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Monitoring diel and seasonal activity of voles and shrews at Hardangervidda using camera trapping.

Overvåking av aktiviteten til stumpmus og spissmus gjennom døgn og sesong på Hardangervidda ved bruk av kamerafeller.

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Abstract

Voles (*Microtinae*) and shrews (*Soricidae*) are keystone species in the northern terrestrial ecosystems, with voles functioning as seed dispersers and vegetation facilitators and all species being important prey for a range of predators. Because of their central part in the ecosystem, they are widely studied species. Voles and shrews have complex population structures, and their activity patterns may be influenced by an array of both biotic and abiotic factors. Earlier studies on the activity patterns of voles and shrews have been conducted in the laboratory, but because of their complex relationship with the ecosystem, studies in the field give results of greater ecological relevance. We therefore set out to examine the daily and seasonal activity patterns of *Microtus* voles, bank voles (*Myodes glareolus*) and shrews (*Soricidae)* in the field. We used camera traps to monitor the activity of the study species at Skinnarbu, Tinn municipality over three years; January 2017-December 2019. Based upon species occurrences on the images we modelled the seasonal and daily activity patterns for the species in question using statistical software.

Using these modelled activity patterns, we found a preference for nocturnal activity in the voles during spring, summer and autumn, with a synchronised rest period in the daylight hours. In winter, there was a shift towards a preference for diurnal activity with an activity peak in the middle of the day. Shrews had the same pattern of nocturnal activity in spring and summer but exhibited a more uniform activity pattern in autumn and winter with activity throughout the 24 hours. Based on our data we suggested that the activity patterns are essentially influenced by sunrise- and sunset- times, predation (although no statistical analysis were preformed), social factors and need for food. We found camera trapping to be a satisfactory non-invasive method of monitoring small mammal activity, with some suggestions for improvement.

Sammendrag

Stumpmus (*Microtinae*) og spissmus (*Soricidae*) er nøkkelarter i terrestriske økosystemer på den nordlige halvkule, hvor stumpmus blant annet bidrar til å spre frø og fasilitere vegetasjon, og der alle artene er viktig byttedyr for et bredt spekter av predatorer. Grunnet deres sentrale rolle i økosystemet er de godt studerte arter. Stumpmus og spissmus har kompleks populasjonsstruktur og aktivitetsmønstrene kan bli påvirket av ulike biotiske og abiotiske faktorer. Tidligere studier på aktivitetsmønstre hos stumpmus og spissmus har blitt utført i laboratorier, men grunnet deres komplekse forhold med økosystemet, gir feltstudier resultater med større økologisk relevans. Derfor valgte vi å se på aktivitetsmønstrene til *Microtus* stumpmus, klatremus (*Myodes glareolus*) og spissmus (*Soricidae*) gjennom døgn og sesong i felt. Vi benyttet kamerafeller til å overvåke aktiviteten til studie-artene ved Skinnarbu, Tinn kommune over tre år; januar 2017-desember 2019. Basert på forekomst av art på bildene, modellerte vi mønstre for sesong- og døgnaktivitet for studie-artene ved hjelp av statistisk programvare.

Gjennom de modellerte aktivitetsmønstrene fant vi en preferanse for natt-aktivitet hos stumpmus på våren, sommeren og høsten, med en synkronisert hvile-periode i timene med dagslys. Om vinteren var det en preferanseendring mot dagaktivitet med en aktivitetstopp midt på dagen. Spissmus viste samme mønster med natt-aktivitet om våren og sommeren, men hadde et mer uniformt aktivitetsmønster om høsten og vinteren med generell aktivitet gjennom døgnet. Basert på vår data foreslo vi at aktivitetsmønstrene er spesielt påvirket av tider for soloppgang og solnedgang, predasjon (ingen statistiske analyser ble gjort på dette forholdet), sosiale faktorer og behovet for mat. Vi kom frem til at kamerafeller viste seg å være en tilfredsstillende ikke-invaderende metode for å observere aktivitet av småpattedyr, med noen forslag til forbedringer.

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1. Introduction

Small mammals, and especially voles (*Microtinae*) and shrews (*Soricidae*), are important key-stone species in northern terrestrial food webs (Soininen et al., 2015). They are important prey for a range of predators; owls (*Strigiformes*), raptors (*Accipitres*) and carnivorous mammals (*Carnivora*) (Halle, 2000b; Ylönen et al., 2019). In addition, voles and shrews contribute to the flow of energy as consumers of plants or insects (Churchfield, 1979; Halle, 2000b; Ylönen et al., 2019). Microtine rodents (i.e., voles and lemmings and shrews also typically appear in great numbers, making them popular species for ecological studies (Churchfield, 1979; Merrit & Vessey, 2000). They also have a wide geographical distribution making them accessible study species (Bennie et al., 2014). Voles are also a well-studied species group because of their density fluctuations, or more commonly termed, population cycles (Andreassen et al., 2019; Halle, 2000b). Voles and lemmings are living in strongly seasonal environments and have been of special interest because of their pronounced cycles (Boonstra et al., 1998; Hansen et al., 1999; Ylönen et al., 2019). As well as influencing fluctuations in the population, the nature of the seasons might also shape the activity of voles and shrews.

When studying the ecology of animals, considering at what time the activity of said animal takes place is of great importance (Enright, 1970). There are generally two states of behaviour for all animals: rest and activity. The most prominent activities performed during the active phase is foraging (Daan & Slopsema, 1978), exploration, search for mates (Halle & Stenseth, 2000) and defence of home range (Lehman & Sommersberg, 1980). During the active phase, the animals are also in a state of increased mortality risk due to for example predators (Halle, 1993) and harsh weather conditions (Halle & Stenseth, 2000). The daily activity patterns of animals are an alternation between these two behavioural states, since neither one can be retained permanently. These recurring alterations result in one or several activity cycles during the 24-h day. These repeated activity cycles are commonly called the "diel activity pattern", or just the "activity pattern" of a species (Bartness & Albers, 2000). This creates a daily rhythm timed by internal clocks in the animals. There are four types of such clocks, each named after the four periodicities in the environment: the tides, day and night, the lunar cycle and the seasons (Aschoff, 1984). The internal clocks that are run by the rhythms of day and night are called circadian clocks. "Circa" is latin for about or around, while “dies” or “dian” means day (Bartness & Albers, 2000). This clock runs in synchrony with the day/night-cycle (Aschoff, 1984; Enright, 1970), with a frequency that slightly deviates from the mimicked 24-h cycle, this is achieved through entraining signals from periodic factors in the environment termed zeitgebers (Aschoff, 1954; Aschoff, 1984). Zeitgebers for daily activity can be all events that affects the organism in question (Aschoff, 1954). In the circadian rhythm, the light/dark-cycle (hereafter termed LD-cycle) is the most powerful zeitgeber, but as activity patterns are distinct for each species, the zeitgebers for the circadian clocks may be an array of different factors (Aschoff, 1984). Hence, the factors influencing the activity patterns differ with ecological habits of the species (Halle & Stenseth, 2000). It may be connected to predator/prey relationships (Halle, 1993; Lehman & Sommersberg, 1980), digestion and metabolism (Churchfield, 1979), social interactions (Lehman & Sommersberg, 1980) or simply owed to unfavourable environmental conditions. Activity patterns of small mammals, as well as other animals, differ with species and there is a wide variety of strategies of activity (e.g.Daan & Aschoff, 1981; Halle, 2006).

As an adaptation to the LD-cycle, two basic strategies of activity have evolved: nocturnal species are active during darkness and diurnal species are active in the daylight, however there are exceptions to these patterns. Nocturnal and diurnal species are monophasic, meaning they are almost exclusively active during day or night**.** These types of activity patterns are also most commonly unimodal, i.e., they have one activity peak (Halle & Stenseth, 2000). Crepuscular species, however, primarily roam about under the twilight conditions of dawn and dusk, and some species exhibit short activity bouts of a few hours length, and as a result of this are active both day and night (Halle & Stenseth, 2000). These patterns of several bouts of activity and rest in a day are termed polyphasic (Daan & Aschoff, 1981; Halle & Stenseth, 2000). Microtine rodents are the most prominent representatives for this type of activity pattern (Halle & Stenseth, 2000; Halle, 2006; Ylönen et al., 2019), and shrews are also known to have short-term rhythms in activity (Daan & Aschoff, 1981; Halle, 2006). Hence, the feature that shapes microtine activity is not the circadian rhythm, but the period shorter than this, ultradian rhythms (Aschoff, 1984; Daan & Aschoff, 1981; Halle & Stenseth, 2000). Contrary to circadian rhythms, these short-term rhythms are not connected to environmental periodicity (Daan & Aschoff, 1981). This pattern of polyphasic rhythm has been observed for voles both in the field (Greenwood, 1978; Halle & Lehman, 1987; Halle & Lehman, 1992) and in laboratories (Erkinaro, 1961). The same observations have also been made for shrews in the field (Ivanter & Marakov, 2002) as well as in laboratories (Rust, 1978; Saarikko & Hanski, 1990). Studying above-ground activity of small mammals in the field by passage counters or radio tracking only reveals the ultradian activity (Halle, 2006). This above-ground activity most likely represents routine behaviour, such as foraging (Halle & Stenseth, 2000; Halle, 2006), and can most likely also be captured using camera traps in the field.

Camera trapping is a relatively new method of monitoring small mammals in the field. The method has not been as frequently used in earlier studies due to images being of poor quality, making it difficult to determine species. But higher image quality is now more available making this a valuable method in observing small mammals (DeSa et al., 2012). Wildlife scientists can use this method to detect rare species, determining numbers of one species, to look at behaviour and much more (O'Conell et al., 2011). Even though it is possible to determine species, it is not possible to distinguish between individuals by looking at images. Therefore, this method is more suitable for looking at populations (DeSa et al., 2012). Camera trapping also opens the opportunity of monitoring interactions in the field, like predator prey interactions (Soininen et al., 2015). Since camera trapping is a relatively new method for small mammal monitoring, different study designs are still being evaluated. Several studies have placed the camera horizontally (Karanth & Nichols, 1998; Villette et al., 2016), but these studies have mostly been conducted on larger animals. Studies on small mammals, like voles and shrews, now typically places the camera so that pictures are seen from a vertical view (McCleery et al., 2014; Soininen et al., 2015). This allows for more accurate detection of the small mammals. Other studies on small mammals design a “box” in which the camera is placed, and this is beneficial due to constant distance from the camera lens making identification of small animals easier (McCleery et al., 2014; Soininen et al., 2015). Even though different study designs of camera trapping are still being tested, camera trapping has several benefits when monitoring small mammals in the wild.

Using camera traps opens the possibility to “be present” in the field 24-hours a day, without the time consuming and expensive field work. The camera traps are designed to be outside for a long period of time, and this could allow new dimensions to monitoring small mammals in the field. Camera trapping is beneficial because it is less invasive than common methods of observing small mammals in the field, like live trapping and pitfalls (Halle & Stenseth, 2000; Villette et al., 2016). Because it is less invasive, the animals will experience less stress compared to live trapping (Fletcher & Boonstra, 2006). Camera trapping also demands fewer working hours in the field, personnel working on the study will be using their time to analyse images (McCleery et al., 2014). Camera traps allows for monitoring small mammals in the subnivean environment, which is an important part of small rodent runways during the winter (Soininen et al., 2015). This means that there is opportunity to collect data on small mammal movement in the winter that has previously not been well studied. Considering all of these benefits, it is not surprising this technology has given us an improved understanding of ecological relationships, population dynamics and activity patterns (Karanth & Nichols, 1998; O'Conell et al., 2011).

The majority of studies on vole and shrew activity has been performed in the laboratory, only simulating similar conditions to their natural habitat (Halle & Stenseth, 2000; Richardson, 1973; Saarikko & Hanski, 1990). Measurements on vole and shrew activity in their natural habitat will allow a study on activity with an ecological dimension that most likely cannot be considered in cage experiments and live-trapping experiments (Halle & Stenseth, 2000). Also, camera trapping allows for long-term monitoring of small mammal activity in the field, possibly allowing further assessment of influences on these activity patterns. Using camera trapping, we aim to investigate the daily and seasonal activity patterns of *Microtus* voles (*Microtus agrestis* and *Microtus oeconomus*), bank voles (*Myodes glareolus*) and shrews (*Sorex araneus, Sorex minutus* and *Neomys fodiens*) at Skinnarbu, Tinn municipality.

2. Methods

The following chapters contain information on methods used in this project. We provide descriptions of the study area and study species as well as give insight into methods used to sort the data material and statistical analyses performed on the data.

2.1 Study area

Data collection and camera deployment was conducted at Skinnarbu in Tinn municipality in Vestfold and Telemark county, about 1000 m a.s.l (59°48′46.2172″ N, 8°18′27.66459″ E) (Fig.1). The study area is located within Europe's largest mountain plateau, Hardangervidda, Norway. Hardangervidda encompasses about 8,600 km, including one of Europe's largest national parks. The study area is dominated by sub-alpine forests of dwarf-birch (*Betula* *nana*) (Bakkestuen et al., 1999), but there are also graminoids, mosses, lichens and ericaceous shrubs (e.g bilberry, *Vaccinium myrtillus*) in the area (Steyaert et al., 2018). The habitat is relatively open, with the dwarf-birch providing sparse cover.

