Remote Sensing in Ecology and Conservation
Open Access

ORIGINAL RESEARCH

# Under the snow: a new camera trap opens the white box of subnivean ecology

Eeva M. Soininen, Ingrid Jensvoll, Siw T. Killengreen & Rolf A. Ims

Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Naturfagbygget Dramsveien 201, 9037 Tromsø, Norway

**Keywords**
Activity patterns, camera trap, mustelid, population dynamics, rodent, small mammal monitoring, snow cover, snowpack

**Correspondence**
Eeva M. Soininen, Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Naturfagbygget Dramsveien 201, 9037 Tromsø, Norway. Tel: +47 776 46393; Fax: +47 776 46333;
E-mail: eeva.soininen@uit.no

**Funding Information**
This study was financed by the Fram Centre though the Climate-Ecological Observatory for Arctic Tundra.

Editor: Rob Williams
Associate Editor: Natalie Kelly

Received: 13 January 2015; Revised: 31 March 2015; Accepted: 10 April 2015

doi: 10.1002/rse2.2

## Abstract

Snow covers the ground over large parts of the world for a substantial portion of the year. Yet very few methods are available to quantify biotic variables below the snow, with most studies of subnivean ecological processes relying on comparisons of data before and after the snow cover season. We developed a camera trap prototype to quantify subnivean small mammal activity. The trap consists of a camera that is attached facing downward from the ceiling of a box, which is designed to function as a snow-free tunnel. We tested it by placing nine traps with passive infrared sensors in a subarctic habitat where snow cover lasted for about 6 months. The traps were functional for the whole winter, permitting continuous data collection of site-specific presence and temporal activity patterns of all three small mammal species present (the insectivorous common shrew, *Sorex araneus*, the herbivorous tundra vole, *Microtus oeconomus*, and the carnivorous stoat, *Mustela erminea*) as well as abiotic conditions (presence/absence of snow cover and subnivean temperature). Based on their successful functioning (only 6% of the photographs appeared empty or were of poor quality, whereas ca 80% were of small mammals and the remaining of birds and invertebrates), we discuss how the new camera trap can enable subnivean studies of small mammal communities. This greatly increases the temporal resolution and extent of data collection and thereby provides unprecedented opportunities to understand population and food web dynamics in ecosystems with snow cover.

## Introduction

Annually, snow covers up to 40 million square kilometers of the northern hemisphere (Brown and Robinson 2011), often for more than half of the year. Snow conditions play a major role for various ecological processes, of which many are subnivean – that is taking place on the ground under the snowpack (Stenseth et al. 2004; Nobrega and Grogan 2007; Kausrud et al. 2008; Hansen et al. 2011; Olofsson et al. 2011). However, research of subnivean ecology is by no means easy, as quantifying biotic variables below the snow mostly requires repeated disturbance of the snowpack and results in a significant change in conditions (Bilodeau et al. 2013c). The vast majority of studies that consider ecological winter-time processes therefore use data on biotic variables collected before and after the snow cover season to infer what has happened during the snow cover period (Olofsson et al. 2011; Bilodeau et al. 2013a; Korpela et al. 2013; Ravolainen et al. 2014). Since many ecological variables are likely to change during winter quantifying them as the difference between autumn and spring could lead to a major loss of temporal resolution.

Winters up to 9 months long with several meters deep snowpacks present the single most important barrier for understanding northern small rodent population fluctuations (Krebs 2011, 2013). Small rodents are one of the most important study systems for the development of population ecology theory and models (Berryman 2002; Turchin 2003; Krebs 2013) and, moreover, are key-stone species in northern terrestrial food webs (Ims and Fuglei 2005; Krebs 2011; Legagneux et al. 2014). Small rodent population cycles are both suggested to be caused by processes happening during winter (i.e. predation by mustelid rodent specialists (Hanski et al. 1991; Gilg et al. 2003; Hansson and Henttonen 1985) and to be disrupted by snow conditions (Hansson 1999; Ims et al. 2008; Kausrud et al. 2008; Stien et al. 2012). However, "the consequent lack of information can result in some impossible demographic statements about, for example, how much population growth can occur over winter, or how much population decline over winter may be caused by predators" (Krebs 2013).

Indeed, very few studies have attempted to quantify small rodents below the snow (Schweiger and Boutin 1995; Yoccoz et al. 2001; Korslund and Steen 2006). Furthermore, not all attempts have been successful (Bilodeau et al. 2013c). Given that unsuccessful studies rarely get published, we suspect that the real number of such attempts is higher than the number of publications. Additionally, below-snow trapping is extremely work intensive and therefore mostly restricted to few events at spatially small scales. Finally, manipulation or disturbance of the snowpack is an inherent problem of trapping rodents through snow.

The challenges presented by the snowpack can, however, partly be overcome by employment of automatic measurement methods. In spite of being developed primarily for detection of large mammals, the tradition of small mammal camera traps is long (Pearson 1959) and novel camera trapping methods are increasingly being used to census small mammals as well (Meek et al. 2012; Glen et al. 2013; Rendall et al. 2014). Camera traps have the potential to enable continuous subnivean observations throughout the winter without destruction of the snow cover. However, we are not aware of any previous attempts to apply camera traps below the snow. We therefore developed a prototype of a small mammal camera trap for below-snow conditions and tested it during a sub-arctic winter for 9 months, covering a 6 month snow cover period. Specifically, our aims were to (a) document how the technical aspects of the below-snow camera trap functioned, (b) suggest how eventual remaining difficulties could be solved and (c) exemplify how such camera trap data could be used to study small mammal predator–prey interactions and mammal–snow interactions.

