Specialerapport

Behavioral response of European hares towards a simulated predator

Dagmar Hedvig Fog Bjerre

AARHUS UNIVERSITY

Behavioral response of European hares towards a simulated predator.

Dansk titel: Adfærdsmæssig respons hos haren (Lepus europaeus) på simuleret tilstedeværelse af predator.

Specialerapport udarbejdet af Dagmar Hedvig Fog Bjerre, årskort nummer: 201303468

Biologi, 60 ETCS, Aarhus Universitet.

Afleveret: 1 november 2018

Hovedvejleder: Trine Bilde, sektion for Genetik, Økologi og Evolution.

Medvejleder: Peter Sunde, sektion for Faunaøkologi.

Medvejleder: Martin Mayer, sektion for Faunaøkologi.

AARHUS UNIVERSITY

Forord

Denne specialerapport er udarbejdet som min afsluttende opgave på min kandidatgrad i biologi. Formålet med opgaven er at bidrage til vores viden om harens adfærd i forbindelse med et projekt om haren der kører sideløbende.

Efter aftale med mine vejledere, består opgaven af et manuskript til en videnskabelig artikel rettet mod et videnskabeligt tidsskrift og et vidensblad rettet mod lægfolk.

Præmissen for udarbejdelsen af den videnskabelige artikel var at den skulle være baseret på et felteksperiment og have et omfang på ca. 10 sider (24000 anslag). Denne artikel skal betragtes som 'hovedproduktet' i min afhandling.

For i tillæg at træne og demonstrere mine almene formidlingsevner, skulle jeg endvidere udarbejde et vidensblad rettet mod den almindelige dansker. Vidensbladet skulle være udarbejdet i et let forståeligt sprog, og kort og præcist gengive de vigtigste pointer fra min artikel. Vidensbladet skulle fylde 2 sider, svarende til forsiden og bagsiden af et A4-ark, og have et tekstomfang på omkring 500 ord.

Jeg vil gerne sige tak til mine tre vejledere Trine, Peter og Martin, for feedback og konstruktiv kritik som har hjulpet mig den rigtige vej. En særlig tak skal dog lyde til Martin som trofast har stillet op og hjulpet med alt det praktisk i forbindelse med feltarbejdet, og som uanset hvornår jeg havde behov for hjælp eller feedback har stået klar.

Derudover vil jeg gerne sige tak til de lodsejere som har lagt jord til mine felteksperimenter, Lyngbygård gods, Naturstyrelsen, Kirstineborg, Kaj Jeppesen og Niels Kanstrup.
En tak skal også lyde til Starfox rævefarm i Sæby for at stille ræve ekskrementer til rådighed til mit forsøg.

Behavioral response of European hares towards a simulated predator

Abstract

When faced with increased predation risk, prey species alter their behavior accordingly by using different types of anti-predator behavior. In this study, I investigated the behavioral response of the European hare (*Lepus europaeus*) toward the simulated presence of a red fox (*Vuples vulpes*). The behavior was registered with pictures taken from camera traps, first for the control period and afterwards for the treatment period. Butyric acid was used as control to test if a reaction was due to fox scent or just an unfamiliar scent. Analysis showed different changes in behavior. Both abundance and activity decreased when faced with the simulated presence of fox. Further, an increase in vigilance and a decrease in foraging were observed in the presence of a predator cue. The change in behavior affected by the increased predation risk can have consequences both on survival and reproduction.

Introduction

The fear of a potential predator can trigger different behavioral responses in prey species, even when the predator is not visible (Weterings et al. 2016). Predators do not only have direct top-down effects on the prey population by increasing mortality, but they can also have indirect effects, for example by triggering a change in behavior (Lima and Dill 1990). As a response to the possibility of a predator being present nearby, a prey species must try to balance the costs of remaining in their preferred habitat (e.g. increased risk of predation) against the benefits (e.g. higher food quality). For example, Creel et al. 2005 showed that elks shifted their habitat use from their normal preferred foraging grounds to areas with more cover when wolves were present. There is a trade-off in the activity of prey species as searching and harvesting foods require movement, but movement also increases the encounter rate of predators in enhances the possibility of detection (Werner and Anholt 1993; Brodin and Johansson 2004). A higher activity can give an increase in the food amount consumed and therefore a higher growth rate which is important in relation to survival and mating success (Werner and Anholt 1993; Brodin and Johansson 2004). In general, there will be a selection towards individuals that find the optimal balance of cost-benefit as this gives an increased reproduction and survival rate (Lima 1998). Which kind of behavioral response the prey will show to the predation risk is influenced both by the way the predator hunts (Creel et al. 2005; Weterings et al. 2016), and on the internal state of the prey as the hunger level could affect the willingness to take chances on feeding in a risky habitat (Lima 1992), and also by the habitat itself. Thus, low vegetation can result in an increased probability to be detected by a predator, but it will also give an advantage of detecting the predator sooner and an enhanced escape possibility (Lima 1992). Conversely, high vegetation might facilitate hiding, but hinders escape and predator detection (Lima 1992). Thus, a change in habitat structure can alter the predation pressure (Hummel et al. 2017), and trigger costly antipredator behavior (Weterings et al. 2016) such as reduced foraging time and movement (Creel et al. 2005).

One of the most common types of anti-predator behavior is increased vigilance. When perceiving a predator it is important for the prey to adapt its behavior and increase vigilance according to the perception, especially when the predator is not in sight, as a wrong choice can result in death (Brown 1999; Brown et al. 1999). Not being vigilant enough will increase the risk of being predated, whereas if the animal is too vigilant it could lead to a decrease in fitness over time, because vigilance will often be at the expense of foraging time (Laundré et al. 2001; Creel et al. 2005). Another anti-predator behavior that is often used is avoidance behavior were prey avoid specific areas perceived to be at high risk. Earlier studies have shown that predation can cause prey to shift their habitats so that an area with a predator will be avoided altogether (Apfelbach et al. 2005). Habitats with high food quality are not necessarily the same habitats which are the safest, which can force the prey to either forage in low quality areas or to forage in more risky habitats where the chance of being predated is larger (Rohner and Krebs 1996; Creel et al. 2005). This means that when foraging in a more risky habitat the feeding rate has to be higher to balance out the increased risk of being predated (Brown 1999).

In this study, I investigated how the simulated presence of a red fox (*Vulpes vulpes*) affects abundance, activity and behavior (vigilance and foraging) of the European hare (*Lepus europaeus*, hereafter hare). I simulated the presence of fox with a scent experiment by using fox scat as an olfactory cue. Hare populations have declined all over Europe since the 1960s (Tapper and Parsons 1984), and studies have shown that the intensification of agriculture plays a major role (Smith et al. 2005; Jennings et al. 2006). The change in habitat structure to a more homogeneous structure does not only give a deficient food supply but it also increases the risk of being predated, as the hare is in need of a more heterogenic structure with both high vegetation, providing cover, and low vegetation with a good overview while foraging (Hummel et al. 2017).

