Behavioural Responses of Ungulates to Sound Systems
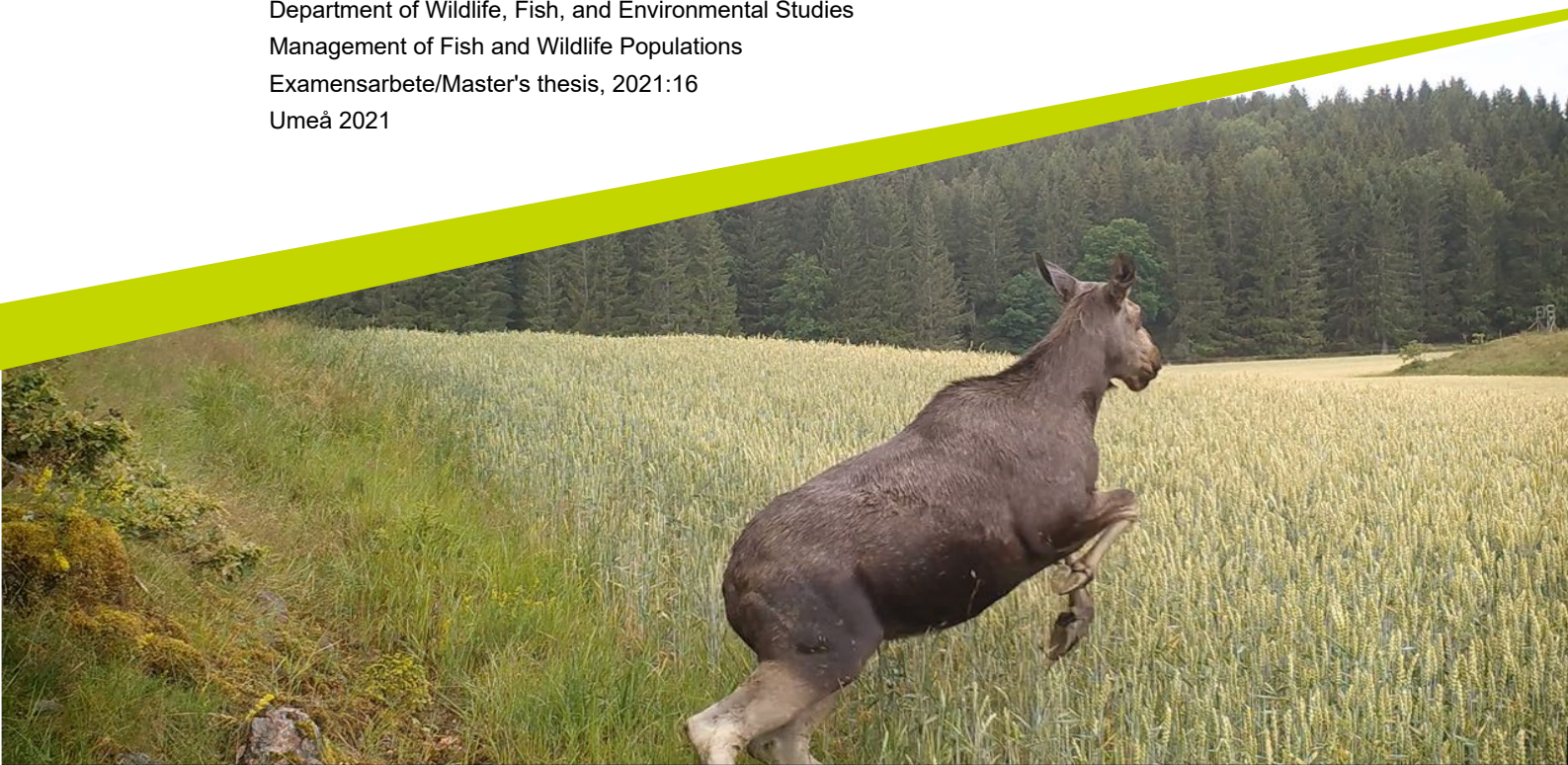## – Can simulated risk influence behaviour?

Klövvilts reaktion av ljudsystem – Kan simulerad risk påverka beteende?

Carolin Veronika Berndt

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Abstract

Increasing ungulate densities all over Europe are intensifying the ongoing human-wildlife conflict, embodied by mainly economical losses through damages in forestry and agriculture. Given the current circumstances, farmers and forest owners prefer a decrease in ungulate numbers through direct population control, whereas other stakeholders, such as hunters, wildlife watchers or photographers, prefer higher wildlife numbers. This challenging contradiction requires novel management approaches. The landscape of fear theory implies behavioural changes in prey by not the direct killing, but the fear of predators, which can cause trophic cascades down to vegetation level. Here, I used Automated Behavioural Response systems (ABR) to experimentally induce this landscape of fear for ungulates in two study areas in southern and northern Sweden and to evaluate three behavioural responses: leaving rate, foraging behaviour, and vigilance behaviour. I used different risk sounds (human, dog and wolf sounds) and a non-risky control sound (different native bird species). The ABRs were placed along the edges of crop fields and close to other lure types, such as salt licks, to test for fear responses in situations where resources were plentiful. The results show that ungulates were significantly more likely to abandon the site when they were exposed to risk sounds than to control sounds, where the effect of the human sound exceeded the other risk sounds by far, and therefore supports the 'human super-predator' theory. Furthermore, they decreased foraging time and increased vigilance levels for risky sounds. Distance of the animal to the sound source played an important role for behavioural responses, as well as group size (only applied for fallow deer), which reflects a known anti-predatory strategy. With increasing distance, ungulates left the area fewer times, increased their foraging time, and decreased their time being vigilant. The same behavioural response patterns were shown for larger fallow deer groups compared to single individuals.

Overall, human sounds showed to be most effective, followed by wolf sounds. Dog sounds played only a minor role in altering ungulates' behaviour. The results of this study show that it is possible to affect and alter ungulates behaviour through a locally human-made landscape of fear. Thus, the knowledge about the behavioural effects could contribute to a potential conflict minimisation of the ongoing human-ungulate issue.