## Materials and Methods

### Design of the camera trap

We used Reconyx™ SM750 HyperFire™ License Plate Capture Cameras (Reconyx Inc., Holmen, WI, USA) as a starting point for the camera development, as this model had the fastest trigger speed among Reconyx cameras. Standard features of this camera model are a No-Glow™ High Output Covert Infrared illuminator (Reconyx Inc.), which enables infrared images to be taken in the dark and a trigger speed (i.e. the length of time from an animal entering the detection zone to when an image is taken) of 1/10 sec, allowing three images to be taken per 1 sec (information provided by the manufacturer). The camera case is weatherproof and for each image taken the camera also logs temperature. The cameras were custom-modified by Reconyx by changing the sensor to a faster one (High sensitivity passive infrared sensor, hereafter PIR) and the camera lens to a wide-angle lens with focal distance of 15 cm. The cameras were also modified to be able to attach an external battery. As yet, the final product has no specific model name, but was called by Reconyx "High speed camera for mice".

In order to have attachment for the camera under snowpack and to provide a subnivean tunnel in which photographs could be taken at a standardized focal distance, the cameras were attached inside a plywood box. They were vertically aligned (i.e. facing downward) under the ceiling of boxes, which were open on both ends (Fig. 1). The boxes were 23 cm high, 17 cm wide and 50 cm long, with a removable lid. Based on our measurements, the width of the detection zone at the bottom of the camera trap was 5 cm. The field of view covered the whole bottom of the box (Figs. 1 and 2). To direct small mammals under the sensor, we inserted two blocks at the entrance of the boxes (Fig. 1), narrowing the entrance down to 7 cm. The entrance width was chosen as a trade-off between the narrow detection zone and the range of animals that could enter the trap, with only extremely small animals (<1 cm wide) entering the trap undetected. The detection zone was not uniformly wide on both sides of the detector and to maximize the width of the detection zone we aligned the camera case with the non-blocked edge of the box (Fig. 1). We painted the inside of the bottom of the trap box with white, flat paint to avoid reflection of light. To prevent snow from entering the boxes, we installed two plates at the ends so that only $7 \times 6.5$ cm opening remained (Fig. 1). No lure is used with the traps because, (i) based on our previous experience we expected that small mammals would readily enter tunnels/cavities making baiting unnecessary, and (ii) the lure could not be renewed during the snow cover season.

### Field study

We tested the camera traps during winter 2013–2014 on the island of Håkøya, in Troms, Northern Norway (N 69.67° E 18.83°). The site is in a birch forest close to sea level where the field layer vegetation consists of various tall grasses and forbs. During the last 10 years, average snow-season length has been 7 months (data for Tromsø weather station, available from www.eklima.no).

 

