariates, and occupancy probability without covariates.

We defined primary sampling occasions as five-day units (59 primary sampling occasions in the study period). Five days was chosen to be in line with the recommended sample sizes

of MacKenzie and Royle (2005) and so that this period would be short enough for the local population at a given trap site not to change considerably. The occupancy rates were estimated for these time units. Within the primary occasions (i.e., the five-day units), the presence or absence of the different species was recorded each day (secondary occasion). As the camera traps recorded relatively few numbers of lemmings, the records of all three rodent species and shrews were combined to model a single stronger data set. To be able to obtain species-specific parameter estimates (White et al. 2013), the model was extended by a "species dimension". The presence-absence observations (y) at site i in primary occasion (five-day unit) t and secondary occasion (day) j for species s, can be described with a Bernoulli distribution:

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

where $z_{i,t,s}$ denotes the true state of occurrence and $p_{i,t,s}$ the detection probability.

Detection probability (p): Through a logit link function, species-specific detection probabilities were modelled as a function of two categorical environmental covariates snow and water. The equation for detection probability was thus

(2)	$\text{logit}(p_{i,t,s}) = pb1_{\text{snow}_{i,t,s}} + pb2_{\text{water}_{i,t,s}}$

where $pb1$ and $pb2$ are the coefficients that describe the effect of the environmental covariates. As the three-level categorical covariates snow and water (see section "Image data") in eq. (2) are specified at the temporal resolution of primary occasions t (five-day periods), although they were recorded from time-lapse photos each day (i.e., at secondary occasions j), the scores for the covariates were set to the highest recorded value (0–2) per trap and secondary occasion. Records of NAs for the covariates at any given site (e.g., scores of 3) were replaced with the median of the scores of the other sites within a block.

Occupancy probability (Ψ): The initial occupancy probability (Ψ_1 = occupancy probability of small rodents in the first primary occasion) was modelled as

(3)	$\text{logit}(\Psi_{i,t=1,s}) = a_s$

where a_s is a species-specific intercept. The development of the occupancy changes over time (Ψ_{t+1}, here z) was modelled as a function of site colonization (γ) and extinction (ε) events:

(4)	$z_{i,t,s} \sim \text{Bernoulli}(z_{i,t-1,s} \times (1 - \varepsilon_s) + (1 - z_{i,t-1,s}) \times \gamma_s)$

Extinction (ε) and colonization (γ) probability: Both were modelled similar to Ψ_1 with a logit link:

(5)	$\text{logit}(\gamma_s) = gb_s$

and

(6)	$\text{logit}(\varepsilon_s) = eb_s$

The model of the four parameters (p, Ψ, γ, and ε) 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 160 000 iterations were run and the first 10 000 iterations were discarded as burn-in and 40 000 was used as adaptations. The model was checked and indicated chain convergence as all $\hat{R}$ values were <1.1 (Gelman et al. 2013) and trace plots showed that the

chains were mixed well. We ascertained that the model was fit for the data set by performing a posterior predictive check (Kéry 2010). All occupancy estimates are provided with 95% credible intervals based on their posterior distributions.

Results

Camera trap functionality and ambient conditions

Of the 40 cameras that were technically functional from the onset of the study, four ceased to function in autumn and a further 12 had water-induced hardware damage associated with flooding during the spring thaw period in May–June (Fig. 4). Thirteen traps were infiltrated by snow and five traps were flooded by water to the extent that it prohibited detection of animals (snow and water category 3) for shorter or longer periods during the winter and spring (Fig. 4).

The first snow was recorded in late September (Fig. 4). However, this shallow snow cover (snow 1) melted soon and caused some water (water 1) in most traps. A closed snow cover (snow 2) established quite simultaneously across the sites/blocks in mid-October. In the turn of October–November, snow 2 transitioned to snow 0/1, associated with the presence of water in some of the traps (Fig. 4). A permanently closed snow cover (snow 2) was present from early November until the spring thaw period when a lot of water (water 2 and 3) was prevalent in many of the traps (Fig. 4).