Keywords: Ungulates, Landscape of fear, Behavioural response, Predation risk, Playback experiment, ABR, Management strategies

Table of contents

List of tables

List of figures

Abbreviations

ABR	Automated Behavioural Response System
GLMM	Generalized Liner Mixed Model
SLU	Swedish University of Agricultural Sciences
SMHI	Swedish Meteorological and Hydrological Institute

1. Introduction

During the last decades European ungulate densities and their ranges have been increasing and expanding (Apollonio 2010; Deinet et al. 2013; Linnell et al. 2020), which in many areas has led to changes in species composition from single species systems to multi-species communities (Linnell et al. 2020). Large parts of Sweden are now inhabited by moose (*Alces alces*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) (Linnell et al. 2020). The feeding types of those different ungulate species partly overlap (Hofmann 1989), which can result in inter- and intraspecific competition for food resources (Bleier et al. 2012; Spitzer et al. 2020). Moreover, increasing populations of these species may cause damages to forestry and agriculture through trampling or foraging. Both these issues are seen as a main management challenge all over Europe and in Sweden (Gordon 2009; Naturvårdsverket 2018; Valente et al. 2020). Increasing densities and resulting intensified competition for resources, might deepen this human-wildlife conflict (Spitzer et al. 2020). Even though no overall reliable numbers are available for damages on agricultural fields caused by wild ungulates, already in 2011 a study estimated that wild boar alone causes an economic loss of 80 million Euro per year in Europe (Reimoser & Putman 2011). In some countries, compensation payments are made (Valente et al. 2020), but Swedish farmers have to cope with the economic losses themselves (Naturvårdsverket 2018). So far, the main management strategy in most European countries is population control by reducing ungulate numbers with the aim to concurrently reduce the damage caused by them (Reimoser & Putman 2011; Linnell et al. 2020). Simultaneously, however, high ungulate numbers are favoured for recreational purposes, such as wildlife watching, photography or hunting (Naturvårdsverket 2018; Linnell et al. 2020). This trade-off between some stakeholders preferring high numbers of ungulates, while others aim at minimizing the damage caused by them can be considered a vicious circle.

Predators are known to modify ungulate communities through direct effects on their populations by reducing their numbers (Creel & Christianson 2008; Clark & Hebblewhite 2021). In Europe's modified landscapes, the main predator of ungulates is the human (Theuerkauf & Rouys 2008; Darimont et al. 2015). Hunting is usually the main cause of death for ungulates and, for example, during the hunting season 2019/2020 hunters shot about 400,000 ungulates in Sweden (Viltdata 2021).

Collisions with vehicles represent another major cause of death triggered by humans (Seiler 2004; Seiler et al. 2004). Historically, wolves have also been an important European predator (Apollonio 2010). Although they went extinct during the 20th century in Sweden (Ericsson et al. 2018), they recolonized Sweden several decades ago and are now expanding, especially in the southern part (Eriksson & Dalerum 2018; Svensson et al. 2021).

Despite the direct lethal effects of predators on their prey (Curio 1976), there is increasing evidence that indirect, non-lethal, effects of predators can play a similar or even more important role (Schmitz et al. 1997). Those indirect effects of predators on their prey's behaviour and habitat use (Brown et al. 1999; Laundré et al. 2001) can have implications on lower trophic cascades (Suraci et al. 2016), such as vegetation (Ripple & Beschta 2004, 2012; Donadio & Buskirk 2016). Prey usually alter their behaviour to minimize the risk of predation (Lima & Dill 1990). This individually perceived predation risk create a 'Landscape of Fear' for prey species (Laundré et al. 2010, McArthur et al. 2014). This landscape of fear concept is increasingly used in ecological studies and states fear as a main behavioural driver (Bleicher 2017). However, animals are also driven by finding food resources to maintain or increase survival and fitness. This individual food-fear trade-off is also influenced by various other factors, such as evolutionary factors, energetic state of the animal, landscape structure, food availability, predation intensity, intraspecific & interspecific competition, and others (Bleicher 2017).

Typical direct behavioural responses to perceived risk can include changes in vigilance (Wolff & van Horn 2003; Creel et al. 2014), reduced foraging (Winnie & Creel 2007; Donadio & Buskirk 2016; Suraci et al. 2016) and increased aggregation (Creel & Winnie 2005), as well as generally avoiding areas with higher predation risk (Suraci et al. 2016). Increased vigilance levels can be advantageous if a detection of a potential predator can be made in sufficient time. This time, which is spent being vigilant, leads to a loss in available time for other activities. Studies have shown that this usually goes at the expense of time spent foraging (Pulliam 1973; Brown et al. 1999; Kuijper et al. 2014). However, Creel et al. (2014) emphasized that this might not be the case for all species and thus species-dependent. An immediate avoidance of risky areas as well as increased vigilance levels at the expense of time spent foraging should both lead to less browsing pressure. Those different behavioural responses can have energetic as well as physiological consequences for the prey, which alter not only survival but also reproduction and can therefore have a major impact on their population dynamics. Another tactic to reduce predation risk can be flocking behaviour. Large groups usually provide safety in numbers based on the dilution and confusion effect (Rosenzweig et al. 1997; Wood & Ackland 2007). An additional side-effect of that behaviour can be that bigger groups allow an individual to decrease the time spent being vigilant, which can then be used to increase foraging time.

Those "non-consumptive" effects of predators on their prey and the landscape of fear they create, are generally difficult to test experimentally in the field. Suraci et al. (2017a) developed an Automated Behavioural Response system (ABR), which comprises a motion-sensitive speaker system paired with a camera trap. This system allows to remotely record and quantify behavioural responses of animals to playback experiments. Many studies have used this particular system for different purposes, such as experimentally testing behavioural responses to sounds of humans, competitors, predators, or anthropogenic noise in South Africa, Canada, and the US (Smith et al. 2017; Suraci et al. 2017b; Suraci et al. 2019b; Gambra Caravantes 2020). Besides the already proven ecological impacts and trophic cascades caused by the fear, this approach is relatively new to use as a potential management method to influence and steer animals behaviour.

Human sounds and cues of human presence have been shown to create a landscape of fear for several wildlife species reaching from Capercaillie (*Tetrao urogallus*) (Rösner et al. 2014) and porcupines (*Hystrix cristata*) (Mori 2017) to top-predators such as pumas (*Puma concolor*) (Suraci et al. 2019b). Studies from Smith et al. (2017) and Suraci et al. (2019b) showed that human sounds had the biggest impact on pumas and led to them spending less time on their feeding site. Since humans are the apex predator of ungulates, it is likely that they also play a major role in affecting ungulates' behaviour. Analysis from Ciuti et al. (2012) illustrate that the effect of humans on elk (*Cervus elaphus*) even exceed those of their natural predators. Dogs (*Canis lupus familiaris*), as the most abundant terrestrial carnivore (Vanak & Gompper 2009), can also be considered to be a potential threat to ungulates. Especially free-roaming or feral dogs have the ability of direct killing. Besides perceiving dogs as predator, the strong association of dogs to humans, as pet or a hunting dog, might also lead ungulates to perceive dogs as a threat (Silva-Rodríguez & Sieving 2012; Mori 2017). For pumas, however the sound of dogs did not affect their behaviour (Suraci et al. 2019b).