Predators on voles and shrews in the area include stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*), which are regarded as specialist rodent predators (Selås, 2020a). Other important predators on voles and shrews known to be present in the area are Tengmalm's owl (*Aegolius funereus*), common buzzard (*Buteo buteo*), European viper (*Vipera berus*) and red fox (*Vulpes vulpes*). During the study period, the temperatures at Skinnarbu ranged from -8.9-16.1°C (data for Møsvatn weather station, available from www.eklima.no). Annual precipitation is on average 860 mm (data for Møsvatn weather station, available from www.eklima.no). The area normally has snow cover from November to April (data for Møsvatn weather station, available from www.eklima.no).

Figure 1: Map (© kartverket/norgeskart.no) of the study area. Camera trap study area for *Microtus* voles, bank voles and shrews located in Central Southern Norway, Tinn municipality, during November 2016 to January 2020. 5 sites were chosen randomly for camera deployment (Kartverket (Norges Geografiske Oppmåling), 2020).

2.2 Study species

The three study species in this project were *Microtus* voles, bank voles (*M. glareolus*) and shrews. In the following sections we will give short descriptions of and relevant information on each of the three study species.

2.2.1 *Microtus* voles

In our study area, there are two known voles of the genus *Microtus*, the field vole (*M. agrestis*) and the tundra vole, or root vole (*M. oeconomus*). Both species are common over large parts of North-and Middle-Europe, with the field vole having a wider distribution. These two species are very similar and the teeth are the best way to separate them (Bjärvall & Ullström, 1997). As a consequence of this, the two species were pooled, as *Microtus* voles could not unambiguously be identified to species by looking at the images. The size of these voles is normally between 78-145 mm with a tail length of about 18-49mm. Fig.2 shows an example of an individual determined to be a *Microtus* vole. *Microtus* voles have a general preference for open habitats but are not restricted to a specific type of surrounding (e.g sparse birch-forest, croplands and at the seashore) (Seatnan et al., 2009). This group of voles is herbivorous, and graminoids is the most important food (Hansson, 1971). *Microtus* voles reproduce between April and September, but this period can be prolonged if the access to food is good and the number of competing individuals is low. This group of voles have home ranges between 200 and 1000 m2, with the home-range size for males double that of females (Myllymäki, 1977).

Figure 2: Image from the camera trap showing an adult *Microtus* vole, December 2016.

2.2.2 Bank voles

The size of the bank vole ranges from 80-135mm with a tail length of 35-72mm. The tail length is considerably longer than that of *Microtus* voles. Fig.3 displays an example of a bank vole. Bank voles are relatively common over large parts of Europe. They prefer forests with rich ground vegetation as their habitat, but have no special preference for deciduous forests or coniferous forests (Bjärvall & Ullström, 1997; Wegge & Rolstad, 2018). Bank voles are herbivorous-graminivorous, and their diet mainly consists of seeds, moss, herbs, fruit, grass, fungi and roots, but from time to time they also eat insects and other small animals (Hansson, 1971). Bilberry is important in the bank vole diet and has been shown to have a connection to bank vole population cycles (Selås et al., 2002; Selås, 2020a). They reproduce from April until September/October, but this period can be prolonged until January if the conditions for survival are good. Their home range has been found to be between 700 to 11 000 m2 (Karlsson & Paptov, 1998), and they are a territorial species (Halle, 2000b) meaning their guard their own territory.

Figure 3: Image from the camera trap showing an adult bank vole (*M. glareolus*), August 2019.

2.2.3 Shrews

Common shrews (*Sorex araneus*), pygmy shrews (*Sorex minutus*) and water shrews (*Neomys fodiens*) were pooled together because we were unable to separate them unambiguously on the images. Fig.4 shows a picture of a shrew from the camera trap. Shrews are found over a wide range of habitats, and are commonly found in woodlands, grasslands and hedgerows (Churchfield, 1979). Water shrews (*N. fodiens*) have a preference for wetter habitats with substrates of rocks, gravel and mud (Greenwood, 1978), while pygmy shrews (*S. minutus*) prefer moist grounds (Feldhamer et al., 1993). Our study area is relatively dry, and we therefore assume that most shrews were common shrews. Water shrews would also have been easily recognisable because of their darker back and lighter stomach. Because we grouped several species together, there is a large variation in size of the individuals. The sizes range from 42-87 mm, but all of the species have a characteristic, pointed snout making them easily identifiable. All shrew-species are insectivorous, and a metabolic rate far exceeding that of other small mammals (Churchfield, 1979). Shrews reproduce between March/April and September/October and are generally found to be less active in the wintertime than in the summer (Baláž & Ambros, 2006; Churchfield, 1979). Shrew species generally have small home-ranges (Bjärvall & Ullström, 1997).

Figure 4: Image from the camera trap showing a shrew, August 2018.

2.3 Study design

Our study consists of five trap-boxes containing camera traps. They were placed on the ground in close proximity to each other at Skinnarbu. In the following paragraphs we are going to describe their design and how the images were sorted.

2.3.1 Trap-box

The trap-boxes with the cameras were set up in November 2016 and have been running 24-hours a day ever since. In our study we have used data for three whole years, this being January 2017 to December 2019. Tab.1 displays number of hours for each season and how many of these hours each species was present or not present. This is for the entire dataset and each hour-block was scored with either present or not present. The design of the trap-box was based on the trap-box in a study of subnivean ecology by Soininen et al. (2015)**.** They designed a box that was supposed to be a part of the small mammal’s runway system. They had a square box with one entry point and one exit point. The bottom of this box was metal painted white, so the identification of the species would be easier. The camera was placed in the lid of the box (Soininen et al., 2015). Our trap-box follows this design, but with some alterations. We used wood as material in our trap-box, which suited the study area. As shown in Fig.5C the floor of our trap box was the ground, which was more natural for species passing through the box. We placed the camera in the lid of the trap-box, the constant distance between the camera and the ground made species identification easier (Fig.5B). All five trap-boxes in this study had the same design.

The trap-boxes were constructed with one entry point and one exit point making them a natural part of small mammal movement (Fig.5A). The trap-boxes included a Reconyx PC900HyperFire™ camera trap with No-glow™ high-output covert infrared technology (Reconyx Inc., WI, USA). This camera is classified as a good quality camera on the market (Rovero et al., 2013). The camera was customised to have the lens in focus at 30-40 cm. The cameras were active 24-hours and had passive infrared sensors (PIR) which responded to movement. The camera was isolated from the surroundings by the trap-box, this limits the number of false triggers.

The camera captured still images when there was movement through the trap-box. Due to the absence of light inside the box the pictures were in black and white. The camera had a “rapid fire” function, taking up to 3 images per second, and there was no delay. Due to the camera capturing every movement, the viewing of the images was experienced as a video. One individual could trigger the camera several times causing a long series of pictures of the same individual. The images were stored on 32 GB secure Digital (SDHC®) Memory Card (hereafter SD-card). The data from the memory cards were collected about four times a year.

When data from the memory cards were collected, the batteries were changed with charged batteries. In the camera trap Nickle-Metal Hydride (NiMH), which are rechargeable batteries, were used. This was advantageous because they could be used multiple times. In his review of camera traps, Rovero et al. (2013) recommend this as long as it does not interfere with the camera traps performance. The trap-boxes were located in an area where frequent visits were possible, and therefore changing batteries was not a problem. Because easy access was an important factor when the trap boxes were placed, they are in close proximity to each other.

Table 1: Number of hours for each season with small mammal present (1) or not present (0) by the hour block for each study species.

	Season	Total	Not present	Present
***Microtus* vole**				
	Spring	33120	32861	259
	Summer	33120	31305	1815
	Autumn	33655	32630	1025
	Winter	39214	39146	68
Bank vole				
	Spring	33120	33062	58
	Summer	33120	32753	367
	Autumn	33655	33221	434
	Winter	39214	39166	48
Shrews				
	Spring	33120	33000	120
	Summer	33120	32127	993
	Autumn	33655	33014	641
	Winter	39214	39047	167

Figure 5: (A) The trap box from the outside. Entry-and exit-points on either side of the box. (B) The trap box photographed opened. The lid of the box with the camera attached. (C) The box photographed from inside. The wooden squares guide the animals in front of the PIR-sensor of the camera.

2.3.2 Sorting the images

After the SD-cards containing the images were collected, we manually determined species by examining the images. Images from the camera traps were sorted using Windows Photo Viewer (Microsoft Corp., Redmond, WA) and Finder (Apple Inc., Cork, Republic of Ireland). Before we sorted the images some of them were sorted in another project at NMBU, but we controlled their sorting. We first had to determine if there was an animal present on the image. If there was an animal present, species had to be determined. There were mostly images of voles or shrews, but sometimes other small animals in the area were captured on camera. We created folders for “Bank vole”, “Bank vole juvenile”, “*Microtus* vole”, “*Microtus* vole juvenile”, “Vole”, “Shrews”, “Lemmings (*Lemmus lemmus)*”, “Stoat”, “Least weasel”, “European Viper”**,** “European Lizard (*Zootoca vivipara*)” and “Other”. In the “Other”-folder, we gathered the observations of other species, such as Eurasian red squirrel (*Sciurus vulgaris*), Passerines (*Passeriformes*) and bugs. In the “Vole” folder we placed images that contained voles, but we were not able to tell if it was a *Microtus* vole and bank vole. For the *Microtus* and bank vole we could identify some individuals as juveniles (Fig.6 and 7 displays examples). The data from the camera traps confirmed the reproduction times suggested by literature, April-September/October, but due to low sample size (Tab.2) and uncertainty we decided to merge adults and juveniles for *Microtus* voles and bank voles. Grey sided voles (*Myodes rufocanus*) might be mistaken as *Microtus* voles on the images, but they are very rare in our study area (Framstad, 2020).

Figure 6: Images from the camera trap, to the left an adult bank vole and to the right a juvenile bank vole.

Figure 7: Images from the camera trap, to the left an adult *Microtus* vole and to the right a juvenile *Microtus* vole.

The voles were separated by looking at the length of the tail. If the tail was longer than half the body, we classified it as *M.glareolus* and if the tail was shorter than half the body it was classified as *Microtus* vole. This relatively large difference made it possible to differentiate the two species. The shrews differed from the voles both in shape of the snout and the texture of the fur (Braanaas, 1997; Brink & Valum, 1972).

Table 2: Total number and proportion of trigger events in the five camera traps between November 2016 and January 2020.

Trigger event category	**Number**	**Proportion (%)**
Bank vole	6226	15%
Bank vole- juvenile	1415	3.3%
Microtus vole	21327	49%
Microtus vole-juvenile	2883	6.7%
Shrews	7778	18%
Lemming	12	0.03%
Vole	3051	7.0%
Least Weasel	135	0.3%
Stoat	36	0.08%
European viper	89	0.2%
Lizard	29	0.07%
Species not determined	117	0.30%

2.4 Statistics

Statistical analyses were performed using the statistical software R, version 3.6.1 (R Development Core Team, 2019). To extract the information from the sorted folders (species group, time and date), we used a custom-made R-script with a call to Exiftool.exe. https://exiftool.org/ (to read exif-data from the images). The end product was a data frame with all the observations recorded, ready for the analysis. The analyses of diel activity rhythms were based on linear mixed effects regression models within the *lme4* package (R Development Core Team, 2019). Time of day is not a linear function, because the 24-h day runs in cycles. To account for this, the periodic component of time series was represented by pairs of sine and cosine functions. Photographic events were recorded as binary response variables and used as an index of activity around the clock. Each hour-block was scored as either “1” (voles or shrews observed) or “0” (no voles or shrews observed), and we modelled the outcomes using logistic regression with a binomial distribution. We fitted the fixed explanatory variable “Time of day” using the cosinor-method. M0 was the null hypotheses, equivalent of no pattern in activity. M1 had one harmonic component, capturing a top or bottom in activity. M2 and M3 had two and three harmonies, respectively. By adding more harmonies, the models became more detailed and captured more tops and bottoms in activity. The activity models were specified as:

$$\mathbf{M0}: logit\big(f(x)\big) = a_0 + \epsilon$$

$$\mathbf{M1}: logit\big(f(x)\big) = a_0 + (a_1 cos\frac{2\pi x}{24} + b_1 sin\frac{2\pi x}{24}) + \epsilon$$

$$\mathbf{M2}: logit\big(f(x)\big) = a_0 + \left(a_1 cos\frac{2\pi x}{24} + b_1 sin\frac{2\pi x}{24}\right)$$
$$+(a_2 cos\frac{2 \cdot 2\pi x}{24} + b_2 sin\frac{2 \cdot 2\pi x}{24}) + \epsilon$$

$$\mathbf{M3}: logit\big(f(x)\big) = a_0 + \left(a_1 cos\frac{2\pi x}{24} + b_1 sin\frac{2\pi x}{24}\right)$$
$$+\left(a_2 cos\frac{2 \cdot 2\pi x}{24} + b_2 sin\frac{2 \cdot 2\pi x}{24}\right)$$
$$+a_3 cos\frac{3 \cdot 2\pi x}{24} + b_3 sin\frac{3 \cdot 2\pi x}{24}) + \epsilon$$

with x as “Time of day” and $\in$ as the random effect “site ID”. Using *AICmodavg* (R Development Core Team, 2019) we calculated the Aikaie’s Information Criterion (AIC) for each model. Site ID was included as a random effect to account for possible variations between sites. This package also produces model selection tables based on the AIC and the second-order AIC (AICc), which we used to evaluate each model’s fit (M1-M3) comparing the AIC values with the model that included only the random term (M0). This comparison determined whether a given harmonic term was included in the final model, i.e. whether it contributed statistically to the characterization of the waveform (Steen & Barmoen, 2017). We ranked the model fit according to their AICc values, with the lowest AICc value being considered as the best fit. Models in which difference in AICc relative to AICcmin is <2 can be considered to have substantial support (Burnham & Anderson, 2002). When modelling the activity for small rodents and shrews we chose the most parsimonious model with the fewest amount of predictor variables. Graphical presentations of the activity patterns were constructed using the package *graphics* (R Development Core Team, 2019). The 95% confidence intervals of the fitted line were computed by model-based parametric bootstrapping for mixed models (*bootMer* function, 1000 simulations, *lme4* package). The mean of the modelled activity curve (MESOR) was calculated for each model, and it is represented by a horizontal threshold line on all the activity plots. The time of day the modelled activity was above MESOR indicated an increase in activity (Navarro et al., 2013). We created these activity patterns for each season. The following partitioning was used: March, April and May were spring-months, June, July and August were summer-months, September, October and November were autumn-months and December, January and February were winter-months. We also created bubble plot depicting seasonal activity of the study species.

