Examensarbete
i ämnet biologi

2013:15

Effects of brown bear (Ursus arctos) odour on the patch choice and behaviour of different ungulate species

Sonja Noell

Sveriges lantbruksuniversitet
Fakulteten för skogsvetenskap
Institutionen för vilt, fisk och miljö
Examensarbete i biologi, 30 hp, A2E

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Effekter av odör från brunbjörn på olika klövvilts beteende och områdesutnyttjande

Sonja Noell

Keywords: risk effects, odour, fallow deer (Dama dama), roe deer (Capreolus capreolus), red deer (Cervus elaphus), moose (Alces alces), wild boar (Sus scrofa), Öster Malma

Handledare: Joris Cromsigt och Ellinor Sahlén
Examinator: John P Ball

30 hp, A2E
Kurskod EX0633
Program: Inget

SLU, Sveriges lantbruksuniversitet
Fakulteten för skogsvetenskap
Institutionen för vilt, fisk och miljö

Swedish University of Agricultural Sciences
Faculty of Forestry
Dept. of Wildlife, Fish, and Environmental Studies

Umeå 2013

Abstract

The return of large predators to regions where they were previously extirpated has created a need for knowledge about their effect on prey species, not only their lethal but also their behavioural or risk effects. In this study the behavioural risk effects of brown bear (*Ursus arctos*) were tested on fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), moose (*Alces alces*) and wild boar (*Sus scrofa*). This was done by using patches of fur to simulate the presence of the novel predator (brown bear), a novel non-predator (reindeer (*Rangifer tarandus*) and no fur as control. These three treatments were then compared. The response variables measured were increased vigilance, decreased feeding time and change in patch use. The results for fallow deer supported the hypothesis that there are fewer individuals present during the bear treatment (change in patch use). Red deer and roe deer changed the individuals present during treatments as well but they were least present during the reindeer treatment and most during control. The results for roe deer support the hypothesis that there is more time spent on vigilance behaviour during the bear treatment by showing more ‘sniffing in the air’ behaviour during bear treatment than during reindeer and control treatments. As well as showing more ‘combined vigilance’ during bear treatment than during reindeer treatment (increased vigilance). The results for wild boar support the hypothesis that there is less feeding behaviour during bear treatment by spending less time on ‘feeding on the ground’ during bear treatment than during control treatment (decreased feeding time). The hypothesis that feeding height is an aspect of vigilance behaviour and is therefore influenced by the bear odour was not supported. The fact that every species reacted differently shows that studying risk effects in this manner outside under natural conditions is possible but requires detailed knowledge of species behaviour to be able to tailor experiments exactly right to detect these effects.

Återkomsten av stora rovdjur till områden där de tidigare utrotats har skapat ett behov för kunskap om hur de påverkar sina bytesarter, inte endast gällande dödliga effekter men också av beteenden, så kallade riskeffekter. I den här studien testades riskeffekterna av brunbjörn (*Ursus arctos*) på dovhjort, rådjur, kronhjort, älg, och vildsvin. Detta gjordes genom att använda delar av päls för att simulera närvaro av en predator (brunbjörn), en icke-predator (ren), och en kontroll utan päls. Dessa tre behandlingar blev sedan jämförda. Responsvariablerna som mättes var ökad vaksamhet (vigilance), minskad födotid och ändrat områdesutnyttjande. Resultaten för dovhjort stödde hypotesen att färre individer var närvarande under björnbehandling (ändrat områdesutnyttjande). Kronhjort och rådjur ändrade antalet individer närvarande under de olika behandlingarna men de var minst närvarande under renbehandling och mest under kontrollen. Resultaten för rådjur stödjer hypotesen att mer tid är spenderad på vigilancebeteenden under björnbehandling genom att visa mer ”sniffande i luften”-beteende vid björnbehandling än under ren- och kontrollbehandling. De visade även mer ”kombinerad vigilance” under björnbehandlingen än under renbehandling (ökad vaksamhet). Resultaten för vildsvin stödjer hypotesen att det uttrycks mindre födobeteende under björnbehandling eftersom vildsvinen spenderade mindre tid på ”äta på marken” med björndoften än under kontrollen (mindre födotid). Hypotesen att födohöjd är ett sorts vigilancebeteende och därför påverkas av björndoft stöddes inte. Faktumet att varje art reagerade på olika vis visar att riskeffekter kan studeras under naturliga förhållanden med denna metod, men att det krävs detaljerad kunskap om arternas beteende för att kunna skräddarsy exmeriment på ett sätt som fångar dessa effekter.

Introduction

Large carnivores were seen as direct rivals to people and where therefore hunted to extinction in certain parts of the world, Europe being a prime example. In recent years people's perception of what nature is and means has seen some radical change, which has lead to predators naturally returning to and settling in areas where they were not present in the last years (European Commission 2013). From a scientific perspective this leads to very interesting fields of study since in many European countries these top predators were extinct for some time or were only present in very small numbers in small areas effectively stunting a whole trophic level for decades (European Commission 2013). In these countries the missing trophic level had effects on the entire ecosystem not yet fully realised and certainly not exhaustively researched (Estes and Palmisano 1974). The effect of apex predators moves top-down, if this involves three or more trophic levels (Predator -Herbivore-Plant) this is called a trophic cascade (Berger et al. 2008, Ripple and Beschta 2004). The causal link between apex predators and such trophic cascades has been studied extensively in Yellowstone National Park since the return of the wolves in 1995 (Matthew et al. 2010, Halofsky 2008, Fortin et al. 2005, Ripple et al. 2004, 2010, Creel et al. 2009, Berger et al. 2008, Christianson and Creel 2008, White and Garrott 2005, Ripple and Beschta 2006, 2012). It may even lead to secondary cascades where the effect branches out to more than one herbivore species and therefore more than one plant species (Ripple et al. 2010). However, there has been intense debate on how apex predators cause this effect. It is taken as a given that there is a density mediated effect meaning that the predator has a direct effect on prey population numbers though their successful hunting activities, since there are less prey individuals (reduced density), these eat fewer plants equalling a trophic cascade (Kauffman, et al. 2010). The competing hypothesis, that there are also behaviour mediated trophic cascades, is more controversial. Behaviour or trait mediated means that the mere presence of the predator causes what is called a risk effect, where the behaviour of the prey species changes due to this perceived threat, which leads to a change for the plants involved again equalling a trophic cascade (Kauffman et al. 2010).

Risk effect refers to those species-specific anti-predator behaviours, invoked as a reaction to predatory threats, to minimise their probability of meeting a predator and reduce the probability of being killed by this predator. (Halofsky 2008, Thaker et al. 2011, Creel and Christianson 2008). These anti-predator strategies often involve behavioural changes in vigilance, foraging, aggregation and habitat use, but also influence reproduction, mortality and other life history factors of the prey species, therefore carrying costs for the prey individual (Creel and Christianson, 2008). That these risk effects not only exist, but can be greater than direct lethal effects, has been shown in various studies including spiders (Schmitz et al. 1997), insects and fish, summarized by Creel and Christianson (2008). Through studies on mammals are rare, Boonstra et al. (1998) show that the decline in the snowshoe hare (*Lepus americanus*) population (in the classic research done on predator-prey interaction where the population cycle in population of lynx (*Lynx lynx*) is linked to the population of snowshoe hares) is not due to limited food supply as previously assumed, but to risk effects, in this case near constant stress. The risk effect on ungulates has often been studied indirectly through the trophic cascade effect they have on plants such as aspen (*Populus tremuloides*) and willow (*Salix spp.*) (Creel et al. 2009, Fortin et al. 2005, Halofsky 2008). Although there are also studies that look at risk effects more directly for example Christianson and Creel (2008) who show that reduced reproductive success in elk (*Cervus elaphus*) is greater than can be explained by wolf (*Canis lupus*) kills of calves. There is also the study by Halofsky and Ripple (2008) who look at vigilance of elk. Risk effect is often not studied because most research focuses on indirect observations of life history factors, such as fecundity, and in these studies risk effects are easily interpreted as a result of any number of bottom-up limiting factors such as food supply (Creel, et al. 2008). Risk effect need to be studied directly because they are “the product of hundreds or thousands of small actions” (Creel et al. 2008) taken by prey to sometimes indirect cues of predator presence.

