Automatic camera traps in monitoring small mammals: The effect of predation risk on activity and foraging in winter and spring

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ABSTRACT

Along the predicted climate change scenarios, it is important to monitor animal populations and communities effectively under changing environmental conditions. Modern trail cameras allow monitoring in natural habitats without large manpower or extensive trappings. This study aimed at testing the use of trail cameras in natural small mammal communities and enclosure populations in winter and spring. Climate change will predictably lead to shorter and unstable snow cover affecting directly food supply and survival of small-mammals, spending their winter under the snow. Predation by small mustelids, like weasels and stoats, may strongly influence survival and behavior of prey small mammals. The aim of this study was i) to experimentally study predation risk effects in form of weasel odor on small mammal foraging and activity and ii) to automatically monitor wintering small mammal communities in several forest study areas. Predation risk effect experiments were done both in the forest and in the field enclosures using camera traps and feeding trays. During the forest monitoring period the number of rodent or shrew visits in the camera traps decreased as the winter progressed. Visit decrease may have been due small mammals moving less during freezing temperature, but more likely due to declining population density. In the predation risk experiment I hypothesized that small mammals would avoid fresh weasel odor but that the effect of odor would fade with time. For foraging I used the Giving-Up-Density -method (GUD), which measures how fast an animal abandons the foraging site when predator odor is either fresh or aged. The results show that there were more visits in the weasel odor boxes in the natural forested areas compared to the enclosures. It may be that small mammals in their natural environment inspect the odor source to assess the true predation risk. This was the first time to use camera traps in Finland for collecting information of small mammal communities, decline of numbers and activity. The information was collected from natural forest habitats over the winter and from experimental enclosures in spring.

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TIIVISTELMÄ

Ilmastonmuutoksen myötä on tärkeää seurata vaihtuvissa ympäristöolosuhteissa eläviä eläinpopulaatioita- ja yhdyskuntia. Modernit riistakamerat mahdollistavat eläinten tarkkailun luonnollisessa ympäristössä. Tämä tutkimus tähtäsi riistakameroiden käytön testaamiseen luonnontilaisissa piennisäkäsyhteisöissä sekä tarhatuissa populaatioissa talvella ja keväällä. Ennusteiden mukaan ilmastonmuutos tulee aiheuttamaan lumipeitteen määrän laskua ja maantieteellistä epätasaisuutta. Tämä vaikuttaa suoraan lumipeitteen alla talvensa viettävien pienjyrsijöiden ruuan saantiin ja selviytymiseen. Pienten näätäeläinten, kuten lumikon ja kärppien, saalistuspaineella voi olla suuri merkitys pienten nisäkkäiden käyttäytymiseen ja selviytymiseen. Tämän tutkimuksen tavoite oli i) kokeellisesti tutkia lumikon hajun muodossa saalistusriskin vaikutuksia piennisäkkäiden ruuan etsintään ja aktiivisuuteen niin metsässä kuin tarhoissakin ja ii) seurata talvehtivia piennisäkäsyhteisöjä useassa metsätutkimuskohteessa. Tarkkailujakson aikana talven edetessä piennisäkkäiden vierailut laatikoissa vähenivät. Tämä saattaa johtua niiden vähäisestä liikkumisesta pakkasilla, mutta todennäköisemmin vierailut vähenivät piennisäkkäiden määrän laskettua jyrkästi talven aikana. Saalistusriskiä tutkittaessa oletuksena oli, että piennisäkkäät välttävät tuoretta lumikon hajua, mutta hajun vaikutus heikkenee ajan myötä. Ravinnonkäytön seuraamiseen käytin Giving-Up-Density (GUD) metodia, joka mittaa kuinka nopeasti eläin hylkää ruokintapaikan, kun saalistajan haju on tuore tai vanhentunut. Tulokset osoittavat, että luonnontilaisessa metsämaastossa pikkunisäkkäät vierailevat useammin lumikon hajua sisältävissä laatikoissa, kun taas tarhaolosuhteissa vierailuja hajulaatikoissa on vähemmän. Piennisäkkäät, jotka elävät luonnollisissa olosuhteissa, saattavat tarkastaa hajun lähteen arvioidakseen todellisen saalistusriskin. Tämä oli ensimmäinen kerta, kun Suomessa kerättiin tietoa piennisäkäsyhteiskunnista riistakameroiden avulla. Tietoa kerättiin niin luonnontilaisesta metsästä koko talven ajalta kuin tarhaolosuhteista keväällä.

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1. INTRODUCTION

Small ground-dwelling mammals are an important part of animal communities and they are key-stone species in the terrestrial food webs in the northern hemisphere (Ims & Fuglei 2005). Predation pressure by small mustelids, weasels and stoats influence the activity and foraging of small mammals, such as bank voles (Hanski, Hansson & Henttonen 1991). Specialist predators are also one of the main causes for small mammal cyclic dynamics (Korpimäki, Norrdahl, Klemola, Pettersen & Stenseth 2002). Small mammals have a highly developed olfactory system and they make behavioral decisions based on odors (Slotnick 2001). Prey species avoid predators through antipredator responses, which causes multiple changes in their behavior. This affects to the dynamics of the population (Jędrzejewska and Jędrzejewski 1990, Sundell & Ylönen 2004).

Hansson & Henttonen (1985) discovered that there is a strong correlation between population variations and snow cover, snow thickness and latitude. Voles spend approximately 4-6 months per year under the snow in Fennoscandia (Johnsen *et al.* 2017) and other small rodents spend most of their time in the sub-nivean space as well (Korslund & Steen 2006). The diminishing or instability of the snow cover has an effect to ground-dwelling small mammals, which spend their winter mainly in the sub-nivean conditions, between the ground and the snow pack (Korslund & Steen 2006). Winter time creates challenges when trying to determine the abundance and activity of small mammal populations or communities. Trail cameras offer a possibility to monitor small mammal communities under the snow in their natural environment.

1.1 Predator odor

Voles and other small mammals use olfaction not only for reciprocal interaction and foraging but also to detect and avoid predators (Jędrzejewski, Rychlik &

Jędrzejewska 1993; Borowski 1998; Bytheway, Carthey & Banks 2013). Predator odor affects mammalian prey species in multiple ways. Prey individuals alter their behavior when predator odor, such as fur, urine or feces, is present. They forage and groom themselves less frequently and even delay spring reproduction. (Apfelbach, Blanchard C.D., Blanchard R.J., Hayes & McGregor 2005; Haapakoski *et al.* 2012). Mice and rats (Apfelbach *et al.* 2005, Bytheway *et al.* 2013) have been shown to decrease their locomotory activity and in bank voles the activity response is variable from increasing in form of fleeing (Jędrzejewska & Jędrzejewski 1990) or decreasing if scared individuals chose inactivity or freezing as antipredatory adaptation (Sundell & Ylönen 2004).

It is not known, if the prey changes its behavior based on the information that temporal variation of predator cue offers. It can either be prepared for predator attack or reduce antipredator behavior by recognizing that the cue is old and the predator is not likely to be near (Bytheway *et al.* 2013). When encountering a predator scent, prey might need to approach and investigate the odor instead of fleeing. Prey examines the odor to have more information about the predation risk (Zöttl, Lienert, Clutton-Brock, Millesi & Manser 2012). This "predator inspection" is useful, as it is important for the prey to assess the true predation risk correctly (Fishman 1999; FitzGibbon 1994). Fresh scent marks indicate that there is probably a higher risk of predation compared to old cues (Parsons *et al*. 2017). Prey species have to constantly assess the possible predation risk and costs of fleeing compared to the benefits of for example foraging (Fishman 1999; Parsons *et al*. 2017). This is why the assessment has to be done precisely: being too cautious might lead to starvation but being too optimistic can lead to death (Lima and Bednekoff 1999). It is not yet well known how accurately and correctly prey individuals can read cue information.