We also used the *activity* package (R Development Core Team, 2019) in R to create the kernel-density plots. When creating the kernel-density plots, we added a 30 min gap to the data to avoid pseudoreplication. This was performed by the use of a custom-made R-script. All images triggered within a 30 min time interval for a given species was merged to one observation.

3. Results

3.1 General activity 24/7/365

Microtus voles were generally more active in the darker hours, with more individuals captured on camera before sunrise and after sunset (Fig.8A). This pattern was most evident in the spring- and summer-months (months 5-9), with the bubbles being visibly larger in the dark hours. Further, more individuals were captured in these snow free months, expressed by larger circles.

Bank voles had a generally lower sample size, and the bubbles were therefore less pronounced (Fig. 8B). There was an indication that bank voles followed the same pattern as *Microtus* voles, and this was most evident in the late summer- and autumn-months (8-10). In the summer-months, shrews exhibited the same pattern of diel activity as the other study species (Fig.8C). In autumn, however, the activity pattern of shrews changed to be more uniform, with no clear preference for time of day.

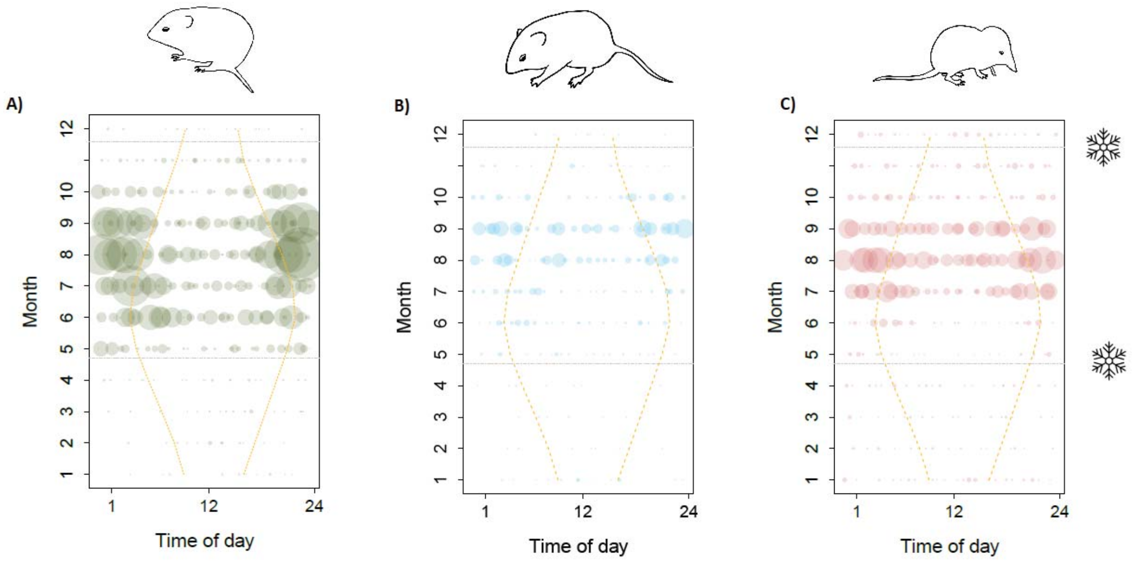


Figure 8: Bubble plot showing diel activity throughout the year (2017, 2018 and 2019 pooled) in A) *Microtus* voles, B) Bank voles and C) Shrews. The number of individuals captured by the camera is depicted by the dots. The size of the dots (bubble size) represent number of occurrences of the observations for a given time of day and month. The vertical, dashed yellow lines represent sunrise (left) and sunset (right). The horizontal dotted grey lines illustrate the median start and end of snow cover.

3.2 Seasonal activity

In the following chapter, we present daily activity curves for *Microtus* voles, bank voles and shrews. The hour blocks for each season were scored for presence/absence of animal.
The sample size for the other species was too low to do any further analysis (Tab.1 and 2).

3.2.1 *Microtus* voles

In springtime it was clear that *Microtus* voles had a resting period during daytime and increased their activity during the dark hours (Fig.9A). The main dip in activity was in hour-blocks 10-12, but the general resting period was during hour-blocks 04-18. M3 was the best model (Tab.3), the other models had considerably lower support ΔAICc ≥2.0.
We saw the same pattern during summer as we did during spring (Fig.9A and 9B), less activity during daytime, although with a longer period of activity. The lowest dip in activity was in hour-block 15-16, but the general period with lower activity was in hour-blocks 08-16 (Fig.9B). This showed that the lowest activity occurs later in the day compared with the activity curve for spring (Fig.9A). For summer, M3 was the best model, the other models had considerably lower support ΔAICc ≥2.0 (Tab.3). For autumn in Fig.9C, we saw the same pattern as for spring and summer (Fig.9A and 9B), less activity during daytime (Fig.9C). There was a general period of lower activity in hour-blocks 09-15. M3 was the best model for autumn activity, the other models had considerably lower support ΔAICc ≥2.0 (Tab.3).
For the winter months, M1 was the best model, the other models had considerably lower support ΔAICc ≥2.0. (Tab. 3). And here we saw a unimodal peek on the activity index for the daylight hours (Fig.9D). This was the opposite of what we saw for the rest of the seasons.

Table 3: Model selection table showing number of parameters (K), AICc, ΔAICc, AICc weights (AICcWt), cumulative weight (Cum.Wt) and log-likelihood (LL) for *Microtus* voles.

	Model	**K**	**AICc**	**ΔAICc**	**AICcWt**	**Cum.Wt**	**LL**
Spring							
	M3	8	2992.43	0.00	0.69	0.69	-1488.21
	M2	6	2995.36	2.93	0.16	0.85	-1491.68
	M1	4	2995.52	3.09	0.15	1.00	-1493.76
	M0	2	3020.22	27.79	0.00	1.00	-1508.11
Summer							
	M3	8	13213.63	0.00	0.94	0.94	-6598.81
	M2	6	13219.14	5.52	0.06	1.00	-6603.57
	M1	4	13230.46	16.84	0.00	1.00	-6611.23
	M0	2	13552.62	338.99	0.00	1.00	-6774.31
Autumn							
	M3	8	8622.42	0.00	0.98	0.98	-4303.21
	M1	4	8631.03	8.62	0.01	1.00	-4311.52
	M2	6	8634.25	11.63	0.00	1.00	-4311.12
	M0	2	8845.07	222.65	0.00	1.00	-4420.54

Winter

M1	4	986.48	0.00	0.69	0.69	-489.24
M3	8	989.39	2.91	0.16	0.85	-486.69
M2	6	989.94	3.46	0.12	0.98	-488.97
M0	2	993.24	6.76	0.02	1.00	-494.62

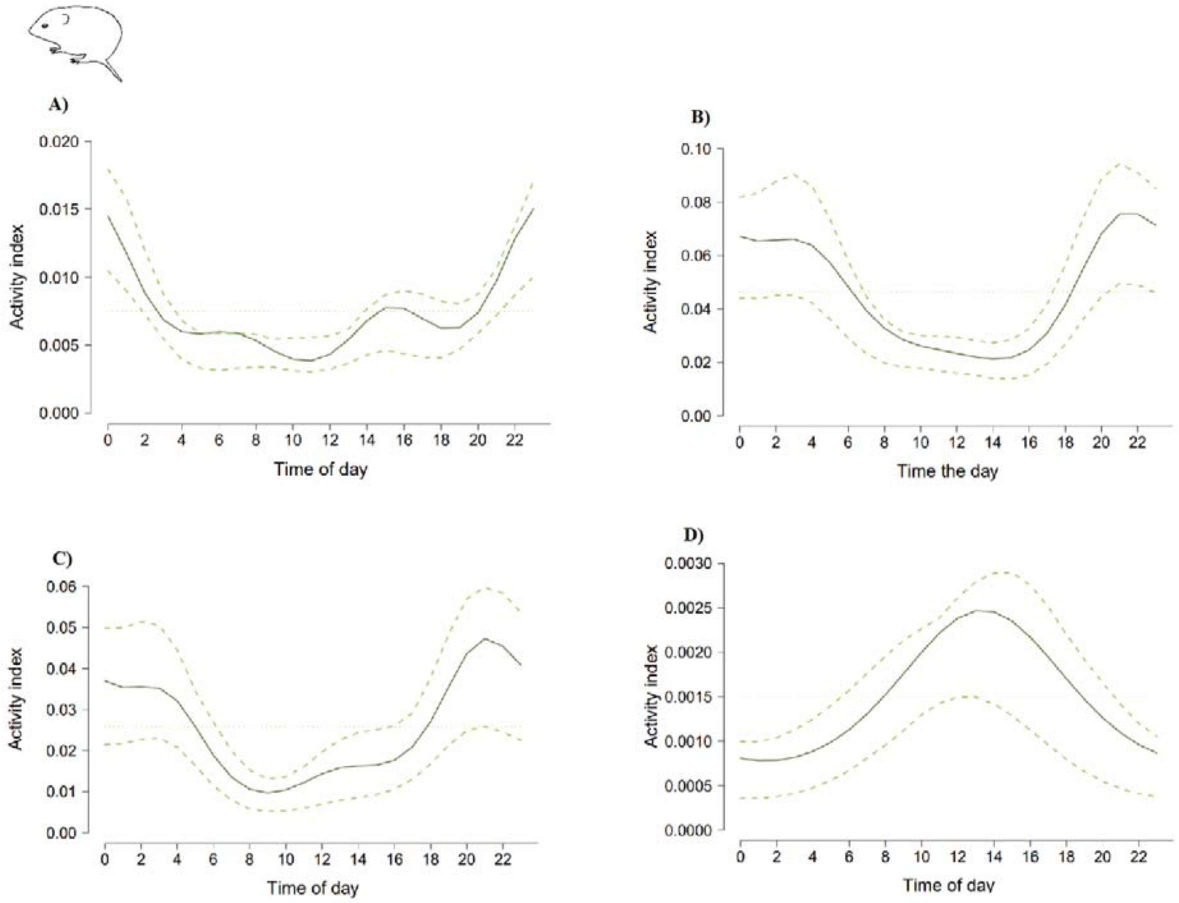


Figure 9: Modelled diel activity of *Microtus* voles from camera trap data, for A) Spring, B) Summer, C) Autumn and D) Winter. Fitted line in solid and upper and lower 95% CI in dashed lines. The MESOR (mean of the modelled activity curve) is indicated with a dotted line and parameter estimates are given in Tab. 4.

Table 4: Parameter estimates from the best-fitted model for *Microtus* vole activity. For spring, summer and autumn M3 was the best fit and for winter M1 was the best fit.