In this study, I used ABRs to test how ungulates in two study areas in northern and southern Sweden respond to sound playbacks of risky and non-risky sounds. The use of playbacks is a suitable method to simulate the presence of a potential predator (Hettena et al. 2014; Suraci et al. 2017b) and to create an experimental landscape of fear (Smith et al. 2017; Suraci et al. 2019a). Here, I used four different playback sounds. Three of them were considered to be perceived as potential risk for ungulates species; human, dog, and wolf sounds. The ungulate species in my two study sites in Sweden frequently experience the presence of humans and dogs in the landscape. On the other hand, wolves as the main natural top-predator (Okarma 1995) have been absent for many decades in large parts of Sweden (Ericsson et al. 2018), including my two study areas, and ungulates may have lost their fear to them, due to lack of experience. If this is true, that would mean that they would not show anti-predator behaviour to wolves, since they are not

accustomed to them anymore (Berger et al. 2001). However, other studies have shown that ungulate species were able to recognize predators, even a long time following local extinction of the predator (Hettena et al. 2014; Dalerum & Belton 2015). To be able to compare the behavioural responses, I also used non-risky control sounds; the sound of different native bird species.

If the risk sounds created a landscape of fear, I expected ungulates to avoid my experimental plots when they heard a risky sound and spend less time there relative to when they heard a non-risky sounds (Hypothesis I). Furthermore, I hypothesize that ungulates would change their behaviour and spend less time foraging (Hypothesis II) and more time being vigilant (Hypothesis III) in response to risky sounds relative to non-risky control sounds. Moreover, I would predict that the extent of these different anti-predator responses is influenced by group size since larger groups might be less susceptible to risk sounds and, on average, spend less time being vigilant than solitary animals (Hypothesis IV(3)). As a result, the foraging time might even increase for larger groups (Hypothesis IV(2)) and they would spend more time in the particular area (Hypothesis IV(1)). Since several of the common ungulate species present in Sweden (moose, roe deer) are usually solitary animals, I tested this effect of group size only for fallow deer (*Dama dama*), which can display a large variation in group size. They can be solitary, but usually form larger groups as an antipredator strategy (Apollonio et al. 1998). The distance to the sound source may also influence the strength of the ungulates' response. Since the noise of sound is decreasing with increasing distance, I predicted that the perception of animals to the sound, and therefore their anti-predator response, would be less intense for animals that were further away from the ABR. So, ungulates would leave the site fewer times (Hypothesis V(1)), increase their foraging time (Hypothesis V(2)), and decrease their time being vigilant (Hypothesis V(3)) with increasing distance for risky sounds. For non-risky sounds, there should not be any difference in behaviour depending on the distance or group size.

The results of this study could deepen the knowledge of ungulates' behavioural responses to non-lethal cues of risk in the Swedish landscape. This might be useful for various management purposes and could have potential to contribute reducing this ongoing economic human-wildlife conflict.

2. Materials and methods

2.1. Automated Behavioural Response (ABR) System

The Automated Behavioural Response system has been developed by Suraci et al. (2017a) and was used in several studies (Zanette et al. 2011; Clinchy et al. 2016; Suraci et al. 2016; Smith et al. 2017; Suraci et al. 2017b; Suraci et al. 2019a). It consists of a video-enabled camera trap, which is paired to a sound system. The camera trap (Model: Browning BTC-8FHD-PX) with passive infrared sensors detects movement and then starts to record a video. The ABRs were scheduled to record video lengths of 30 seconds, and to activate the sound 3 seconds after the start of the video for the duration of 10 seconds. The playback types were divided into risk sounds (human, dog, wolf) and control sounds (different bird calls). Each sound type category itself had a variety of different sound tracks (human: 10; wolf: 9; dog: 11). The sound exemplars of the human playback represented both women and men (5 each) conversationally talking in Swedish. Dog playbacks contained the sound of various barking dogs, whereas the wolf sounds involved barking and howling sounds of different wolves. The control, non-risky, sounds consisted of three different native bird species, which were played depending on their natural occurrence of the time of the day. For day time, I used nine different barnacle goose (*Branta leucopsis*) recordings, for crepuscular times ten different raven (*Corvus corax*) tracks, and during the night ten different tawny owl (*Strix aluco*) recordings. All three bird species are abundant throughout the study area and are neither predators, competitors or prey of ungulates and therefore suitable to function as control sound.

Every sound track had approx. the same length of 10 seconds as well as the same volume (average 100.4 dB at 1m) to ensure an equality of the sound perception as well as to display a natural volume of those sounds. The different tracks of the same treatment type (bird, dog, human, wolf) were then composed into 15 min playlists and programmed to switch among the treatments every 15 minutes. An animal, which continuously triggered the camera could thus hear different tracks of the same sound type (e.g. dog). In other words, if a dog sound was triggered, it would play dog sounds for the next 15 minutes. If triggered after 15 minutes, the ABR

would play a different sound type. Also, the playlists alternated in different frequencies. The "full-risk" treatment contained equal amounts of each sound type, which represents in conclusion a higher amount of possible risk sounds compared to control sounds. The "half-risk" treatment meant that the control sounds (different bird species) were played twice as much as risk sounds. The time of the triggering of the camera thus determined which sound was played and was therefore random. However, the probability of which sound category was played differed between the two treatment types (full- and half-risk).

The camera was attached to a pole at a height of approx. 1.5 m (Figure 1) to enable the capture of the targeted ungulate species within the trigger range of approx. 25 m. The sound device was attached under the camera trap in direction towards the camera's field of view (Figure 1).
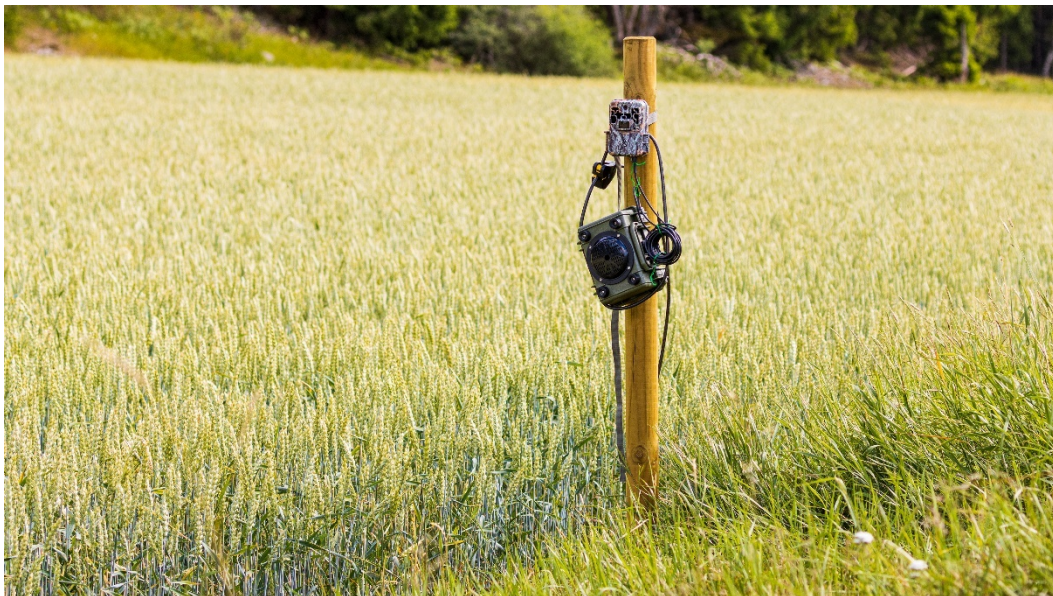
Figure 1: Setup of the ABR system (Study site: Öster Malma). Camera trap is connected to a pole at a height of approx. 1.5 m. The speaker is attached below facing in the camera's view direction. Photo: © Ingemar Parck.