1.2 Cyclic dynamics

Small mammal populations in the northern hemisphere often show cyclic dynamics (periodic oscillation) of 3-5 years in their abundance (Hansson & Henttonen 1985; Lindström & Hörnfeldt 1994; Johnsen *et al*. 2016). According to the studies of Radchuk, Ims and Andreassen (2016) and Krebs (1996) the combination of extrinsic (predation, food) and intrinsic (sociality and dispersal) factors causes cyclic periods. The effect predation has on prey population dynamics is depending on whether the predator is a generalist or a specialist (Hanski, Hansson & Henttonen 1991). Unlike a generalist predator, for example the red fox (V*ulpes vulpes*), a specialist, such as the least weasel (*Mustela nivalis*), affect the cyclicity of small mammalian rodents more severely. It has been shown that mustelids are the main reason causing the cyclic dynamics in voles. (Hanski *et al.* 1991; Norrdahl & Korpimäki 1995; Sundell 2002).

1.3 Snow cover

Climate change is most profoundly affecting the thickness and the duration of snow cover in northern hemisphere (Räisänen & Eklund 2012). Snow cover has many important elements and as an insulator, it does not only efficiently protect the ground from heat loss in winter, but also offers thermal insulation to many animal and plant species (Zhang 2004; Räisänen & Eklund 2012). According to Callaghan et al. (2011), Pomeroy and Brun (2001) state that the insulating properties of snow affect not only the soil surface, but also the near-soil surface temperatures: in the middle of the winter, when the air temperature is as low as -20 degrees Celsius, the soil surface temperature stays around zero when there is 50 cm snow coverage on the top (Haapakoski, Sundell & Ylönen 2012).

The change in the snow cover has not been systematic or geographically uniform (Räisänen & Eklund 2012). In the Northern Hemisphere, the snow cover has reportedly started to disappear faster in the spring (Brown & Mote, 2009; Räisänen & Eklund, 2012, Lemke *et al.* 2007). During last century in southern and central

Finland snow depth has been increasing due to increased precipitation but the snow season is shorter than before (Hyvärinen 2003). The climate model simulations show that there is a stronger instability expected in the snow cover in the future (Brown & Mote, 2009; Räisänen & Eklund 2012). Depending on the study and the methods used, there are dramatic or more modest speculations about the future changes in climate. Milder winters increase rainfall and decrease snowfall thus the snow coverage decreases and melts earlier. In the coldest regions the temperatures will not necessarily increase so drastically so the snow cover is not affected as much. (Räisänen, 2008; Räisänen & Eklund 2012). According to climate model simulations in most part of the Northern Hemisphere there will be a decrease in snowfall in spring and autumn but during mid-winter the snowfall will increase (Krasting, Broccoli, Dixon & Lanxante 2013). Vehviläinen & Lohvansuu (1991) predict that there is going to be a strong shortening of winters in the northern and central Finland. The maximum amount of snow might be decreasing by up to 80 %.

In addition to insulation, thick snow pack offers shelter from predators (Lindström & Hörnfeldt 1994; Kausrud *et al*. 2008). Increasingly wet winters decrease the thickness of snow pack and lead to the forming of ice, which prevents the access to food supplies (Johnsen *et al.* 2017) and splits the sub-nivean space up complicating the movement of small rodents (Korslund & Steen 2006).

1.4 Camera traps

During winter time, it is laborious and difficult to trap small mammals and monitor their lives without destroying the snowpack. Modern camera traps could bring a solution to this problem, because with durable trail cameras it could be possible to observe sub-nivean space throughout the winter without any disturbance. (Soininen, Jensvoll, Killengreen & Ims 2015).

The trail camera collects information wirelessly, which enables long-term monitoring without any disturbance to over-wintering environment or animals.

1.5 Aim of the study

There were two parts in this study. The aim was to study how a cue of predation risk in form of fresh or aging weasel odor affects ground-dwelling small mammals' movement activity and foraging decisions during early winter and in late spring. One of the objectives was to survey with a new camera trap –method, what kind of effects winter and forest snow cover would have to the abundance of small mammal communities.

1.5.1 Research questions and hypothesis

i) How does the predation risk simulated by weasel odor affect activity and foraging of small mammals?

The hypothesis was that small mammals react to the fresh weasel smell by avoiding entering or spending time in the camera boxes. There would be more visits in the control boxes than fresh weasel smell boxes and the frequency of visits and foraging would increase in the odor boxes as the weasel smell ages. I also hypothesized that the fresh weasel smell will age quickly and when the odor ages, the avoidance diminishes rapidly and finally stops entirely just in a matter of a few days. This means that in about two days there should be a significant difference in foraging rates in boxes with aged smell compared to the boxes with fresh smell. The argument for this hypothesis comes from previous studies (Bytheway *et al.* 2013; Jędrzejewski *et al.* 1993; Borowski 1998).

ii) What kind of effect winter and snow cover have to the abundance of small mammals' overwintering forest communities?

I hypothesized that during winter monitoring period there would be a lot of observations mainly of bank vole and common shrew, because they are the most common small-mammals in Finland and both exploit especially forest habitats. I expected to see also other vole and shrew species, yellow necked mouse and least weasels. I presumed that the rodents could seek shelter from the boxes. The hypothesis was that the abundance of small mammals would decrease during winter.

2. MATERIALS AND METHODS

2.1 The experiment

The study had two parts. The first part was monitoring what kind of effect aging weasel smell have on the behavior of the small mammals in the forest community. The second part was to monitor the abundance of small mammal winter communities. (Table 1.) The first part was carried out at onset of winter from the middle of November to the middle of December 2017 and was repeated in spring in May 2018. The aim was to measure the effect of presence and aging of predator odor on small mammal visitation rate, and foraging behavior, by measuring their activity and foraging using Giving-Up-Density -method (GUD) (Brown 1999). During November-December 2017 I made three experiments: three monitoring weeks followed by GUD experiments. Twelve trail cameras were used for the first two monitoring weeks and GUDs. Six study camera boxes with fresh weasel odor and six control boxes with clean wood shavings were placed in the forests of Jyväskylä and Konnevesi. The boxes were placed pairwise: Two of the boxes were always placed in the same area, 10-15 meters apart. The camera boxes stayed in one place for one week. Then started the two-day GUD experiment and the GUD boxes were placed in every 12 camera boxes. After that the camera boxes were moved to another location and the same experiment was repeated. This led to six separate study areas: three in Konnevesi and three in Jyväskylä. Acquiring more trail cameras and boxes allowed the usage of eighteen camera boxes during the third monitoring week so it was possible to increase the amount of study areas from six to nine. All together in the three monitoring + GUD studies there were nine study areas: four in Jyväskylä and five in Konnevesi. This adds up to 21 separate sample sites during onset of winter: on the first and second week I used 6 sites with 12 camera boxes and on the third week I used 9 sites with 18 camera boxes. (Table 2. Figures 1. and 2). The new location inside a sample site varied approximately from 50m to 2 km and was randomly chosen depending on the forest cover, vegetation and landscape.

Table 1. The experiment had two parts, part I and II. Part I included four separate monitoring and Giving Up Density- experiments. Part II was to monitor small mammal winter activity.

		The experiment	
Study period	Location	Part I	Part II
November 2017	Forest	monitoring+GUD	
November-December 2017	Forest	monitoring+GUD	
December 2017	Forest	monitoring+GUD	
May 2018	Enclosures	monitoring+GUD	
December 2017-February 2018	Forest		winter monitoring

Table 2. The locations of monitoring period followed by GUD. KV=Konnevesi, JKL=Jyväskylä. Weasel odor box and control box were placed pairwise in the same location. The numbered locations function as “sub-locations”: the boxes have been moved to a different place inside the same location.