In total, the cameras recorded 60 547 images of which 40 346 were motion-triggered. The number of motion-triggered images per camera across the whole study period (290 days) ranged from 14 to 4726 with a mean of 506. Of the motion-triggered images, 10.4% did not show a presence of animals in the trap despite good-quality images. Moreover, 4.2% of the motion-triggered images were of such bad quality because of malfunctioning cameras, or ice or dew on the lens, that animals would not be visible even if they were present (Appendix A, Table A1). When rodents were recorded, the species could be identified in almost all cases, i.e., only 0.3% were classified as unknown voles (Appendix A, Table A1) that were discarded from the analysis.

The grey-sided vole was recorded most frequently (64.5% of the trigger images; Appendix A, Table A1) with the largest and most even spatial distribution across sites and blocks (Fig. 4). Tundra voles were the next-most frequent species and with most of the records aggregated on two of the blocks. The Norwegian lemming had the most restricted distribution of the rodents, whereas shrews appeared more scattered in time and space than the rodents (Fig. 4). Least weasels and ermines were recorded on three and two sites, respectively (Appendix A, Table A1).

Occupancy modelling

The estimated occupancy probabilities (Ψ) of all small mammal species decreased during October–November contemporary with the abrupt shift in ambient conditions in terms of a drop in temperature and the emergence of a closed snow cover (Fig. 5; see Appendix A, Table A2 for estimates of other parameters). Thereafter, the occupancy probabilities of the most prevalent species — the grey-sided vole — became remarkably stable for the rest of the winter and spring. Tundra vole occupancy continued to have a declining trend until the spring thaw when occupancy rates increased. The lemming exhibited a long period of complete absence after the decline in the early winter. Shrews had quite low occupancy rates with more short-term variability than the rodents.

The estimated detection probability ($p_{i.t.s}$) ranged between 0.065 and 0.909 depending on the species and ambient conditions (Fig. 6). Shrews had mostly lower detection probabilities than the rodents. The detection probabilities for the lemming were more affected by the ambient conditions than for the two vole species, with a peak associated with the