2.2. Study areas and study designs

In this study, two study areas were involved, one in the southern part of Sweden, around Öster Malma (central point: 16°56'33"E 58°56'30"N) and one in the northern part of Sweden, around Nordmaling (central point: 19°41'27"E 63°31'18"N) (Figure 2). Both study areas are very different in their biotic and abiotic components. Due to external circumstances, the study period and the study design differed between the two sites, which is explained below in detail. However, the overall aim was to place the ABRs close to attractive places for ungulates, which would allow for more videos, respectively data, based on higher visitation rates.

Figure 2: Overview map (left) of the two study sites in Sweden with detailed maps (right).
⬠ *represents the ABR positions (Note: one symbol correlates to one ABR in Nordmaling; one symbol correlates to one field, respectively to two ABRs in Öster Malma).*
▨ *represents the approx. wolf territory (Ärla left, established 2017; Sjunda right, established 2014 (Pers. Com.: I. Parck Länsstyrelsen Södermanland (2021)).*
Source overview map: © Esri, Maxar, Earthstar Geographics, USDA FSA, USGS, Aerogrid, IGN, IGP, and the GIS User Community.
Source detailed maps: © Lantmäteriet.

In both areas, the landowners gave permission for conducting the study. Also, no animal was physically harmed and the influence of the ABRs and the potentially caused fear for the animal was very temporary and local. The influence of the ABR and the experiment was minimized directly after the exposure and not considered to cause further distress or severe consequences for the animal's health.

2.2.1. Öster Malma

The study was carried out between 27 June and 09 of August 2020 in a study area located in the south-eastern part of Sweden, in the county of Södermanland, between Nyköping and Gnesta (Figure 2). The average day temperature in this time period was 17.3 °C, with a maximum average temperature (per day) of 23.2 °C and a minimum of 11.4 °C, respectively (SMHI 2021b). The mixed landscape covers high amount of forests as well as open country and expanses of water. In this area the ungulate species fallow deer, roe deer, red deer, moose, and wild boar coexist, where fallow deer are most abundant (up to 127 individuals/10 km²) and moose least common (3-5 individuals/10 km²) (Velin 2021). However, the abundance of

those ungulates differ locally. Wolf packs are not established in the particular area of the different field sites (see Figure 2), which is why a personal encounter of ungulates with this predator has most likely never taken place. Nevertheless, since some years two wolf packs have territories close to the study sites (closest site approx. 10 km distance to "Ärla" territory). Since wolves roam freely in that area (Rovbase 2021), it is theoretically possible that some ungulates have had an encounter with them or perceived other cues of this natural predator.

The period of this study correlated approx. with the sowing and harvesting date of the agricultural fields, on which nothing but wheat was planted. In total, the area including all the study sites captures approx. 530 km² (North-to-south extension: approx. 25 km; East-to-west-extension: approx. 20 km).

Study design

The study area contains seven different agricultural fields. To ensure an independence among the fields, the different fields were at least three km distance from each other (average 7.2 km). Two ABRs with a minimum distance of 500 m in between were placed on each field, resulting in 14 ABRs in total. All ABRs played all four different playback sounds. However, the potential frequency of risky versus non-risky sounds was different between the two ABRs in each field. One of the ABRs always contained the "full-risk" playlist and the other one the "half-risk" playlist, respectively. The systems were placed on the field edges close to the surrounding forest. During the study period, they were checked at least once. The precise positions of the ABR systems were based on ungulate occurrence clues, such as tracks, faeces, etc. to maximize the amount of possible encounters and therefore videos. To be able to evaluate the distance of the animals to the ABR in the video, I recorded myself at the exact positions of 5 to 25 m in 5 m steps straight along the field-forest edge (straight camera view) as well as along a transect at a 45° angle towards the agricultural field. The sound volume of four different ABRs was exemplarily measured on the site for the different distance classes (Figure 15 Appendix 3).

2.2.2. Nordmaling

This study area covers in total ca. 150 km² and is located in the northern part of Sweden, in the county of Västerbotten around Nordmaling, which is situated approx. 45 km south of Umeå (Figure 2). It is dominated by forest areas, mainly consisting of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula* sp.), sporadically also mixed with mires and agricultural lands. The ungulate community contained, similar to the study site in Öster Malma, also fallow deer, roe deer, red deer and moose, but no wild boar (Spitzer et al. 2019). The study period was in the winter season and ranged from 04 November 2020 to 11 January 2021. In this time, the average day temperature was 1.6 °C (SMHI 2021a).

Study design

Because this study occurred during winter, it did not make sense to place ABRs - as in Öster Malma - along agricultural wheat fields. Instead, I used other lures, which were attractive for the ungulates during this time of the year, and would increase the likelihood of visitation. Ten different independent sites were chosen with at least one km distance in between (average 2.1 km). They were located close to different human-made lures, ranging from salt lick stones (on five sites) to game fodder fields (on five sites). Those were established before the start of the study, so that local ungulates were already used to the occurrence of them. The potential difference among the sites regarding their attraction, might balance out since they all provide either a food source or provide animals with necessary minerals needed in this time of the year.

In contrast to the study setup in Öster Malma, only one ABR system was installed per site, which was only containing the "full-risk" playlist and thus proportionally playing more risk sounds than control sounds. The ABR was placed close to the lure, with an approx. distance of 5 m, locally different based on the conditions. Wolf territories are not established in this particular area and also not close to it (Svensson et al. 2021), which means that ungulates in the Nordmaling site most likely never have experienced this predator itself or cues of it. In this study area, I was not able to conduct distance measurements from the ABR system. Therefore, I estimated the distance through the comparison with natural objects visible in the video.

2.3. Behavioural analysis

The analysis of the behavioural response of the ungulates to the ABRs was coded with the program Solomon Coder (Péter 2019). I scored the behaviour of each animal in each video, resulting in high-quality data on individual level. The possible overall behavioural response was divided into two main groups: movement and attention/action, which were further separated in several behavioural categories (Table 1). Those behavioural classes were aligned to recognized ungulate behaviour from earlier studies (Winnie & Creel 2007; Kuijper et al. 2014; Dalerum & Belton 2015; Wikenros et al. 2015), but slightly modified.