	Locations		
Cameras	1 monitoring+GUD 13-22.11.17	2 monitoring+GUD 22.11-2.12.17	3 monitoring+GUD 5.12-14.12.17
1	Station1, Kv	Station2, Kv	Station3, Kv
2	Station1, Kv	Station2 , Kv	Station3, Kv
3	Sukeva1, Kv	Sukeva2 , Kv	Sukeva3, Kv
4	Sukeva1, Kv	Sukeva2, Kv	Sukeva3, Kv
5	Rinteenmäki1, Kv	Rinteenmäki2, Kv	Rinteenmäki3, Kv
6	Rinteenmäki1, Kv	Rinteenmäki2, Kv	Rinteenmäki3, Kv
7	Erkintie (Urtti1), JKL	Erkintie (Urtti3), JKL	Fish tanks, Kv
8	Erkintie (Urtti1), JKL	Erkintie (Urtti3), JKL	Fish tanks, Kv
9	Urtti 2, JKL	Urtti4, JKL	Autiolahdentie, Kv
10	Urtti 2, JKL	Urtti4, JKL	Autiolahdentie, Kv
11	Sääksvuori, JKL	Etelä-Keljo1, JKL	Urtti5, JKL
12	Sääksvuori, JKL	Etelä-Keljo1, JKL	Urtti5, JKL
13			Haapavuorentie, JKL
14			Haapavuorentie, JKL
15			Etelä-Keljo2, JKL
16			Etelä-Keljo2, JKL
17			Etelä-Keljo3, JKL
18			Etelä-Keljo3, JKL

Figure 1. Sample sites in Jyväskylä area

Figure 2. Sample sites in Konnevesi area.

The small mammal abundance was really low after the winter, so the spring GUD experiment was conducted in the eight enclosures in Konnevesi. The enclosures are situated in an old field in Sukeva located approximately 12 kilometres from the Konnevesi Research Station (see Figure 2.). The size of one enclosure is 2500 m^2 and the vegetation is grass with shrubs and some spruce. Each of the enclosure is surrounded by steel sheets, which prevent the voles form escaping and any small predators from entering the enclosures. (Trebatická, Suortti, Sundell & Ylönen, 2012). For this experiment 16 camera boxes were used: one control and one weasel smell box in each of the enclosures.

Five females and four males were released to each of the eight enclosures. The individuals were born during spring/summer 2016 and overwintered in the laboratory at the Konnevesi Research station. Males weighted 18.3 g ± 1.2 g, and females weighted 16.6 g ± 1.4 g (mean ± standard deviation).

The second part of the experiment was to monitor the numbers and visitations of forest small mammals undisturbed without any manipulation throughout the winter from December 2017 to February 2018 (see Table 1. and 3.3 Winter monitoring).

2.2 Study location

The experiments (part I and II) were conducted between November 2017 and May 2018. The study areas for the experiment between November 2017 and February 2018 were *Vaccinium myrtillus* -type forests, mixed spruce and deciduous forest with typical shrub undercover, situated in the Jyväskylä and Konnevesi area. The areas were chosen as "optimal bank vole habitat" according to the forest type and the distant location from settlement and roads. For the experiment in May (part I) I used the vole enclosures of the Mammalian Ecology Research Group situated in Konnevesi because small mammal populations crashed during winter. Doing the experiment in the enclosures was to ensure the sufficient amount of vole visits so that there would be enough data.

2.3 Cameras and boxes

When using trail cameras in winter, it is reasonable to place the camera inside a box so it will be sheltered place for the small mammals to enter. I used Uovision UM785-HD SMS 12MP 3G trail cameras (Figure 3). The cameras use infra black flash, resulting in no visible cue for the animals. It also sends pictures and videos automatically to selected email addresses. The cameras tolerate both humidity and cold temperatures so they are weatherproof. (Uovision Europe web-page http://www.uovisioneurope.com/en/trail-camera/30-uovision-um785-3g-sms-12mp-wireless-3g.html Visited 15.11.2017.). These qualities are essential, since the cameras were going to be continuously outside in the winter. The cameras were attached to external batteries, guaranteeing full functionality for a prolonged period at low temperatures.

The cameras were attached in to the wall inside wooden boxes (Figure 4). The boxes were 60 cm long, 40 cm wide and 30 cm high. The lids were attached with a hinge, so the boxes could be opened. There was an entrance tube attached to both sides of the camera boxes for the small mammals to enter. For the spring experiment the camera boxes were altered with cutting the entrance tube in half to make it easier for the animals to enter through a plain hole. There was a tube only inside the camera box so that the animal would become in front of the camera instead of staying in the edge of a shooting area. The angle of the camera was placed so that the area of sight would be as large as possible. When in forest, the camera boxes were covered with camouflage nets to reduce the visibility of the boxes.

The cameras were set to take videos up to 15 seconds with a lag of one second. This means that the camera started to record again after one second if there was movement. The cameras automatically sent the videos to the Seneram (www.seneram.com) internet service, which is specifically made for this purpose.

The functionality and settings of the trail cameras were tested in Konnevesi Research Station in mid- November 2017. The experimental set-up was tested during a one-week trial period to assure full functionality of the cameras. When analyzing the autumn and winter results I noticed that there were some small mammals that spend time in the corners unseen from the camera. A net was added inside a box in May to avoid the animals going to the corners beyond the shooting range.

Figure 3. Uovision UM785-HD SMS 12MP 3G trail camera

Figure 4. A camera box with Uovision trail camera and an external battery

2.4 Experimental set up

The aim was to observe the effect of predator odor aging in wild populations. This was done by weekly monitoring periods during late autumn before onset of permanent snow cover, in mid-winter, and during spring after the snow melt. In November 2017 – December 2017 every one-week monitoring was followed by a foraging efficiency monitoring using the Giving Up Density method (see 2.4.2 Giving Up Density –method (GUD)). The cameras were used pairwise: each pair included a camera box with predation risk cue and a camera box with control. In November 2017 – December 2017 experiments, the location of the box-pair was changed inside the same larger forest sample site approximately 50 metres to 2 kilometres after one week of monitoring and the Giving Up Density-tests. This was done to increase the sample size of each area for every study period during November -December 2017 (study periods: see Table 1.).

2.4.1 The odor treatment

The odor treatments were prepared according to Haapakoski, Sundell & Ylönen (2012). The weasel odor treatment (here after w) was made by collecting two deciliters of weasel latrine beddings including feces of two different individuals of least weasel (*Mustela nivalis nivalis*) from the weasel cages at Konnevesi Research Station. Those latrine beddings were put into a bucket, mixed with 3 deciliter of water and 1.8 liter of sawdust, and sealed with an air-tight lid. The mixture was placed in 4 °C for overnight. This ensured that the odor, moisture and other components were evenly distributed in the mixture. The control treatment (here after c) was prepared with mixing 2 liter of sawdust with 3 deciliter of water and was stored also in 4° C. This ensured the similar consistency of treatment in every box.

2.4.2 Giving Up Density –method (GUD)

The threat that predator odor causes to the rodents can be measured with Giving Up Density method (here after GUD). GUD is measured with food trays containing a known initial number of food items mixed with a constant amount of sand. (Brown 1999). If an animal eats only a few easy-to-find items and leaves, it feels afraid and the GUD will be high; if an animal spends a lot of time searching for and finding seeds, animal is considered to feel safe and the GUD will be lower (Brown 1999). I conducted the experiment with 40 sunflower seeds mixed with one liter of fine sand. GUD boxes were changed after 24 hours and GUD was monitored for two days. If insectivorous shrews visit the boxes, they should not affect the GUDs eaten by granivorous rodents, and can be neglected in discussing foraging effects.

2.4.3 Winter monitoring

The second part of the study was carried on from December 2017 until February 2018 for monitoring the small mammal activity and species composition throughout the winter. For this experiment seventeen camera boxes out of eighteen were used due to a malfunction of one of the cameras. The camera boxes were left to the same tried and tested locations where experiments were conducted before: six in Konnevesi and 11 in Jyväskylä. I placed several boxes to some of the biggest sample sites (Figures 5 and 6). For this experiment there were no smell but a small amount of sunflower seeds added to each of the boxes when they were placed. This was done to make the boxes more attractive for the small mammals to visit.