Cues for predator presence can be classified as direct or indirect. Direct cues are always those that only occur when the predator is actually present, the most obvious being a visual presence but can include others depending on the prey animal’s senses. Indirect cues are more diverse in that they involve anything that a prey animal can sense that indicates the predator’s presence at some other time. The most useful are the species specific cues such as fur, faeces, urine, and gland secretions. For risk effect studies, indirect cues are the more important ones, since these are left behind over a large area and will forewarn the prey that a predator might be present even if they are not directly detectable at the moment. In this study the focus is on ungulates, which through evolutionary history have a strong sense of smell and are therefore able to detect the above mentioned indirect cues. Various studies have been done to test the effectiveness of these cues as for example repellents, with varying success (Apfelbach et al. 2005, Müller-Schwarz 1972, Melchoirs et al. 1985, Nolte et al. 2001, Swihart et al. 1991, Lindgren et al. 1995). Most research showing the reaction of prey to predator odour is being done in laboratories with rodents reacting to smells from predators such as cats and foxes. Since these are not only predator smells but also unknown smells to the rodents, synthetic odours which are also unknown to the rodents are used as controls. Results are often inconsistent between studies (Apfelbach et al. 2005). When studies are done on ungulates it is usually in captivity, the predator odours are faecal, urinary, or synthetic products using either of these as base. The odours are sprayed on the food or placed in containers in the food troughs. Since these are captive animals they are unfamiliar with predators, especially because some of the predator samples are not native predators to the ungulates in the experiment, however, no controls are used to control for a reaction to an unfamiliar smell (Müller-Schwarz 1972, Melchoirs et al. 1985, Nolte et al. 2001, Swihart et al. 1991, Lindgren et al. 1995). At the end of their review Apfelbach et al. (2005) state that the most effective and consistent results occur when predator fur is used and the predator and prey have evolutionary history together, this is one of the few instances where a comparison of odour source and its effects are remarked upon at all.

In this study the focus is on how ungulate species react to the indirect cues left behind by predators. That behaviour changes when prey species react to risk has been established already and these changes include; an increase in vigilance and a decrease in feeding behaviour (Apfelbach et al. 2005). However, it has not been studied extensively whether foraging as such changes, or if it is just a change in diet because the animal has moved to a different habitat. In this case a closer look was taken at feeding height since height may have an important role in vigilance behaviour. All types of animals try to achieve a view from the top to be able to see threats earlier and have more time to react. For ungulates species this is usually represented in the type of habitat they use and how their habitat use changes according to perceived risk level. However, there is not much known about whether ungulates increase the height at which they feed to be able to have a better overview of their surroundings even while feeding resulting in kind of partial vigilance. Partial vigilance is known to exist in herbivores where time while chewing is spent on vigilance and therefore increased vigilance does not have as large an effect of decreased feeding time as previously assumed (Fortin et al 2004). Therefore the possibility of feeding height being part of vigilance behaviour will be tested on this study.

This study was done to ascertain how the return of large predators might affect ungulate species in Europe, which are; fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), moose (*Alces alces*) and wild boar (*Sus scrofa*). The study was done in southern Sweden and the brown bear (*Ursus arctos*) was chosen as the predator, since this is a natural predator in this area but has been extirpated for some time and has not yet returned (Katajisto 2006). This fulfils the requirement of the predator and prey having evolutionary history. Since the extirpation of said predators in most of Europe has led to predator naive ungulates the study area was chosen to represent this setting. Bear fur was used to create the illusion of bear presence, so that the risk effects conveyed via the indirect cue of bear odour could be studied. To be able to differentiate between the effect of an unknown predator and the effect of it just being an unfamiliar smell reindeer fur was used as a control. Reindeer (*Rangifer tarandus*) was used because as an herbivore it is not a lethal threat to the ungulates. It also fulfils the requirement of being native but not present in the region. Another control with no fur was used to control for the effect of the equipment alone. The behavioural risk effects tested for were; increased vigilance, decreased feeding time, and change in visitation rate and feeding height as well as seeing whether species reacted differently.

To examine how herbivores may alter their behaviour in response to a predator in the area, I tested:

- If fewer individuals were present at experimental sites when bear presence was simulated with odour
- If fewer were videos taken at experimental sites when bear presence was simulated with odour
- If more time was spent on vigilance behaviour when bear presence was simulated with odour
- If less time was spent on feeding when bear presence was simulated with odour
- If species fed more at eye level height when bear presence was simulated with odour
- If responses to the simulated bear presence with odour were species specific

Methods

The study was conducted during six consecutive weeks, separated into two periods of three weeks. The first period was between the 6th to the 29th of March 2013 and the second from the 27th March to the 19th of April 2013.

Study Area

The study area is located in southern Sweden about 90 kilometers south of Stockholm in the county Södermanland. Virtually in the centre is Öster Malma (N 58°57' - E 17°09') and the closest city is Gnesta (See Figure 1) (Öster Malma 2012).

The area is mostly covered in managed forests (spruce and pine) and a few agricultural fields, with some lakes completing the landscape. Average temperature during the study month is 1.3°C in March and 3.5° in April (SMHI 2013). However this year in March the average temperatures per day ranged from -10°C to +5°C, where the coldest temperature at night reached -18°C. In April the average temperatures per day ranged from -5°C to +5°C. There was also a much longer period with snow cover than on average.

The area was chosen for its high density of different ungulate species; fallow deer, roe deer, red deer, moose and wild boar. There have been sightings (unconfirmed) of wolf and lynx in the area but no bears (Katajisto 2006). Hence this area was chosen, as it might give a clear indication of how ungulate species will react to an unknown predator appearing in their area after it had been extirpated for some time.

The land on which the experimental sites were located belonged to five different landowners, including the Svenska Jägareförbundet (Swedish Association for Hunting and Wildlife Management). The 30 experimental plots were spread over all of their lands at locations where supplementary feeding stations are maintained for the ungulates during the winter months and early spring. The ungulates were therefore used to human disturbance as well as food availability at these sites. The feed was mostly made up of silage, sometimes with the addition of an electronic wheat dispenser.

Figure 1: Study area with experimental plot locations used to test effect of brown bear odour on ungulate behaviour in south-eastern Sweden, spring 2013.

Experimental Setup

In each of the two periods 15 sites were chosen in forested areas at supplementary feeding sites within the study area. At these 15 locations a camera trap was set up in such a way that it faced a feeding tree which contained wheat silage (See Figure 2). The feeding tree was a wooden structure with silage attached at 5 different heights (See Figure 2), which was set up additionally to the silage the landowners spread on the ground. This was done so that when to individuals came to eat the height at which they fed could be estimated. Within close proximity to the feeding tree wooden structures containing the fur treatment were attached so that the smell would permeate the area (See Figure 2). In total 30 sites were covered in this way in six weeks.

Figure 2: Set up of the experimental plots to test effect of brown bear odour on ungulate species in south-eastern Sweden, spring 2013.