Fig. 4. Records of ambient conditions (snow and ice) and the presence of small mammals at 40 camera trap sites during the 9.5 month study period from mid-September 2014 to early July 2015. Each cell represents a five day sampling period per site. The sites (i.e., the rows) are grouped according to the four blocks shown in Fig. 1. For the snow and water panels, the white squares indicate occasions where the cameras were malfunctioning, i.e., not recording information of ambient conditions. For the animal species panels, the white squares also include images of bad quality and record snow 3 and water 3.
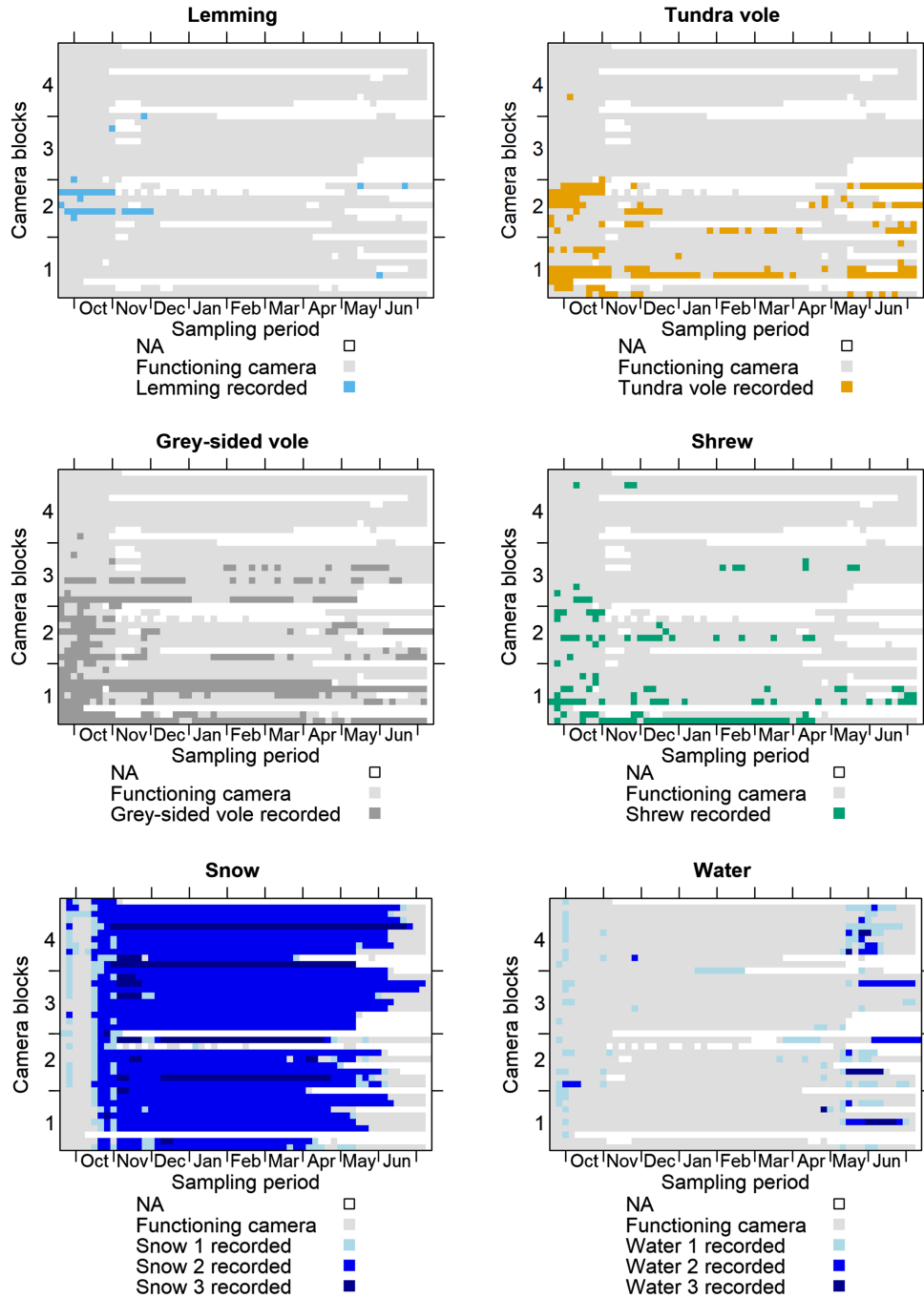
Fig. 5. Small mammal occupancy dynamics and ambient conditions per five-day units during the 9.5 month study period. Occupancy rates are