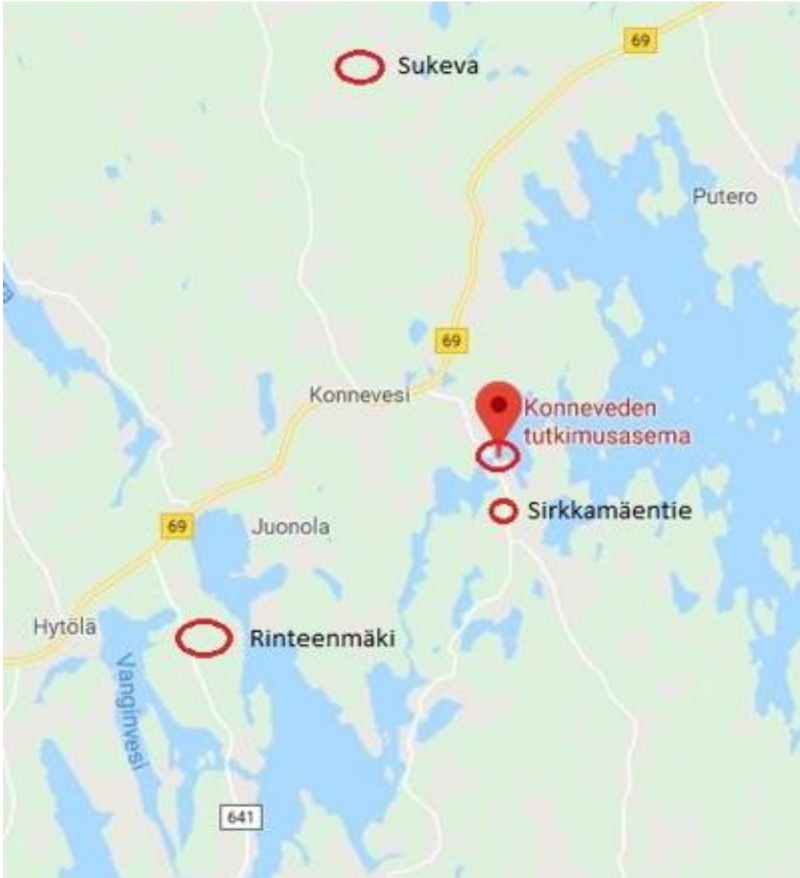

Figure 5. The sample sites in Konnevesi during the winter monitoring period. The camera boxes were located as follows: Two in Sukeva, two in Rinteenmäki, one in the station and one in Sirkkamäentie.

Figure 6. The sample sites in Jyväskylä during the winter monitoring period. The camera boxes were located as follows: Three in Etelä-Keljo, two in Sarvivuori, three in Urtti, one in Haapavuorentie and two in Kinkomaa area.

2.5 Video analysis

I had to decide a time lag when I would start treating an observation as a new individual, because it was impossible to tell apart each individual from the black and white videos (Figure 7.). I set a threshold of 5 minutes for the animals entering and leaving the boxes. For the experiment, however, it was not significant whether the individual that visited the box was the same or a different one, so I did not count individuals but visits. This been said if an individual went in and out from the box constantly (couple of seconds between visits) I counted it as one visit. I made this kind of interpretation for example of a shrew who carried all of the seeds out from the camera box one by one, so there was dozen visits during 30 seconds. If there were several videos repeating after each other and the animal was sitting in the camera box all the time, I concluded that it was the same individual. This assumption was made only if I never saw the animal leaving the box.

Figure 7. A still image from one of the videos from camera traps. The recognition between individuals from black and white footage was not possible.

2.6 Data analysis

I analyzed the results of GUD and monitoring periods with SPSS Statistics 24 using generalized linear mixed models (GLMMs). This analyzing method includes both fixed and random variable effects. With the mixed models, I was able to account the pseudo replication caused by control and odor camera box being close to each other, so that the same individual could visit both of the camera boxes. In the analysis I used Poisson distribution and a log linear link function for visit as a dependent variable. When analyzing the Giving Up Density the seeds were used as a target and sub location as a random factor. As fixed effects I used study day and treatment and two-way cross classification of day and treatment together. When analyzing GUD data from the enclosures I also used two-way cross classification of treatment and day, and enclosure as random factor. The GUD results were analyzed from autumn 2017 with fixed two-way effect: day * treatment.

The number of visits of spring data from the enclosures were analyzed separately with fixed effects day and treatment and with sub-location (several places inside one location, see Table 2.) as a random effect. I also analyzed the GUD data from forests (autumn) and enclosures (spring) of bank voles together using day and treatment as fixed effects and two-way interaction of treatment and enclosures.

For monitoring period, I used number of visits as a dependent variable and sub-locations as a random factor. I analyzed all the species separately (vole, mice, shrew) and visits of all of the species pooled as a dependent variable. As fixed effects I used day and treatment and two-way cross classification of day and treatment and treatment and season. I run the analysis with combined forest (autumn results) and enclosures (spring results) and separately for them both.

2.7 Small mammals

The target species were mainly bank voles (*Myodes glareolus*) and common shrews (*Sorex araneus)* which are the most common small-mammals in Finland and both exploit especially forest habitats.

2.8 Least weasel (*Mustela nivalis*)

The world's smallest carnivore, the least weasel is dependent on small rodent prey, including the bank vole in forested habitats. It hunts small rodents in burrows and sub-nivean tunnels (Trebatická et al. 2012). As the weasel is a natural enemy for small mammals, it was optimal to use weasel smell in the experiment.

3. RESULTS

3.1 The effect of predator odor aging on small mammal visitation rate

3.1.1 Natural forest habitats: The odor treatment

When analyzing the November – December 2017 results separately there was a significant difference between the vole visitation rate (all the days combined) and treatment ($F_{2,207}$=4.5, p < 0,012) (Figure 8.).

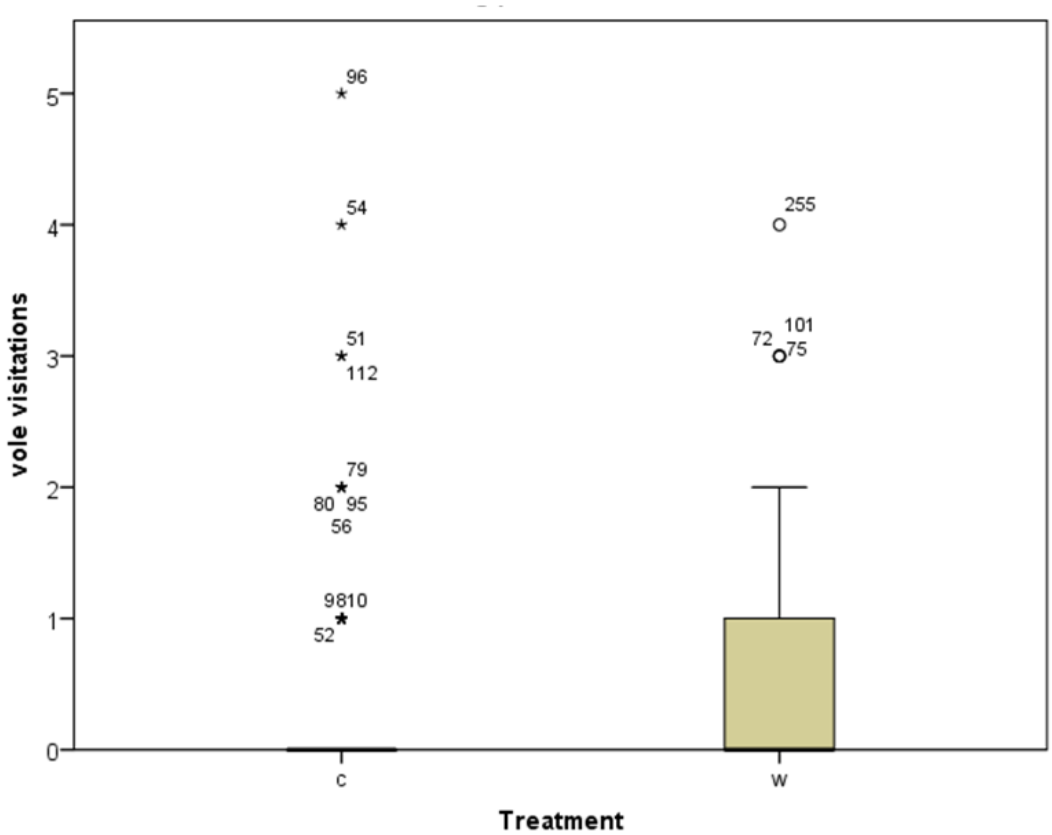

Figure 8. Monitoring period mean of visitations and treatment (c=control, w=weasel smell) in autumn. Line shows median, and whiskers 95 % confidence interval. There were more visits in the weasel smell boxes.