	Fixed effects	**Estimate**	**Std. Error**	**Z value**	**Pr (>|z|)**
Spring					
	(Intercept)	-4.960	0.155	-31.927	<0.001
	$I(\cos\left(2\pi\cdot\frac{hour}{24}\right))$	0.417	0.093	4.510	<0.001
	$I(\sin\left(2\pi*\frac{hour}{24}\right))$	-0.169	0.095	-1.781	0.075
	$I(\cos 2*\left(2\pi*\frac{hour}{24}\right))$	0.131	0.094	1.398	0.162
	$I(\sin 2*\left(2\pi*\frac{hour}{24}\right))$	0.046	0.093	0.499	0.618
	$I(\cos 3*\left(2\pi*\frac{hour}{24}\right))$	0.191	0.091	2.098	0.036
	$I(\sin 3*\left(2\pi*\frac{hour}{24}\right))$	-0.146	0.091	-1.598	0.110
Summer					
	(Intercept)	-3.122	0.302	-10.349	<0.001
	$I(\cos\left(2\pi*\frac{hour}{24}\right))$	0.663	0.039	17.089	<0.001
	$I(\sin\left(2\pi*\frac{hour}{24}\right))$	0.063	0.037	1.725	0.085
	$I(\cos 2*\left(2\pi*\frac{hour}{24}\right))$	-0.061	0.037	-1.620	0.105
	$I(\sin 2*\left(2\pi*\frac{hour}{24}\right))$	-0.106	0.038	-2.783	0.005
	$I(\cos 3*\left(2\pi*\frac{hour}{24}\right))$	-0.111	0.036	3.058	0.002
	$I(\sin 3*\left(2\pi*\frac{hour}{24}\right))$	-0.020	0.040	-0.405	0.685
Autumn					

(Intercept)	-3.756	0.278	-13.531	<0.001
$I(\cos\left(2\pi * \frac{hour}{24}\right))$	0.666	0.061	13.122	<0.001
$I(\sin\left(2\pi * \frac{hour}{24}\right))$	-0.242	0.050	-4.818	<0.001
$I(\cos 2 * \left(2\pi * \frac{hour}{24}\right))$	0.012	0.050	0.240	0.811
$I(\sin 2 * \left(2\pi * \frac{hour}{24}\right))$	0.057	0.051	1.113	0.266
$I(\cos 3 * \left(2\pi * \frac{hour}{24}\right))$	-0.182	0.048	-3.800	<0.001
$I(\sin 3 * \left(2\pi * \frac{hour}{24}\right))$	-0.056	0.048	-1.162	0.245

Winter

(Intercept)	-6.581	0.277	-23.747	<0.001
$I(\cos\left(2\pi * \frac{hour}{24}\right))$	-0.543	0.180	-3.022	0.003
$I(\sin\left(2\pi * \frac{hour}{24}\right))$	-0.205	0.174	-1.176	0.240

3.2.2 Bank voles

Based on AIC modelling for spring bank vole activity, the null model (M0) was the most parsimonious model. This indicated that there was no apparent pattern to be found in our data for spring activity. We used the next-best fitted model, M1, to create the activity curve for spring activity, this model had ΔAICc=1.47. When modelling activity for summer, several models had ΔAICc <2.0. We selected the most parsimonious model with as few predictor variables as possible. For summer bank vole activity, we chose M1, with ΔAICc=0.78.
A graphical representation of the activity is shown in Fig.10A. There was an indication that the activity peaks in the dark hours of the night (between hour-blocks 22-03). There was a clear period of inactivity in the light hours of the day, during hour-blocks 08-18 (Fig.10A). The bank voles were distinctly night active in the summer. When modelling autumn activity for bank voles, two models had ΔAICc <2.0. We chose M1, with ΔAICc= 1.17. The activity

clearly ceased during the daylight hours, between hour-block 06 and 16 (Fig.10B). There was also a peak in activity during the darker hours, between hour-block 20 and 01(Fig.10B).
M1 was the most parsimonious model for winter activity of bank voles, the other models had considerably lower support ΔAICc ≥2.0. The activity pattern in wintertime was unimodal and concentrated in the daylight hours, with a peak in activity in hour-blocks 10-14 (Fig.10C).

Table 5: Model selection table showing number of parameters (K), AICc, Δ AICc, AICc weights (AICcWt), cumulative weight (Cum.Wt) and log-likelihood (LL) for bank voles.

	Model	**K**	**AICc**	**ΔAICc**	**AICcWt**	**Cum.Wt**	**LL**
Spring							
	M0	2	839.53	0.00	0.64	0.64	-417.76
	M1	4	841.00	1.47	0.30	0.94	-416.50
	M2	6	844.71	5.19	0.05	0.99	-416.36
	M3	8	847.34	7.81	0.01	1.00	-415.67
Summer							
	M2	6	3923.94	0.00	0.43	0.43	-1955.97
	M1	4	3924.72	0.78	0.29	0.73	-1958.36
	M3	8	3924.88	0.94	0.27	1.00	-1954.44
	M0	2	3948.66	24.72	0.00	1.00	-1972.33
Autumn							

	M3	8	4490.39	0.00	0.54	0.54	-2237.19
	M1	4	4491.57	1.17	0.30	0.84	-2241.78
	M2	6	4492.77	2.37	0.16	1.00	-2240.38
	M0	2	4546.90	56.50	0.00	1.00	-2271.45
Winter							
	M1	4	724.76	0.00	0.70	0.70	-358.38
	M2	6	726.77	2.02	0.26	0.96	-357.38
	M3	8	730.55	5.80	0.04	0.99	-357.28
	M0	2	734.50	9.75	0.01	1.00	-365.25

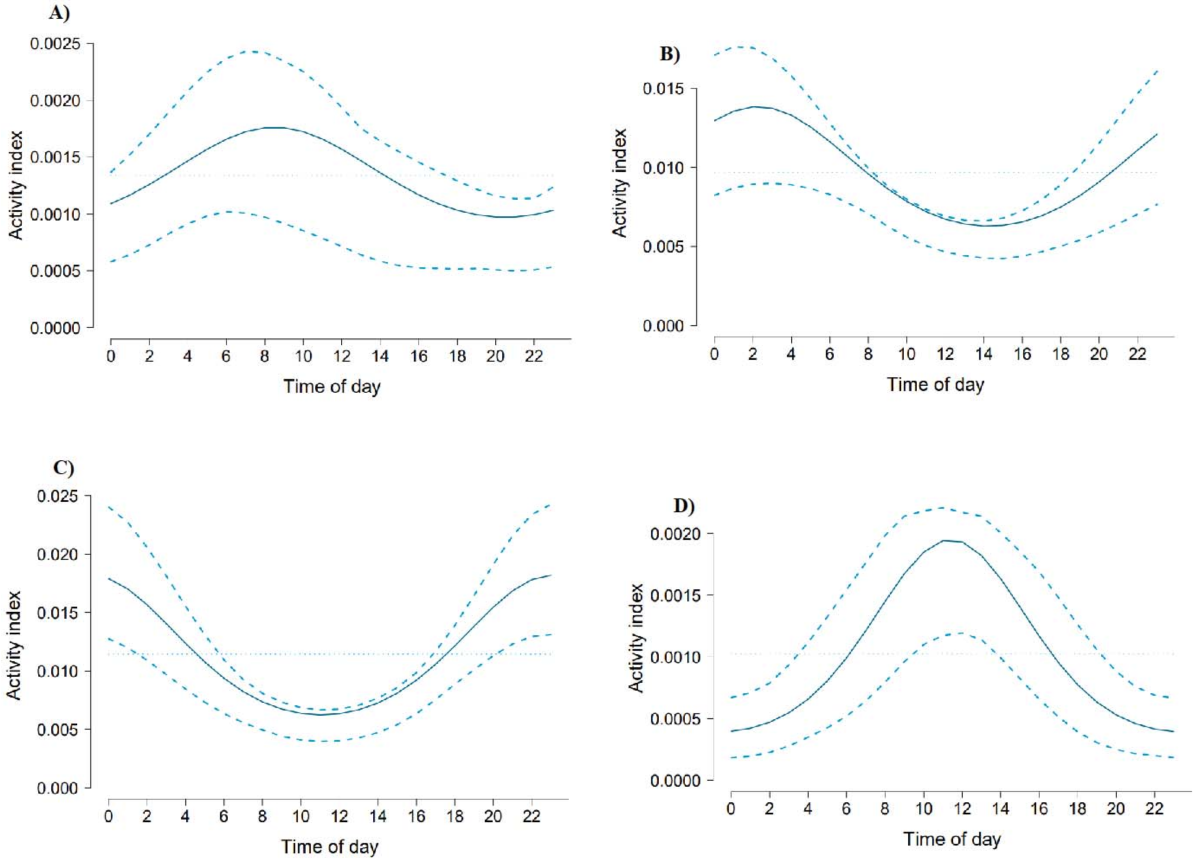


Figure 10: Modelled diel activity of bank voles from camera trap data, for A) Spring, B) Summer, C) Autumn and D) Winter. Fitted line in solid and upper and lower 95% CI in dashed lines. The MESOR (mean of the modelled activity curve) is indicated with a dotted line and parameter estimates are given in Tab. 6. M0 was the best-fitted model for spring, but the next-best fitted model was used to model activity.

Table 6: Parameter estimates from the best-fitted model for bank vole activity. For spring M0 was the best fitted model, but M1 AIC was < 2.00 and was therefore included. For summer, autumn and winter M1 was the best fit.

	Fixed effects	Estimate	Std. Error	Z value	Pr (>|z|)
Spring					
	(Intercept)	-6.637	0.393	-16.886	<0.001
	$I(\cos\left(2\pi \cdot \frac{hour}{24}\right))$	-0.182	0.185	-0.982	0.326
	$I(\sin\left(2\pi \cdot \frac{hour}{24}\right))$	0.237	0.186	1.275	0.202
Summer					
	(Intercept)	-4.910	0.299	-16.396	<0.001
	$I(\cos\left(2\pi \cdot \frac{hour}{24}\right))$	0.342	0.082	4.152	<0.001
	$I(\sin\left(2\pi \cdot \frac{hour}{24}\right))$	0.280	0.082	3.363	<0.001
Autumn					
	(Intercept)	-7.164	0.301	-23.808	<0.001
	$I(\cos\left(2\pi \cdot \frac{hour}{24}\right))$	1.730	0.298	5.794	<0.001
	$I(\sin\left(2\pi \cdot \frac{hour}{24}\right))$	-0.249	0.223	-1.117	0.264
Winter					
	(Intercept)	-7.040	0.315	-22.318	<0.001
	$I(\cos\left(2\pi \cdot \frac{hour}{24}\right))$	0.792	0.226	-3.514	<0.001
	$I(\sin\left(2\pi \cdot \frac{hour}{24}\right))$	0.124	0.210	0.592	0.554

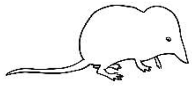
3.2.3 Shrews

M1 was the most parsimonious model for spring activity of shrews, the other models had considerably lower support ΔAICc ≥2.0. A graphical representation of the activity is shown in Fig.11A. The model showed an inactive period in the middle of the day, from hour-blocks 08 to 17 (Fig.11A). M3 was the most parsimonious model for summer activity of shrews, the other models had considerably lower support ΔAICc ≥2.0. Fig.11B shows the activity pattern of shrews in summertime. The activity pattern showed an increase in activity during the dark hours, between hour-blocks 21 and 05 (Fig.11B). A peak in activity was apparent between hour-blocks 02 and 04 (Fig.11B). There was also an inactive period in the daylight hours between hour-blocks 07 and 17 (Fig.11B). M1 was the most parsimonious model for autumn activity of shrews, the other models had considerably lower support ΔAICc ≥2.0. A graphical representation of the activity is shown in Fig. 11C. The model shows an inactive period in the middle of the day, from hour-blocks 09 to 13 (Fig.11C). Based on AIC modelling for winter shrew activity, the null model (M0) was the most parsimonious model (Tab.7). This indicated that there was no apparent pattern to be found in our data for winter activity. We used M1 to create an activity pattern for winter, M1 had ΔAICc=2.28, so the activity pattern is not significant.

Table 7: Model selection table showing number of parameters (K), AICc, ΔAICc, AICc weights (AICcWt), cumulative weight (Cum.Wt) and log-likelihood (LL) for shrews.