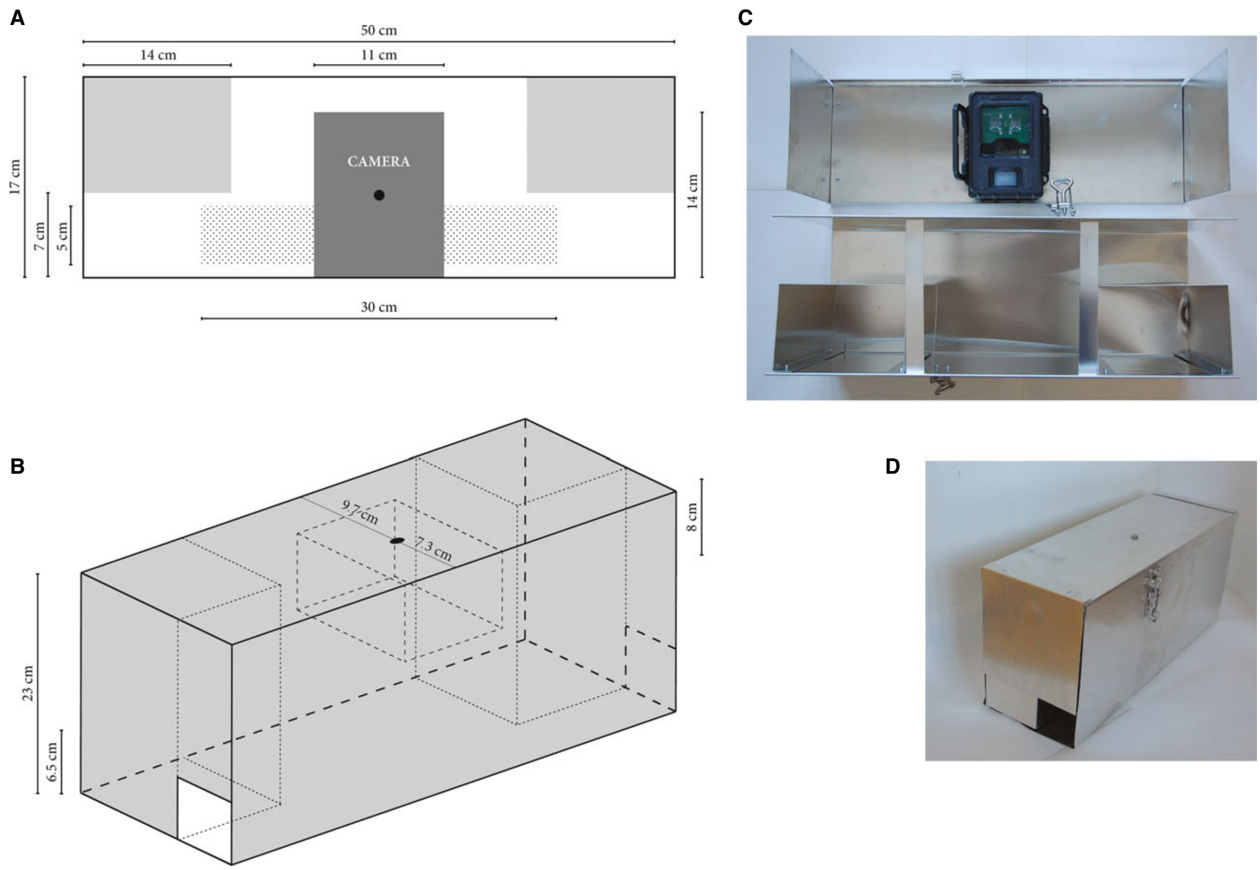


**Figure 1.** The subnvean camera trap box. Parts A and B give the internal measures of the box. On the left side are measures of the box, on the right side measures of the camera. Black circle denotes the attachment location of the camera. Parts C and D portray the aluminum version of the camera trap box. (A) The trap box from above. Pale gray rectangles indicate blocks inserted in the box in order to direct animals below the movement sensor. Patterned rectangle below the camera shows the extent of the detection field of the camera trap. (B) The trap box from outside. Middle point of the camera attachment screw is indicated. (C) The trap box photographed from opened. Above; lid of the box with camera attached. Note that plates that block snow from entering the box are attached on the lid. Below; bottom part of the box. Note that (i) the blocks guiding animals below the PIR sensor are hollow, allowing storage of external battery, (ii) the box structure is supported by two aluminum straps crossing the box. (D) The trap box photographed from outside.

The small mammal community residing under the snow in winter is composed of three species; the herbivorous tundra vole (*Microtus oeconomus*), the insectivorous common shrew (*Sorex araneus*) and the carnivorous stoat (*Mustela erminea*).

We set out nine camera traps on 23 August 2013, spatially overlapping a live-trapping transect (45 traps) for small rodents along an edge of a birch forest and a shore meadow. All camera traps were placed in a line close to the shore (5–30 m), *c.* 20–80 m from the closest neighboring camera trap and along obvious runways of rodents. Adjustable features of the cameras and the settings we used are given in Table 1. In order to maximize the time the camera traps would be functional without visits, we equipped all traps with 12 Lithium batteries and a 32 GB memory card. We checked the batteries and memory cards in all traps on 11 September 2013. The first snowfall occurred in mid-October (Fig. 3B), after which the traps gradually became covered with snow. On 2 December 2013, four of the traps were dug out of the snow and the batteries and memory cards were checked. Even though the batteries indicated they were 99% full, we equipped these cameras with an additional external battery. We recorded the trap snow cover status (below snow/at least partly exposed) on 23 February 2014. After snowmelt, all traps were collected (28 May 2014). Live-trapping was conducted in the area twice; 29 September to 1 October 2013 and 28 to 30 May 2014 (R. A. Ims, unpubl. data).

## Data analysis

We used the program MapView™ (Reconyx) to quantify images. For the first images of the three images taken per a trigger event, we noted the number and species of small

 

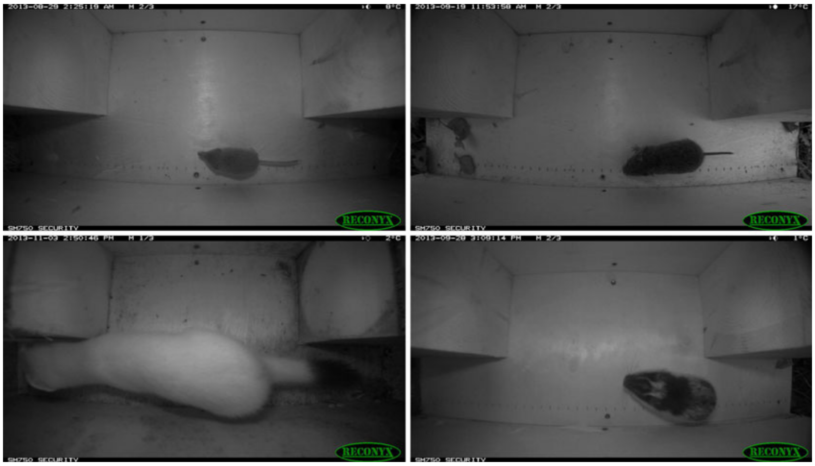

**Figure 2.** Examples of small mammal images taken by the subnivean camera trap. From top left to bottom right; common shrew (*Sorex araneus*), tundra vole (*Microtus oeconomus*), Norwegian lemming (*Lemmus lemmus*), stoat (*Mustela erminea*).