3.1.2 Enclosures: The odor treatment

There were no significant effects of day on the visitation rate from the spring monitoring period (p = 0.191). I pooled all the days starting from odor treatment (7 days before GUD), fixed effects being day and treatment. The results show that there was a significant difference in visitations between treatments (treatment $F_{1,35} = 15.0$ $p < 0.001$), there were more visits in the control boxes (130 observations) than in the weasel smell boxes (81 observations) (Figure 9).

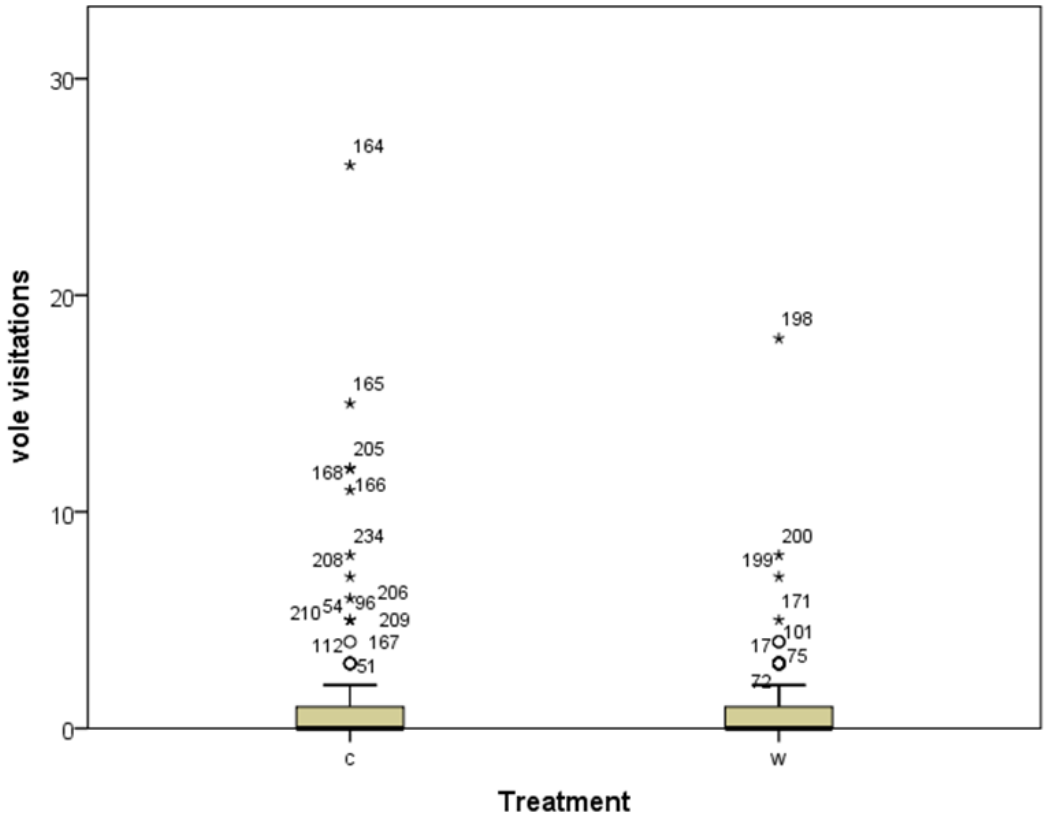

Figure 9. Monitoring period box plot of visitations and treatment (c=control, w=weasel smell) in enclosures in May 2018. There were more individual visits in the control boxes than in the weasel smell boxes (all days combined). Line shows median, and whiskers 95 % confidence interval.

What was common to all of the small mammal visitations was that the first day seemed to be the least visited day though this was not statistically significant (autumn p = 0.434, spring p = 0.191). This was repeated in all of the boxes despite the location, treatment and season or if there was food in the box or not (Figures 10: autumn and 11: spring).

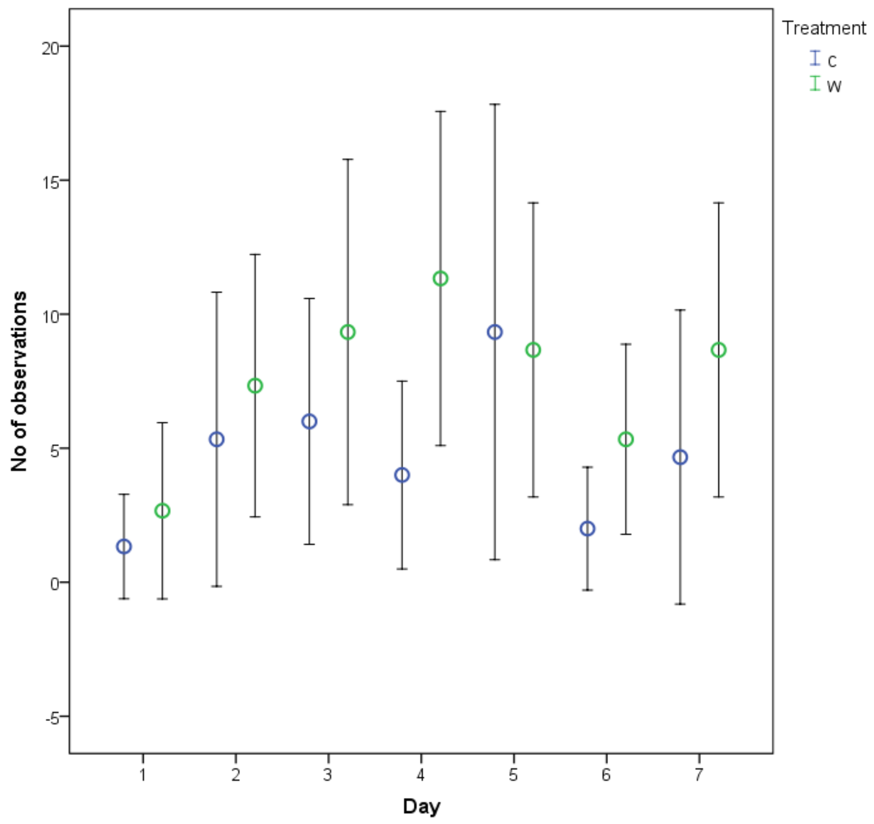

Figure 10. Total visitations per day of autumn monitoring periods combined. Treatments: weasel odor (w) and control(c). Circle shows mean of all the boxes and separate trials and whiskers 95 % confidence interval.