the means of the posterior distribution of Ψ averaged over sites with functional camera traps. Water and snow are the proportion of functional camera traps (sites) with records of the three snow and water categories. Temperatures are highest recorded daily air temperature per five-day unit from the nearest weather station (Båtsfjord) and recorded by the camera traps (averaged over all functional traps).
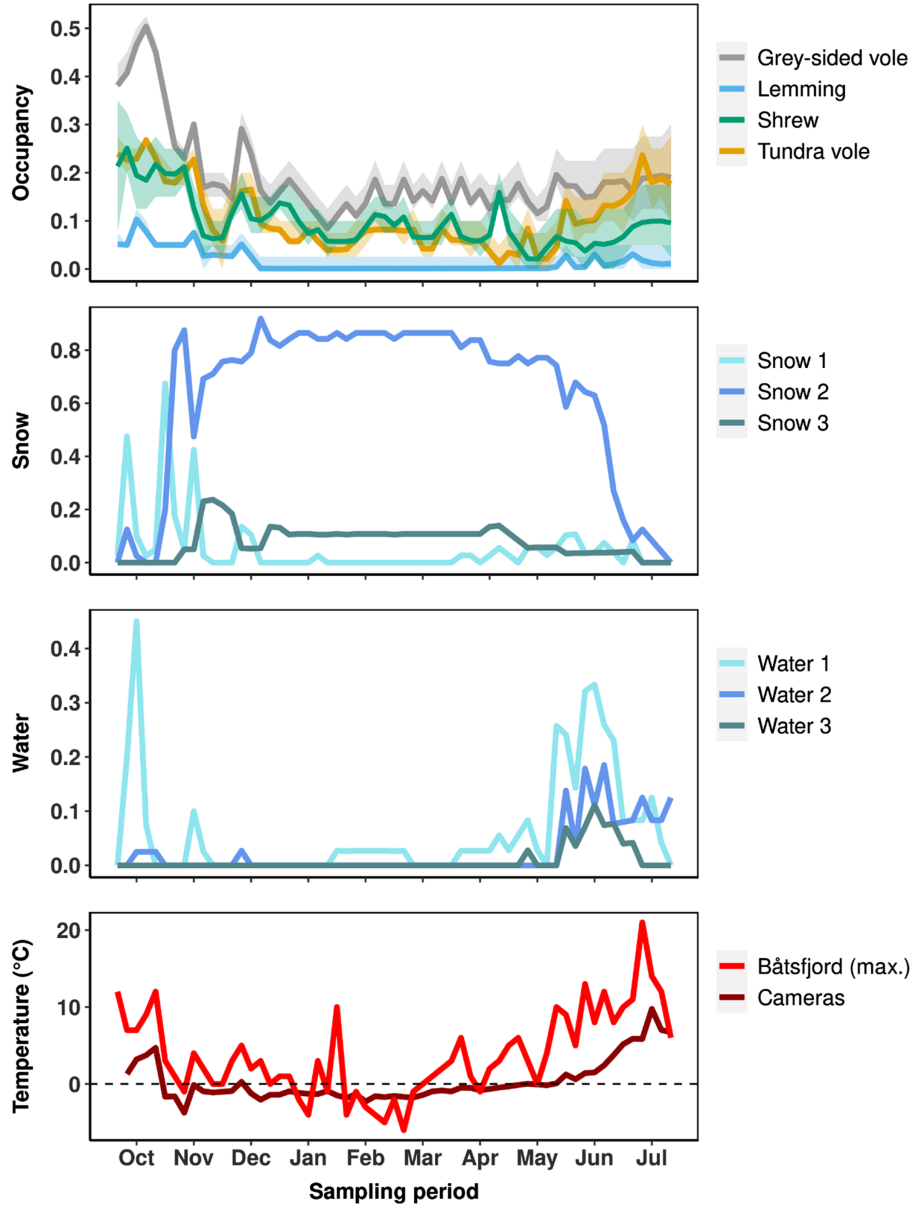
appearance of shallow snow (snow 1) at the onset of the winter, and a sharp drop with the presence of water (water 1 and 2) in the traps. Of note, the development of a closed snow-pack (snow 2) as compared with snow-free tundra (snow 0) only appeared to have a negative effect on the detection probability of the tundra vole (Fig. 6).