Hares are nocturnal animals, living in open lands. They have a home range of about 20-40 ha, providing them both with year round cover (Hummel et al. 2017) and sufficient food resources (Tapper and Barnes 1986; Smith et al. 2005). The main predator of the hare is the red fox (Goszczyński J and Wasilewski M 1992; Lindstrom et al. 1994; Reynolds and Tapper 1995; Panek 2009), and especially leverets are predated (Hummel et al. 2017). However, martens *(Martes martes),* badgers (*Meles meles)* domestic cats (*Felis catus),* common buzzards (*Buteo buteo),* European polecats (*Mustela putorius)* and owls (*Strigiformes)* also predate on hares (Balestrieri et al.; Erlinge et al. 1984). In a study by Weterings et al. (2016) on hares response to elevated predation risk in low vegetation, it was shown that the structure of the vegetation is important when looking at anti-predator behavior. The same study showed that when faced with increased predation risk from a dog (*Canis lupus familiaris)*, hares were shown to spend more time in higher vegetation, and if only low vegetation is available, the reactive movement of the hare will be higher (Weterings et al. 2016).

I hypothesized that the presence of a simulated red fox would cause a change in the abundance and activity of the hare, particularly that areas with fox present would have a lower abundance and activity. Further, I predicted that I would observe a smaller change in areas with low vegetation than in areas with high vegetation, as hares to a large extent use their sight to assess the predation risk (Bang et al. 1969; Hansen 1991). I also hypothesized that a change in behavior would be observed, more specific that an increase in vigilance and a decrease in foraging would be observed in the presence of a simulated fox.

Material and Methods

Study area

The study was carried out in six areas in Denmark (Fig 1), but one was removed due to absence in hares: one area on Mols in Syddjurs municipality and four areas around Aarhus. These areas are dominated by agricultural fields of different types. This study was conducted in one area with barley (*Hordeum vulgare*), one apple plantation and three pastural fields. The study took place from May to August.

Experimental design

I set up camera traps of the model Bushnell Trophy cam HD (Bushnell Outdoor Products, 9200 Cody Overland Park, KS, United States). The cameras were placed in different areas with different vegetation types and heights. The cameras were placed in a grid consisting of two transects with 50 m in between each camera and with five cameras in each transect. The grid was made in ArcGIS by creating a fishnet with 50 meters between points (Fig. 2). I placed the camera traps on poles in a height of 40-80 cm depending on vegetation height and habitat structure, generally facing in the same direction with the best visibility. The cameras were active 24 hours a day and set to take one picture at a time with an interval of 2 sec between two pictures when movement was registered. The pictures from the camera traps were collected twice, first after the control week and then after the week of treatment.

In order to simulate the presence of a predator, fox scat was used. Scat from male red fox were collected from Starfox fox farm in Sæby in Northern Jutland. The scat was collected in one-liter buckets and kept frozen until use, each bucket containing scat from only one individual.

I separated the observation period into a one-week control period followed by a one-week treatment period. During the control period, no olfactory cue was brought out on either transect. During the treatment period, I placed an olfactory cue at a distance of 3-5 m in front of each camera trap, where one transect served as the treatment transect and the other one as the control transect (assigned randomly). I used scat from one individual per area to avoid pseudo replication (Kroodsma et al. 2001). To simulate the natural scent-marking behavior of a fox (4-10 times per km traveled) (Goszczynski 1990; Arnold et al. 2011) one fox scat, with an approximate weight of 13 g, per camera was placed in the treatment transect, and 3 mL diluted butyric acid (1:3) per camera trap were placed in the control transect. The butyric acid is a strong-smelling acid and it was used as a control to check if a possible response to the scent was due to the scent of fox, or just because of an unfamiliar scent (Sullivan et al. 1985; Epple et al. 1993). Both olfactory cues where brought out in round plastic containers with a height of 3 cm and a diameter of 4 cm. The scats were placed directly in the container, and the butyric acid was applied to a sponge which was placed in the container.

The vegetation height is expected to have a great influence on the movement of the hares and their area use. To be able to take this into account the vegetation height was measured with a measuring tape. This was done once for the control and once for the treatment period.

Data preparation

The pictures were sorted in a Microsoft Access database, where every picture was registered with area and camera number, the time of day, vegetation height, visibility, species and behavior. Pictures with only moving vegetation were disregarded. The pictures were classified according to behavior, based on the classification of Kuijper et al 2014. The classification had to be adjusted as it is originally used for ungulates in dense forest (Kuijper et al. 2014), and one behavior was substituted. I categorized behaviors into eight groups: 1) *Vigilance*, defined as standing or sitting still with the head raised and ears pointing directly up or twitching. 2) *Foraging,* head to the ground or visible chewing. 3) *Walking*, i.e., moving slowly without foraging, hares are seen clearly in the picture. 4) *Running,* moving fast either so the picture is blurry or hare in the air fully stretched out or on the ground with hind legs clearly in front of front legs. 5) *Sudden Rush*, i.e., when the animal went from standing still to running. 6) *Sniffing/exploring* when the animal was sniffing the container with scent 7) *checking camera*, when walking directly towards the camera or sniffing the camera. 8) *Sitting*, when sitting or lying down without being vigilant. For the activity analysis, I used all observations of hares to see if there were a difference in the amount of time spent in front of the camera between control and treatment period. For the abundance analysis, I used an index for abundance defined as observations pr. day pr. camera with a minute in between, a minute was chosen to minimize the number of pictures which was from the same visit, this is still an overestimate of visits as some stay for more than a minute.

Statistical analysis

If the simulated presence of red fox has an effect on behavior, I expect to see it in both the abundance, activity and behavior of the hare. To analyze if this was the case I used three generalized linear mixed models (GLMM) using the lme4 package in R (Bates et al. 2015). The GLMM was used because I worked with both fixed and random variables as the observations were not independent as there were multiple observations per camera. For the behavior analysis I grouped the behavior into three groups: (1) *vigilance*, containing vigilance, sudden rush, and sniffing/exploring, (2) *foraging*, containing only foraging, and (3) *other*, containing the remaining groups. The abundance and activity data was non-normal distributed, but showed a negative binomial distribution, which I accounted for by setting the family of error structure to negative binomial in the GLMM For the two first analyses, activity and abundance, I started with a GLMM with the hare abundance or activity as the response variable and vegetation height, treatment, period, different types of predators, and competitors for resources as fixed effects and the camera location as a random intercept. There was no correlation between the fixed effects (all $r < 0.6$). Model selection was based on Akaike information criterion (AIC). The model with the lowest AIC is the most parsimonious model. In order to find this model, the step function in the lmerTest package in R was used. This function performs an automatic backward selection removing non-significant fixed effects.

For the behavior analysis, the proportions of the three behavior groups were calculated in R by using the cbind function. For each behavior group, the proportion was used as response variable, vegetation height, treatment and period as the fixed effects, and the area as a random intercept. As an addition to the behavioral analysis, the proportion of each behavioral group was calculated in excel for each of the four test groups (two control groups and two treatment groups) and plotted to visualize the change in the proportion of the different behaviors.

Results

In total, there were 1339 hare observations distributed over the five areas (Table 1). Other animals such as red fox, roe deer (*Capreolus capreolus)*, badger, cat, dog, and different bird species were also observed (Table 2). Of the observations 855 were made in vegetation under 25 cm, 456 in vegetation between 25-50 cm, and 28 in >50 cm high vegetation.

Abundance and Activity

The hares showed a significant shift in their abundance and activity between treatment areas (Table 3). In the areas treated with butyric acid hare activity and abundance increased compared to the control period (no scent), and in the area treated with fox scat activity and abundance decreased compared to the control period (Figs. 3 and 4). Vegetation height was shown to have a negative influence on both hare abundance and activity. When looking at the other observed animals, roe deer was the only species with a correlation, here there was a positive correlation on the hare abundance and activity. The model describing the abundance and activity the best was the model with vegetation height, roe deer activity or abundance, treatment and period as explanatory variable and the camera ID as a random factor. Not all the variables in the best model was informative when looking at the confidence interval as for some variables the confidences interval went from negative to positive, but they were kept in the model anyway (Table 5).