**Table 1.** Adjustable features of the Reconyx™ SM750 HyperFire license plate capture cameras and the settings used in this study.

| Feature | Specification | Options | Set to |
|---|---|---|---|
| Trigger | PIR sensor | On/off | On |
| | Sensitivity | From low to high | High |
| | Pictures per trigger | 1–10 | 3 |
| | Picture interval | From RapidFire™ near-video speed to 10 sec | Rapid fire |
| | Quiet period | From no delay to 5 min | No delay |
| Time lapse | | Hours of day and days of week | Off |
| Resolution | | 720P or 1.3 MP | 1.3 MP |

mammals; tundra vole, stoat or common shrew. To account for images with only a small part of an animal visible we also included a category "vole or shrew". If no animals were observed in the first image, we inspected the two subsequent images of the same trigger event, always including data of one image per trigger event in the data-set. All trigger events were scored, even though sometimes the same animal had apparently released the trigger several times. We also noted if the image was of very poor quality and the likely reason for that (e.g. trap filled with snow, humidity on the lens, etc.). Further, we noted if no animals were observed in the image. One of the traps was filled by vole nest material by mid-December, and data from this trap were excluded from further analyses and comparisons. All further data handling was done using the statistical software R, version 3.1.1 (R Development Core Team 2014).

As tundra voles were the most common species observed, we use them to exemplify our data. To assess the relationships between vole activity patterns, snow conditions and predator occurrence, we calculated occurrence of voles per camera per day and daily proportion of camera traps with vole occurrence (i.e. proportion of camera traps with at least one trigger event with any number of tundra voles recorded). We plotted this index of vole activity against days with stoat occurrence in at least one trap and with data on snow depth and precipitation data acquired from Tromsø weather station, which is at a distance of *c.* 4 km from the study site. Winter precipitation was classified as rain at temperatures above 1°C, otherwise as snow (according to Hansen et al. (2013)).

To assess snowpack impact on vole activity patterns within 24-h, that is, diel patterns (Halle 1995), we calculated occurrence of voles per hour for the three traps that were below snow the whole winter. For each hour, we first recorded whether one or several voles were present at least once. Based on duration of snow cover season, defined by temperature data recorded by the camera traps (see below), we divided the data between before and after the onset of snow cover. We then summed, for each time period respectively, the number of occasions vole activity occurred during a given hour of the day. In order to include only unambiguously snow-free or snow-covered days, we included data for September only for the period before snow cover and data for December- April for during snow cover.

In order to assess to what extent the temperature data collected by the camera traps could be used to determine snow cover duration, we calculate daily average, minimum and maximum temperatures across the camera traps that were observed to be below snow the whole winter. We compared these with the snow depth and precipitation data described above.

 

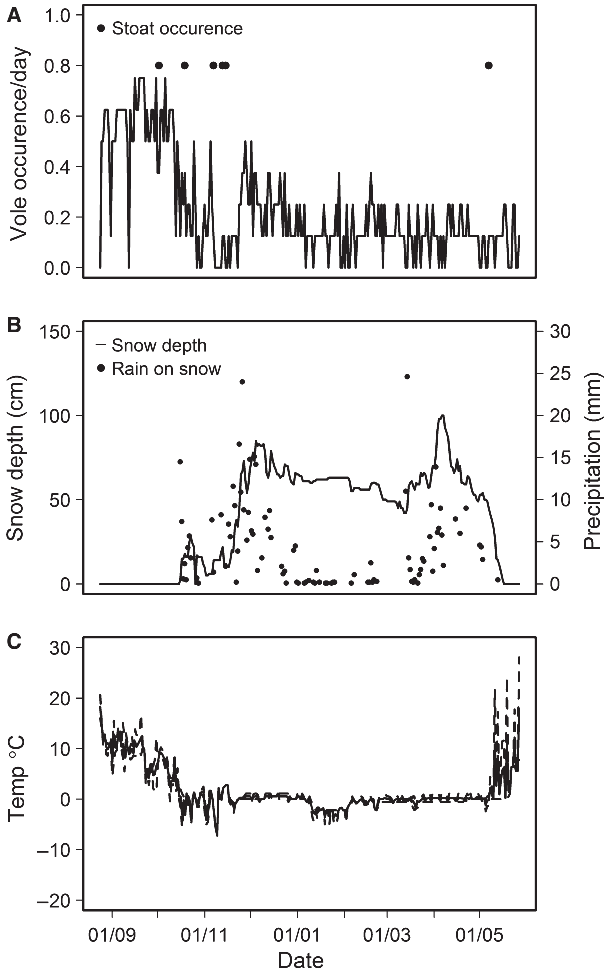


**Figure 3.** Vole and stoat occurrence, snow conditions and temperature in snow-covered camera traps during winter 2013–2014. (A) Vole occurrence per date (for each date, the proportion of camera traps where at least one vole was present at least once) and stoat occurrence (date with stoat occurrence in any camera trap) through the season. (B) Snow conditions through the season; daily snow depth measurement and 24 h accumulation of rain (defined as temperature >1°C and precipitation >1 mm) measured at Tromsø weather station. (C) Temperature measured by the camera traps; daily mean, minimum and maximum temperatures (dotted lines) aggregated across the traps that were observed to be beneath snow throughout the snow cover season.

To assess the relationship between the vole activity index achieved by camera traps and the number of voles observed during live-trapping, we enumerated the total number of vole individuals observed during each live-trapping session. For the camera trapping, we calculate the average proportion of camera traps with vole occurrence at least once a day during the week preceding each live-trapping session. We compared the magnitude of change from autumn to spring between the measure of live-trapping and camera trapping.