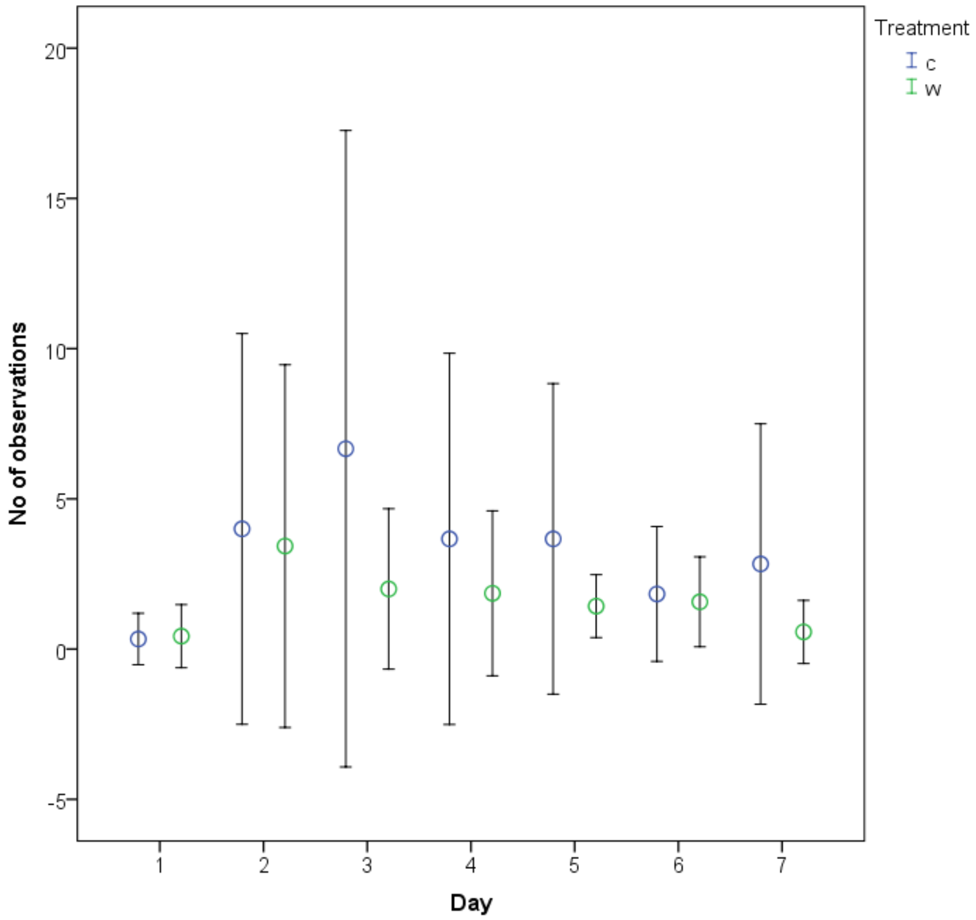

Figure 11. Total visitations per day of spring monitoring periods combined (mean). Treatments: weasel odor (w) and control(c). Circle shows mean of all the boxes and separate trials and whiskers 95 % confidence interval.

3.2 Giving Up Density -method (GUD)

3.2.1 GUD: natural forest habitats

Only 15% of the GUD boxes (13 out of 84) were visited in natural forested habitats. There was a significant difference in the day and the seeds eaten (day $F_{1,13} = 21.5$, $p < 0.001$) (Figure 12). The seeds were eaten less during the first day. Day * treatment interaction is significant.

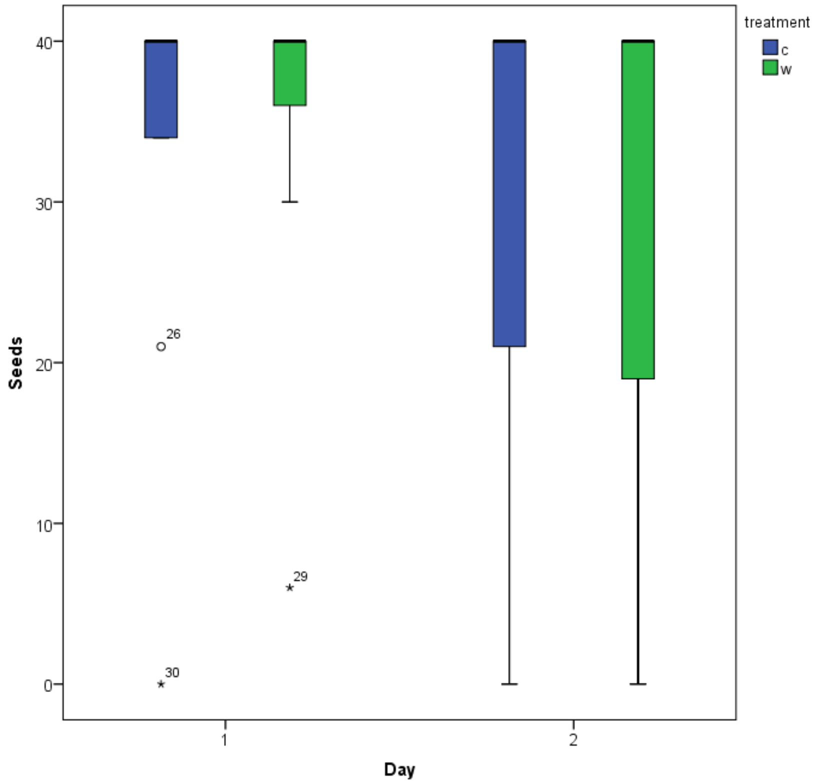

Figure 12. Treatments form November – December 2017 of weasel odor (w) and control(c). Y - axis shows the number of seeds remaining in the box. There were 40 seeds in each seed tray in the beginning of the experiment. Line shows median, and whiskers 95 % confidence interval.

3.2.2 GUD: enclosures

GUD done in the enclosures in May resulted in 56% visitation rate: 18 boxes out of 32 were visited. Analyzing the spring results from the enclosures separately with fixed effects day and treatment, there were significant differences between the seeds eaten, the day and treatment.: there were more seeds eaten from the control boxes than from the weasel smell boxes (treatment $F_{1,34} = 15.5$ $p < 0.001$) and on the second day (day $F_{1,34} = 15.2$ $p < 0.001$) (Figure 13).

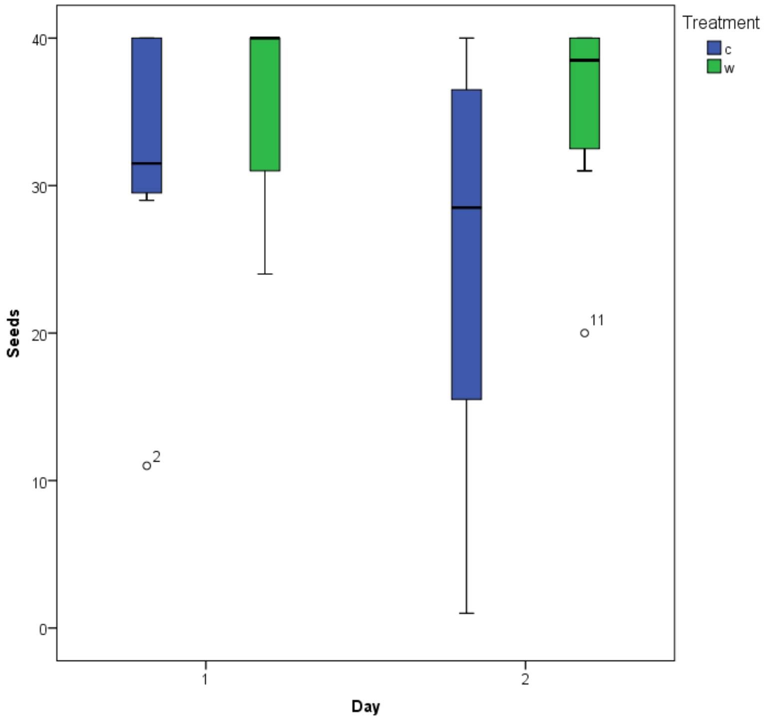

Figure 13. Enclosures: treatments of weasel odor (w) and control (c). Y - axis shows the number of seeds remaining in the box. There were 40 seeds in each seed tray in the beginning of the experiment. Line shows median, and whiskers 95 % confidence interval.

3.3 Winter monitoring

According to Finnish Meteorological Institute, February 2018 was the coldest month in Central Finland last winter with average -11,2 degrees Celsius (Measurement point: Jyväskylä airport). The precipitation was fairly high through December, January and February and the snow depth was thickest in March (mean 660mm) (Figure 14).