Behavior

Hares spent more time foraging in the area treated with butyric acid and less time in the area with fox scat (Fig 5), the vegetation height did not influence the amount of foraging. Vigilance behavior increased for both treatments, but there was no difference between groups (Fig 6), and the vegetation height did not seem to influence the amount of vigilance behavior. No significant change was observed in the behavioral group *Other* (Fig 7), but the vegetation height has a significant negative influence on the behavioral group other. For the the three behavior models all fixed varibles were kept both the informative and the uninformative as there was a difference between which variables that were informative in the three different behavior models and to make them easier comparable all variables were kept.

Discussion

In this study, I investigated the behavioral response of hares when exposed to simulated fox presence. As hypothesized, when comparing the area treated with fox scat to the area treated with butyric acid, lower abundance and lower activity were observed in the area treated with fox scats in the treatment period. This indicates that hares avoid areas that have been treated with fox scat, which also was the expected result as the red fox is the main predator of hares and is responsible for most of the predation on hares (Goszczyński J and Wasilewski M 1992; Lindström et al. 1994; Reynolds and Tapper 1995; Panek 2009; Hummel et al. 2017). When the activity is lowered the chance of being detected is also lowered, especially in cryptic prey, so this will help reduce the predation risk. A lowered activity when faced with increased predation risk is also seen in other species such as Coho salmon and kangaroo rats is as way to lower predation risk (Daly et al. 1990; Martel and Dill 1995). Even though a reduction in activity can help the prey to stay undetected it can have consequences as searching for food patches and mating possibilities require movement. So, reducing activity is a good anti-predator behavior if the predator is only present for a short time, but if the predator is present most of the time the reduced activity might end up killing the hare as they would not get sufficient food. Reduced abundance and activity were not observed in the area treated with butyric acid, which indicates that the response is due to the smell of predator and not an unfamiliar scent in general. In the butyric acid area an increase in abundance and activity was seen, which could be because the hares might not recognize this smell as a threat. Thus, hares might move away from the area with fox scat and into the area with butyric acid, which is considered safe. Another explanation for the increase in abundance and activity in the area treated with butyric acid could be that hares spent more time investigating the unfamiliar scent of butyric acid, whereas the two hypotheses are not mutually exclusive.

For both the area treated with butyric acid and the area treated with fox scat an increase in vigilance was observed, so even though the hares did not avoid the area treated with butyric acid it still seems to affect them by increasing their vigilance. However, the time spent foraging did not decrease so it probably will not affect the energy intake. This was also found in a study on mountain beavers (*Aplodontia rufa)*, where butyric acid had no effect on the feeding behavior (Epple et al. 1993). In a study on snowshoe hares it was shown that butyric acid did not suppress feeding behavior, so that the feeding rate was higher in the area with butyric acid than in the control area (Sullivan et al. 1985). For the area treated with fox scat an increase in vigilance and a decrease in foraging was observed, indicating that the increased vigilance is on the expense of foraging time. This was also reported in studies on elk (*Cervus canadensis*) and bison (*Bison bison)* bison in North America when faced with increased predation risk from wolves, where especially females with calves were more vigilant. The increase in vigilance could influence the survival rate, if this increase is at the expense of foraging. This is because a decrease in foraging could affect body condition, which could have an influence on reproduction success as the energy for giving birth and caring for leverets would be lower. A decrease in foraging could also cause the hare to be more reckless and take chances as hunger levels rise, which would increase the risk of being predated. However, if vigilance were not increased, the predation risk would also be higher, because the hare might detect the predator too late to escape. A decrease in the frequency of foraging when exposed to fecal smell from a predator was also found in black tailed deer *(Odocoileus hemionus columbianus)* (Muller-Schwarze 1972). The fecal smell of fox also decreased foraging and increased vigilance and avoidance behavior in the European rabbit (*Oryctolagus cuniculus)*, but in the study it was discussed if the presence of fox scats close to a foraging point had an influence on the food intake as herbivores are not forced to graze in limited areas but could move to another area (Monclús et al. 2005). If all areas with possible feeding potential were of the same food quality then this would be true, but as the vegetation differs in food quality, then it could mean that moving to another area would lower the quality of the food. The amount of time spent foraging would then have to increase to get the same energy intake which would mean spending more time where the prey could be predated easier.

The results show that vegetation height have a negative influence on both abundance and activity. This fits well with the expected results as hares to a great extend use their eyesight when checking for predators, so in high vegetation where the visibility is low the chance of detecting a predator is reduced (Bang et al. 1969; Hansen 1991) and the hares therefor might have to rely more on their sense of smell. Also, hares are known for their great ability to escape a predator, but this ability is limited by high vegetation (Goszczyński J and Wasilewski M 1992; Lima 1992). Generally, an increase in the number of hares was seen in the treatment period compared to the control period (Table 4). For the area treated with fox scat, it was a small insignificant one, but for the area treated with butyric acid there was almost a doubling in the number of hares present in the treatment period compared to the control period. This increase was mostly seen in the areas where the vegetation became lower in the treatment period, which also indicates that hares prefer low vegetation. Another explanation for the lower abundance and activity in the high vegetation could be that the food quality isn't as good in the high vegetation compared to the low, as the high vegetation often will be dryer and less energy rich than low vegetation. This could also explain the positive correlation between the number of roe deer and the number of hares, as more hares were observed in areas where there were also more roe deer. The roe deer also seemed to prefer the low vegetation and as they don't have the same requirements for low vegetation for visibility and escape as the hares and mostly use high vegetation for cover (Sempere et al. 1996). They must prefer the low vegetation due to higher food quality as they prefer soft energy-rich foods containing much water (Sempere et al. 1996). The composition of the vegetation can play a role as a study has shown that unpreferred plants affect the foraging in an area as the feeding rate was seen going up when removing unpreferred plants and decreased when planting unpreferred plants in the area (Kuijper and Bakker 2008). I wanted to investigate if hares avoided higher vegetation more when a predator was present, but because I only observed one hare in vegetation over 25 cm in the area treated with fox scat, this was not possible.

The simulated presence of fox seems to have an influence on the behavior of the hares by increasing anti-predator behavior. An increase was found both in avoidance behavior and in vigilance behavior, and a decrease in activity. The avoidance behavior could have a great influence on the hare population as there generally have been a decrease in suitable habitats for hares and they already have a hard time in intensively farmed areas. So, an additional presence of predators might add extra costs both in terms of habitat use, by avoiding areas with fox presence, but also by effecting foraging efficiency by reducing time spent feeding. A reduction in foraging could affect the reproduction and as the fox already is known to especially predate on leverets the same predation on fewer leverets could end up in a decreasing population size.

Bibliography

Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS. 2005. The effects of predator odors in mammalian prey species: A review of field and laboratory studies. Neurosci Biobehav Rev. 29:1123–1144. doi:10.1016/J.NEUBIOREV.2005.05.005. [accessed 2018 Jun 11]. https://www.sciencedirect.com/science/article/pii/S0149763405000989?via%3Dihub.

Arnold J, Soulsbury CD, Harris S. 2011. Spatial and behavioral changes by red foxes (*Vulpes vulpes*) in response to artificial territory intrusion. Can J Zool. 89:808–815. doi:10.1139/z11-069. [accessed 2018 Mar 19]. http://www.nrcresearchpress.com/doi/10.1139/z11-069.