There were three different treatments. One was the bear scent, one was reindeer and the third was the fur-less control. Reindeer as well as the bear are unfamiliar smells to the ungulates species in this area. Therefore, to be able to recognize the difference between a reaction to an unfamiliar smell and the reaction to a predator smell reindeer was included as a second control. The different smells were created by pieces of animal fur being nailed to a wooden structure (See Figure 3). The bear fur was acquired from the Swedish International Veterinary Institute (SVA). The reindeer fur was bought from a Sami herder, the indigenous reindeer herders in northern Sweden. All fur was frozen when fresh and stored frozen until use. The control was an empty wooden structure, without fur.

Figure 3: Treatment Structure used to test effect of brown bear odour on different ungulate species in south-eastern Sweden, spring 2013.

The treatments were rotated every week, meaning that each site hosted all three treatments by the end of the three weeks. The first treatment was assigned arbitrarily and then the order of the following two weeks was predetermined to include all possible combinations within the 15 sites. There were always two wooden structures with the current treatment. When the treatments were moved to the new site one fur piece was replaced with a fresh one to ensure fresh smell. Only one could be renewed due to a shortage of bear fur, equaling 40 fur pieces per treatment species used over the course of the study period. Whenever the treatments were exchanged the wheat silage on the feeding tree, which had been eaten, was replaced to ensure the same conditions as in the week before.

The cameras (Company - HCO outdoor products, Model – ScoutGuard SG560C) (See Figure 4) were set to record videos for 30 seconds every two minutes when triggered by the motion sensor. The sensitivity chosen was the normal setting, which was recommended for outside use. The two minutes were chosen to keep disturbance to a minimum, since the flash was a normal white light flash and is therefore seen by the animals. The 30 seconds were selected, since when tested with fallow deer in an enclosure, this duration was shown to be long enough for them to stop staring at the flash after getting disturbed by it and not too long to create data overflow, while also saving battery power.

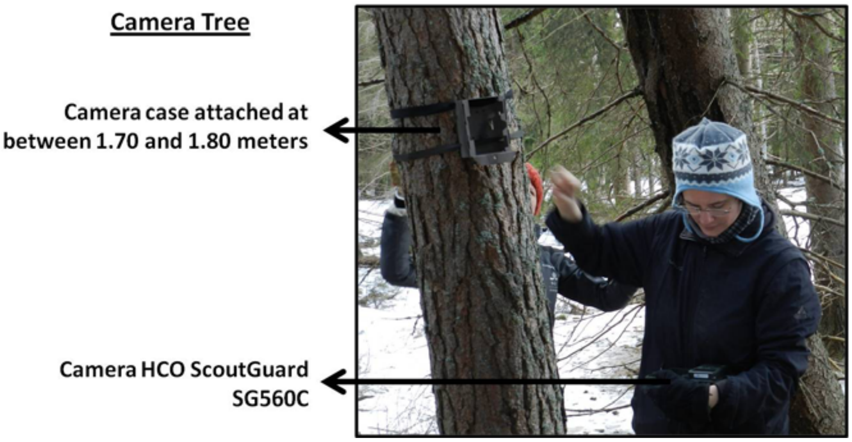

Figure 4: Camera Set up used to test effect of brown bear odour on different ungulate species in south-eastern Sweden, spring 2013.

Data analysis

For all statistical calculations R version 2.13.2 (2011-09-30) was used with the packages Rcmdr, pgirmess, lme4, multcomp, nlme

Of the 2620 videos taken (excluding ones which had no relevant species present) 451 had to be discarded because the video length was under 30 seconds. Of the remaining videos not all could be comprehensively analysed in time for this master thesis.

For the questions pertaining to behaviour only videos taken during the second day and the seventh day of each week were analysed, resulting in 730 videos. These days were selected to include the beginning as well as the end of the week and still get a full 24 hour undisturbed time period for each day of the data sample.

Visitation rates to plots were also analysed independent of behaviour. For this analysis videos taken on the second, the fourth, fifth and seventh day of each week were included, resulting in

1448 videos. Since analysis of videos without including behaviour was quicker, four days were analysed to include more than half the data and therefore have more certain results. The days were spread throughout the week so that changes within the week would be included in the average.

The location of the individual on the ‘site’ was included in the analysis to test if the effect of smell cues had a limited range around the feeding tree. Locations were separated into three ranges: the range directly at the feeding tree, meaning that the mouth of the individual can potentially reach the feeding tree without the need of walking; the second range was the range where at night the individual was well visible owing to the flash (up to 15 meters away); the third range was anywhere outside of the flash range (further away than 15 meters). Duration of behaviour (See Table 1) was tested separately for each location. All behaviour shown in the location ‘outside range’ was later removed from the analysis because behaviour could not be quantified accurately due to low visibility.

Site was chosen as a replicate to avoid pseudoreplication, since animals could not be recognised individually.

Analysis of visitation rate data

Individuals were summed up by ungulate species on each video and then averaged over all videos taken during each day. Zeros were added to the data when a species was not present on a particular site during a particular day. For the number of videos taken at each site the same approach was used; the number of videos was summed up for each species on each day, then zeros were added.

A linear mixed effect model was used to analyse the number of individuals present, because it allows for a Poisson distribution which is necessary when modelling count data as well as making it possible to distinguish between fixed and random factors. The inclusion of random factors made it possible to include any effect ‘site’ might have in the calculation. The linear mixed-effect model was also used to correct for repeated measure effects of measuring the same site and treatment for multiple days. So as a random variable, ‘day’ was nested within ‘species’ and ‘species’ within ‘site’. The same thing was done for the number of videos taken.

For both response variables (number of videos per day, and number of individuals per day), models were tested with the variables ungulate species and fur treatment. Single variable models were run as well as the additive and interaction model including both variables. These were then compared with a log-likelihood test to find the best fitting model with lowest number of variables.

Analysis of behavioural data

There were 21 different behaviours recorded. Of these the seven in the table below (See Table 1) were analysed as relevant for the study.

Table 1: Analysed Behaviours and Grouping

Behaviour	**Group**
Feeding on the ground (not from the feeding tree)	Feeding
Feeding on the feeding tree at different heights	Feeding
The individual is not moving except to blink (freezing)	Vigilance
The individual is looking around	Vigilance
The individual is sniffing the air	Vigilance
The individual is lying down and chewing	Partial Vigilance
The individual is standing and chewing	Partial Vigilance

Analysis was done on the groups defined in Table 1 as well as on some of the single behaviours within these groups such as ‘sniffing in the air’ since it is considered the most important vigilance behaviour concerning the treatment. ‘Feeding’ behaviour was again analysed in different groups such as ‘all feeding behaviour together’, then separately ‘feeding on the ground’ and ‘feeding on the feeding tree’. ‘Feeding on the ground’ was analysed separately from ‘feeding on the feeding tree’ because the area where it can take place is much larger compared to the area of each feeding height on the feeding tree, even when standing directly at the feeding tree. Feeding on the feeding tree was also analysed separately for each feeding height to test the hypothesis that feeding height is indicative of vigilance behaviour. Feeding from the feeding tree two meters above the ground (F5) was removed from the analysis because there was no feeding at this height. Feeding at the feeding tree as well as the analysis of feeding height influence was only calculated at the feeding tree range because at both other ranges feeding can only be done on the ground.