Fig. 6. Small mammal detection probabilities for the recorded categories of snow and water (see text for a description of the categories). The violin and box plots show estimated posterior distributions obtained from the dynamic occupancy model. The estimates for the three snow categories were obtained for water 0, whereas the estimates for three water categories were obtained for snow 0.
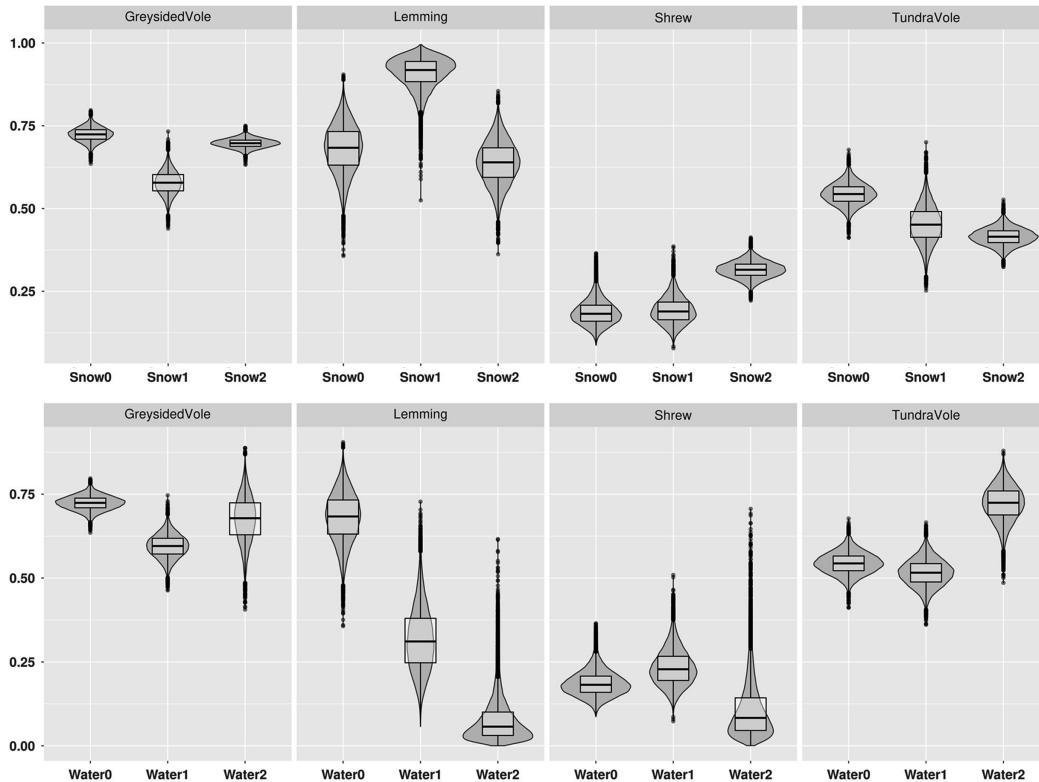
Discussion