The behavioural category is exclusive per main group. An animal can either stand or walk, not both. The overall behavioural response was then defined by a combination of usually one response from each main group. So, an animal could stand and look at the camera at the same time (Figure 3). However, in some cases, this precise scoring was not possible since the head was for example out of the camera's sight. A certain behavioural response was coded for every 0.2 seconds. So, there were 150 possible continuous behavioural responses possible for one

animal in the camera's sight of view, during the total length (30 sec) of one video. Furthermore, the time of appearance and the leaving time of each animal was noted as well as the start and end of the sound. Other additional information were also registered when possible, namely sound type, species, gender, age, group size and distance of the animal to the camera. The distance of the animal to the camera was taken on the position where it was situated when the sound started playing. Further changes in the distance to the camera during the course of the recorded video could not be analysed. Group size represents the maximum number of individuals seen in each video. To compare behavioural responses for the factor group size, I defined three group size categories for fallow deer: Single individuals, when only one individual was visible during the course of the video; small groups, consisting of two to five individuals; and large groups when more than five individuals were visible in the video. The information to age class was divided into 'adult' and 'juvenile', where the latter category represented all animals estimated to be not older than approx. one year. As adult were all animals older than one year considered. If it was not possible to define age or sex properly, I categorized those as 'unknown'.

Table 1: Categories of ungulate behavioural responses divided into two main groups: Movement and Attention/Action. The behavioural categories within the main group were exclusive (only one category per main group could occur at the same time) and then the behavioural response from each main group was combined into the overall behavioural response.

Category	Description
Movement	
Standing	The animal is in an upright position and remaining in one location. But it can make three or less steps in any direction to check the surroundings.
Walking	The animal takes more than three consecutive steps in a direction, where left and right legs alternate.
Running	The animal took more than three consecutive steps in a single direction at speed greater than walking. Left and right legs move together.
Fleeing	Animal is moving fast (running) away from the sound source. This behavioural response is only possible after the sound started.
Approaching	The animal is approaching the camera/sound system.
Laying down	The animal is laying on the ground and resting and/or sleeping.

Category	Description
Attention/Action	
Foraging	The animal is foraging planted crops. (Study site Nordmaling: Animal is eating on the different baits, respectively licking on salt lick; depending on the particular site.)
Foraging Other	The animal is foraging on something else than the planted crops, respectively the intended bait. This can be e.g. trees, etc..
Head-up	The animal was standing with its head above the shoulders. The head could move for scanning. None of the other attention or action behaviours were performed.
Head-down	The animal was standing or walking with its head below the shoulders.
Chewing	The animal is chewing (usually head-up & not directly on the plant). This includes chewing as directly following of foraging as well as chewing from rumination processes.
Looking at camera	The animal was standing or walking with its head raised up and was looking directly at the camera with both eyes visible.

The attention behaviours "Looking at the camera" and "Head-up" (Table 1) represent different alertness states of an individual and were – as all other behavioural responses in each main group – exclusive. An animal which was standing with the head up and looking at the camera was scored as "Standing – Looking at camera". I considered "Looking at camera" as a sign of more alertness then only head-up, since the animals attention is directly focused on the sound source. Similar assumptions were made for the differentiation between "Head-up" or "Head-down", etc. to "Chewing". In this case the behaviour was classified as "Chewing", because this states a non-vigilant response and vigilance is usually performed at the exclusion of foraging or chewing (Underwood 1982; Winnie & Creel 2007). That is why vigilance behaviour is here considered to be only represented by the behavioural category "Looking at camera". Foraging, on the other hand, represents a very unvigilant state of behavioural choice, since the focus is on the plant and the detection of a potential predator is less likely.

Figure 3: Example of a male fallow deer group in the study site Öster Malma showing the combined behavioural response "Standing (Movement category) - Looking at camera (Attention Category)" to a dog sound. For other example pictures of the coded behaviour see Figure 14, Appendix 1.

2.4. Statistical Analysis

2.4.1. Calculation of behavioural response categories

For the analysis, I excluded the videos which were empty, contained non-ungulate species or species which could not be identified, and videos in which the animal left the site before the sound started playing. All other ungulates, which were still in the camera's view when the sound started, were considered to be interested in the lure (agricultural field, respectively other bait types) and intended to spend time there.

As described above, I considered "Foraging" and "Foraging Other" in the behavioural response "Foraging", since it was in this study not of importance what kind of plant the animal was browsing on. For the vigilance response, I only included the behavioural response "Looking at camera", since this represents a high alert to the sound source and therefore a state of high vigilance.

For the calculation, I counted the behavioural responses (one value per 0.2 sec), in which the animal was foraging (Yes) to those, it was not foraging (No) and calculated the proportion of foraging behaviour to not-foraging behaviour per individual animal in each video. The same approach was applied for the vigilance behaviour. To analyse if animals avoid the particular site based on the sound, I determined if an animal left the field of view of the camera within the video duration (Yes) or not (No) and used that as binary response variable.

2.4.2. Generalized Linear Mixed Models (GLMM)

Since I could not control if the same individuals were returning to the same or another site and therefore were exposed to several treatments, I used Generalized Linear Mixed Models (GLMM). This model type can account for this temporal pseudoreplication and potential data dependencies (Crawley 2015). GLMM's are widely used in ecology and can handle nonnormal binary data as well as proportional data and implement random effects (Bolker et al. 2009).

To analyse all three behavioural responses; abandoning the particular site within the video time (binary data), time spent foraging (proportional data), and time spent being vigilant (proportional data), I applied for each response several GLMMs to answer the different sub-hypothesis to sound type, distance and group size (Table 2). I used all data entries, so all individuals in all videos and accounted for that as a random effect in the model. Thus, I used a nested random intercept and nested video within ABR location. The ABR location displays the study site combined with the individual ABR number.

Table 2: Generalized linear mixed model structures for each factor and the corresponding data basis. The different response variables for each factor, respectively model were: abandoning the site within the video time (binary), time spent foraging (proportional data) and time spent being vigilant (proportional data). The nested random intercept was for each model 'video' within 'ABR location'.

Factor		Model structure	Data
Sound type category	(1)	Response ~ Sound type category (Control vs. Risk sounds)	All individuals in each video
Treatment sound	(2)	Response ~ Sound type (All 4 different treatment types)	
Distance	(3.1)	Response ~ Distance	All individuals in videos with **control sounds**
	(3.2)	Response ~ Distance	All individuals in videos with **risk sounds**
Group size	(4.1)	Response ~ Group Size	All **fallow deer** individuals in videos with **control sounds**
	(4.2)	Response ~ Group Size	All **fallow deer** individuals in videos with **risk sounds**

I performed separate tests for the different factors of interest as more complex models including more than one factor did not converge properly. For all behavioural responses, I tested first differences between control and risk sounds (model 1) and then the differences among all four sound treatments (model 2) (Table 2). For testing differences for the factors 'Distance' and 'Group size', I had to subset the data entries into control and risk sounds and tested the factor distance,

respectively group size, on those subsets for each behavioural response. Thus, I first tested the effect of distance to the according response variable for all individuals, which were exposed to control sounds (model 3.1) and then for those which heard a risk sound (model 3.2). I applied the same for the factor group size (model 4.1 and model 4.2) (Table 2). To compare the different categories of the factors, I applied for each model a pairwise Tukey post hoc comparison test. The significance level was considered to be p = 0.05.