Behaviour was recorded for each individual present in each video separately. It was recorded in second intervals for all 30 seconds of each video. Resulting in a sum of seconds for each behaviour shown in this video for each individual present. Furthermore, the position (range) within the experimental site was recorded for each individual, for each of these seconds as well. To be able to use ‘site’ as a replicate, behaviour duration was averaged over all individuals per site and treatment, separated by range. For each behaviour per ungulate species this resulted in a maximum of 30 average durations of the behaviour per treatment per site and range within site. However, species did not visit all sites or display all behaviours at all sites.

Hence the resulting data set was unbalanced with different sample sizes for different species-treatment groups. This meant that no models with more than one explaining variable could be used. There was also too little data on two species, moose and red deer, and they were therefore removed from the behavioural analysis calculations altogether.

All response variables (behaviours) was analysed with linear models, using ungulate species and treatment as predicting variables, whenever residuals were distributed normally and ‘site’ did not have an effect. If ‘site’ did have an effect then a linear mixed effect model was used where species was nested within site. When the residuals were not normally distributed the Kruskal-Wallis test was used to evaluate effects of variables, and multiple comparisons (using the kruskalmc test in the pgirmess package in R) to pinpoint which levels of a variable were significant. The advantage of using “kruskalmc” is that the p-value is adjusted to the number of consecutive Kruskal-Wallis tests that are done (similar to the Bonferoni correction). This multiple comparison test returns results for pair-wise comparisons as either being TRUE when significant or FALSE when not significant. In the following results section the p-value in these cases is always given as <0.05 when the test returned as TRUE when testing for significant results or <0.1 when testing for trends.

Results

Is there a significant influence of treatment on number of individuals present?

Four linear mixed effect models were run and the log-likelihood comparison is summarised below.

Table 2: Models for Individuals

Name	**Model Formula**
LMER.1	No.of.Indiv ~ Treatment + (1 | Site/Species/Day)
LMER.3	No.of.Indiv ~ Species + (1 | Site/Species/Day)
LMER.4	No.of.Indiv ~ Species + Treatment + (1 | Site/Species/Day)
LMER.2	No.of.Indiv ~ Treatment * Species + (1 | Site/Species/Day)

Table 3: Comparisons between Models for Individuals

Model	Df	AIC	BIC	logLik	Chisq	Chi Df	Pr(>Chisq)
LMER.1	6	5927.5	5960.5	-2957.8			
LMER.3	8	5952.5	5996.5	-2968.	0.000	2	1
LMER.4	10	5881.6	5936.6	-2930.8	74.897	2	<0.0000
LMER.2	18	5790.1	589.0	-2877.1	107.513	8	<0.0000

The model with both fur treatment and species as well as their interaction (LMER.2) has the best fit (See Tables 2 and 3).

Table 4: LMER.2 Results

Species	**Treatment**	**Effect**	**Std.Error**	**Pr(>|z|) compared to bear**
Red Deer	Bear	0.0016	2.8154	
Red Deer	Control	0.0041	1.3160	0.0006
Red Deer	Reindeer	0.0005	1.6093	0.0154
Roe Deer	Bear	0.0222	1.8912	
Roe Deer	Control	0.0334	1.1171	0.0002
Roe Deer	Reindeer	0.0114	1.1590	<0.0000
Fallow Deer	Bear	0.1208	1.7749	
Fallow Deer	Control	0.1899	1.0597	<0.0000
Fallow Deer	Reindeer	0.1745	1.0608	<0.0000
Moose	Bear	0.0013	3.7870	
Moose	Control	0.0004	3.7399	0.4048
Moose	Reindeer	0.0013	2.5412	0.9999
Wild boar	Bear	0.1968	1.7670	
Wild boar	Control	0.2196	1.0789	0.1479
Wild boar	Reindeer	0.2018	1.0805	0.7446

For red deer the least number of individuals were present during reindeer treatments weeks and the most were present during control treatment weeks, this can be seen in the table above (See Table 4), for roe deer the pattern is the same. The pattern is different for fallow deer, they were present most during control weeks and least present during bear weeks (Table 4). The number of individuals present for moose and wild boar did not differ between treatments (See Table 4).

The average number of individuals present can be seen in Figure 5.

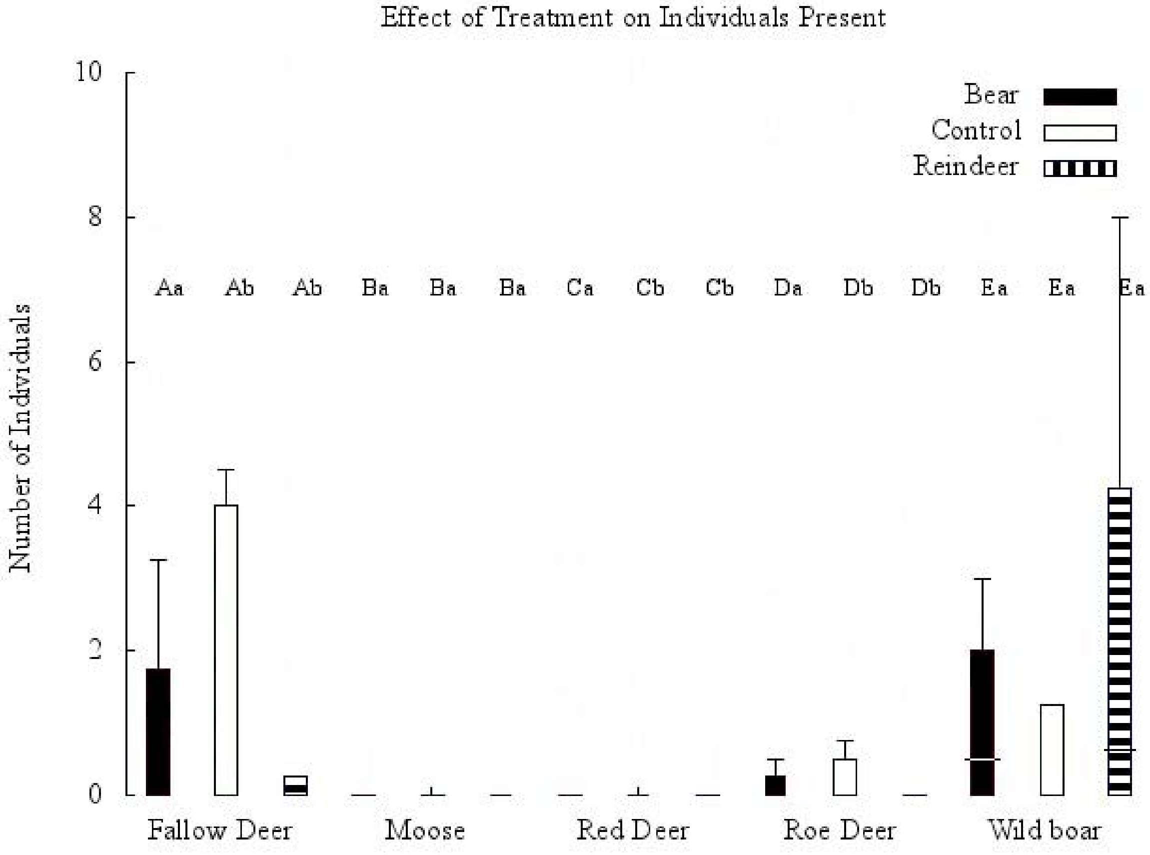

Figure 5: Comparison of odour treatment effects on average number of individuals of ungulate species present on experimental plots in south-eastern Sweden, spring 2013.

The line within the box is the median. The boxes represent the first and third quartile and the whiskers are one standard deviation above the mean of the data. The little letters above the error bars depict which value is significantly different to the others, Aa is significantly different to Ab but would not be to another Aa, and Aa and Ba were not in the same group and therefore not compared. The b values are not neccesarily not different, since control and reindeer were not tested against each other.