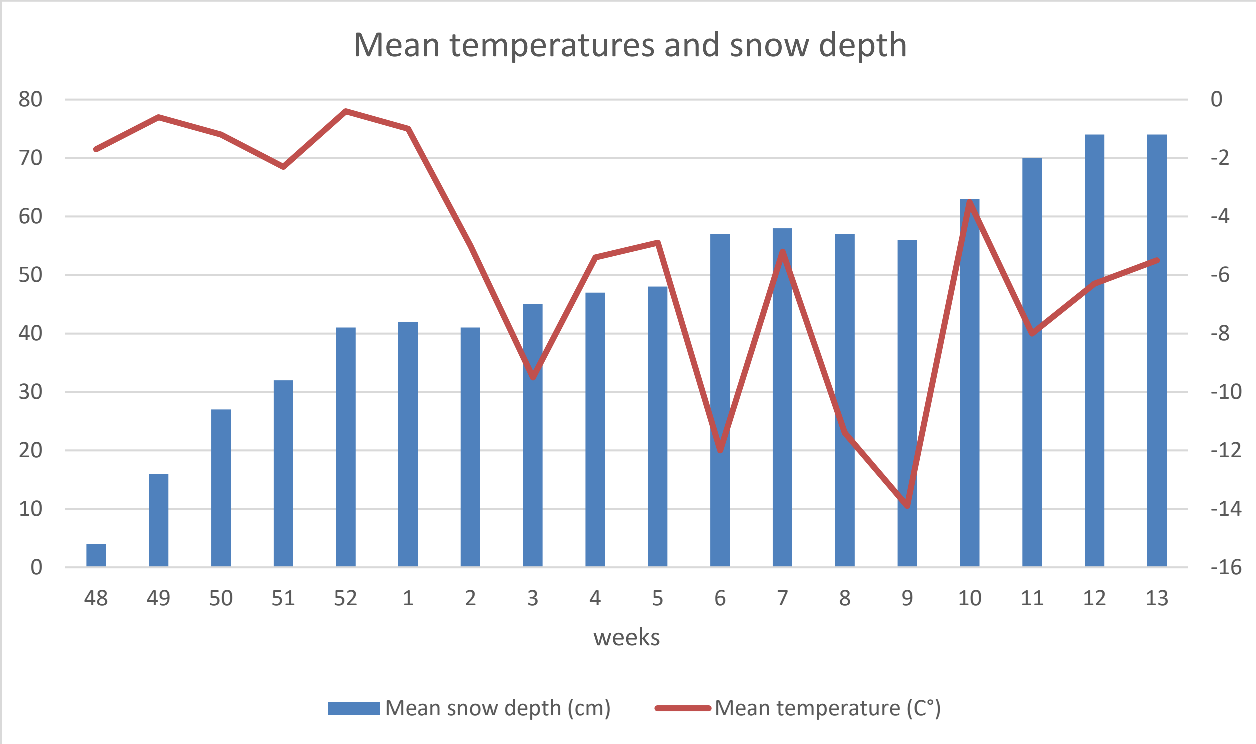

Figure 14. Weekly mean temperatures and snow depth December 2017 - March 2018, measured from Jyväskylä airport. (Finnish Meteorological Institute).

The small mammal species to visit the camera boxes under the snow were bank voles and shrews. The winter was a decline period of the cyclic vole populations in Central Finland as the amount of individual observations diminished drastically over winter due to the crashing of vole populations (Figure 15). In the beginning of the winter the visitation rate was high but in the end of February the numbers of visitations were already really low.

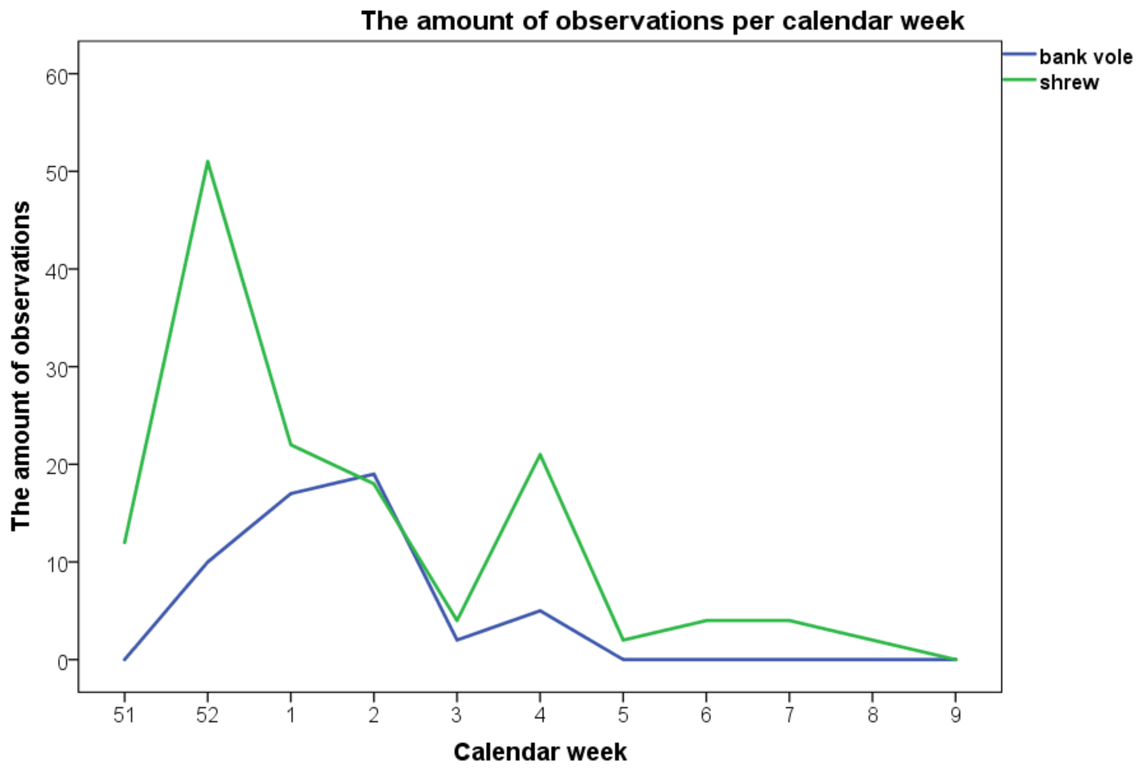

Figure 15. Individual observations of bank voles and shrews during winter monitoring weeks (December – February).

4. DISCUSSION

Camera traps have not been used before in Finland to monitor small mammal community events over winter, from snow free early winter over snow covered mid-winter to spring. This method gave information about the small mammal abundance and shows a strong decline in their numbers over winter. Further, measuring the responses of small mammals to odor cues of the main predator, the least weasel, provides information of species behavior like foraging and variability of the response to fresh or aged weasel odor. I found out that small mammals in open forest plots visited weasel boxes more often than control boxes whilst this was vice versa in the enclosures. The hypothesis for the fresh weasel smell was that the small mammals avoid entering or spending time in the camera boxes when the odor is fresh and the aging of the smell would increase the visitation rate. This was observed in the spring, when the experiments were done in the enclosures. Interestingly though small mammals visited also the fresh weasel odor boxes when the experiment was done in natural forest habitats during autumn.

4.1 The effect of predator odor on small mammal community

Small mammals may need to have more information about the predation landscape so they investigate also the weasel odor boxes. This backs up the theory that small mammals need to inspect the smell more often, especially when the odor ages (Parsons *et al*. 2017).

The visitation rate differs whether the study is conducted in natural forest habitats in autumn or in the enclosures in spring. In the enclosures the voles visited control boxes more often than odor boxes but in autumn it was the other way around. Bank voles living in the forested habitats surprisingly visited the weasel odor boxes more frequently. The aging of the odor had no significant effect on the visitation rate either in the forest or in the enclosures. On the contrary to previous study (Bytheway *et al.* 2013) there were no indication that aged predator odor would have a difference in GUDs of small mammals. In the forested areas there were more seeds eaten in the second day, but from both the control box as well as from the weasel odor box. In the enclosures the seeds were eaten also more during the second day, but not from the weasel odor box, but from the control box. In fact, there were only a few seeds eaten more on the second day from the weasel odor box compared to the first day. To have more data about the effect aging of predator cue has on the behavior of small mammals, there is a need for further study with larger sampling. Instead of using latrine beddings and feces as a source of odor, it would be sensible also to test the effect of fur or skin derived odors, as some research show that they have more intense lasting effect on prey (McGregor, Schrama, Ambermoon and Dielenberg 2002; Masini, Sauer & Campeau 2005).

When placing the boxes in to the forest, the control boxes were 10-15 meters away from the weasel odor boxes. Any small mammal crossing a box would be interested in a novel object and investigate it at some point no matter if there was a weasel smell or not. Also, the weasel odor is so strong that it can function as attractant to voles, so they would have to inspect the source of the odor. They are curious and the box could offer them shelter as well.