Balestrieri A, Remonti L, Ruiz-González A, Vergara M, Capelli E, Gómez-Moliner BJ, Prigioni C. Food habits of genetically identified pine marten (Martes martes) expanding in agricultural lowlands (NW Italy). doi:10.1007/s13364-010-0015-8. [accessed 2018 May 21]. https://link-springer-com.ez.statsbiblioteket.dk:12048/content/pdf/10.1007%2Fs13364-010-0015-8.pdf.

Bang P, Hvass H, Jensen B. 1969. Danmarks dyreverden.

Bates D, Mächler M, Zurich E, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. [accessed 2018 Sep 27]. https://arxiv.org/pdf/1406.5823.pdf.

Brodin T, Johansson F. 2004. CONFLICTING SELECTION PRESSURES ON THE GROWTH/PREDATION-RISK TRADE-OFF IN A DAMSELFLY. [accessed 2018 Oct 22]. https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1890/03-3120.

Brown JS. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. Evol Ecol Res. 1:49–71. [accessed 2018 Feb 12]. http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.489.6835&rep=rep1&type=pdf.

Brown JS, Laundre JW, Gurung M. 1999. THE ECOLOGY OF FEAR: OPTIMAL FORAGING, GAME THEORY, AND TROPHIC INTERACTIONS. [accessed 2018 Feb 12]. http://www.jstor.org.ez.statsbiblioteket.dk:2048/stable/pdf/1383287.pdf?refreqid=excelsior%3Afd2c71f23086af6383aa1eea60a842bc.

Creel S, Winnie J, Maxwell B, Hamlin K, Creel M. 2005. Elk Alter Habitat Selection as an Antipredator Response to Wolves. Source Ecol. 86:3387–3397. [accessed 2018 Feb 19]. http://www.jstor.org/stable/3450747.

Daly M, Wilson M, Behrends PR, Jacobs LF. 1990. Characteristics of kangaroo rats, Dipodomys merriami, associated with differential predation risk. Anim Behav. 40:380–389. doi:10.1016/S0003-3472(05)80934-0. [accessed 2018 Oct 17]. https://www.sciencedirect.com/science/article/pii/S0003347205809340.

Epple G, Mason JR, Nolte DL, Campbell DL. 1993. Effects of Predator Odors on Feeding in the Mountain Beaver (Aplodontia rufa). [accessed 2018 Oct 9]. https://www.jstor.org/stable/pdf/1382293.pdf?casa_token=gOSTWCAAwf4AAAAA:Z2OLbBIkF7oGI7lVibMUnd77bBjSbkAfcIduxqDVxJEZ-yAlql60n2cA40-EoMIJEPtXmAAWNxRYnekt3cIbvncA7NbA1rDpyhiIG3Yif_JppLuAcXQ.

Erlinge S, Frylestam B, Goransson G, Hogstedt G, Liberg O, Loman J, Nilsson IN, Von Schantz T, Sylvan M, Erlinge S, et al. 1984. Predation on brown hare and ring-necked pheasant populations in southern Sweden. Holarct Ecol. 7:300–304. [accessed 2018 May 21]. http://www.rana.se/Jon/pdf/predhare84.pdf.

Goszczynski J. 1990. Scent marking by red foxes in Central Poland during the winter season. Acta Theriol (Warsz). 351:7–16. [accessed 2018 Apr 5]. http://rcin.org.pl/Content/11714/BI002_2613_Cz-40-2_Acta-T35-nr2-7-16_o.pdf.

Goszczyński J, Wasilewski M. 1992. Prédation of foxes on a hare population in central Poland. Acta Theriol (Warsz). 37:329–338. [accessed 2018 Oct 8]. http://rcin.org.pl/Content/11806/BI002_2613_Cz-40-2_Acta-T37-nr30-329-338_o.pdf.

Hansen K. 1991. Hare. In: Danmarks Pattedyr 1.

Hummel S, Meyer L, Hackländer K, Weber D. 2017. Activity of potential predators of European hare (Lepus europaeus) leverets and ground-nesting birds in wildflower strips. Eur J Wildl Res. 63:102. doi:10.1007/s10344-017-1158-6. [accessed 2018 Jan 7]. http://link.springer.com/10.1007/s10344-017-1158-6.

Jennings N, Smith RK, Hackländer K, Harris S, L PC, White Jennings PC. 2006. Variation in demography, condition and dietary quality of hares Lepus europaeus from high-density and low-density populations. White Source Wildl Biol Wildl Biol. 12121792. [accessed 2018 Jan 7]. http://www.bioone.org/doi/full/10.2981/0909-6396%282006%2912%5B179%3AVIDCAD.

Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu W-C. 2001. COMMENTARIES Pseudoreplication in playback experiments, revisited a decade later. Anim Behav. 61:1029–1033. doi:10.1006/anbe.2000.1676. [accessed 2018 Sep 27]. http://academic.brooklyn.cuny.edu/biology/jbasil/KroodsmaPseudoreplication.pdf.pdf.

Kuijper DPJ, Bakker JP. 2008. Unpreferred plants affect patch choice and spatial distribution of European brown hares. Acta Oecologica. 34:339–344. doi:10.1016/J.ACTAO.2008.06.007. [accessed 2018 Oct 16]. https://www.sciencedirect.com/science/article/pii/S1146609X08000994.

Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K. 2014. What Cues Do Ungulates Use to Assess Predation Risk in Dense Temperate Forests? PLoS One. 9:84607. doi:10.1371/journal.pone.0084607. [accessed 2018 Aug 13]. www.plosone.org.

Laundré JW, Hernández L, Altendorf KB. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Can J Zool. 79:1401–1409. doi:10.1139/z01-094. [accessed 2018 Feb 12]. http://www.nrcresearchpress.com/doi/10.1139/z01-094.

Lima SL. 1992. Strong Preferences for Apparently Dangerous Habitats? A Consequence of Differential Escape from Predators Strong preferences for apparently dangerous habitats? A consequence of differential escape from predators. Source: Oikos. 64:597–600. [accessed 2018 Feb 22]. http://www.jstor.org/stable/3545181.

Lima SL. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions Nonlethal Effects in the Ecology of Predator-Prey Interactions What are the ecological effects of anti-predator decision-making? Source Biosci. 48:25–34. [accessed 2018 Feb 22]. http://www.jstor.org/stable/1313225.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. [accessed 2018 Feb 23]. http://gambusia.zo.ncsu.edu/readings/Lima and Dill 1990.pdf.

Lindström ER, Andrén H, Angelstam P, Cederlund G, Hörnfeldt B, Jäderberg L, Lemnell P-A, Martinsson B, Sköld K, Lindstrom ER, et al. 1994. Disease Reveals the Predator: Sarcoptic Mange, Red Fox Predation, and Prey Populations DISEASE REVEALS THE PREDATOR: SARCOPTIC MANGE, RED FOX PREDATION, AND PREY POPULATIONS'. Swenson Source Ecol Ecol. 75:1042–1049. [accessed 2018 Jan 7]. http://www.jstor.org/stable/1939428.

Lindstrom ER, Andrtn H, Jaderberg L, Lemnell P-A, Martinsson B, Skold K, Swenson JE. 1994. DISEASE REVEALS THE PREDATOR: SARCOPTIC MANGE, RED FOX PREDATION, AND PREY POPULATIONS'. [accessed 2018 Oct 8]. https://about.jstor.org/terms.