We performed the first assessment of the applicability of camera traps for providing data on small mammal community dynamics during the Arctic winter. Whenever functional, the camera traps developed by Soininen et al. (2015) yielded data suitable for dynamical occupancy modelling with generally high detection probabilities — especially for the three rodent species that were present in our study area. The detection/non-detection data acquired from camera traps do not provide the kind of abundance estimates/indices that have been the standard way to study Arctic rodent population dynamics (Krebs 2013; Ehrich et al. 2020). However, at a landscape scale cyclically fluctuating rodents can be considered as metapopulations that are driven by local-scale extinction and colonization events (Glorvigen et al. 2013). The year-round data collection enabled by camera traps thus provides a means for assessing the link between such metapopulation events and potentially influential ambient events such as snowfalls, snowmelt, and flooding. Our camera traps provide daily site-specific data on such ambient events that can be used as covariates in occupancy models. This allows both to correct for their influence on the detection rates as done in the present study, and to estimate their impact on metapopulation processes (e.g., colonization and extinction rates) in future multi-annual studies. Ultimately, this approach will yield improved knowledge about how Arctic climate change

impacts Arctic rodent community dynamics. Our results on snow and water indicate that such ambient conditions need to be modelled as species-specific parameters.

This study revealed some important challenges due to the severe ambient conditions in Arctic tundra during winter and spring that resulted in reduced camera trap functionality. Drifting snow caused some cameras to be clogged with snow to the extent that it hindered data capture for shorter or longer periods through the winter. An action that can reduce snow infiltration through the trap entrances, is to erect piles of stones around the camera traps (Appendix A, Fig. A2) functioning as snow fences, but still leaving gaps for passages of small mammals. In tundra areas without access to stones, the camera traps can be differently designed, for instance, with entrances formed as angled tubes that will likely prevent snow from clogging the main compartment of the trap.

Flooding due to melting snow, particularly during the spring thaw, permanently damaged a proportion of the cameras. This problem can be counteracted by avoiding placing the camera traps in topographic features such as small-scale depressions, where water is likely to accumulate. Waterproof cameras will prevent damage to hardware, but water-logged traps will still hinder passages of terrestrial small mammals and cause loss of data — so sites that are vulnerable to such events should be avoided.

We experienced only minor problems with frost or dew on the camera lenses contrary to what has been reported from a High Arctic study site with very cold permafrost and profound vertical temperature gradients in the snow packs (Kalhor et al. 2019). The Varanger Peninsula has only sporadic warm permafrost (Farbrot et al. 2013) and we recorded subnivean temperatures that were only slightly below zero (Fig. 4). Hence, the camera traps used in the present study should be tested under a wider range of ambient conditions to verify their general functionality.

It is still uncertain whether data from camera traps will be able to yield the same numerical aspects of population arithmetic as conventional trapping data (removal sampling and capture–recapture). It is, however, promising to notice that the abundance relations between rodent species and the observed overwinter decrease obtained by camera trapping (Fig. 5) and snap-trapping (Fig. 2) show similar patterns. Furthermore, the occupancy estimates showed the characteristic drop at the onset of the winter previously found by mark–recapture trapping of boreal rodent populations (e.g., Merritt and Merritt 1978; Johnsen et al. 2018), indicating that occupancy estimation is able to show the main features of seasonal and multi-annual dynamics of cyclic rodent populations. However, we encourage future studies to assess how occupancy estimates compare with more conventional metrics of Arctic small mammal population dynamics — such as estimates or indices of population density and growth rate.

To conclude, we find that camera traps can be used to monitor small mammal community dynamics during the Arctic winter. In addition, the camera traps also collect environmental data that can be used to estimate climate-driven colonization and extinction events in Arctic small mammal communities. As the camera traps also provide simultaneous data on presence/absence of mustelids, future more long-term studies that cover all phases of the multi-annual cycle can provide new insights about how the dynamics of mustelids (predator) and rodents (prey) are linked. It is also noteworthy that our relatively modest sample of camera traps was able to capture the seasonal dynamics of the Norwegian lemming, a key species in the focal ecosystem (Ims et al. 2017), given that the lemmings were almost absent in the extensive sample of snap-trapped rodents. Hence, we conclude that subnivean camera traps bear great promise in terms of elucidating novel aspects of the community dynamics of Arctic small mammals and how these communities respond to climate change.

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Author contributions

Conceptualization R.A.I., E.M.S., E.F.K.; Data curation J.P.M., E.M.S.; Formal analysis J.P.M., E.F.K.; Funding acquisition R.A.I., E.M.S.; Investigation J.P.M., E.F.K., R.A.I., E.M.S.; Methodology J.P.M., E.F.K., R.A.I., E.M.S.; Project administration J.P.M., Visualization J.P.M., E.M.S., Writing — original draft J.P.M., Writing — review and editing J.P.M., E.F.K., E.M.S. and R.A.I.

Data availability

The data are available through the COAT data portal (https://data.coat.no/dataset/v_rodents_cameratraps_pilot_v1, doi: 10.48425/0077746).