# Results

## Technical aspects

All of the camera traps took pictures throughout the winter and no cameras had technical failures or malfunctioned. The longest period a camera was unchecked varied between 154 and 236 days. At every check, all lithium batteries were 99% full. The total amount of data per camera trap were on average 289 (min 75, max 451) MB, thus never using more than 1% of the 32GB memory card capacity.

Most of the images were easy to classify to a given animal category. A small number of the images seemingly had no animal present, and a very small number of images were of bad quality, mostly due to snow in the box, moisture on the lens during snowmelt or bright sunshine (Table 2). One of the nine traps was filled by nest material by mid-December and another trap was partly filled by snow between 4 December 2013 and 26 February 2014. Excluding the trap with nest material, the camera traps were triggered in total 9995 times, on average 1249 times per camera (min 355, max 2336). The camera traps which were dug out of the snow in December, had on average somewhat lower vole occurrence after the exposure than the other traps (mean number of days with vole occurrence after 2 December in opened traps was 51, and in non-opened traps 78).

## Data recorded

We detected a range of animals in the traps; tundra voles, common shrews, insects, spiders, great tits (*Parus major*) and stoats (Fig. 2, Table 2). In majority of the cases (80%, Table 2) we identified a mammal to be the cause of trigger release. We mostly observed one animal, but

**Table 2.** Total number and proportion of trigger events in the eight camera traps between August 2013 and May 2014.

| Trigger event category | Number | Proportion |
|---|---|---|
| Tundra vole | 4992 | 0.50 |
| Common shrew | 2861 | 0.29 |
| Vole or shrew | 66 | 0.01 |
| Stoat | 6 | 0.001 |
| Bird | 214 | 0.02 |
| Invertebrate | 1251 | 0.13 |
| Bad quality (sunshine) | 51 | 0.005 |
| Bad quality (snow/moisture) | 56 | 0.005 |
| No animal | 498 | 0.05 |

Bad image quality due to snow or moisture means that either the box was partly filled by snow, or the camera had fog on the lens. The number of invertebrates was not scored, but represents the number of trigger events that were not assigned to any other category.

130 trigger events were caused by two voles and 13 trigger events by two shrews. In the camera trap with a vole nest, three voles were observed during 18 trigger events. A relatively large number of the images taken (13%, Table 2) were of invertebrates.

During September and October, *c.* 80% of the camera traps were visited daily by tundra voles (Fig. 3A). In November, vole activity decreased rather abruptly, and remained at a low level (0–30% of the camera traps being visited daily) for the remaining winter (Fig. 3A). The period of decrease in activity commenced concurrently with both the first recorded rain-on-snow event and with the first observation of a stoat in the camera traps (Fig. 3A and B). The traps that were below snow throughout the winter had a higher level of vole activity than those traps that had melted out in February and were exposed to ambient conditions (Fig. 4). However, the traps that were below snow throughout the winter already had a higher level of activity before the first snowfall (Fig. 4). The observed diel activity pattern of voles was consistent with an ultradian rhythm with 3–4 h between activity peaks (cf. Halle 1995) both before and after the onset of snow cover (Fig. 5).

Temperature data recorded by the cameras reflected snow cover duration well. Temperature of those camera traps that were below snow throughout the snow cover season remained relatively stable around zero and corresponded well to duration of snow cover recorded at the closest weather station (Fig. 3B and C).

The number of tundra vole (i.e. the only species captured during the live-trapping) individuals recorded during the live-trapping decreased from 69 in end of September 2103 to 16 in end of May 2014, that is, by 77%. During the week preceding live-trapping, on average 55% of the traps camera traps were visited at least once a day in the autumn and 8% in the spring, corresponding to a decrease of 85%.

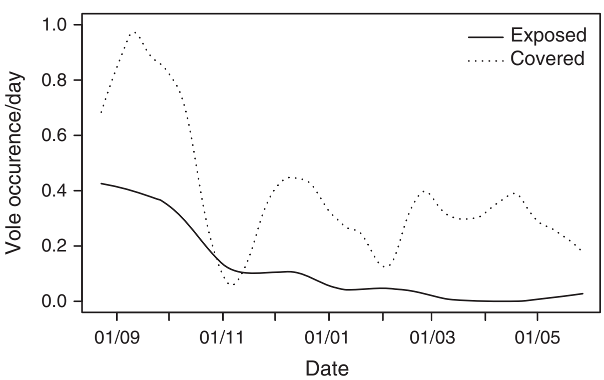


**Figure 4.** Proportion of camera traps with tundra vole occurrence per day for camera traps that were covered by snow ($n$ = 3) or exposed ($n$ = 5) 23.02.2014. Lowess-smoothed curves ($f$ = 1/8).

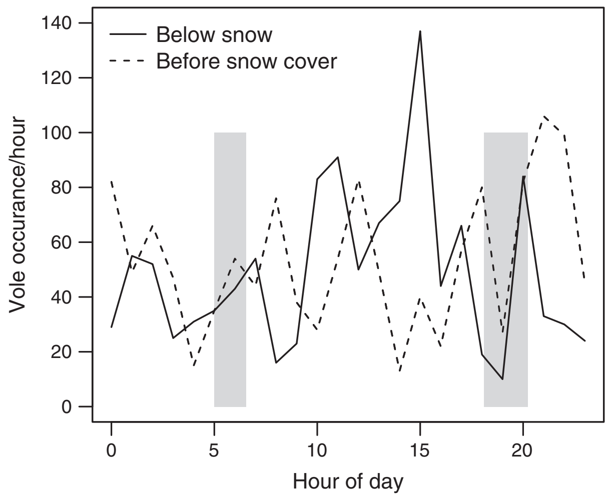


**Figure 5.** Tundra vole ultradian rhythm below snow and before the onset of snow cover. Vole occurrence per hour per camera traps is summed across the camera traps that were covered by snow throughout the winter. Data for "Below snow cover" is from September 2013 and data for "Below snow" from December 2013 – April 2014. Grey blocks denote timing of sunrise and sunset in Tromsø in September 2013.