Martel G, Dill LM. 1995. Influence of Movement by Coho Salmon (Oncorhynchus kisutch) Parr on Their Detection by Common Mergansers (Mergus merganser). Ethology. 99:139–149. doi:10.1111/j.1439-0310.1995.tb01095.x. [accessed 2018 Oct 17]. http://www.sfu.ca/biology/faculty/dill/publications/j.1439-0310.1995.tb01095.x.pdf.

Monclús R, Rödel HG, Von Holst D, De Miguel J. 2005. Behavioural and physiological responses of naïve European rabbits to predator odour. Anim Behav. 70:753–761. doi:10.1016/J.ANBEHAV.2004.12.019. [accessed 2018 Oct 16]. https://www.sciencedirect.com/science/article/pii/S0003347205001922#bib15.

Muller-Schwarze D. 1972. Responses of Young Black-Tailed Deer to Predator Odors. J Mammal. 53:393–394. doi:10.2307/1379188. [accessed 2018 Oct 16]. https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1379188.

Panek M. 2009. Factors Affecting Predation of Red Foxes *Vulpes vulpes* on Brown Hares *Lepus europaeus* During the Breeding Season in Poland. Wildlife Biol. 15:345–349. doi:10.2981/07-042. [accessed 2018 Oct 8]. http://www.bioone.org/doi/abs/10.2981/07-042.

Reynolds JC, Tapper SC. 1995. Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its potential impact on annual population growth. Wildlife Biol. 1:145–158. doi:10.2981/wlb.1995.019. [accessed 2018 Oct 8]. http://www.bioone.org/doi/10.2981/wlb.1995.019.

Rohner C, Krebs CJ. 1996. Owl Predation on Snowshoe Hares: Consequences of Antipredator Behaviour. Source: Oecologia. 108:303–310. [accessed 2018 Jan 7]. http://www.jstor.org/stable/4221419.

Sempere AJ, Sokolov VE, Danilkin AA. 1996. Capreolus capreolus. Mamm Species. 3:1–9. doi:10.2307/3504309/2600733. [accessed 2018 Oct 15]. https://academic.oup.com/mspecies/article-abstract/doi/10.2307/3504309/2600733.

Smith RK, Vaughan Jennings N, Harris S. 2005. A quantitative analysis of the abundance and demography of European hares Lepus europaeus in relation to habitat type, intensity of agriculture and climate. Mamm Rev. 35:1–24. doi:10.1111/j.1365-2907.2005.00057.x. [accessed 2018 Jan 7]. http://doi.wiley.com/10.1111/j.1365-2907.2005.00057.x.

Sullivan TR, Nordstrom LO, Sullivan DS. 1985. USE OF PREDATOR ODORS AS REPELLENTS TO REDUCE FEEDING DAMAGE BY HERBIVORES I. Snowshoe Hares (Lepus americanus). [accessed 2018 Oct 9]. https://link.springer.com/content/pdf/10.1007/BF01012077.pdf.

Tapper S, Parsons N. 1984. The changing status of the Brown hare (Lepus capensis L.) in Britain. Mamm Rev. 14:57–70. doi:10.1111/j.1365-2907.1984.tb00339.x. [accessed 2018 Feb 20]. http://doi.wiley.com/10.1111/j.1365-2907.1984.tb00339.x.

Tapper SC, Barnes RFW. 1986. Influence of Farming Practice on the Ecology of the Brown Hare (Lepus europaeus). [accessed 2018 Oct 8]. https://www.jstor.org/stable/pdf/2403079.pdf.

Werner EE, Anholt BR. 1993. Ecological Consequences of the Trade-Off between Growth and Mortality Rates Mediated by Foraging Activity. [accessed 2018 Oct 22]. https://www.jstor.org/stable/pdf/2462815.pdf.

Weterings MJA, Zaccaroni M, van der Koore N, Zijlstra LM, Kuipers HJ, van Langevelde F, van Wieren SE. 2016. Strong reactive movement response of the medium-sized European hare to elevated predation risk in short vegetation. Anim Behav. 115:107–114. doi:10.1016/J.ANBEHAV.2016.03.011. [accessed 2018 Jan 7]. https://www-sciencedirect-com.ez.statsbiblioteket.dk:12048/science/article/pii/S0003347216000865.

Figures

Figure 1 Overview of the 5 experimental areas

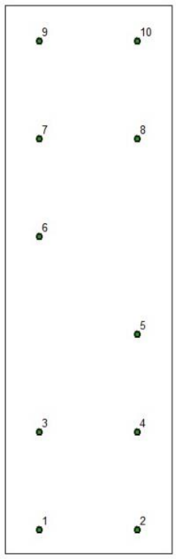

Figure 2 Baseline experimental setup

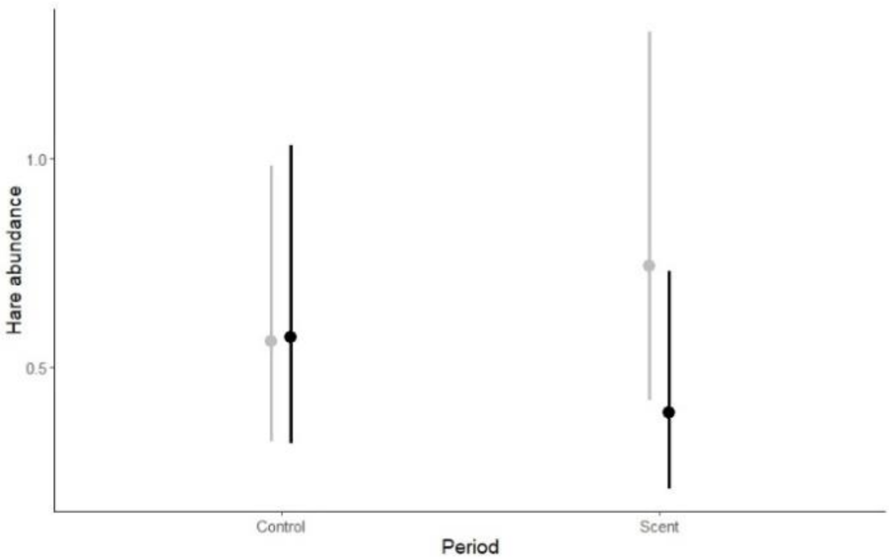

Figure 3 Hare abundance, grey shows the abundance for butyric acid area, and black shows the abundance for Fox scats area, error bars shows 95 % confidence interval, the high confidence interval is due to the high difference in abundance between the five areas. There is no diffenrence between the two control periods, but we see an increase the abundance for the butyric acid and a decrease for the fox scats