	Model	**K**	**AICc**	**ΔAICc**	**AICcWt**	**Cum.Wt**	**LL**
Spring							
	M1	4	1550.72	0.00	0.59	0.59	-771.36
	M3	8	1552.32	1.60	0.27	0.86	-768.16
	M2	6	1553.57	2.85	0.14	1.00	-770.78
	M0	2	1562.95	12.23	0.00	1.00	-779.48

Summer							
	M3	8	13213.63	0.00	0.94	0.94	-6598.81
	M2	6	13219.14	5.52	0.06	1.00	-6603.57
	M1	4	13230.46	16.84	0.00	1.00	-6611.23
	M0	2	13552.62	338.99	0.00	1.00	-6774.31
Autumn							
	M1	4	6174.26	0.00	0.76	0.76	-3083.13
	M2	6	6177.65	3.39	0.14	0.90	-3082.82
	M3	8	6179.50	5.24	0.06	0.95	-3081.75
	M0	2	6179.90	5.64	0.05	1.00	-3087.95
Winter							
	M0	2	2141.20	0.00	0.70	0.70	-1068.60
	M1	4	2143.49	2.28	0.22	0.93	-1067.74
	M2	6	2146.01	4.81	0.06	0.99	-1067.00
	M3	8	2149.50	8.30	0.01	1.00	-1066.75



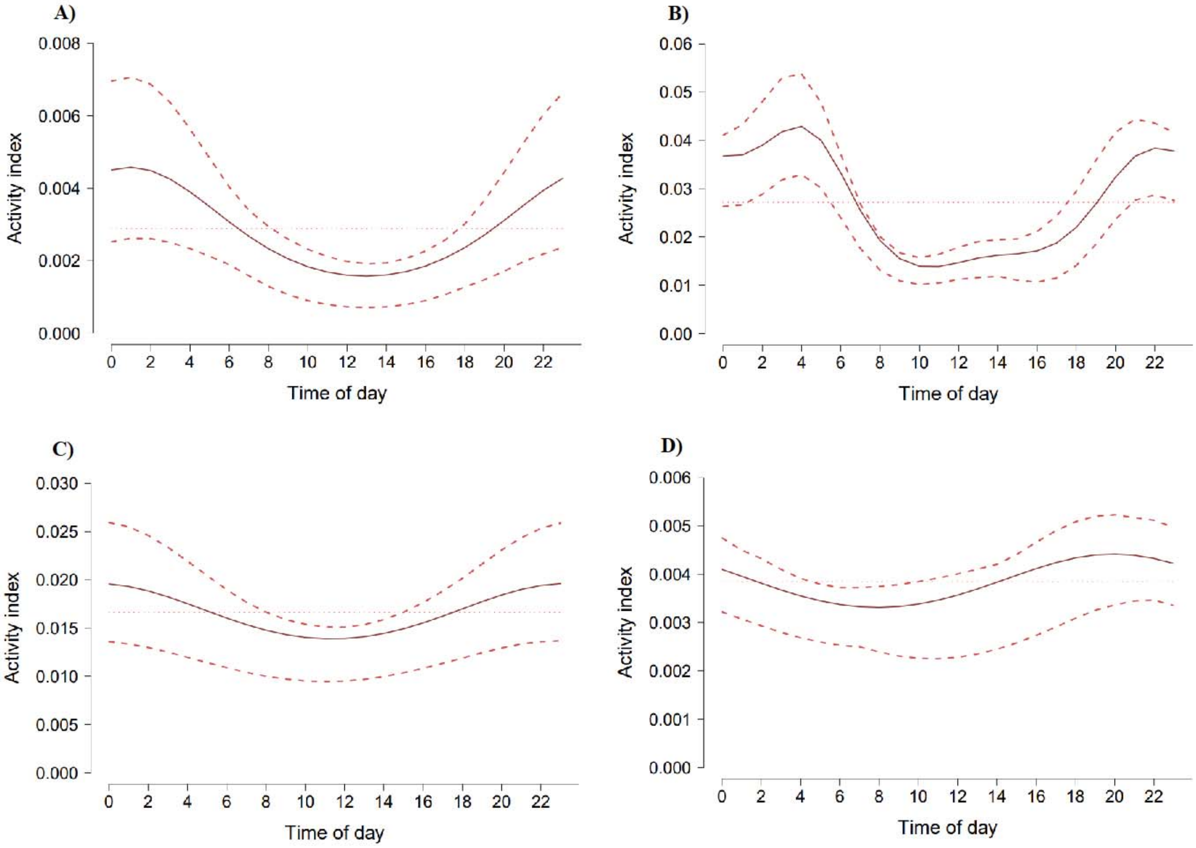


Figure 11: Modelled diel activity of shrews from camera trap data, for A) Spring, B) Summer, C) Autumn and D) Winter. Fitted line in solid and upper and lower 95% CI in dashed lines. The MESOR (mean of the modelled activity curve) is indicated with a dotted line and parameter estimates are given in Tab. 8. M0 was the best-fitted model for spring, but the next-best fitted model was used to model activity. The modelled activity for winter was not significant.

Table 8: Parameter estimates from the best-fitted model for shrew activity. For spring and autumn M1 was the best fit, for summer M3 was the best fit. And for winter M0 was the best fit, but M1 is included.

	Fixed effects	**Estimate**	**Std. Error**	**Z value**	**Pr (>|z|)**
Spring					
	(Intercept)	-5.916	0.362	-16.331	<0.001
	$I(\cos\left(2\pi\cdot\frac{hour}{24}\right))$	0.519	0.135	3.844	<0.001
	$I\left(\sin\left(2\pi\cdot\frac{hour}{24}\right)\right)$	0.132	0.131	1.007	0.314
Summer					
	(Intercept)	-3.660	0.220	-16.616	<0.001
	$I(\cos\left(2\pi\cdot\frac{hour}{24}\right))$	0.561	0.051	11.081	<0.001
	$I(\sin\left(2\pi\cdot\frac{hour}{24}\right))$	0.119	0.048	2.486	0.022
	$I(\cos\left(2\cdot 2\pi\cdot\frac{hour}{24}\right))$	-0.077	0.049	-1.575	0.115
	$I(\sin\left(2\cdot 2\pi\cdot\frac{hour}{24}\right))$	0.050	0.049	1.002	0.316
	$I(\cos\left(3\cdot 2\pi\cdot\frac{hour}{24}\right))$	-0.090	0.048	-1.891	0.057
	$I(\sin\left(3\cdot 2\pi\cdot\frac{hour}{24}\right))$	-0.094	0.048	-1.983	0.047
Autumn					
	(Intercept)	-4.090	0.237	-17.283	<0.001
	$I\left(\cos\left(2\pi\cdot\frac{hour}{24}\right)\right)$	0.174	0.057	3.058	0.002
	$I\left(\sin\left(2\pi\cdot\frac{hour}{24}\right)\right)$	-0.030	0.057	-0.523	0.601

Winter

(Intercept)	-5.562	0.229	-24.309	<0.001
$I\left(\cos\left(2\pi\cdot\frac{hour}{24}\right)\right)$	0.070	0.109	0.639	0.523
$I\left(\sin\left(2\pi\cdot\frac{hour}{24}\right)\right)$	-0.126	0.110	-1.152	0.249

3.3 Optional method for creating activity curves

In spring, *Microtus* vole activity was characterized by a general dip in activity during the daylight hours, and an increase in activity during the dark hours (Fig.12). *Microtus* voles showed similarities in the activity pattern in summer and autumn. The peak in activity differed between the two seasons. In summer, the peak in activity was in the morning, while the peak was more evident in the evening in autumn. In wintertime, however, there was an opposite pattern with increased activity during the light hours of the day (Fig.12). Bank voles showed no obvious pattern of activity in the spring, with a flatter curve and large variation in both lower and upper CI, and with only a small peak just before midday (Fig.12). In the summertime, bank voles had a clear dip in activity during the daylight hours. The most pronounced resting period was in hour-blocks 12-17 (Fig.12). Bank voles showed the same pattern in autumn as in summer. In winter, the activity pattern was the opposite, with increased activity during the daylight hours, peaking in hour-block 12. In springtime shrews were generally less active during the daylight hours, with a pronounced decrease in activity after sunrise. This pattern persisted in the summer, which also had a resting period in the daylight hours. In autumn, however, shrews had a more uniform pattern of activity, with only a slight tendency of a dip in the daytime (Fig.12). In wintertime, there was no evident activity pattern for shrews. The curve was quite flat, and there was large variation in the upper and lower CIs (Fig.12).

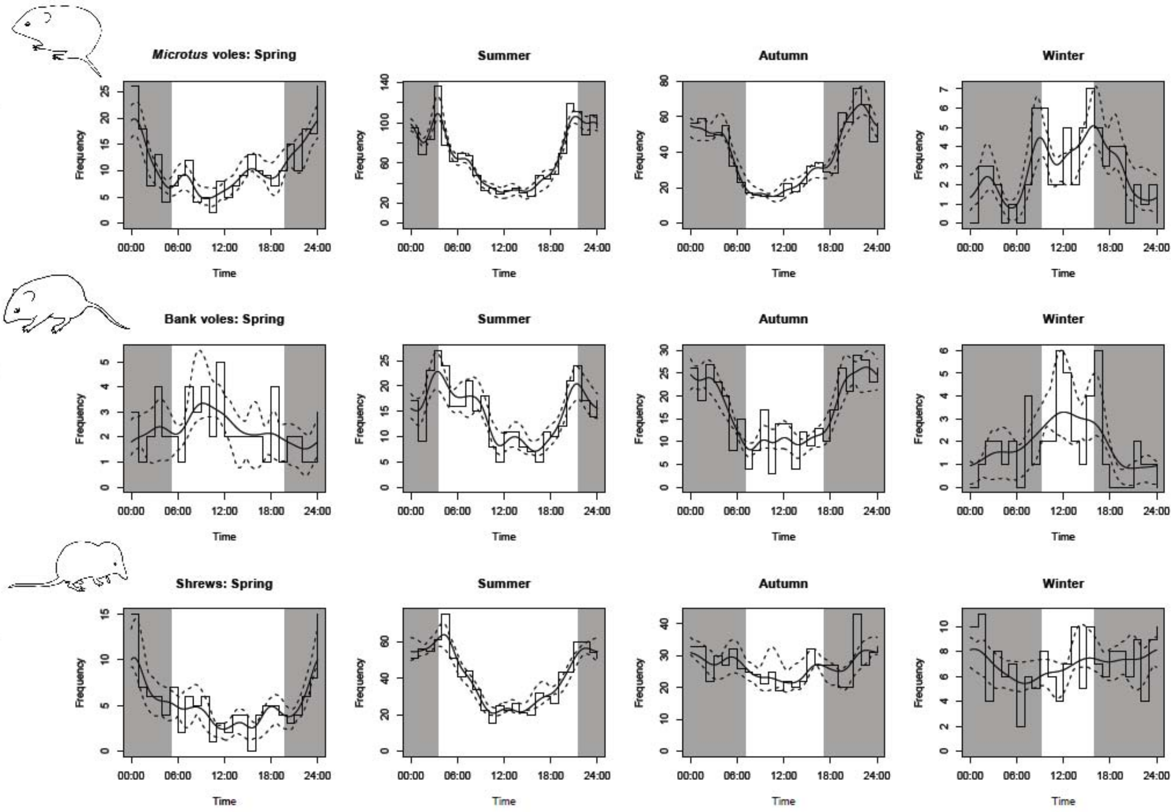


Figure 12: Kernel density estimation of species diel activity for all seasons. Shaded grey areas represent sunrise and sunset. Fitted line in solid and upper and lower 95% CI in dashed lines.

4. Discussion

4.1 Discussion of Methods

Using camera traps allowed us to monitor the study species over an extended period of time in their natural habitat (O'Conell et al., 2011). Because of the complex ecology of small mammals, laboratory experiments are not so suitable for ecological-evolutionary discussion (Halle & Stenseth, 2000). The activity patterns of small mammals also exhibit a high degree of plasticity, and therefore only analyses under natural conditions could yield relevant information (Halle & Lehman, 1987). We therefore believe that the results derived from this field study will to a greater degree represent the natural activity-patterns of *Microtus* voles, bank voles and shrews. In addition to observing the study species in their natural habitat, the cameras also allowed us to study the species around the clock over several years. Our data consists of three years of data pooled, and we are not sure how this has affected our results. When creating the activity curves for each season the years were pooled so the sample size would be higher. For the bubble plot we also created plots for each year separately (Fig. 1-3, Appendix), this demonstrates the low sample size for some of the years. There are most likely differences in snow cover, temperature, precipitation and population size between the different years. The onset and end of snow cover varied between the years. However, when creating the bubble plots, we used the median for all years (Tab. 1, Appendix). The summer of 2018, for example, was extremely warm compared to the other years (data for Møsvatn weather station, available from www.eklima.no). We suspect that this had an effect on the habitat and interactions in our study area. The delayed response of this warm summer might explain the small amount of data in 2019. But then again, populations of small mammals are adapted to the variations in their habitat and fluctuations in small mammal populations is well known and studied (Dobrinskii, 2017; Halle & Lehman, 1987; Oli, 2003). Therefore the activity curves we have generated might give a better understanding of their activity compared to a study done for only one year or one season (Soininen et al., 2015). But it is important to note that our study is of populations, and not individual activity.

When monitoring small mammals in the wild through camera traps, it is not possible to distinguish between individuals, like Johnsen et al. (2019) did when using capture-recapture. There was therefore no way of knowing if we had captured the same individual on camera several times. Our data could therefore be heavily influenced by a few individuals of the population being more active than the majority. However, because of the length of our study period, we deem it less likely that these individuals would have a big impact on our activity-data. One individual could also stay in the trap-box over a longer time-period and trigger several releases. To account for this possible flaw in our methods, we chose to score the hour-blocks for presence rather than number of animals. When using the dataset to create kernel-density, we applied a 30 min gap to avoid pseudoreplication as a consequence of these extended visits. It seems like most researchers have set a time-gap they see fit for their study. O'Brien et al. (2003) did a study on tigers in Indonesia where they set a 30 min gap because they observed that another individual did not visit the camera before 30 min had passed. We therefore decided, based on examining the images, that a 30 min gap was suitable for our study. This decision is supported by the similar result for both methods used to create activity curves. By using camera trapping, we could also not acquire data on sex, age or reproductive status to use in further analyses. Because of their complex interactions between the individuals, data on such properties is perhaps important for explaining the nature of their activity patterns. Not being able to distinguish between individuals of the same species could therefore have an unknown effect on our data.