For the analysis I used the packages "lme4" (Bates et al. 2015) "ggResidpanel" (Goode & Rey 2019), and "multcomp" (Hothorn et al. 2008) within the R software (R Core Team 2019). Furthermore, I visually inspected the model diagnostic plots for each model.

3. Results

3.1. Sampling results

Ungulate species were recorded in 13 of 14 locations in the study area in Öster Malma and in 8 of 10 sites in Nordmaling, respectively. In total, 2,344 individuals in 645 videos have been coded, where most of the videos as well as data entries (all scored ungulate individuals in each video) were from the study site in Öster Malma (Table 3; Table 5 in Appendix 2). Each ABR recorded different amount of individuals, ranging from 0 to 775 animals.

Fallow deer was the most recorded species (88.5% of all data entries) in both study sites (Figure 4). The other ungulate species appeared less in both areas, whereas in Nordmaling proportionally more roe deer, red deer and moose occurred than in Öster Malma (Figure 4). The average group size was the highest for fallow deer (mean 5.3; min. 1; max. 32). Wild boar had an average group size of 3.4 with a maximum of nine animals. The other species were mostly solitary (mean group size moose 1.07; red deer 1.3; roe deer 1.2). The amount of videos per group size category was evenly distributed for fallow deer, resulting in 148 videos for single individuals, 147 videos for small groups and 140 for large groups. Proportionally
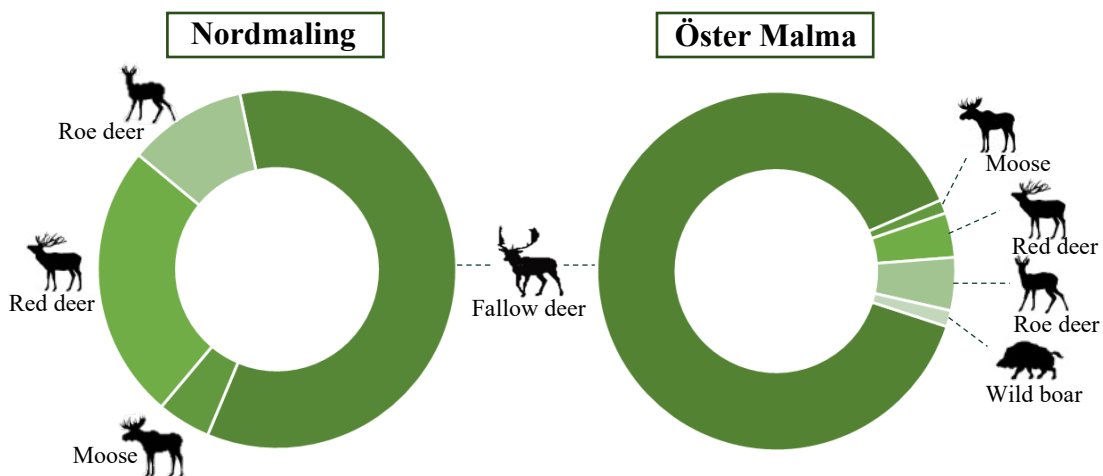
Figure 4: Data entries (all scored ungulate individuals in each video) per species in the two study sites (Nordmaling N=290; Öster Malma N=2054).

more male ungulates (84%) have been recorded than females and the most common distance to the ABR was 10 to 15 m, where approx. a third of all individuals were located. Furthermore, the majority of the ungulates were adult (82%).

There were more videos (Table 5 Appendix 2), as well as data entries (Table 3), gathered for risk sounds compared to control sounds. The amount of the different risk sounds categories (human, dog, wolf) was fairly high. However, especially the sample size per species per sound type was too low to perform species-specific analyses (Table 4 Appendix 2).

Table 3: Number of data entries per sound type category and study site.

	Control	Risk				
	Bird	*Pooled*	*Human*	*Dog*	*Wolf*	**Total**
All data entries	1030	1314	306	663	345	**2344**
Öster Malma	963	1091	239	554	298	**2054**
Nordmaling	67	223	67	109	47	**290**

3.2. Direct response: Abandoning the site

One of the direct behavioural changes contains adapting the habitat choice and leaving the particular site. Ungulates were more likely to leave the field of view of the camera when risk sounds were played (proportion left: 0.29) compared to when control sounds were played (proportion left: 0.19; p = 0.014; Figure 5 and Table 6 Appendix 4). However, the comparison of the three risk sounds showed that there are major differences among them (Figure 5). Animals which were exposed to dog sounds had even a slightly lower leaving rate (proportion left: 0.186) than for control sounds. Wolf sounds led to an abandoning proportion of the site of 0.28. In contrary, human sounds made ungulates leave the site more than twice as often (proportion left: 0.53) than for control sounds and showed also a significant higher leaving rate compared to the other risk sounds (Figure 5; Table 7 Appendix 4). So, only the human sound led to significant higher leaving values (p<0.001) compared to the control sounds. Both, dog (p=0.28) and wolf (p=0.056) sounds showed no significant difference to the control sound (Table 6 Appendix 4). However, based on those values, there is a strong indication that animals responded also to wolf sounds.
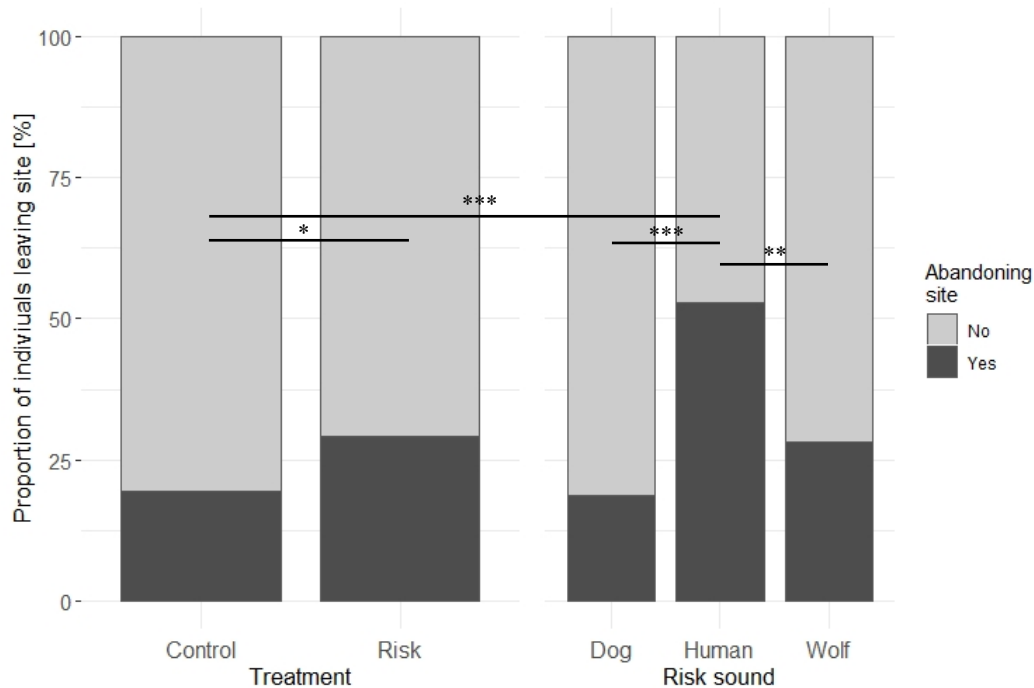
*Figure 5: Proportion of individuals abandoning the site within the video time divided into control and risk (all risk sounds pooled) treatments (left) and the different risk sounds on its own (right). Horizontal lines and stars indicate significance values between categories (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1). See Table 6 and Table 7 in Appendix 4 for accurate statistical values.*