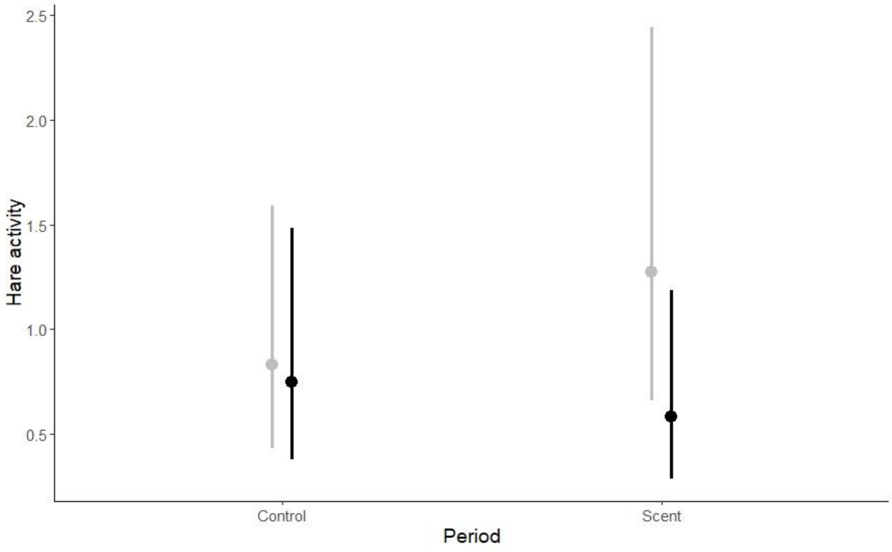

Figure 4 Hare activity, grey shows the activity for butyric acid area, and black shows the activity for the fox scats area, error bars shows 95 % confidence interval, the high confidence interval is due to the high difference in activity between the five areas. There is no diffenrence between the two control periods, but we see an increase the abundance for the butyric acid and a decrease for the fox scats.

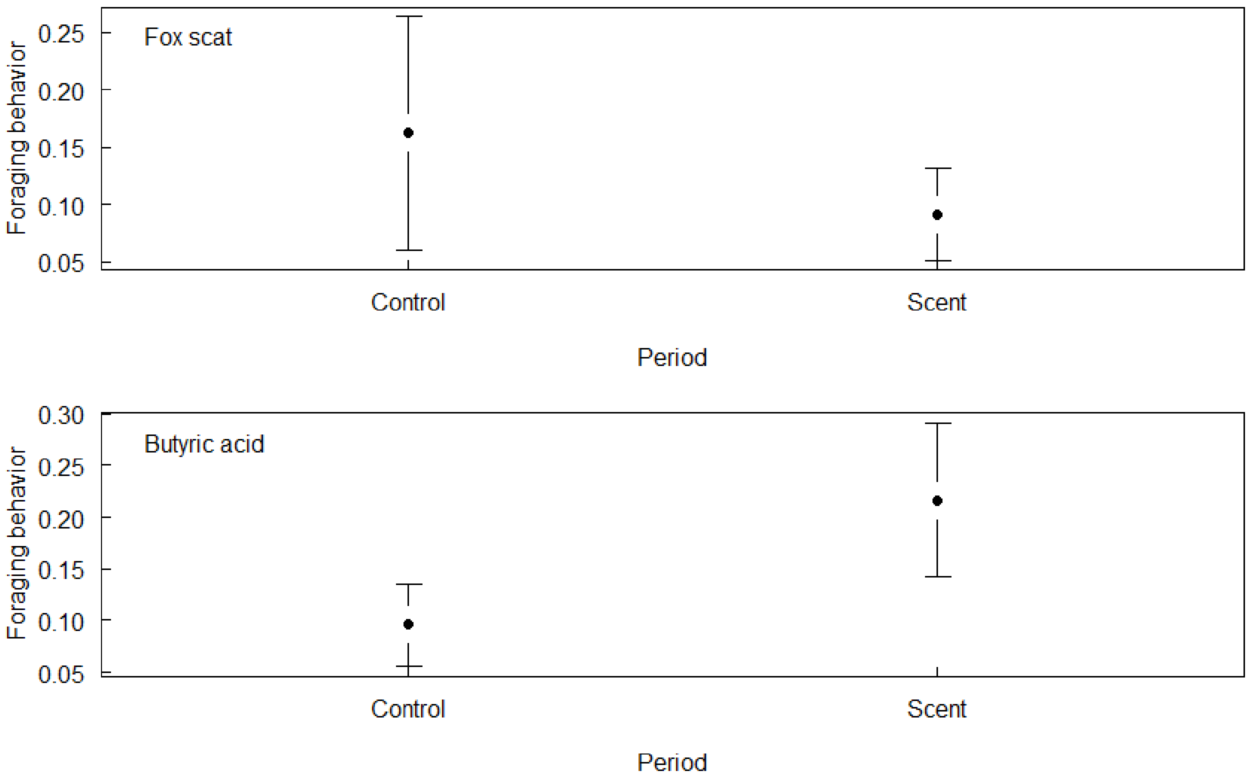

Figure 5 Mean proportion of foraging behavior, error bars shows 95 % confidence interval the high confidence interval is due to the high difference in foraging behavior between the five areas. There is no observed difference between the two control periods, a slightly increase in foraging is observed in the butyric acid area, and a decrease is observed in the fox scat area.

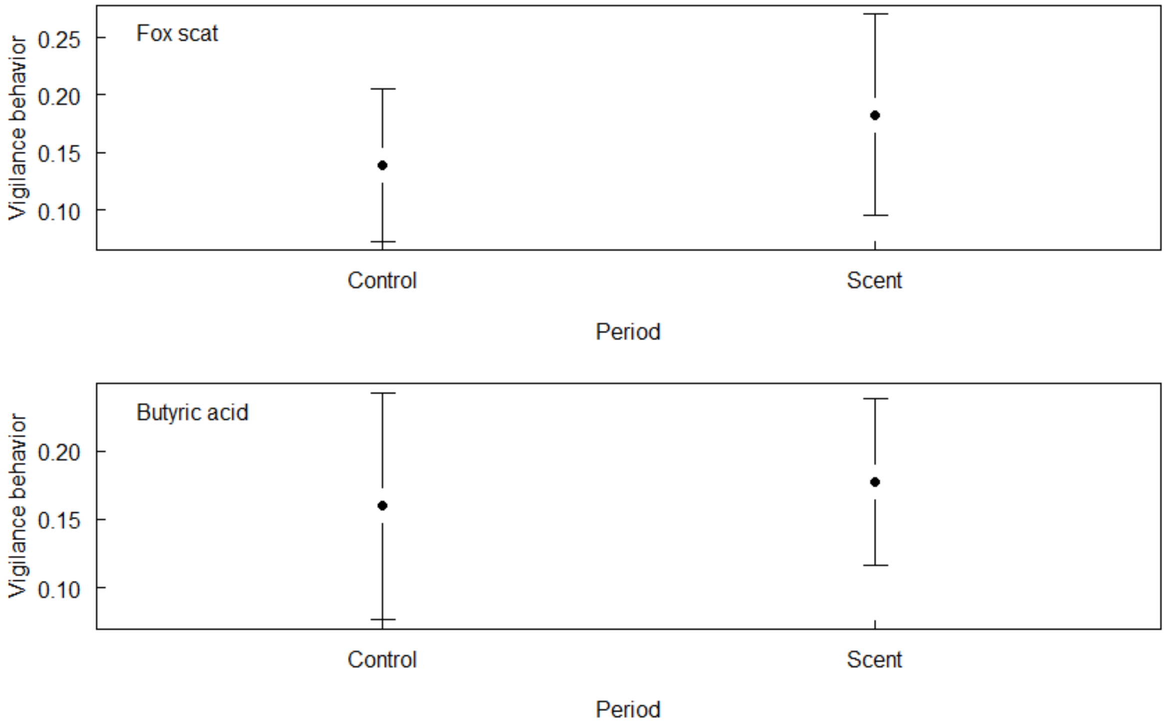

Figure 6 Mean proportion of vigilance behavior. Error bars shows 95 % confidence interval the high confidence interval is due to the high difference in vigilance behavior between the five areas. There is no observed difference