Is there a significant difference between treatments in number of videos taken?

Four mixed effect models were run in this analysis as well, the summary can be seen below.

Table 7: Models for Videos

Name	**Model formula**
LMER.6	No.of.Vids ~ Treatment + (1 | Site/Species/Day)
LMER.5	No.of.Vids ~ Species + (1 | Site/Species/Day)
LMER.7	No.of.Vids ~ Treatment + Species + (1 | Site/Species/Day)
LMER.8	No.of.Vids ~ Treatment * Species + (1 | Site/Species/Day)

Table 8: Comparison between Models for Videos

Model	Df	AIC	BIC	logLik	Chisq	Chi Df	Pr(>Chisq)
LMER.5	6	2511.6	2544.6	-1249.8			
LMER.6	8	2513.6	2557.5	-1248.8	2.0847	2	0.3526
LMER.7	10	2463.5	2518.5	-1221.8	54.0161	2	<0.0000
LMER.8	18	2439.6	2538.5	-1201.8	39.9624	8	<0.0000

Again the model including fur treatment and species as well as the interaction between them (LMER.8) has the best fit (See Table 7 and 8).

Table 9: LMER.8 Results

Species	**Treatment**	**Effect**	**Std. Error**	**Pr (<|z|) compared to Bear**
Fallow Deer	Bear	0.1196	1.5987	
Fallow Deer	Control	0.1942	1.1081	<0.0000
Fallow Deer	Reindeer	0.1372	1.1189	0.221
Red Deer	Bear	0.0003	2.3836	
Red Deer	Control	0.3140	1.5405	0.0255
Red Deer	Reindeer	0.0449	2.0220	0.164
Roe Deer	Bear	0.0034	1.6842	
Roe Deer	Control	0.2574	1.1675	<0.0000
Roe Deer	Reindeer	0.0911	1.2160	0.164
Moose	Bear	0.0003	2.9212	
Moose	Control	0.0399	3.8690	0.417
Moose	Reindeer	0.1196	2.6034	1.00
Wild boar	Bear	0.0245	1.5862	
Wild boar	Control	0.1423	1.1161	0.1142
Wild boar	Reindeer	0.1345	1.1178	0.2930

This table shows that there were more videos taken during control weeks than during bear weeks for fallow deer, red deer and roe deer. For wild boar and moose the number of videos did not differ between treatments. For red deer, roe deer and fallow deer the number of videos did not differ from reindeer treatment weeks to bear weeks (See Table 9).

To see the average number of videos taken, see Figure 6.

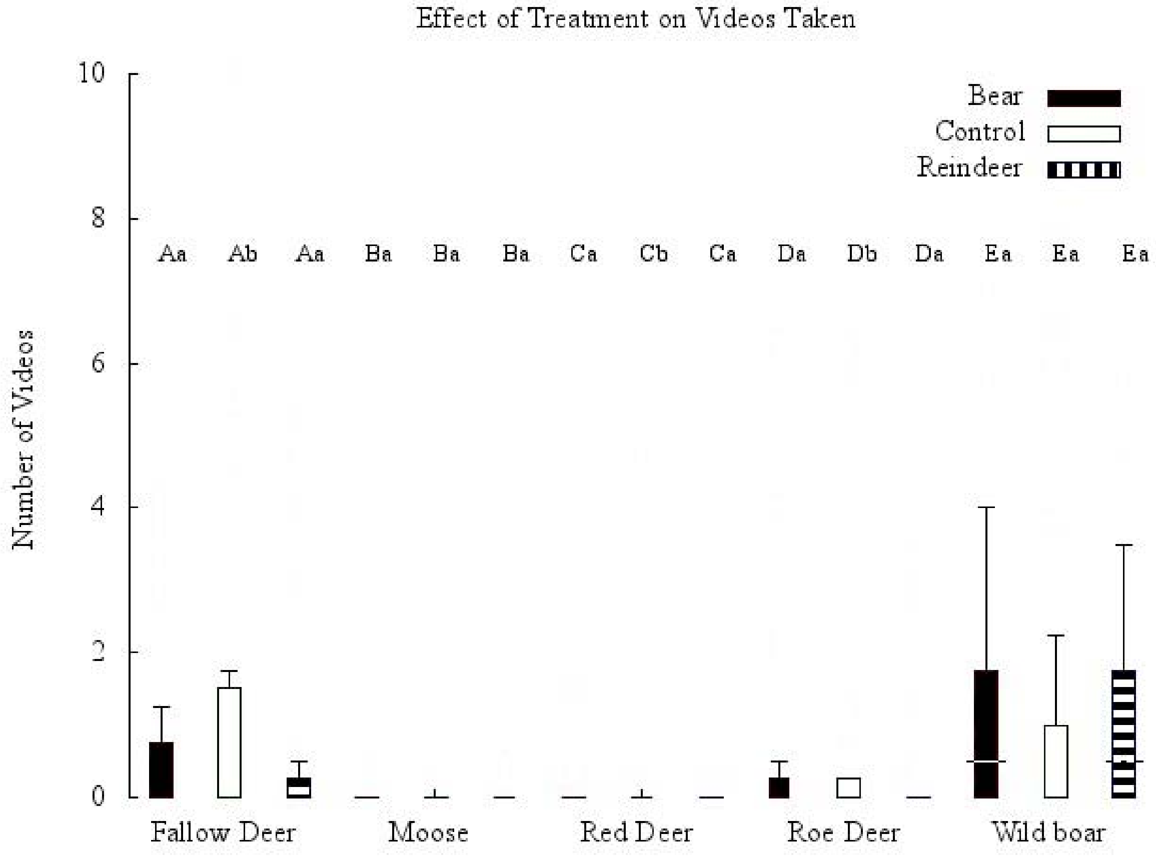

Figure 6: Comparison of odour treatment effects on the average number of videos taken of different ungulate species on experimental plots in south-eastern Sweden, spring 2013.

The line within the box is the median. The boxes represent the first and third quartile and the whiskers are one standard deviation above the mean of the data. The little letters above the error bars depict which value is significantly different from the others, Aa is significantly different to Ab but would not be to another Aa, and Aa and Ba were not in the same group and therefore not compared. The b values are not neccesarily not different, since control and reindeer were not tested against each other.

Is there a significant difference between treatments in behaviour?

Analysis of behaviours taking place within the feeding tree range:

‘Combined feeding’ did not differ between treatments for any of the species (Fallow Deer p-value = 0.3436, Roe Deer p-value = 0.8499, Wild boar p-value = 0.1385). However, it varied between species (p-value: 0.0066), roe deer spent less time with ‘combined feeding’ behaviour than fallow deer (p value = 0.0053).

‘Feeding on the ground’ did not differ among treatments for any of the species (Roe Deer = p-value: 0.5817, Fallow Deer = p-value 0.5817, Wild boar = p-value: 0.235). However, for wild boar there was a trend (p-value = 0.0919) towards less time spent on ‘feeding on the ground’ during bear weeks versus control weeks (See Figure 7).