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Appendix A

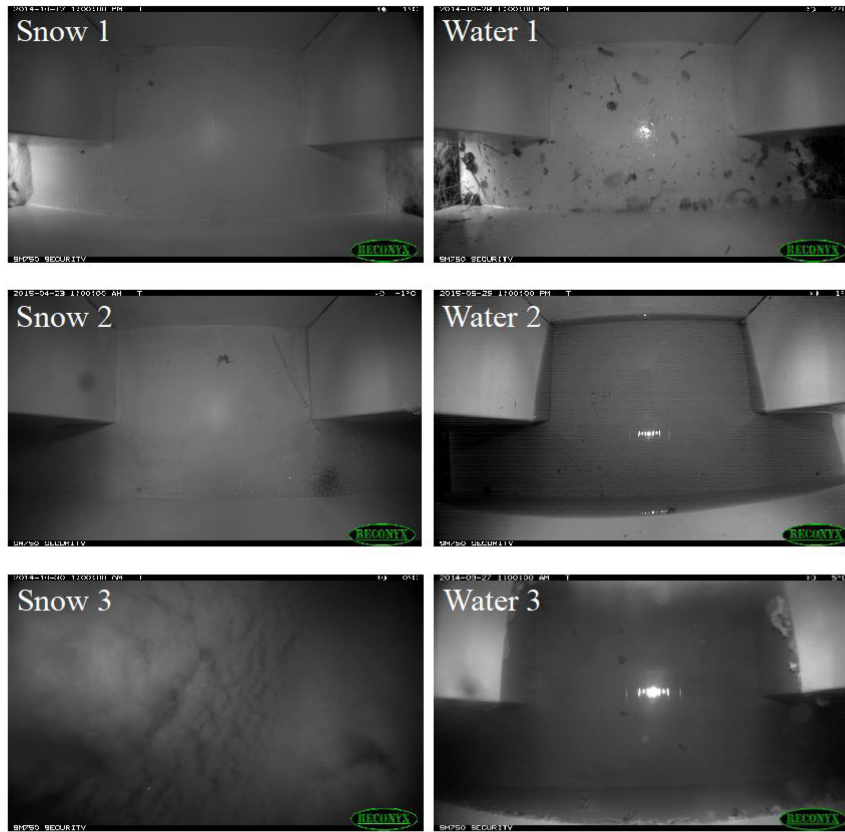**Fig. A1.** Example images of recorded classes of snow and water described in the main text.

Fig. A2. Example of a camera trap embedded in a stone pile made to prevent infiltration of drifting snow that may clog the trap as shown in Fig. A1, Snow 3.

Table A1. Summary statistics of observations of presence of different image categories.

Observation	No. camera traps	No. five-day units	No. days	No. triggers
Lemming	10	31	92	830
Grey-sided vole	26	398	1336	13 019
Tundra vole	19	203	526	2596
Unknown vole	8	15	25	48
Shrews	23	148	278	716
Ermine	2	2	2	2
Least Weasel	3	7	10	15
Bad quality	14	96	172	845
Total	40	636	3238	20 172

Note: Row "total" refers to the number of sampling units that were available for observations, i.e., sum of active camera traps included in the study, total number of five-day units, camera trap and days, and the total number of movement trigger releases.

Table A2. Parameters estimates of colonization probability (γ), extinction probability (ε) and initial season occupancy (ψ) given as the means of the posterior distribution and 95% credible intervals (CI).

Parameter	Species	Posterior mean	95% CI
γ	Lemming	0.005	0.002–0.009
ε	Lemming	0.335	0.180–0.512
ψ	Lemming	0.058	0.010–0.146
γ	Grey-sided vole	0.042	0.032–0.052
ε	Grey-sided vole	0.192	0.154–0.234
ψ	Grey-sided vole	0.383	0.240–0.533
γ	Tundra vole	0.025	0.018–0.033
ε	Tundra vole	0.217	0.156–0.283
ψ	Tundra vole	0.241	0.121–0.386
γ	Shrew	0.026	0.018–0.036
ε	Shrew	0.263	0.185–0.346
ψ	Shrew	0.215	0.046–0.420