3.2.1. Distance effects

For risk sounds, there are significant differences among several distance classes visible (Figure 6 and Table 8 Appendix 4). About 74% of the animals left the site when they were closer than five meters to the ABR system. This high proportion decreases with increasing distance, where the leaving proportion is still 26% for the highest distance class (>25m). The leaving rates of ungulates, which were exposed to risk sounds, were in all distance categories higher than for control sounds, except for the distance class '15 to 20 m', where the leaving proportion was approx. 5% higher for non-risky sounds. However, the differences between risk and control sounds among distance classes were not statistically tested.

For control sounds, the proportion of animals leaving the site was relatively equal over the different distance classes (Figure 6) and there were only few significant differences among some distance classes (Figure 6; Table 8 Appendix 4). However, the highest leaving rate was for the distance class '15 to 20 m' where about 31% of the individuals left the site, whereas the lowest value occurred for the distance category '10 to 15 m', where only 14% left the site.
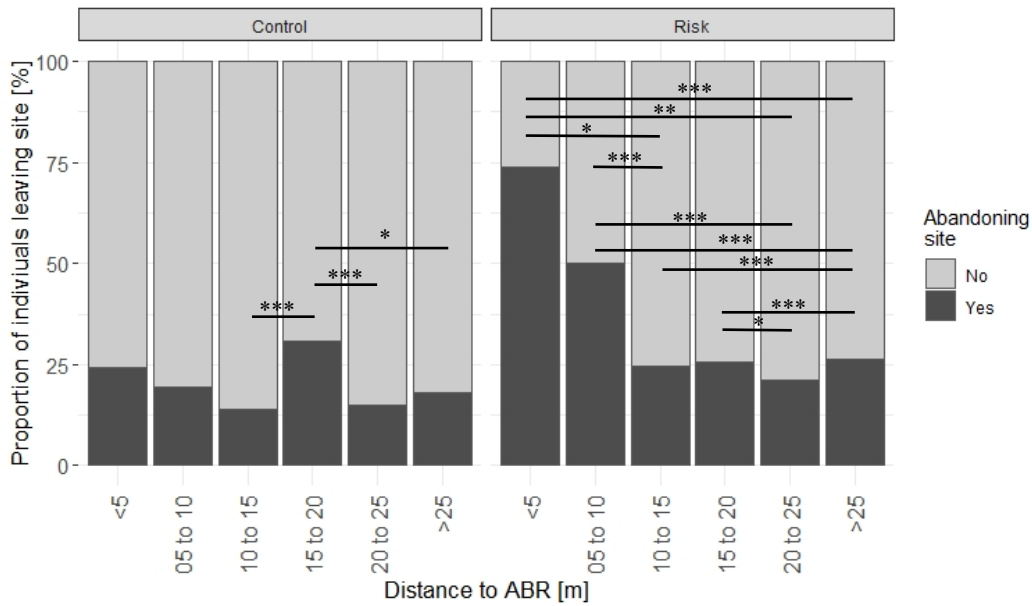
*Figure 6: Proportion of individuals leaving the site within the video time (yes/no) for control and risk sounds (pooled together) depending on the distance of the animal to the ABR. Horizontal lines and stars indicate significance values between categories (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1). See Table 8 in Appendix 4 for accurate statistical values.*

3.2.2. Group size effects

For control sounds, single fallow deer (proportion left: 0.27) and small groups (proportion left: 0.28) left the site fewer times, whereas large groups remained at the site proportionally more (proportion left: 0.11) (Figure 7). The difference between small groups and large groups was significant (p=0.001) (Table 9 Appendix 4). Risk sounds led to a higher leaving rate in all group size categories, where single individuals left the site in 44%, steadily decreasing, where large groups left the site only in 22%. The difference among the leaving rate of single individuals to large groups was also significant (Table 9 Appendix 4).

The proportional difference between risk and control sounds was highest for single individuals (18%) and least visible for small groups, where the difference was only 3% (Figure 7).
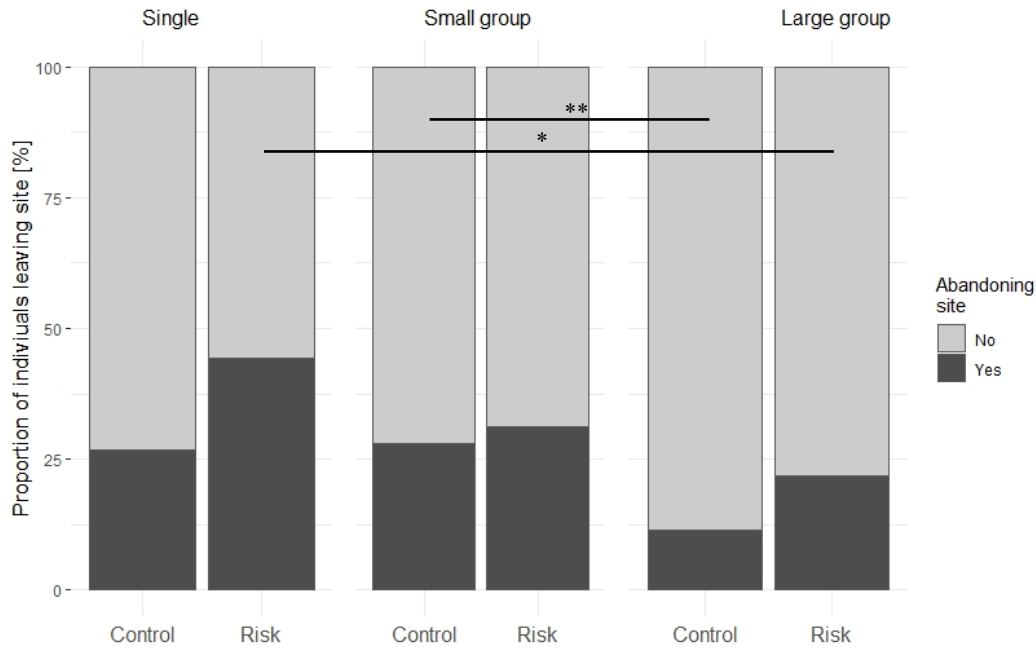
*Figure 7: Proportion of fallow deer leaving the site within the video time (yes/no) for control and risk sounds (pooled together) among different group size classes. 'Single' individuals represent fallow deer, which were alone in the video frame, 'Small group' represent individuals, which were part of a group of two to five animals, and 'large group' include all individuals, which were part of a group with more than five fallow deer visible in the video. Horizontal lines and stars indicate significance values between categories (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1). See Table 9 in Appendix 4 for accurate statistical values.*