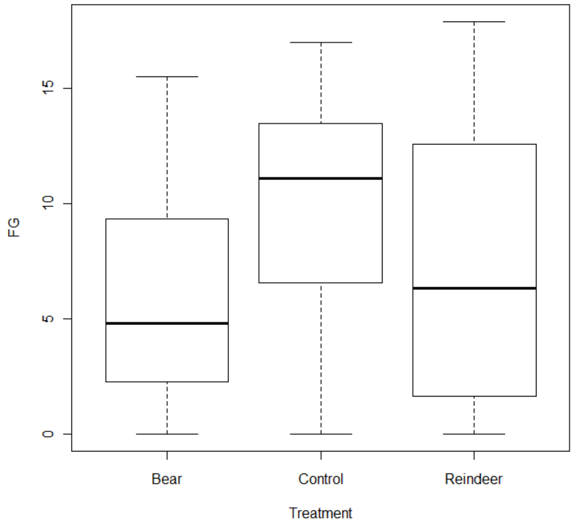

Figure 7: ‘Feeding on the ground’ (FG) behaviour of wild boar at feeding sites during different odour treatment weeks in south-eastern Sweden, spring 2013. FG calculated in average number of seconds spent on this behaviour during a 30 second video. The difference between bear and control has a p-value of 0.09191.

‘Feeding on the feeding tree’ did not differ between treatments for any of the species (Fallow Deer p-value= 0.5798, Roe Deer p-value = 0.6326, Wild boar p-value = 0.1457). There was also no difference between species (p-value = 0.3516).

Feeding time at different ‘feeding heights’ did not differ between treatments for any of the species (See Table 10). The species spent varying amounts of time ‘feeding’ from different ‘feeding heights’, wild boar spent more time ‘feeding’ at F1 than fallow deer (p-value = <0.05), wild boar also spent more time ‘feeding’ at F2 than roe deer (p-value = <0.05).

Table 10: Feeding at different feeding heights

Feeding Height	F1 - ground	F2 – 50 cm	F3 – 1 m	F4 – 1.5 m
Site Influence	p-value 0.1595	p-value 0.3718	p-value 0.395	p-value 0.9766
Same as	F2 p-values >0.1	F1 p-values >0.1	F4 p-values >0.1	F3 p-values >0.1
Different to other Height	F3, F4 p-values <0.05	F3,F4 p-values <0.05	F1,F2 p-values <0.05	F1, F2 p-values <0.05
Difference between Species	p-value = **0.0230**	p-value = **0.0018**	p- value = >0.05	p-value = >0.05
Fallow Deer (FD) – Wild boar (WB)	p-value <0.05 **WB>FD**	NA	NA	NA
Roe Deer (RD) – Wild boar (WB)	NA	p-value <0.05 **WB>RD**	NA	NA
Difference between treatments for fallow deer	p-value = 0.7022,	p-value = 0.6743,	p-value = 0.7603	p-value = 0.4412

Difference between treatments for roe deer	p-value = 0.8039	p-value = 0.527	No Data	No Data
Difference between treatments for wild boar	p-value = 0.8395	p-value = 0.4222	p-value = 0.604	No Data

Time spent on ‘sniffing in the air’ did not differ between treatments within species (Fallow Deer = p-value = 0.328, Roe Deer = p-value = 0.6376, Wild boar = p-value = 0.1844).

‘Combined Vigilance’ (see Table 1 for groupings) did not differ between treatments within each species (Fallow Deer = p-value = 0.3166, Roe Deer = p-value = 0.9343, Wild boar = p-value = 0.7597). However, fallow deer showed a trend (p-value <0.1), spending more time on ‘combined vigilance’ behaviour during control treatment weeks versus bear weeks (See Figure 8). There was a difference between species (significant p-value = 0.0212), where wild boar showed less ‘combined vigilance’ behaviour than roe deer.

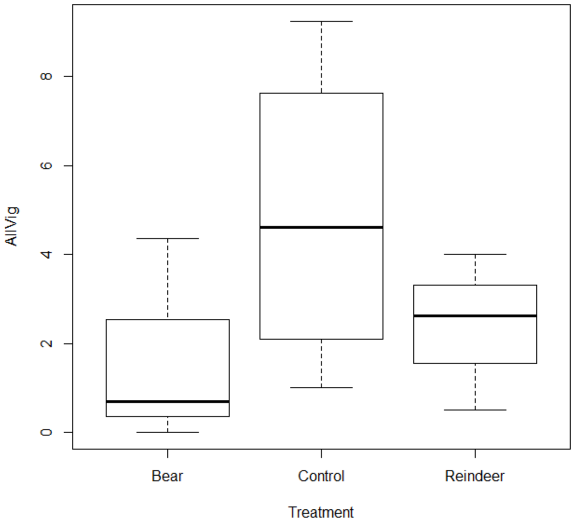

Figure 8: ‘Combined Vigilance’ (AllVig is a combination of behaviours ‘sniffing in the air’, ‘looking around’ and ‘freezing’) behaviour of fallow deer at feeding sites compared during different odour treatment weeks in south-eastern Sweden, spring 2013. AllVig is calculated in average number of seconds spent on this behaviour during a 30 second video. The difference between bear and control has a p-value of <0.1.

‘Combined partial vigilance’ (for grouping see Table 1) did not differ between treatment weeks within species (Fallow Deer = p-value = 0.5756, Roe Deer = p-value = 0.3197, Wild boar = p-value = 0.9656). There is a trend (p-value = 0.0718) indicating that species used this behaviour differently and form the plotted results it can be inferred that wild boar used this behaviour least although p-value is >0.1. (See Figure 9)

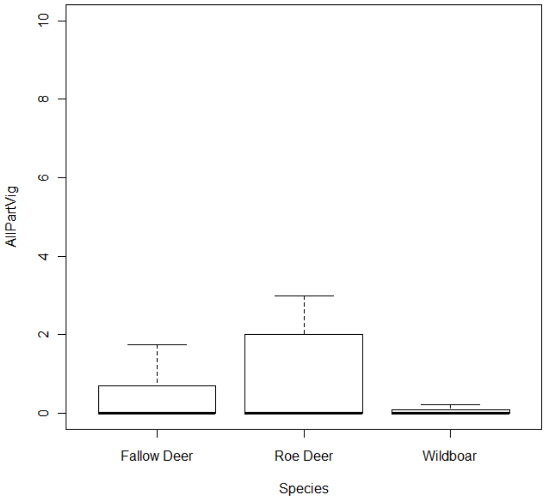

Figure 9: ‘Combined partial vigilance’ (AllPartVig is a combination of the behaviours ‘lying down and chewing’ and ‘standing and chewing’) compared between different ungulate species in south-eastern Sweden, spring 2013. AllPartVig is calculated in average number of seconds spent on this behaviour during a 30 second video. The difference between species has a p-value of > 0.1.

Analysis of behaviours taking place within the flash range:

‘Feeding on the ground’ did not differ between treatments within species (Fallow Deer = p-value = 0.6294, Roe Deer = p-value = 0.6109, Wild boar = p-value = 0.1093). However, for wild boar when comparing bear treatment weeks to control weeks there was a difference (p-value <0.05), spending more time ‘feeding on the ground’ during control weeks (See Figure 10).

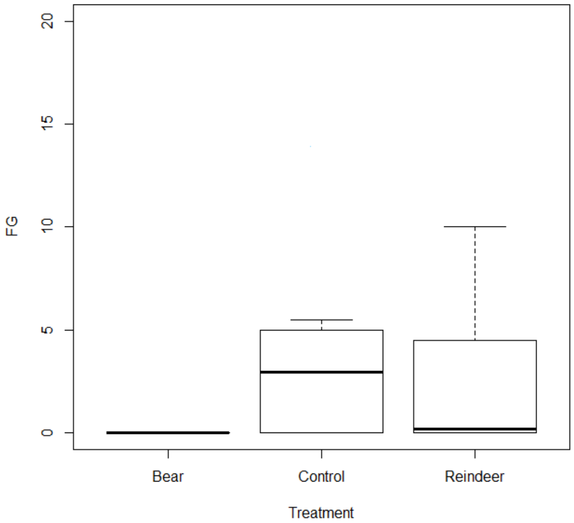

Figure 10: ‘Feeding on the ground’ (FG) by wild boar compared between different odour treatment weeks in south-eastern Sweden, spring 2013. FG calculated in average number of seconds spent on this behaviour during a 30 second video. The difference between bear and control has a p-value of p-value <0.05.