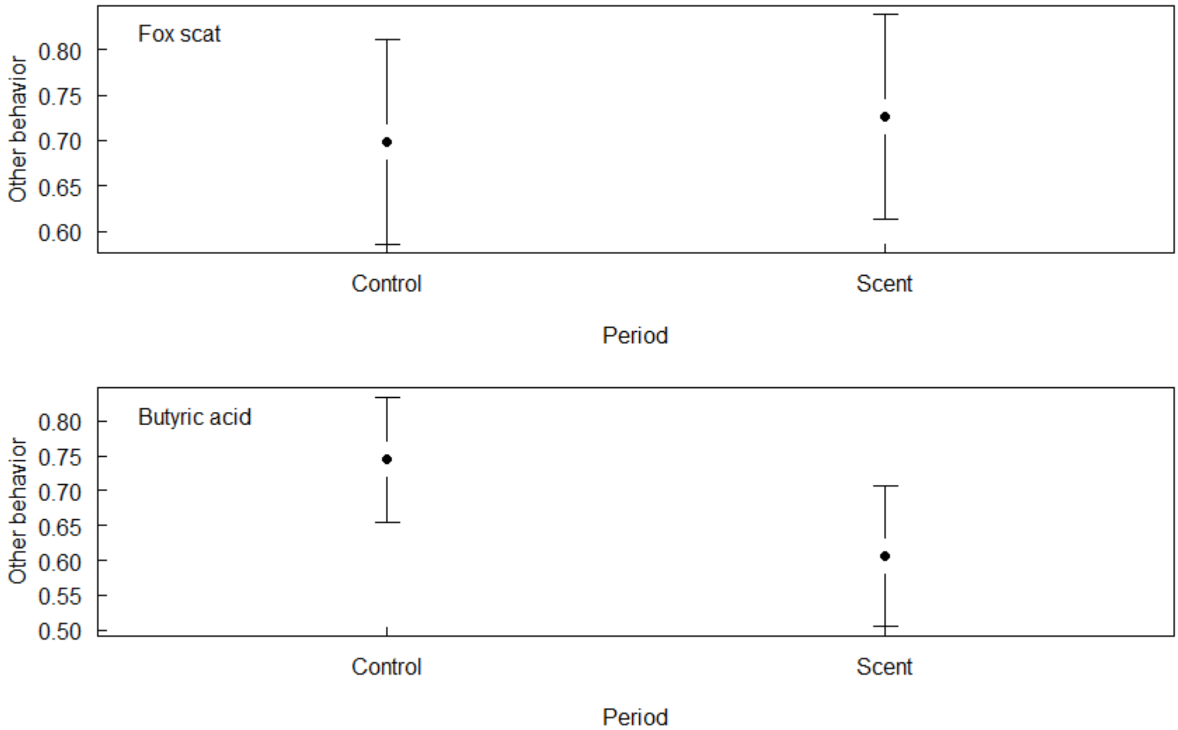

Figure 7 Proportion of other behavior. Error bars shows 95 % confidence interval, the high confidence interval is due to the high difference in other behavior between the five areas. No significant change observed.

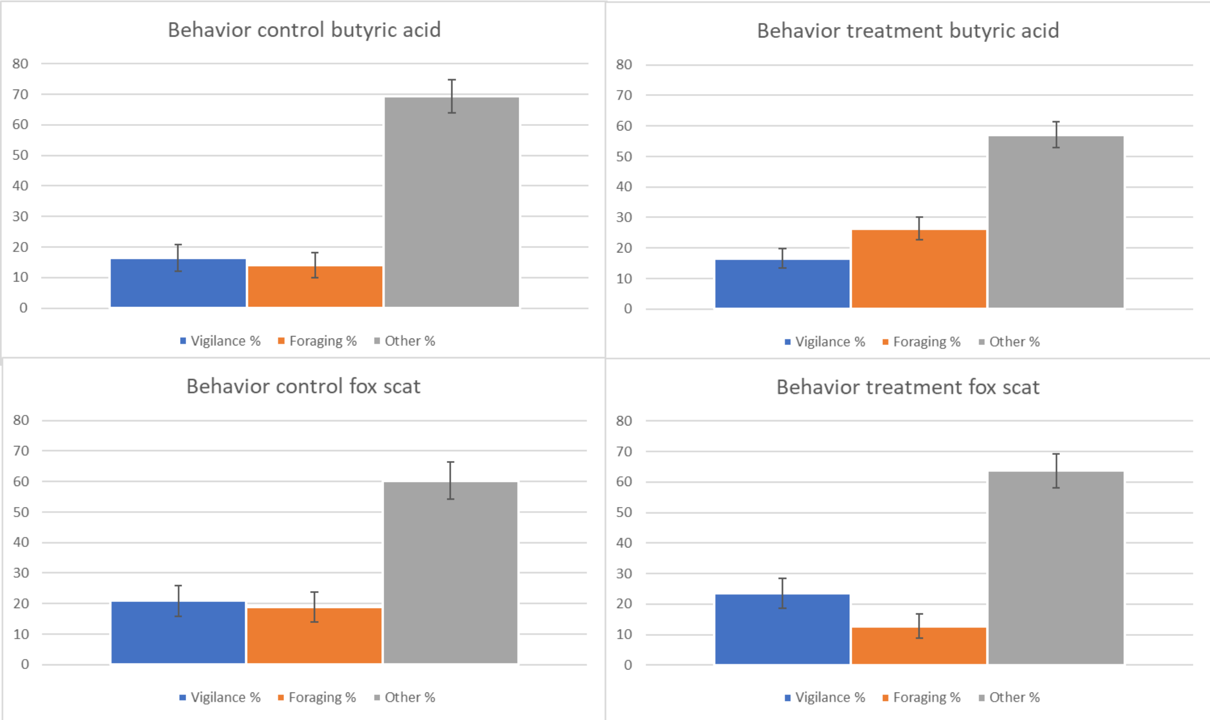

Figure 8 Distribution of the three behavioral groups in the two areas in the control and treatment period.

Tabels

Area	Camera location	Hares	POINT_X	POINT_Y	Vegetation type	start control period	start treatment period	cue
1	1_1	58	578005,2	6232983,9	Apple plantation	29.05.2018	06.06.2018	fox scat
1	1_2	43	578004,2	6233039,5	Apple plantation	29.05.2018	06.06.2018	fox scat
1	1_3	45	578059,8	6233040,5	Apple plantation	29.05.2018	06.06.2018	fox scat
1	1_4	84	578058,8	6233096,1	Apple plantation	29.05.2018	06.06.2018	fox scat
1	1_5	68	578057,8	6233151,6	Apple plantation	29.05.2018	06.06.2018	fox scat
1	1_6	41	578113,5	6233152,7	Apple plantation	29.05.2018	06.06.2018	butyric acid
1	1_7	88	578112,5	6233208,2	Apple plantation	29.05.2018	06.06.2018	butyric acid
1	1_8	138	578168,1	6233209,2	Apple plantation	29.05.2018	06.06.2018	butyric acid
1	1_9	23	578167,1	6233264,8	Apple plantation	29.05.2018	06.06.2018	butyric acid
1	1_10	11	578166,1	6233320,4	Apple plantation	29.05.2018	06.06.2018	butyric acid