# Discussion

We found that the camera traps were able to provide data of small mammal activity below snow throughout the winter, yielding very detailed temporal resolution of small mammal activity dynamics. The change from autumn to spring corresponded well to that found with live-trapping, but the camera traps were able to pinpoint when the decrease happened and provided data to assess the causes of such decrease, that is, data on predator occurrence and snow cover duration. The traps also provided detailed data on the fine-scale temporal organization of vole activity, revealing similar ultradian rhythmicity both before and after the onset of snow cover.

## Technical aspects

Throughout the winter, our camera trap prototype proved to be very functionally reliable. We had no technical problems, with the trigger and camera clearly fast enough to capture animals passing through the trap as we only infrequently recorded empty images where the animal in question had disappeared from the trap prior to camera release. We experienced no issues with batteries or memory cards. It is unlikely that any camera trap below snow would be exposed to such extremely low temperatures that could compromise the battery resilience [trials with cameras in freezers (−20°C) support this; Jensvoll, unpubl. observations]. While the number of images taken does, however, affect the battery life-time, it is difficult to assess how many images would be taken by a camera trap, for example, during a small rodent population peak year. Even the camera trap which was filled with nest material and had therefore taken high numbers of images (6300 images since the nest appeared in mid-December), had used little of the battery and memory card capacity. Lithium batteries and 32GB memory cards are thus likely to be a functional solution under most scenarios of subnivean camera trapping.

We did, however, encounter some issues that could probably be avoided or ameliorated. We observed a relatively large number of images with non-target species (invertebrates, including moth, flies and spiders). However, invertebrates were mainly observed when temperatures were above zero. Excessive numbers of invertebrates are unlikely to occur in camera traps during winter as they are in general inactive during the cold season. Furthermore, we observed humidity on the lens of some of the cameras during snowmelt, which could probably be avoided by plugging the opening for the external battery properly and by inserting a small pouch of silica-gel inside the camera case. Only one of the traps filled with snow, and although it may be impossible to completely avoid this problem, careful placing of the traps in wind-sheltered areas must be considered, especially in open terrain. Voles and shrews frequently stayed in the camera trap for several seconds, resulting in multiple trigger events and, over the winter, a large number of images. The number of images per animal could be reduced by setting the camera trap to have a delay period after each trigger event. The length of such delay should, however, be carefully considered in order to balance the probability of false negative detections of other species (Meek et al. 2014). The first prototypes of the trap were constructed of plywood and had deteriorated during the winter. After this present study, we constructed boxes for long-term use out of aluminum (Fig. 1C and D). In the new version of the box, the blocks that direct animals under the PIR sensor are hollow, allowing one to insert an external battery within the box and thus keep the external battery sheltered (Fig. 1C).

Vole activity records in the traps that we checked once during the winter were, after the disturbance, lower than in nondisturbed traps. The fact that a single disturbance event appeared to have an effect on vole activity indicates that disturbance of the snowpack may be an important issue changing small mammal behavior. However, as we observed the batteries to be very resilient in our camera trap setup, such checking is unlikely necessary during the winter. In contrast, repeated disturbance of snowpack is necessary during live-trapping and the automatic camera traps thus provide a much less disturbed subnivean environment than live-trapping regimes. Small mammals that are active under snow spend their winter in tunnel systems and the camera trap box most likely functions simply as a slightly larger chamber of runway tunnel systems, similarly to naturally occurring chambers (e.g. between rocks, hummocks or tree trunks). Even though the box evidently provides small rodents with a large enough chamber space for constructing a nest, it is very unlikely that such space alone would initiate below-snow breeding behavior. The camera trap boxes, if placed as part of runway systems, thus represent a relatively normal winter environment for subnivean small mammals compared to nest boxes (Bilodeau et al. 2013c) and trap chimneys (Yoccoz et al. 2001; Korslund and Steen 2006) used in subnivean live-trapping.

As only one species of vole has been observed at the study site, we could not quantify our detection ability of different rodent species. However, based on preliminary testing of the camera trap in another study area (mountain birch forest at Kattfjordeidet, N 69.65° E 18.53°, 200 m.a.s.l.) voles were clearly distinguishable from the Norwegian lemming (*Lemmus lemmus*) (Fig. 2). On the other hand, it seems that in most cases we were unable to determine the species of vole (tundra voles vs. red voles *Myodes rutilus*). The lack of species-level resolution could probably be avoided by using a camera with white flash instead of infrared flash. However, white flash may scare animals (O'connell et al. 2011) and its effect on small mammal behavior should be assessed carefully prior to implementation.