When sorting the data-material in this study, it was also difficult to differentiate some of the study species. There were times when the species of the individual captured on camera could not with certainty be determined as *Microtus* vole or bank vole. We therefore created the folder named “voles” to capture these undistinguishable individuals. This accounts for 7 % of the data (Tab. 2). This problem led to a reduction in data for *Microtus* voles and bank voles, which again could have had a possible impact on our activity curves. We were also not able to distinguish between the different species belonging to *Microtus* and shrews in the study area just by looking at the camera trap pictures. It is possible that these species have different activity patterns, and that the merging of these patterns influenced our presented activity-patterns. We have not, however, found any previous studies supporting such intraspecific variation**.** The generalisation might therefore not be a problem for our results. A strong suit for this study is that we were two people identifying the images. In a comparative study of camera traps and traditional live-capture methods, Thomas et al. (2020) also used two examiners to review all photographs, and they advocate this strategy for other camera-trapping studies. In addition to us being two people to determine species from the images, our thesis advisor Ronny Steen controlled our species identification. These failsafes improved our sorting accuracy, and thereby made our data sorting more reliable for further analyses. When sorting and preparing the dataset for further analyses, its size may have been reduced due to difficulty of species identification. However, we accounted for this possible loss of data by setting up several trap boxes in the study area.

We placed five trap boxes in close proximity to each other in our study area, but there might still be differences between the locations. The dataset used to generate the activity curves, both using the cosinor-method and the kernel-density method, included data from all five locations pooled. We observed that the boxes had varying numbers of visits, and some boxes were more frequently visited than others. This could be owed to the fact that the trap boxes were not placed based on knowledge of where the small mammals were known to be. In the cosinor-method, site identity was included as random effect to account for possible variations among sites. We did not locate runway systems before placing the trap boxes. In their paper from 1992, Halle and Lehmann discussed possible weaknesses with their passage counters that could be transferable to our methods: we do not know which type of activity we are observing. Halle and Lehmann say that movement within the runway system can be seen as “routine behaviour” and movement outside these runways is exploratory behaviour. The exploratory behaviour constitutes less of their daily movement (Halle & Lehman, 1992). If our trap boxes were placed in an area where the voles only have exploratory movement, we have less and different data than we could have gathered if the trap boxes were placed as a part of the runway system. Because we used data from the five trap boxes, it is more likely that we have data from both “routine behaviour” and “exploratory behaviour”.

We do not know in which way, or if, the methods used in this study have influenced our results. However, as this study is performed in the field and in the natural habitat of the study species, we see the results as relevant in an ecological context.

4.2 General activity

The data in this study was gathered 24-hours a day, 365 day a year over the course of three years. This allowed us to make activity patterns for all four seasons. In the results we see a panel with a graphical depiction of our three study species, *Microtus* voles, bank voles and shrews. We can see that most of the data was collected during the snow free period. This applies to all our study species. This does not necessarily mean that the voles and shrews are not active during winter, they might just be less trappable during this season. In a study on red squirrels Boon et al. (2008) found that an animals personality is bound to risk taking, and therefore also movement. Hence, the trappability might be linked to risk-taking. In our method the animals are “trapped” when they explore the trap box. We know from literature that voles are active underneath the snow cover in tunnels during winter, while shrews most likely search for food under the snow (Bjärvall & Ullström, 1997). Soininen et al. (2015) had a field study in 2013 where camera traps were used to monitor small mammal activity under the snow cover. In this study they performed a live trapping session before the camera trapping to locate the runways for the small mammals in the study, making it possible to place the cameras in these runways. In our study the trap boxes were placed “randomly” based upon easy accessibility and closeness to vegetation. They were placed close to vegetation so they would take a more natural part of the habitat, being less invasive. The camera inside the trap box did not have white flash (only invisible infrared light), this was to not startle the animals.

Our findings illustrate that the species in this study is somehow bound to the LD-cycle. The vole species (*Microtus* voles and bank voles) show a higher activity level in the dark hours while shrews follow this pattern in the summer but are generally more active throughout the 24 hours in the other seasons. This pattern seems to be more dominant for *Microtus* voles, this might be due to the considerably higher sample size. It has been suggested that the activity of small mammals is synchronised with the LD-cycle (Halle & Stenseth, 2000**).** Halle and Stenseth (2000) pointed out that the LD-cycle reflect changes in temperature, humidity, food availability and predation. It is also precise and consistent, and therefore is likely to act as a zeitgeber for the circadian clock in voles. In addition to the LD-cycle, the population size and the stage in the population cycle also influence the activity level of small mammals. If the population size is small, microtine rodents become less active during the light hours because they are more vulnerable when they are few in numbers (Halle, 2006). According to Halle and Stenseth (2000) the activity of small mammals is dependent on the area and the predators present in this area. They also note that because of the predator threat, the first mammals were probably nocturnal, and it is likely that small mammals have kept this trait.

In addition, we generated a graphical presentation of diel activity for all species for the years 2017, 2018 and 2019 separately (Fig. 1-3, Appendix). From this we can clearly see that we captured most *Microtus* voles on camera in 2017 compared to the other years. This demonstrates a phenomenon found for several rodents, population cycles or fluctuations. Elton (1924) published a paper discussing fluctuations in mammals. He found that voles and lemmings follow a fluctuation every 3-5 years. And these fluctuations in vole populations have been studied in great detail ever since. Elton (1924) suggested climatic factors cause these population cycles, but other factors, such as predators (Oli, 2003) have also been suggested. Some also suggest seasonality as an explanation for the cyclic populations of voles (Andreassen et al., 2019). For our study area the seasons have large variations and we find it likely that the seasons have great impact on the small mammal population. Shrews are also known to have cyclic populations, but these fluctuations differ between geographical areas. Shrews have high metabolism, and are therefore more dependent on climate (Erdakov et al., 2019). To analyse our data, we have three graphical presentations. The graphical depiction of our data, which we have discussed above, activity curves created using the cosinor-method for each study species for the different seasons (only the curves which the pattern could be explained) and a kernel-density plot.

4.3 Seasonal activity

For the seasonal activity, we have created activity curves for each study species for spring, summer, autumn and winter. Spring is March, April and May, summer is June, July and August, autumn is September, October and November, while winter is December, January and February. We generated the activity curves in seasons because a lot of the variation in activity is bound to the seasons. Snow cover is found in all seasons except summer. There is higher variation between the three months for spring and autumn due to the large difference in ambient temperature for day and night. In springtime the day gradually becomes longer, the temperature rises, and the snow cover is melting. The opposite happens in autumn, when the day becomes shorter, temperatures colder and snow cover starts. Sunlight hours are scarce during the cold period, and in summer the sun is up for a large part of the 24-hour cycle. Due to the large variation within and between the seasons we can assume a lot of the activity can be explained by this. Another important factor is the predators in the area.

On the cameras we caught pictures of least weasel, stoat and European viper. All of these predators are known to have small rodents as a part of their diet (Bjärvall & Ullström, 1997; Dolmen, 2008). Although not caught on camera, there are also avian predators, like raptors present in the area (pers. obs.). For shrews the more common predator are owls. Many other predators do not eat them because of their strong smell (Bjärvall & Ullström, 1997). The red fox for example, only kills shrews for entertainment (Selås, 2020b). Erlinge (1975) found in a study on least weasel that they did not prefer shrews, and that they only ate shrews when resources were scarce. This makes voles the more preferred prey. Unfortunately, the sample size for the predators in the area was not large enough to analyse. We will further discuss the possible influence of predators, LD-cycle and foraging on the activity of *Microtus* voles, bank voles and shrews.

4.3.1 *Microtus* voles

Microtus voles exhibited a general pattern of a resting period in the daylight hours for all seasons except winter, both in the cosinor-models and in the kernel-density models. The start of the resting period seemed to follow sunrise-times for the different seasons. In spring, the decrease in activity started in hour-block 02-03. This decrease in activity was also evident in the modelled activity for summer, where the activity of *Microtus* voles decreased in hour-block 06-07. In autumn, the onset of the resting period was in hour-block 05-06. The time of day that the activity of the *Microtus* voles increased from below to above the MESOR (upward crossing) in spring was during hour-block 19-20, with a peak in activity around midnight (hour-block 24). This was consistent with sunset-times for the spring months. In the summertime, the activity curve crossed from below to above the MESOR in hour-block 18-19. It therefore seemed that the resting period of *Microtus* voles is somewhat shortened in the summertime. In autumn the onset of activity after the resting period was in hour-block 17-18, again consistent with sunset-times for the months in question. The pattern for *Microtus* vole activity in the winter differed markedly from the other seasons. The activity in winter was unimodal, with a peak in the daylight hours. The fitted line crossed from below to above the MESOR in hour-block 07-08, which indicated the onset of activity. This was also consistent with the times for sunrise in the winter-months. The peak activity was in hour-blocks 11-14. The activity curves illustrate that there was a resting period in the darker hours, with a decrease in activity that started in hour-block 19-20. There was a clear pattern of preference for nocturnal activity in all seasons except winter, and no evidence of polyphasic activity for *Microtus* voles.

Previous studies have described *Microtus* vole activity as polyphasic (Halle & Lehman, 1987; Halle, 2006; Ylönen et al., 2019) and the voles are known to have short activity bouts throughout the day (Halle, 2000b; Halle, 2006). Our data did not show a clear pattern of polyphasic activity for *Microtus* voles. There was, however, tendencies of activity bouts during the period of lower activity in spring and autumn. Halle reported activity bouts every 2 or 3 hours during daytime for individual *Microtus* voles (Halle, 2006). These activity bouts are largely related to sunrise and sunset, and their placement changes with season. When considering activity of *Microtus* voles, the nature of the circadian clock is often discussed. It is acknowledged that the LD-cycle is an important zeitgeber for the circadian clock (Bartness & Albers, 2000; Halle, 2006). The short-term rhythm (ultradian rhythm) of voles is under control of this circadian clock. We most likely did not detect the clear pattern of activity bouts reported by Halle because our study was done on population level. It is not likely that these short activity bouts are synchronised for all individuals in a population. In his study, Halle also reported a prominent 1-hour activity bout around sunrise (Halle, 2006). This pattern was evident in spring, summer and autumn in our data. In both summer and autumn, there was a small increase in activity before sunset. This pattern is consistent with descriptions made by Halle in his studies on voles and polyphasic activity, where he described an activity bout before the onset of night-activity (Halle, 2006). The observed activity bouts before the rest-period and the onset of activity may be more synchronised in the population than the short activity bouts during the rest period. This would explain why we saw this pattern more clearly. In a more recent study on arvicoline rodents, Halle (2006) described *Microtus* voles as cathermal, with routine activity during the day, night and twilight. This cathermal activity explanation is more relevant for our findings, as we also found a phase shift in preferred time for activity. Our data did not show a clear pattern of polyphasic activity for *Microtus* voles, but rather showed that they have a preference for diurnal activity in winter and nocturnal activity in all other seasons.

The apparent activity pattern might also be interpreted as an anti-predator strategy, as microtines are a prominent prey item for several aerial and ground predators (Halle, 2000b). The predators in the area, such as the stoat, least weasel, European viper, red fox and raptors, all have their own activity timing and time for hunting. Raptors and European vipers are mainly active during the day (Halle, 1993), while Mustelid carnivores (stoat and least weasel) are active about 25% of the 24-h day (Zielinski, 2000). Owls are nocturnal predators (Rajković, 2018). Most studies have found red foxes to be nocturnal and crepuscular (Díaz-Ruiz et al., 2016). Tengmalm's owl is a very prominent predator of voles. It has been suggested that it is favourable to start the daylight period with an inactive phase to reduce the risk of encountering diurnal avian predators (Korslund, 2006). The microtines therefore have to trade-off risk and assess the threat of the different predators. The voles are only available to raptors when they are active, while least weasels can enter their burrows when they are resting (Zielinski, 2000). It is therefore likely that the *Microtus* voles see the daylight as a more favourable time to rest, to avoid the probability of a close encounter with raptors. In the wintertime, *Microtus* voles depend on snow cover for optimal survival. Specialist predators, such as the least weasel, can hunt voles and shrews underneath the snow (Ylönen et al., 2019). Avian predators, on the other hand, mainly use visual cues when hunting, so shelter from the snow could yield higher survival for *Microtus* voles (Sipari et al., 2016).

Even though predation risk is a factor influencing activity patterns in *Microtus* voles, we believe that the activity pattern could be owed to several other factors as well. In a study on predation risk in the life of microtines, Halle found that there were no times of generally high or low predation risk throughout the day. He therefore, like us, believed that the activity of microtines is timed after some other demands as well. He suggested that short-term microtine activity could be timed after e.g. foraging/metabolism or social constraints (Halle, 1993). *Microtus* voles, and microtines in general, are specialised on bulky foods with high cellulose content (Weiner, 2000). This could indicate that the ultradian activity pattern for *Microtus* voles might be causally related to metabolism and digestion constraints. Because of the nature of the fermentation chamber in voles, it is best to add small portions of fresh plant material (Halle, 2006). This could also explain the tendency of activity bursts in spring and autumn. However, this strategy would require almost constant foraging activity, and thereby exposure to predators. It is therefore likely that the short-term rhythm of *Microtus* voles has developed as a trade-off between metabolistic demands and predation risk. While this trade-off could be a likely explanation for the daily pattern of activity, it could probably not explain the observed shift in preference for nocturnality and diurnality.