‘Sniffing in the air’ did not differ between treatments for all species (Fallow Deer = p-value = 0.8069, Roe Deer = p-value = 0.0654, Wild boar = p-value = 0.4055). Roe deer spent more time ‘sniffing in the air’ during bear weeks than during either of the other treatments (both p – values <0.05) (See Figure 11).

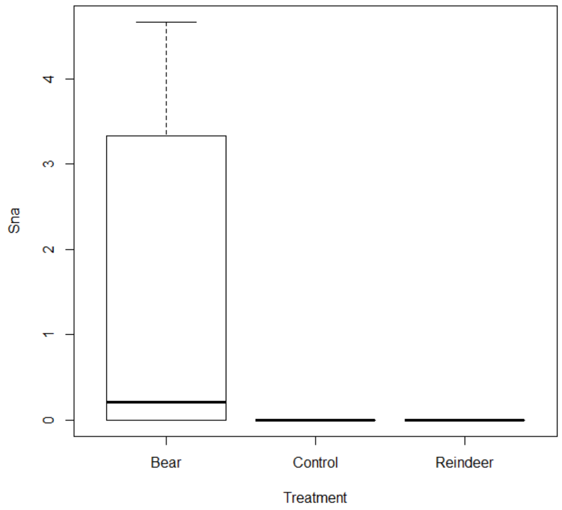

Figure 11: ‘Sniffing in the air’ (Sna) behaviour of roe deer compared between different odour treatment weeks in south-eastern Sweden, spring 2013. Sna is calculated in average number of seconds spent on this behaviour during a 30 second video. The difference between bear and control as well as reindeer has a p-value of <0.05.

‘Combined vigilance’ did not differ between treatments for any of the species (Fallow Deer = p-value = 0.938, Roe Deer = p-value = 0.0845, Wild boar = p-value = 0.9229). However, roe deer spent more time on ‘combined vigilance’ during bear treatment weeks than reindeer weeks (p-value < 0.05) (see Figure 12). Additionally species behaved differently to each other (p-value = 0.0444), roe deer spent less (p-value <0.1) time on ‘combined vigilance’ behaviour than wild boar.

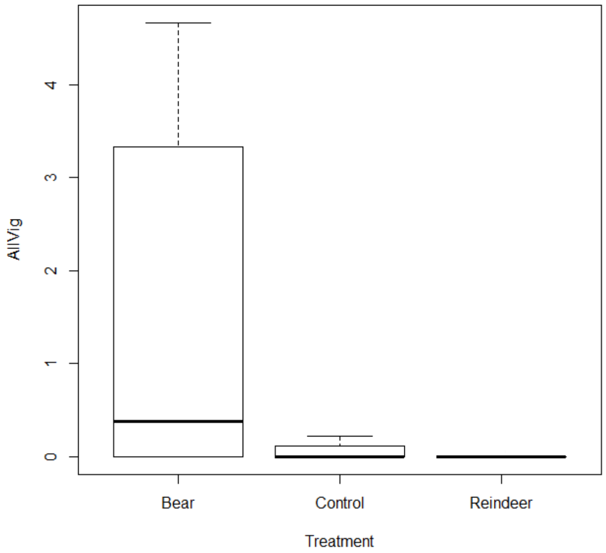

Figure 12: ‘Combined vigilance’ (AllVig is a combination of behaviours ‘sniffing in the air’, ‘looking around’ and ‘freezing’) behaviour of roe deer at feeding sites compared during different odour treatment weeks in south-eastern Sweden, spring 2013. AllVig is calculated in average number of seconds spent on this behaviour during a 30 second video. The difference between bear and reindeer has a p-value of <0.05.

‘Combined partial vigilance’ did not differ between treatments for all species (Fallow Deer = p-value = 0.3402, Roe Deer = p-value = 0.3197, Wild boar = p-value = 0.1385). However, species were not the same (p-value = 0.0011) in their behaviour, fallow deer showed more (p-value <0.1) of ‘combined partial vigilance’ than wild boar.

Discussion

Change in number of individuals and videos between treatments

One hypothesis was that ungulates might use sites with bear smell less than the other sites. When comparing the results using the number of individuals present during each treatments significant differences were discovered. For fallow deer the least amount of individuals were present during bear treatments while during both reindeer and control treatments there were significantly more individuals present. This result is consistent with the hypothesis that ungulates, in this case fallow deer avoid sites with indirect cues of bear presence (Thaker, et al., 2011). Slightly more difficult is the effect discovered for red deer and roe deer. Here there was also a significant difference between treatments, however, in both cases the least amount of individuals were present during reindeer treatment, while the most were present during control weeks with the number of individuals being in between these two during bear treatment. The fact that their presence was highest during control and less during both treatments with unfamiliar smell can be interpreted as avoidance of the unknown. However, why red deer and roe deer avoid the reindeer smell more than they do the bear smell cannot be said. For moose and wild boar there was no significant difference between treatments. This could either mean that these two species did not register the treatments or reacted in a way that did not change the number of individuals visiting the sites. These are also both species where research has shown that healthy adults are not usually hunted by bears (Grzimek 1968, Stubbe 1989), which could be a reason for their non reaction. For moose there is also the possible explanation that there were too few sightings and therefore too much variance, which is given credence by the large standard errors for the moose estimates (2.46 to 3.67). To summarise only fallow deer avoided bear treatment more than other treatments, while red deer and roe deer avoided both fur treatments. Hence fallow deer confirmed the anti-predator response while the other two species were more in line with avoiding unknown smells.

The fewest videos were taken during the bear treatment weeks and the most videos were taken during control weeks, for red deer, roe deer and fallow deer. However, although the difference in number of videos between bear and control was always significant, the difference between bear and reindeer was not. For fallow deer combining this result with the earlier one about number of individuals yields no new information: there were fewer individuals at bear sites, so naturally if nothing else changed there would be fewer videos. For red and roe deer, however, this result is somewhat contradictory, for both of them to be correct the number of individuals present on each video must have changed. For there to be equal number of videos at reindeer and bear site but less individuals during bear treatments than reindeer treatments more individuals must be present on reindeer treatment videos. The most logical explanation for there being more individuals visible is that the group size is larger during bear treatment weeks. This is consistent with research done on response to increased risk on for example Wildebeest (Thaker, et al., 2010). Testing for group size change directly was not possible due to the small sample size analysed. For wild boar and moose the number of videos did not change depending on treatment. Therefore, the conclusion is that wild boar and moose do not react to the treatments perhaps because bear means little threat to healthy adults (Grzimek 1968, Stubbe 1989). With moose, this may also once again be due to minimal overall presence.

To summarize, my analysis revealed that only fallow deer strongly exhibited the anti-predator response because both the individuals present as well as the number of videos taken coincided with bear treatments.