## A word of caution on study designs

In this study, we focused on testing the technical aspects of the camera trap prototype, illustrating potential ways to use data gained by this method. For any ecological study employing below-snow camera traps the best sampling strategy will vary according to the ecological questions and it is therefore important to thoroughly consider issues of study design and modeling approach before setting out camera traps for a larger study. Various aspects of camera trap study designs, such as the underlying assumptions and appropriate study designs for abundance, density and occupancy estimation have been discussed in recent publications (O'connell et al. 2011; Hamel et al. 2013; Rovero et al. 2013). Animal space use is involved in critical assumptions for many camera trapping applications, such as occupancy estimation (O'connell et al. 2011; Rovero et al. 2013). The issue is of especial relevance for subnivean camera trapping, as the current knowledge on subnivean space use of small mammals is extremely scarce (Korslund and Steen 2006; Hoset et al. 2008; Haapakoski and Ylönen 2013). Assumptions related to the below-snow space use should therefore be done consciously and preferably tested, before interpreting the results. Furthermore, the below-snow camera traps are especially prone to false-negative detectability, as the traps may sometimes fill up with snow. This can, however, be easily monitored by setting the cameras to take a daily time-lapse picture (Hamel et al. 2013).

### New avenues for subnivean ecology

Here, we focused on exemplifying the potential of below-snow camera traps specifically for studies of predator–prey and rodent–snow interactions. The current methods for studying mustelids are challenging and most studies within population and community ecology use indirect methods (Gilg et al. 2009; Haapakoski et al. 2012; Bilodeau et al. 2013b). Concurrently, most data series of small rodent population dynamics are based on few trapping events per year (see e.g. Krebs 2013 and references therein). Thus, the possibility to gain simultaneous and continuous data on small rodents and their mustelid predators enables analyses of their relationships at an unprecedented level of detail. Likewise, subnivean camera traps provide, for the first time, the possibility to relate timing of changes in winter weather to those of small mammal activity, as illustrated here by the comparison of winter rain timing and rodent activity. Moreover, these new traps provide the possibility of assessing the fine-scale organization of small rodent activity patterns (diel rhythmicity) under the snow in natural conditions. Indeed, we are aware of only one publication data on subnivean diel rhythms of rodents (Korslund 2006). The type of data provided in Figure 5 can, for instance, be used to infer whether the ultradian pattern is an adaptation to avian predation pressure during the snow-free season (Gerkema and Verhulst 1990), metabolic constraints differing according to snow cover (Aars and Ims 2002), or whether ambient light conditions function as zeitgebers (Halle 1995).

However, applications of the subnivean camera trap extend beyond those illustrated in this study. Importantly, the attachment of the camera on the box leads to images being taken of animals at a fixed distance from the camera, unlike most previous small mammal camera trap applications, where the image may be triggered across a range of different focal lengths (Glen et al. 2013). Thus, it would be possible to assess the relative size of the observed individuals and categorize them as juveniles or adults. Continuous subnivean observations of the reproductive status of the focus population would, for example, provide for the first time, data on the extent and timing of reproduction under snow – a critical aspect of boreal and arctic rodent ecology (Ims et al. 2011; Krebs 2011). Furthermore, camera traps present an opportunity to gain better data on trap-adverse species (Rendall et al. 2014), such as the Norwegian lemming. In areas where the species is an important component of the small mammal guild snap trapping of rodents remains the standard; a situation that could be amended by applying camera trapping methods.

In conclusion, the subnivean camera trap greatly increases the temporal extent and resolution of data collection on small mammal activity in cold ecosystems and provides new opportunities to establish subnivean interactions between predators and prey and the impact of climatic variation and change. Major advances of small mammal research and small rodent population ecology can therefore be expected through the use of the new trap as it allows the physical barrier of snow to be penetrated, leading to more detailed observations.

## Data Accessibility

Camera trap data are available in Dryad Digital repository (http://dx.doi.org/10.5061/dryad.9fg6p). Weather data are available from the Norwegian Meteorological Institute.

## Acknowledgments

We thank all of those who contributed to the design of the camera (Justin Thiner and Jamie Ratajczek at Reconyx), provided help with planning, testing and constructing the camera trap design (Atle Lilletun, Gunnar Johansen, Frode Hansen, Johan Nils Svärd, Eivind Flittie Kleiven, Marita Anti Strømeng and Mari Jacobsen), participated in fieldwork (Sissel Kaino), helped with illustrations (Tove Midtun) and checked the English (Helen Anderson). We also thank all of those who provided ideas, opinions and knowledge about trapping rodents through snow (Frederic Bilodeau, Eva Kallio). This study was financed by the Fram Center though the Climate-Ecological Observatory for Arctic Tundra.

### References

Aars, J., and R. A. Ims. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology 83:3449–3456.

Berryman, A. A. 2002. Population cycles: the case of trophic interactions. Oxford University Press, Oxford.

Bilodeau, F., G. Gauthier, and D. Berteaux. 2013a. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia 172:1007–1016.

Bilodeau, F., G. Gauthier, and D. Berteaux. 2013b. Effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian Arctic. J. Mammal. 94:813–819.

 

Bilodeau, F., A. J. Kenney, B. S. Gilbert, E. Hofer, G. Gauthier, D. G. Reid, et al. 2013c. Evaluation of a technique to trap lemmings under the snow. Arctic 66:32–36.

Brown, R. D., and D. A. Robinson. 2011. Northern hemisphere spring snow cover variability and change over 1922-2010 including an assessment of uncertainty. Cryosphere 5:219–229.