2	2_1	1	578087,0	6232766,6	Arable land (cereal)	29.05.2018	06.06.2018	fox scat
2	2_2	0	578085,9	6232822,2	Arable land (cereal)	29.05.2018	06.06.2018	fox scat
2	2_3	0	578141,6	6232823,2	Arable land (cereal)	29.05.2018	06.06.2018	fox scat
2	2_4	1	578140,6	6232878,7	Arable land (cereal)	29.05.2018	06.06.2018	fox scat
2	2_5	1	578139,6	6232934,3	Arable land (cereal)	29.05.2018	06.06.2018	fox scat
2	2_6	2	578195,3	6232935,3	Arable land (cereal)	29.05.2018	06.06.2018	butyric acid
2	2_7	5	578194,3	6232990,9	Arable land (cereal)	29.05.2018	06.06.2018	butyric acid
2	2_8	6	578249,9	6232991,9	Arable land (cereal)	29.05.2018	06.06.2018	butyric acid
2	2_9	0	578248,9	6233047,5	Arable land (cereal)	29.05.2018	06.06.2018	butyric acid
2	2_10	9	578247,9	6233103,0	Arable land (cereal)	29.05.2018	06.06.2018	butyric acid
4	4_1	5	563928,7	6224566,2	Pasture	26.06.2018	04.07.2018	fox scat
4	4_2	62	563961,4	6224591,9	Pasture	26.06.2018	04.07.2018	fox scat
4	4_3	0	563891,2	6224594,7	Pasture	26.06.2018	04.07.2018	fox scat
4	4_4	0	563931,3	6224633,4	Pasture	26.06.2018	04.07.2018	fox scat
4	4_5	4	563852,4	6224634,7	Pasture	26.06.2018	04.07.2018	fox scat
4	4_6	0	563892,5	6224673,4	Pasture	26.06.2018	04.07.2018	butyric acid
4	4_7	0	563813,6	6224674,7	Pasture	26.06.2018	04.07.2018	butyric acid
4	4_8	0	563853,7	6224713,4	Pasture	26.06.2018	04.07.2018	butyric acid
4	4_9	39	563815,4	6224818,9	Pasture	26.06.2018	04.07.2018	butyric acid
4	4_10	4	563814,9	6224753,4	Pasture	26.06.2018	04.07.2018	butyric acid
5	5_1	1	572899,1	6233835,3	Pasture	26.06.2018	04.07.2018	fox scat
5	5_2	2	572952,8	6233820,8	Pasture	26.06.2018	04.07.2018	fox scat
5	5_3	17	573006,6	6233806,3	Pasture	26.06.2018	04.07.2018	fox scat
5	5_4	10	573060,3	6233791,7	Pasture	26.06.2018	04.07.2018	fox scat
5	5_5	0	573114,1	6233777,2	Pasture	26.06.2018	04.07.2018	fox scat
5	5_6	82	572913,7	6233888,9	Pasture	26.06.2018	04.07.2018	butyric acid
5	5_7	102	572967,4	6233874,4	Pasture	26.06.2018	04.07.2018	butyric acid
5	5_8	0	573021,1	6233859,9	Pasture	26.06.2018	04.07.2018	butyric acid
5	5_9	85	573074,9	6233845,4	Pasture	26.06.2018	04.07.2018	butyric acid
5	5_10	39	573128,6	6233830,9	Pasture	26.06.2018	04.07.2018	butyric acid
6	6_10	12	592613,3	6239791,9	Pasture	05.07.2018	13.07.2018	fox scat
6	6_9	82	592612,1	623984,7	Pasture	05.07.2018	13.07.2018	fox scat
6	6_8	1	592667,7	6239848,6	Pasture	05.07.2018	13.07.2018	fox scat
6	6_7	32	592610,9	6239902,9	Pasture	05.07.2018	13.07.2018	fox scat
6	6_6	1	592666,5	6239904,1	Pasture	05.07.2018	13.07.2018	fox scat

6	6_5	65	59260,8	6240013,9	Pasture	05.07.2018	13.07.2018	butyric acid
6	6_4	25	592664,1	6240015,1	Pasture	05.07.2018	13.07.2018	butyric acid
6	6_3	13	592607,3	6240069,3	Pasture	05.07.2018	13.07.2018	butyric acid
6	6_2	32	592662,9	6240070,5	Pasture	05.07.2018	13.07.2018	butyric acid
6	6_1	0	592661,7	6240126,0	Pasture	05.07.2018	13.07.2018	butyric acid

Tabel 1 Overview of study areas. Area, camera number and location, vegetation type, start date for the control and treatment period and used treatment at each camera.

Red Fox	Roe deer	Badger	Cat	Common Buzzard	Dog	Birds
66	1359	5	27	5	3	1956

Tabel 2 Overview of other animals than hares observed during the study

		Hares pr. day pr. area	±SD
Abundance	Control Fox scat	4.86	1.91
	Treatment Fox scat	5.31	1.27
	Control Butyric acid	4.57	1.82
	Treatment Butyric acid	7.57	2.87
Activity	Control Fox scat	7.11	3.86
	Treatment Fox scat	8.03	2.48
	Control Butyric acid	7.94	4.04
	Treatment Butyric acid	15.17	6.29
Vigilance	Control Fox scat	1.43	0.92
	Treatment Fox scat	1.89	1.06
	Control Butyric acid	1.17	0.67
	Treatment Butyric acid	2.49	1.42
Foraging	Control Fox scat	1.34	1.02
	Treatment Fox scat	1.03	0.66
	Control Butyric acid	1.11	1.06
	Treatment Butyric acid	4.0	2.59
Other	Control Fox scat	4.29	2.13
	Treatment Fox scat	5.11	1.46
	Control Butyric acid	5.51	8.66
	Treatment Butyric acid	8.66	4.75

Tabel 3. Average abundance and activity pr day pr area. Average vigilance, foraging and other behavior pr day pr area

	Butyric acid		Fox scat			
Area	N before	N after	N before	N after	control	treatment
1	59	242	160	138	219	380
2	13	9	3	0	16	9
4	24	19	17	54	41	73
5	138	170	20	10	158	180
6	44	91	49	79	93	170

Tabel 4 Number of hare observations in each area before and after treatment divided into treatments, and total numbers of hares observed in each area in the control and treatment area.

			Confidence interval	
Abundance	Estimate	Std. Error	2.50%	97.50%
(Intercept)	0.508235	0.353428	-0.184472435	0.012009416
Veg_height	-0.04545	0.008798	-0.06269671	-0.02820837
roe_deer	0.071488	0.040716	-0.008313025	0.1518949
PeriodScent	0.276850	0.163817	-0.044224757	0.59792466
TreatmentFox scats+urine	0.016657	0.409584	-0.786113743	0.81942722
PeriodScent:TreatmentFox scats+urine	-0.657672	0.243240	-1.13441238	-0.18093083

			Confidence interval	
Activity	Estimate	Std. Error	2.50%	97.50%
(Intercept)	0.784064	0.398861	0.002311838	1.56581672
Veg_height	-0.041047	0.009093	-0.058869346	-0.0232249
roe_deer	0.021147	0.012710	-0.003763881	0.04605691
PeriodScent	0.428298	0.193760	0..048535752	0.80805995
TreatmentFox scats+urine	-0.103429	0.478343	-1.040965154	0.83410634
PeriodScent:TreatmentFox scats+urine	-0.676256	0.291402	-1.24739874	-0.10511816

Tabel 5 Overview of model estimates for the abundance and activity analysis, including standard error and confidence interval