There was a clear shift from a preference for nocturnal activity to diurnal activity related to season. In an experimental study on *Microtus* voles, Erkinaro (1961) found evidence of diurnal activity in the first 4 months of the year (January-April). In May, he found a change in the pattern toward nocturnal activity. This pattern of nocturnality lasted until January. In our study, we found a similar result. We observed a change from nocturnality to diurnality in the winter-months. In the spring-months, we observed a resting period in the daylight-hours, with a tendency of small activity bursts. In his study, Erkinaro also observed a slightly more prevailing diurnal activity in March and April, and this could be comparable to our results for spring. Erkinaro's study was done in glass cages in a loft, with natural daylight to simulate the LD-cycle (Erkinaro, 1961). The conditions during this study were not likely to be the same as in the natural habitat, and this could explain why the results in this study differ from ours. When studying activity *M. agrestis* in the field by passage counters, Halle and Lehman also found that voles shift from nocturnal to diurnal activity (Halle & Lehman, 1987). However, they suggested that the phase shift does not depend on season, but rather is influenced by other factors. In a later study, they found the same pattern of phase shifts, and hypothesized that it could be correlated with the different stages of the population cycle (Halle & Lehman, 1992). Predation could also be a factor in the observed seasonal phase shift from nocturnality to diurnality. Halle suggested that if the numbers and activity of microtine voles are unpredictable, it could prevent predators from adapting to the otherwise stereotypical activity pattern (Halle, 1993). As the activity patterns of *Microtus* voles are generally very complex, we believe it to be more likely that the observed seasonal phase shift is owed to several different factors. As the LD-cycle is an important zeitgeber for the circadian pattern, we believe that a change in photoperiod could influence this phase shift. Additionally, we consider the stage in the population cycle as an important factor in defining the seasonal activity patterns of *Microtus* voles.

4.3.2 Bank voles

The seasonal activity of bank voles generally followed the same pattern as *Microtus* voles with resting periods in the daylight-hours, and increased activity in the dark hours. For spring activity of bank voles, the null model (M0) was the best fit. This indicated that there was no apparent pattern for activity in the spring. This was supported by the kernel-density model for activity, where there was huge variation around the prediction. We did model spring activity with the cosinor-method using the second best fitted model, M1. In this model, there was a tendency of a preference for diel activity. The resting period in summer was clear both in the kernel-density model and the cosinor-model, with a decrease in activity that started in hour-block 08-09. This dip in activity reached its low point in hour-block 13-14 and did not increase until hour-block 20-21. The pattern for bank vole activity in the autumn was similar to that in summer, with a clear resting period in the daylight-hours. The fitted line crossed from above to below the MESOR in hour-block 05-06 (downward crossing) and indicated the start of the resting period. The line crossed from below to above the MESOR in hour-block 17-18 and indicated the onset of activity. Similar to what we saw in *Microtus* voles, this pattern was reversed in the winter, with a peak in activity in the daylight-hours and decreases in activity during the night. There was a clear peak in activity in the middle of the day (hour-blocks 10-12). The fitted line crossed from below to above the MESOR in hour-block 05-06 and indicated the onset of activity. In hour-block 17-18, the fitted line crossed from above to below the MESOR and indicated the end of the active period and the start of the resting period. There was, however, a large variation (indicated by a large difference in upper and lower CIs) in activity in peak-hours of activity. The kernel-density model also had substantial variation around the prediction. The variation in activity in the darker hours was smaller in both models. In this study, bank voles exhibited a diurnal pattern in winter and a nocturnal activity pattern in autumn and summer.

Previous research on the activity patterns of bank voles show a variety of results. In a field study on bank voles, Greenwood (1978) found bank vole activity to be diurnal with activity peaks at dawn and dusk. This is the opposite of our findings, which indicated activity peaks during the dark hours of the night. However, this study was only conducted in the summer-months and may therefore not apply to the other seasons. The activity pattern is also based on data collected by monitoring the individuals in an area by sight, as compared to our data that was collected using camera trapping. In a field study, Ylönen (1988) found bank vole activity similar to what we found in this study. He found bank voles to have a preference of nocturnal activity in the autumn and spring. The modelled activity for autumn showed a clear nocturnal activity pattern. In spring, however, our results showed a peak in activity during the daylight hours. This is not consistent with the findings of Ylönen. Ylönen also found that bank voles had the same preference for nocturnal activity in summer, similar to our findings. He found the voles to be significantly more active during the light hours from autumn to the onset of breeding in the spring (Ylönen, 1988). Our findings of a unimodal diurnal activity in winter is similar to this finding. Ylönen used both live trapping and camera-monitoring of feeding sites to estimate activity patterns and feeding patterns. He found the feeding pattern to be similar to that of general activity, with a preference for nocturnal feeding in the spring, a uniform pattern in summer, feeding at dusk in autumn and a diurnal feeding-pattern in winter (Ylönen, 1988). Our findings are most similar to those of Ylönen (1988), where there is a clear preference for nocturnal activity in summer and autumn.

The observed pattern of nocturnal activity in summer and autumn could be related to predator avoidance. Bank voles generally have the same predators as *Microtus* voles, with several predator groups posing as threats. The mammalian predators, such as the stoat, least weasel and the red fox, tend to be more active at night, while raptors and other avian predators are more active in the daylight hours (Halle, 1993). Like mentioned when discussing predator-avoidance strategies in *Microtus* voles, least weasels can hunt microtine rodents in their burrows as well as above ground. Bank voles (and other microtine species) might therefore adjust their activity after the hunting pattern of other predators. Assuming bank voles deem avian predators as the largest threat, it is logical that they have a period of inactivity during the active hunting phase of these diurnal predators. If this is the case, it would also explain the similarities in the activity patterns for *Microtus* voles and bank voles. The confidence intervals on the activity models also showed relatively little variation in the inactive periods. This indicated a synchronised rest period in the middle of the day. Halle and Stenseth (2000) suggested that synchronising resting periods gives energetic benefits due to thermoregulation. For the dark hours, on the other hand, the variation in activity was quite large. Synchronous activity might result in an increase in individual predation risk (Halle, 2000a) When more prey specimens are active at the same time, predators may concentrate their hunting efforts in that particular time-window or that specific location. It might therefore be advantageous for the bank voles to disperse their activity. On the other hand, synchronous activity might be a way to reduce predation risk, because there is safety in numbers. Halle and Stenseth termed this the dilution effect (Halle, 2000a). When synchronising their activity, voles may also exchange warning signals and thereby increase their chances of survival. As well as being a possible explanation for the observed pattern of nocturnal activity in autumn and summer, predator-avoidance may also be related to the shift toward diurnal activity in winter.

Similarly to the pattern of *Microtus* voles, the winter activity of bank voles was also unimodal and diurnal. A factor that could maybe explain this change in behaviour is increased predation pressure from specialized predators. *Microtus* voles and bank voles share the same predator species, and bank voles are also under threat from least weasels. Jędrzejewska and Jędrzejewski conducted an enclosure experiment on bank voles and weasels to examine whether bank voles adapted their activity in the presence of a specialist predator (weasels). The study was conducted in three enclosures in Poland with populations of voles captured from a nearby location. They found that the diel rhythm of bank vole activity was characterized by distinct peaks at dawn and that the voles were almost completely inactive at night-time (Jędrzejewska & Jędrzejewski, 1990). When there was a weasel present, however, the bank voles distributed their activity more evenly throughout the day. This suggests that the changes in activity patterns could be related to predator avoidance. However, the density of the bank voles and weasels in the pens was unnaturally high, and thus it may be that the results cannot be applied to natural conditions. Although the change in activity could be owed to predator avoidance, this is not likely to be the sole reason. In a study on caged bank voles, Sipari et al. (2016) found that bank voles exposed to fluctuating temperatures adjusted their activity to be more diurnal compared to bank voles exposed to stable temperatures. With a stable subnivean environment, bank vole survival increases, however, some individuals will survive without snow cover as well (Halle & Stenseth, 2000; Selås et al., 2019; Sipari et al., 2016; Ylönen et al., 2019). Early snowmelt or unstable snow cover therefore create stressful environments for bank voles. Temperature differences between night and day are much larger on top of the snow than in the subnivean space, and Sipari et al. (2016) found that this fluctuation caused stress in the bank voles. A lack of snow cover and more fluctuating temperatures could therefore explain the change of the activity pattern in winter. However, when looking at data for snow cover in the study area (data for Møsvatn weather station, available from www.ekilma.no), there was no indication of early snowmelt or reduced quality of snow cover during our study period. We therefore do not think this is the full reason for the observed shift in activity during winter in bank voles. Rather than being owed to one specific cause, we believe that the shift in activity is caused by several factors: predator avoidance, LD-cycle and environmental conditions.

4.3.3 Shrews

The seasonal activity for shrews followed the same pattern as voles, but their dip in activity was not as low. The trend in activity was the same for activity curves created using the cosinor-method and kernel-density plot. For the cosinor-method the null model was the best fit for winter, and we saw this in the kernel-density plot as well due to the wide confidence intervals. Generally, we found a more even activity pattern throughout the seasons for shrews.

For both spring and autumn there was a dip in activity in the middle of the day, this resting period was more visible for spring. The activity curve for spring crossed MESOR in hour-block 06-07 and when activity increased, the line crossed MESOR in hour-block 19-20. The lowest point of activity was in hour-blocks 11-13. For autumn we found the same resting period, but the activity line crossed MESOR one hour earlier both when the activity was lowering and increasing. The lowest point of activity was still in hour-blocks 11-13. For summer we observed a lower activity level during the daylight hours compared to the other seasons. This might be bound to the ambient temperature and shortened dark period. The resting period followed the same time as it did for spring, but the lowest point of activity occurred in hour-block 09-10. This finding is in line with a study Churchfield performed in 1982. She also used a camera in her study, but the method was experimental. She captured shrews and recreated their natural habitat and used video to observe. She claims that shrews have a particular seasonal activity, and the variation in activity is bound to the ambient temperatures and follow the LD-cycle (Churchfield, 1982). We can assume that the temperature is lower for the darker hours and higher for the lighter hours. So, it is likely that the activity we observed also can be explained by ambient temperature. Looking at temperature and activity, we can see there is a tendency for shrews being more active in the cold periods (data on temperature from Møsvatn weather station, available from www.ekilma.no).

Shrews are insectivorous and therefore different from the two other study species which are rodents. Shrews are known to have a high metabolism and therefore they have the need to forage for large parts of the 24-hour cycle. This can be linked to their diet consisting of invertebrates (Bjärvall & Ullström, 1997) which can be more challenging to find than plant material, and their high metabolism resulting in their need to forage throughout the 24-hour cycle. High metabolism results in the heat emission for the body being high, and their fur has poor heat insulating properties (Ivanter & Marakov, 2002). Knowing this, a more constant activity throughout the day and season is not a surprising observation for the shrews.

Shrews have a short lifespan and most commonly only one generation of shrews overwinter. Whitaker and Feldhamer (2005) looked at survival in their study of shrews in 1996 and found that the survival of individuals was lower in autumn due to intraspecific competition between the different generations. And because only one generation overwinters, there is less competition in spring. They can be observed running over the snow, leaves prints, their thick tail leaves distinct marks in the snow. And even if there are no tracks to be found, they can still be present in pellets from owls (Bjärvall & Ullström, 1997).

For winter the null model was the best fit using the cosinor-method and we therefore present an activity model using the next-best fitted model (although not significant). If this non-apparent pattern was a result of reduced activity in general for shrews for the winter months, it can also be because the shrews are avoiding predators. Shrews share some of the same predators as voles which are discussed above, and their main predators are raptors (Bjärvall & Ullström, 1997). In her study, Churchfield found a lower activity in winter, and she suggests predator-avoidance as a possible explanation for the reduced activity (Churchfield, 1982). Although this is one possible explanation for the activity of shrews in winter, we have not got enough data to support this. Another important factor for the activity during winter is the high amount of brown adipose tissue (brown fat) shrews have, with a high amount of brown fat stored the shrews also have energy stored. And Dew et al. (1998) found that the amount of brown fat is related to ambient temperature. Due to this energy storage we believe the shrews might not need to be as active. One reason for the scare data for the winter months might be that shrews do not run in tunnels like the voles, and therefore the trap boxes are less accessible during snow cover. Churchfield suggests that the reduction in activity during the cold periods is to minimise the loss of energy (Churchfield, 1982).