Gerkema, M. P., and S. Verhulst. 1990. Warning against an unseen predator - a functional aspect of synchronous feeding in the common vole, *Microtus arvalis*. Anim. Behav. 40:1169–1178.

Gilg, O., I. Hanski, and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. Science 302:866–868.

Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biol. 15:2634–2652.

Glen, A. S., S. Cockburn, M. Nichols, J. Ekanayake, and B. Warburton. 2013. Optimising camera traps for monitoring small mammals. PLoS ONE 8:e67940.

Haapakoski, M., and H. Ylönen. 2013. Snow evens fragmentation effects and food determines overwintering success in ground-dwelling voles. Ecol. Res. 28:307–315.

Haapakoski, M., J. Sundell, and H. Ylönen. 2012. Predation risk and food: opposite effects on overwintering survival and onset of breeding in a boreal rodent. J. Anim. Ecol. 81:1183–1192.

Halle, S. 1995. Diel pattern of locomotor activity in populations of root voles *Microtus oeconomus*. J. Biol. Rhythms 10:211–224.

Hamel, S., S. T. Killengreen, J. A. Henden, N. E. Eide, L. Roed-Eriksen, R. A. Ims, et al. 2013. Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. Methods Ecol. Evol. 4:105–113.

Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B. E. Saether. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology 92:1917–1923.

Hansen, B. B., V. Grotan, R. Aanes, B. E. Saether, A. Stien, E. Fuglei, et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science 339:313–315.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. J. Anim. Ecol. 60:353–367.

Hansson, L. 1999. Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. Oikos 86:159–169.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents - the importance of latitude and snow cover. Oecologia 67:394–402.

Hoset, K. S., J. F. le Galliard, G. Gundersen, and H. Steen. 2008. Home range size and overlap in female root voles: effects of season and density. Behav. Ecol. 19:139–145.

Ims, R. A., and E. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. Bioscience 55:311–322.

Ims, R. A., J. A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends Ecol. Evol. 23:79–86.

Ims, R. A., N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. PNAS 108:1970–1974.

Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Ostbye, B. Cazelles, et al. 2008. Linking climate change to lemming cycles. Nature 456:93–97.

Korpela, K., M. Delgado, H. Henttonen, E. Korpimäki, E. Koskela, O. Ovaskainen, et al. 2013. Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. Global Change Biol. 19:697–710.

Korslund, L. 2006. Activity of root voles (*Microtus oeconomus*) under snow: social encounters synchronize individual activity rhythms. Behav. Ecol. Sociobiol. 61:255–263.

Korslund, L., and H. Steen. 2006. Small rodent winter survival: snow conditions limit access to food resources. J. Anim. Ecol. 75:156–166.

Krebs, C. 2011. Of lemmings and snowshoe hares: the ecology of Northern Canada. Philosophical Trans. B 278:481–489.

Krebs, C. 2013. Population fluctuations in rodents. The University Press of Chicago, Chicago.

Legagneux, P., G. Gauthier, N. Lecomte, N. M. Schmidt, D. Reid, M. C. Cadieux, et al. 2014. Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nat. Climate Change 4:379–383.

Meek, P., G. Ballard, and P. Fleming. 2012. An introduction to camera trapping for wildlife surveys in Australia. PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia.

Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, et al. 2014. Recommended guiding principles for reporting on camera trapping research. Biodivers. Conserv. 23:2321–2343.

Nobrega, S., and P. Grogan. 2007. Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in birch hummock tundra. Ecosystems 10:419–431.

O'connell, A. F., J. D. Nichols, and K. U. Karanth, eds. 2011. Camera traps in animal ecology. Springer, Tokyo, Dordrecht, Heidelberg, London, New York.

Olofsson, J., L. Ericson, M. Torp, S. Stark, and R. Baxter. 2011. Carbon balance of Arctic tundra under increased snow cover mediated by a plant pathogen. Nat. Clim. Chang. 1:220–223.

Pearson, O. P. 1959. A traffic survey of *Microtus-Reithrodontomys* runways. J. Mammal. 40:169–180.

R Development Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ravolainen, V. T., K. A. Bråthen, N. G. Yoccoz, J. K. Nguyen, and R. A. Ims. 2014. Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. J. Appl. Ecol. 51:234–241.

Rendall, A. R., D. R. Sutherland, R. Cooke, and J. White. 2014. Camera trapping: a contemporary approach to monitoring invasive rodents in high conservation priority ecosystems. PLoS ONE 9:e86592.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. Hystrix-It. J. Mammal. 24:148–156.

Schweiger, S., and S. Boutin. 1995. The effects of winter food addition on the population-dynamics of *Clethrionomys rutilus*. Can. J. Zool. 73:419–426.

Stenseth, N. C., A. Shabbar, K. S. Chan, S. Boutin, E. K. Rueness, D. Ehrich, et al. 2004. Snow conditions may create an invisible barrier for lynx. PNAS 101:10632–10634.

Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, et al. 2012. Congruent responses to weather variability in high arctic herbivores. Biol. Lett. 8:1002–1005.

Turchin, P. 2003. Complex population dynamics: a theoretical/ empirical synthesis. Princeton University Press, Princeton.

Yoccoz, N. G., N. C. Stenseth, H. Henttonen, and A. C. Prévot-Julliard. 2001. Effects of food addition on the seasonal density dependent structure of bank vole *Clethrionomys glareolus* populations. J. Anim. Ecol. 70:713–720.

 