Change in behaviour between treatments

Both ‘feeding’ and ‘vigilance’ are necessary to ensure the survival of any individual, owing to the fact that concentrating on finding and eating food means less time concentration on surroundings in search of danger, there is a trade-off (Fortin et al. 2005). There can of course be other factors influencing the time allocation for any one behaviour such as how desperately the individual needs food, time of day, time of year, sex and age, as well as social standing in the group. Since all the data was collected in a relatively short amount of time in a relatively homogenous area need for food and similar factors were assumed to be the same for all individuals and time of year could be ignored. Sex had to be ignored because there were too few instances where classification was certain, the same goes for social standing. Age was also hard to discern since the young from the year before where almost yearling and adult size, therefore only piglets were classified and not included in the behavioural analysis. Time of day was not analysed because the data set groupings would have become too small. There is also the possibility of there being another type of behaviour displayed such as anything related to mating or territorial behaviour, which is also necessary behaviour, although some studies show that these may also reduced in favour of ‘vigilance’ when risk is high (Apfelbach, et al., 2005). To minimise this possibility both ‘vigilance’ and ‘feeding’ has been analysed and can therefore be compared to one another.

Behaviour in the feeding tree range

From analysing behaviour in the feeding tree range it can be said that there were few differences between treatments. Wild boar showed a trend of showing more ‘feeding behaviour on the ground’ during control weeks than bear weeks but this was not paired with an increase in vigilance behaviour during bear weeks so this is a mixed result. Fallow deer showed a trend of more ‘combined vigilance’ behaviour during control treatment weeks than bear weeks, which is surprising but note that it this was only a trend. ‘Feeding’ from then ‘feeding tree’ from all ‘feeding heights’ over all species showed a trend indication that most ‘feeding’ happened during reindeer treatment weeks and the least during control weeks. Since this is also only a trend no conclusion is drawn. Feeding height was not influenced at all by treatment, which leads to the conclusion that it is not be part of vigilance behaviour. Since all differences are only trends it is a possibility that at the feeding tree range individuals are too preoccupied with feeding that they show only muted concern for threats.

Species, however, did show a few differences in their behaviour at the feeding tree. Wild boar showed less ‘combined vigilance’ overall than roe deer and fallow deer showed more ‘combined feeding’ behaviour than roe deer. This indicates that roe deer is more cautious than either of the other species. There are also indicators that species utilise some behaviours very differently. Although not statistically significant, wild boar for example showed the least amount of ‘partial vigilance’ behaviour, which seems to be more a reflection of the difference between ruminants and omnivores than a difference in vigilance. Wild boar also dominated feeding time on the lower levels of the feeding tree.

‘Sniffing in the air’ did not differ between treatments within species, species themselves or treatments overall. Therefore, this behaviour is equally expressed by all species and is not influenced be the odours used in the experiment. However, there is the possibility that all individuals of all species deliberately did not use the ‘sniffing in the air’ behaviour in favour of other behaviours for example feeding.

Behaviour in the flash range

From analysing the behaviour at the flash range it can be said that species show their vigilance very differently. Wild boar decreased ‘feeding on the ground’ during bear treatment weeks compared to control weeks. Roe deer increased the amount of ‘sniffing in the air’ during bear treatments weeks compared to control weeks. Roe deer also showed more ‘combined vigilance’ behaviour during bear weeks compared to reindeer weeks. That roe deer did not show a decrease in feeding time is unexpected. However, roe deer shows clearly that it recognised the bear fur smell as a possible threat and reacted to this increased risk. Fallow deer showed neither a change in ‘feeding’ behaviour nor a change in ‘vigilance’ behaviour for any of the treatments.

Species differences were visible in ‘combined vigilance’ where wild boar showed more than roe deer. Since roe deer was the only species that increased ‘sniffing in the air’ during bear treatment weeks as well as being the only one that increased ‘combined vigilance’ at the same time the logical conclusion is that wild shows more ‘freezing’ and ‘looking around’ (See Table 1) behaviour than roe deer and this creates the difference between species. Fallow deer shows more ‘partial vigilance’ than wild boar. The fact that fallow deer is a ruminant may account for this difference. Ruminants spend about 30% of their time ruminating during which time they are chewing cud but are still able to observe their surroundings (Ryan and Jordaan 2005).

Combining the results of both plot locations as well as the count data it can be seen that four of the five ungulate species studied are affected by the presence of odours of bear and reindeer. Moose is the only one not at all effected, which could be because it does not consider bear a threat (Grzimek 1968) or that there was too few moose data. Wild boar only decreased feeding but did not actually increase vigilance, which may also be explained by the fact that bear does not usually hunt healthy adult wild boar (Stubbe 1989). Red deer showed a mixed reaction to bear odour, which could possibly be connected with the fact that red deer has evolved where its anti-predator behaviour is geared towards strategies useable on open terrain not in the forest (Stubbe 1989). Fallow deer only reacted with avoidance and no actual change in behaviour while on the experimental plot, which may have to do with the fact that fallow deer is not actually a native species in southern Sweden but was released by people (Grzimek 1968). Therefore, this species which does not have an evolutionary history with the European brown bear may not have another strategy additional to avoidance, to use when faced with a predator even its ancestors did not know. Therefore, roe deer is actually the only ungulate which is in its native range as well as its native habitat faced with a native predator which hunts it. However, roe deer also showed mixed avoidance behaviour in terms of bear since it also avoided reindeer. Roe deer did show increased vigilance, which was in accordance with the hypothesis but did not show a decrease in feeding, which would have been expected as a result. This gives rise to the possibility that feeding time might not have to decrease when vigilance increases. This may be possible if there was more partial vigilance happening than can be detected in the behaviours analysed in this study (Fortin et al. 2004).

What should be mentioned is the fact that the order in which the treatments were placed at the sites was not analysed although the setup of the experiment allows this because sample sizes would have become too small. And interspecies interactions were also not analysed since only 4.7% of the videos showed multiple species.

Conclusion

Turning to the five hypotheses made in the introduction the results of this study are used to answer them: Fallow deer supported the hypothesis that there will be fewer individuals present during bear treatment weeks. The other species do not support this result. My analysis of fallow deer, red deer and roe deer revealed support for the hypothesis that there are fewer videos during bear treatment weeks. Wild boar and moose do not support this hypothesis. Roe deer support the hypothesis that there will be more time spent on vigilance during bear treatment weeks, but only at the flash range. Wild boar supports the hypothesis that there is less time spent on feeding during bear treatment weeks, again only in the flash range. None of the species support the hypothesis that feeding height is effected by vigilance and therefore by the treatments. That species change their feeding height in response to increased risk is therefore refuted. That the first four hypotheses have been support by different species and species combinations indicates that the reaction to the presence of bear odour is different for each species and leads to different vigilance behaviour. While fallow deer mostly changed their patch use, roe deer increased vigilance behaviour directly and wild boar decreased feeding time increasing vigilance indirectly.

In conclusion, my analyses indicates that bear fur seems to work as an indirect cue of predator presence for fallow deer and roe deer, while red deer and wild boar certainly recognise it as a foreign smell. For moose no reaction could be detected. It can also be said that these indirect cues of predator presence change the behaviour of fallow deer and roe deer and therefore may have behaviourally mediated effects on the ecosystem. Wild boar and red deer also change their behaviour when the predator smell is present; however, the distinction to the other foreign odour of reindeer is not as clear. This means that it is possible that the change in behaviour of red deer and wild boar will not persist when the smell is no longer novel and therefore have no effect on the ecosystem.

The fact that every species reacted differently suggests that studying risk effects in this manner outside under natural conditions is possible but requires detailed knowledge of species behaviour to be able to tailor experiments exactly right to detect these effects. Especially for wildlife management, these research results are important when considering how the return of large carnivores in Europe will affect the current ungulate population and the environment they inhabit. There is also the fact that using predator odour to effect ungulate movement has different results on different species.

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