4.4 All species

The observed activity patterns for *Microtus* voles and bank voles were quite similar, with a preference for nocturnal activity in all seasons but winter. The habitat type in the study area leans towards open terrain, with sparse canopy cover. This type of habitat is preferred by *Microtus* voles (Borowski, 2003; Seatnan et al., 2009) while bank voles generally have a preference for more forested areas with a larger degree of canopy cover (Bjärvall & Ullström, 1997; Wegge & Rolstad, 2018). This could explain the difference in sample size for the two species groups, with *Microtus* voles constituting almost 50% of all our data. In a trapping study on voles and shrews, Sundell et al. (2012) found that both vole species could be found in many kinds of habitat during times of high population density, and that parts of the populations may shift to use less preferable habitats. If the bank voles were not in their optimal habitat, this could have affected their activity. This would explain the discrepancies between the observed activity patterns in our study and previous studies on the activity of bank voles.

While the activity patterns for the vole species were similar, activity patterns for shrews differed from those of voles. The dietary preference of voles and shrews are very different. Shrews are insectivorous (Pernetta, 1976), and have a high metabolism (Churchfield, 1979; Halle, 2006). They therefore have to be more active throughout the entirety of the day, which could explain the observed difference in activity pattern from the voles. The different vole species (*Microtus* voles and bank voles) also differ in diet. *Microtus* voles are extreme herbivores with teeth evolved for dealing with large amounts of green vegetation containing large amounts of cellulose (Hansson, 1971). Bank voles have a diverse diet and eat both herbaceous matter, seeds and invertebrates (Butet & Delettre, 2011). These differences are not as drastic as the difference between voles and shrews, and the similarities in activity patterns between the vole species was therefore larger.

We generated activity curves for seasonal activity of *Microtus* voles, bank voles and shrews using both the cosinor-method and a kernel-density method. The curves generated with the kernel-density method show the same activity patterns as the activity curves generated from the cosinor-method. Thus, we have two analyses exhibiting the same pattern, strengthening the results of our study.

5. Conclusion

In this thesis we utilized camera trapping to investigate the daily and seasonal activity patterns of *Microtus* voles, bank voles and shrews at Skinnarbu, Tinn municipality. We found the vole species, *Microtus* voles and bank voles, to be nocturnal in summer, autumn and spring. The resting period in the daylight hours seemed to be entrained by sunrise, while the onset of activity seemed to be at sunset. Shrews followed the same pattern of nocturnality in summer and spring. We hypothesized that these activity patterns are entrained by the LD-cycle, social factors, and being a possible predator-avoidance strategy. For shrews, which are insectivores, their high metabolism probably also had a great influence on the activity patterns we found. When comparing activity patterns across seasons, we found a seasonal phase shift in activity for voles; from nocturnality in summer, autumn and spring to diurnality in winter. In winter there was also only one activity peak, i.e., the activity pattern had a unimodal distribution. This phase shift was possibly owed to changes in optimal light conditions (i.e., the LD-cycle), predation-risk and the stage in the population cycle. When there is snow cover, most of the activity of voles takes place in tunnels underneath the snow, leading to a change in predation risk in the winter-months. This could explain the observed phase shifts for voles in this study. Shrews did not have a phase shift in activity, but we did observe a tendency towards a more uniform activity pattern in autumn and winter. It is possible that this pattern was influenced by the same factors as vole activity (the LD-cycle and predation), as well as their metabolism and trappability in winter. As voles and shrews generally have very complex population structure (population cycles and social interactions), identifying factors influencing activity patterns is challenging.

The camera traps used in this thesis are still active and have the potential to give us further understanding of the factors influencing the activity patterns of voles and shrews. We pointed out predation-risk as an important factor influencing vole and shrew activity patterns, but unfortunately did not have enough data on predators in the area to do further research. Gathering data on the activity of predators in the area would give the opportunity to confirm the hypothesis. Furthermore, data from the running camera traps could yield more information about the population cycles of the voles at Skinnarbu. We suggested social interactions as a possible factor for synchronisation of activity, and that population cycles may be a cause of changes in daily activity of voles and shrews. Data on population cycles can also be useful when looking at the influence of global change on small mammals.

Through this thesis, camera trapping has proven to be a successful non-invasive technique of monitoring small mammals in the field, and that it has the potential to give valuable insight into the daily activity of small mammals. The small mammal species studied in this thesis are important keystone species not only at Skinnarbu, but in northern terrestrial food webs in general. It is therefore of great interest to learn about their ecology and what influences their behaviour.

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Appendix

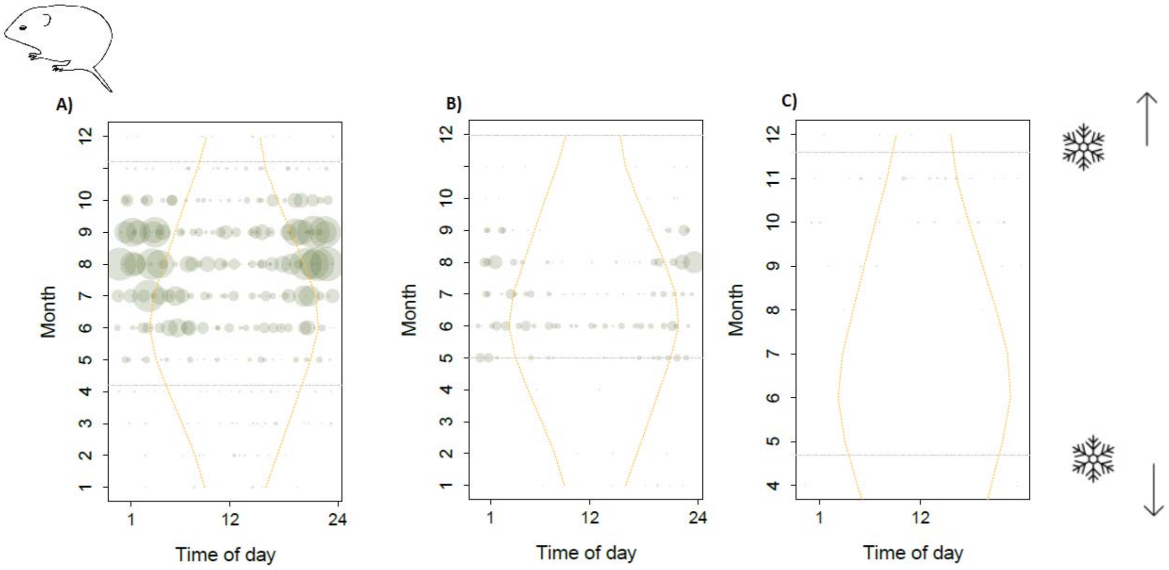

Figure 1: Bubble plot showing diel activity for *Microtus* voles in the years A) 2017, B) 2018 and C) 2019. The number of individuals captured by the camera is depicted by the dots. The size of the dots (bubble size) represent number of occurrences of the observations for a given time of day and month. The vertical, dashed yellow lines represent sunrise (left) and sunset (right). The horizontal dotted grey lines illustrate the median start and end of snow cover.

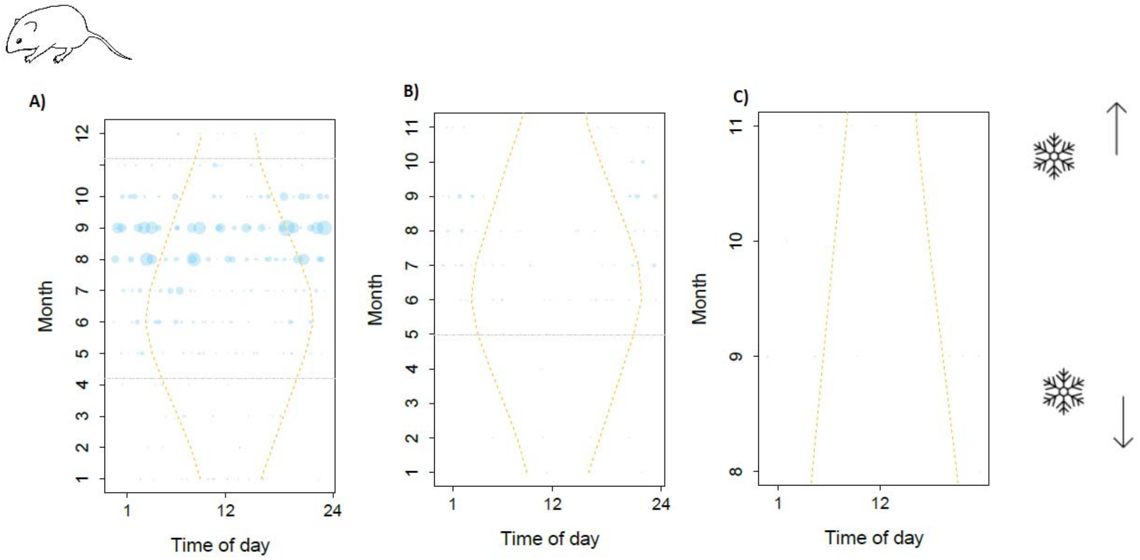

Figure 2: Bubble plot showing diel activity for bank voles in the years A) 2017, B) 2018 and C) 2019. The number of individuals captured by the camera is depicted by the dots. The size of the dots (bubble size) represent number of occurrences of the observations for a given time of day and month. The vertical, dashed yellow lines represent sunrise (left) and sunset (right). The horizontal dotted grey lines illustrate the median start and end of snow cover.

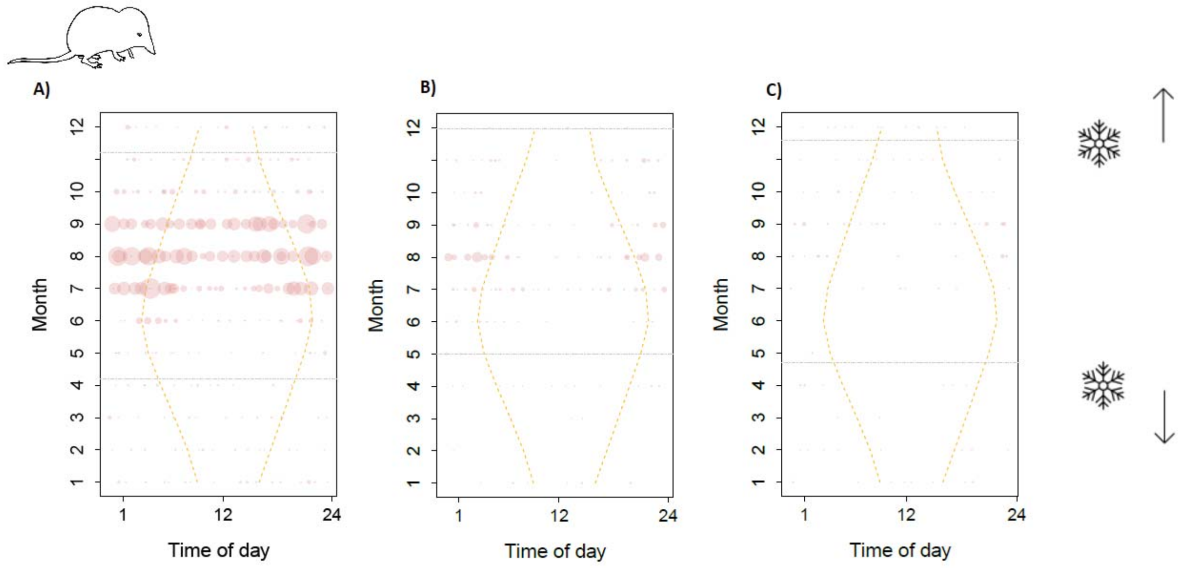

Figure 3: Bubble plot showing diel activity for shrews in the years A) 2017, B) 2018 and C) 2019. The number of individuals captured by the camera is depicted by the dots. The size of the dots (bubble size) represent number of occurrences of the observations for a given time of day and month. The vertical, dashed yellow lines represent sunrise (left) and sunset (right). The horizontal dotted grey lines illustrate the median start and end of snow cover.

Table 1: Snow cover throughout the study period. Data for snow cover from www.eklima.no, Møsvatn weather station.

Year	**Start of snow cover**	**End of snow cover**
2017	05.11	06.04
2018	30.11	30.04
2019	17.11	21.04
Median	17.11	21.04

Table 2: Sunrise and sunset throughout the year (data from https://www.timeanddate.com/sun/).

Month	**Sunrise**	**Sunset**
January	09:11	15:59
February	08:06	17:14
March	06:40	18:28
April	05:09	19:43
May	03:47	20:57
June	03:03	21:49
July	03:31	21:30
August	04:41	20:17
September	05:53	18:47
October	07:05	17:16
November	08:22	15:57
December	09:23	15:19

Table 3: Total number and proportion of trigger events in the five camera traps between November 2016 and January 2020, with 30 min gap.

Trigger event category	**Number**	**Proportion (%)**
Bank vole	841	12%
Bank vole- juvenile	71	1.0%
Microtus voles	2770	39%
Microtus voles-juvenile	344	4.8%
Shrews	1885	27%
Lemming	7	0.09%
Vole	1072	15%
Least Weasel	10	0.15%
Stoat	9	0.13%
European viper	14	0.19%
Lizard	8	0.12%
Species not determined	27	0.38%

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