4.2 Foraging and predation risk: forested habitat

The voles living in natural forest areas visited the weasel odor boxes more than the voles in the enclosures. The food during cold autumn weather might be scarce and the voles living under natural conditions cannot afford to lose possible meal which could keep them alive. During colder times, small mammals do not have necessarily the possibilities to choose where they will collect their food, so in spite of the risk that the fresh weasel odor indicates, they will have to eat or face starvation. Also, it is possible that there were more predators present during early winter and less in spring. When the food is depleting due to the colder weather, it might be beneficial for the voles to gather information about the real presence of the predator, despite of the risk. They need to investigate if the odor is old or fresh to see if there is a real threat of predation or not. And the voles who found a box with food might not be aware that there is another, less risky, box nearby.

4.3 Foraging and predation risk: enclosures

During monitoring periods in autumn, six days out of seven the weasel smell boxes were visited more often than the control boxes (figure 9.). The results from the monitoring periods in enclosures show a different kind of trend: during five days out of seven the control boxes were visited more than the weasel odor boxes (figure 10.).

Natural forest habitat and enclosure differ in many ways as a study area. There is a difference in relief and forest cover, the landscape in the enclosures is quite even and bare of trees and the area is enclosed so the boxes could be fairly easy to find. The forest's undercover might be thicker, the altitude differences greater than in the enclosures and there might be different obstacles such as streams and fallen trees that determine the route the vole will choose. There are also more natural predators in the forests than in the enclosures; the voles probably investigate the odor source more easily to assess the real risk.

The experiments were done in different seasons; in the forest in autumn and in the enclosures in spring. When it is cold or food is scarce, small mammals have to take more risks and investigate the box in terms of a possible meal. The weather was really warm in May so the vegetation started to grow fast offering buds for the voles to eat. During spring the voles did not necessarily have to rely solely on the external seeds to get a meal so they did not have to take unnecessary risks. There is also a possibility that bank voles behave differently on the onset of breeding season and their avoidance of predator odor might be stronger during this time.

The vole density in natural forest is different than in enclosures so the competition is also different. It is not known if the visits are from several different individuals or are they mainly the same individuals that visit the boxes in certain area. In the enclosures the territory is restricted, so the voles cannot exit the area and new individuals cannot enter. This could mean that the same individuals go in and out of the boxes more than in the forest and they a) do not need to inspect the weasel smell box too often and they choose to visit more frequently in the non-risky boxes b) they move around the boxes many times during the day, because they reside in the same area and choose to visit and spend time in the non-risky boxes for shelter. In the enclosures during the monitoring period there are more visits in the weasel odor box during the first 2 days (though only 3 visits on day 1), which indicates that the voles are inspecting the odor source. After 2 days the odor might be already faded so that the aged odor itself becomes irrelevant to the voles and they will have other preferences how to choose which box to enter. In the GUD tests the voles did not eat more seeds from the 2nd day old weasel odor box (figure 8.), which indicates that the odor lasted also during the second day. However, it seems that the voles in enclosures have more possibilities to choose which box to enter and, in the spring, they don't have to take too many risks e.g to find food. The results are in line with the previous studies done in enclosures; bank voles alter their behavior and for example eat less when predator odor is present (Hughes, Korpimäki & Banks 2010; Haapakoski *et al.* 2012).

The first day was always the least visited day in spite of the circumstances (Figures 9, 10, 11 & 12). This kind of behavior could be due to an aversion of novelty. When encountering a new stimulus, it can trigger a fear behavior called neophobia (Greggor, Thornton & Clayton, 2015). Small mammals are cautious towards a new object, a camera box, which has appeared to their territory. Once one individual dares to enter, it leaves a scent mark and others will have the courage to investigate the box as well. The visitation rate then rises after one day.

4.4 The numbers of small mammals declined drastically over winter

There was a distinct belief that the current winter would be an optimal time to conduct this kind of study, because it was thought that as after two years of low populations of voles and almost total absence of weasels, the amount of forest rodents, including the bank vole would be increasing again. According to Natural Resources Center (LUKE) the amount of bank voles was abundant in Central Finland last autumn but the populations crashed during winter (LUKE web page Visited 12.7.2018). This was noticeable also in the field studies as there were distinctly more visitations in the camera boxes during autumn and middle winter compared to late winter.

Shrews are insectivorous but when food is scarce, they eat also seeds, roots and other vegetal based nutrition (Hamilton, 1944). In the videos I saw also many shrews eating or collecting seeds especially during cold winter months. However, shrews foraging behavior differed from voles. Shrews seldom ate the seeds on site but collected the seeds and carried them outside of the camera box one by one. Voles usually ate the seeds right away from where they found them.

4.5 Camera traps under the snow - methodological issues

Over half of the videos appeared empty or with insects, that triggered the camera. The solution to reduce the amount of totally empty videos would be a faster trigger speed. The lag between movement and the point when the camera started recording was approximately two seconds. A lag this long is more than enough for the small mammal to run out of the box before the camera starts recording. Sometimes the empty videos and videos with only digging or gnawing sound repeated after each other. This, and occasional little peaks of fur or tail (sometimes even a shadow), revealed that the animals spend time in the corners, unseen from the camera. For the spring experiment, done in the enclosures, the corners were covered with wiremesh to prevent this, but it didn't block all of the voles from hiding. Placing the camera downwards in to the ceiling of a camera box, so that the shooting range would cover every inch of the box, would prevent the small mammals hiding from the camera (see Soininen *et al.* 2015).

Most of the cameras and external batteries worked nicely throughout the whole study, but there were also some technical difficulties. At first there were problems in receiving the videos from the cameras to the e-mail addresses. This was solved with an internet service meant for trail cameras. All of the videos recorded by the cameras went straight to the Seneram internet service. It was easy to administer the cameras and the videos from the service. There were some malfunctions of some of the cameras and they didn't sent videos at all in a certain period of time. This was during GUD testing, so it didn't so much affect to the study itself. Majority of the videos were clear and it was easy to recognize species from the videos. There were some disturbance sounds and temporary darkness in some of the videos, but nevertheless no animals was left unrecognizable which species it was because of this.

I decided a time lag when I would start treating an observation as a new individual. I decided the 5 minutes threshold for the animals entering and leaving the boxes based on my observations. Many of the observations basically followed a certain pattern. There could have been hours without any observations of small mammals until an individual entered the box. Then the same individual usually stayed in the box for a varying period of time (usually around 30-120 minutes) investigating or sleeping or occasionally moving in and out from the box. If an individual left the box to be returned, it usually took only seconds. After the individual left and did not return, in most of the cases there was a longer period of time (30min-3 hours) before the following observation. In fewer cases the time between the individual observations were shorter. Based on these observations, 5 minutes threshold seemed rational.

4.6 Conclusions

In this study small mammals were observed through camera boxes in Finland for the first time. The results show that bank voles seem to react to the fresh weasel smell by avoiding the weasel smell boxes in the enclosures but not so in the natural forested habitats. Regardless of the circumstances, bank voles might have a fear reaction towards the camera box itself, so they are first cautious to enter the box, whether there is a predator odor or not. The few visits during the first day could be at least partly explained by the possibility that it might take time for the small mammals to find the box from the territory. However, it seems like bank voles have to inspect the smell to have more information about the predator odor or they just need to feed despite the risk. But interestingly the behavior towards the weasel odor box seems to vary depending on the environment and the season. There are however a lot of other factors changing at the same time as well which may affect to the behavior towards the weasel odor box: Population density varies according to the area, landscape: how easy it is to enter the box and even weather to mention a few. Bank voles visited the odor boxes more frequently in the forest plots in autumn than in grassland enclosures in spring, which indicated that the weasel smell seemed to attract the small mammals in the autumn experiments. Cold weather and declining food resources at the onset of winter brings challenges to the ground-dwelling small mammals and the benefits of getting information on predation risk might overcome the risks. So, it seems like small mammals behave more boldly during harsh winter climate in encountering risky environment when searching for food, because that might be the only way to survive. However, autumn experiment was done in natural forest areas and spring experiment in grassland enclosures, so the differences in voles (age, sex etc.), population density, habitat properties and movement possibilities could also have an effect to the results. The research included the observation of sub-nivean space with camera boxes. This enabled the monitoring of small mammals and their natural behavior under the snow without disturbance of the snow pack. This research can act as a baseline for further research with camera traps of the sub-nivean space and the behavior of small mammals.

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