3.3. Foraging behaviour

The proportion of the time spent foraging by an individual was significantly lower for risk sounds (mean=26.7%) than for control sounds (mean=34%) ($p<0.001$) (Figure 8, Table 10 Appendix 5). Ungulates, which heard dog sounds, foraged a similar amount of time as those hearing control sounds ($p=0.38$) (Table 10 Appendix 5). But they spent less time foraging after hearing wolf sounds than after control sounds ($p<0.001$). The strongest response was to human sounds compared to control sounds ($p<0.001$) (Table 10 Appendix 5), with animals foraging for only 19.5% of their time on average (Figure 8). Furthermore, human sounds had also a significant difference to dog sounds ($p<0.001$) and showed also a strong difference to wolf sounds ($p=0.57$) (Table 11 Appendix 5).

Figure 8: Proportion of time spent foraging in percent by an individual for control and risk sounds (pooled together) (left). The risk sound category is subdivided into the different risk sounds (dog, human, wolf) (right). The dot represents the mean per treatment category.

3.3.1. Distance effects

The time individuals spent foraging was – as described above – higher for control sounds than for risk sounds. This overall pattern is also visible among the different distance categories. With increasing distance of the ungulate to the ABR system, the foraging time was increasing for risk sounds (Figure 9). The least time spent foraging was when animals were in a distance between 5 to 10 m. However, this might be based on the relatively low sample size for the distance category below 5 m (n= 19). For the different distance classes between 10 and 25 m, there seems to be similar amount of foraging time of about 21.4%. A steep increase is shown for all individuals, which were further than 25 m away from the ABR. For this category is also no clear difference to the control sounds visible anymore. The differences among some distance classes were significant for risk sounds and control sounds (Figure 9, Table 12 Appendix 5).

For control sounds this distance-foraging relationship seems rather linear and distance seems not to have a severe effect on the foraging time. However, there are still significant effects among some distance categories for control sounds (Figure 9, Table 12 Appendix 5). The highest proportion animals spent foraging was given when they were closer than 5 m to the ABR, whereas the least proportion were spent in a distance between 15 and 20 m for control sounds.

Figure 9: Mean proportion of time spent foraging in percent compared to the total behavioural time divided into control and risk sounds (pooled together) over distance to the ABR system. The dot represents the mean and the lines the according standard error per category. Significant effects (p<0.05) for the treatments among the distance categories are indicated by small letters. See Table 12 in Appendix 5 for accurate statistical values.

3.3.2. Group size effects

For risk sounds, single fallow deer spent proportionally the least time foraging (mean = 14.2%), whereas large fallow deer groups spent in average over 34% with foraging (Figure 10). The differences among group sizes for risk sounds were significant for the category 'large groups' to both 'single' fallow deer, and 'small groups' of fallow deer (Figure 10, Table 13 Appendix 5).

For control sounds, small groups foraged on average at least, where single individuals spent slightly more time foraging, and large groups the most proportion of time (Figure 10). Similar to risk sounds, also here the groups size category 'large group' showed significant differences to both other group size classes ('single' & 'small group') (Figure 10, Table 13 Appendix 5).

Fallow deer, which heard risk sounds, had overall lower foraging proportions compared to control sounds, except for the group size category 'small groups'. Individuals which were part of a 'small group' foraged about 5% more of their time when exposed to risk sounds, compared to control sounds. However, in both cases 'large groups' spend proportionally the most time with foraging (Figure 10).

35
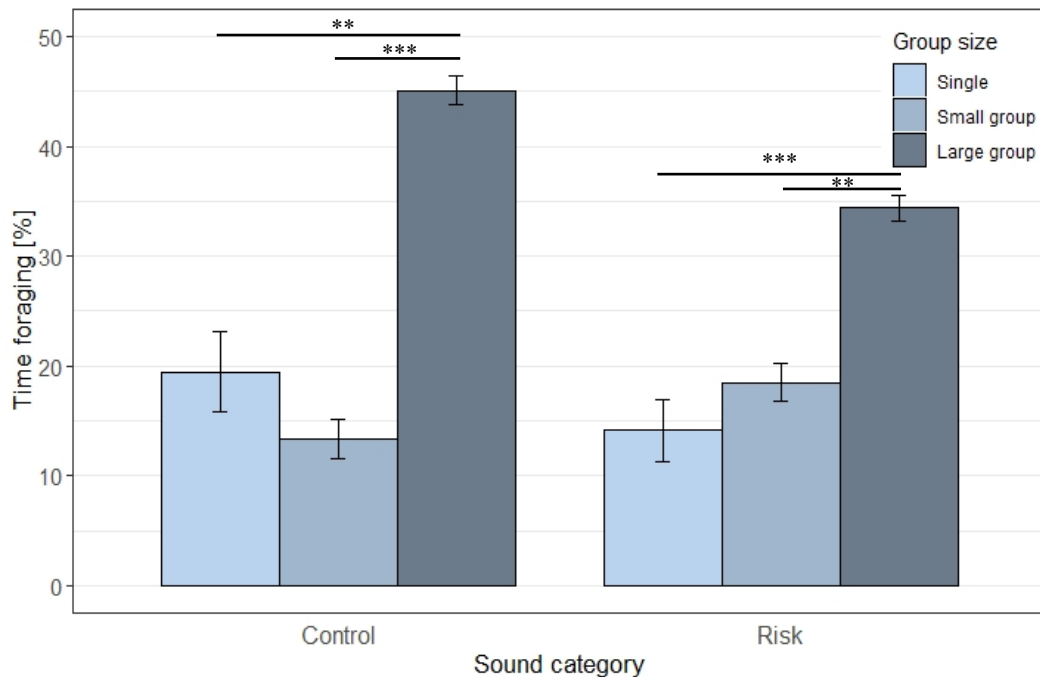
Figure 10: Mean proportion of time spent foraging (+/- standard error) in percent for fallow deer divided into control and risk sounds (pooled together) for the different group size categories. 'Single' individuals represent fallow deer, which were alone in the video frame, 'Small group' represent individuals, which were part of a group of two to five animals, and 'large group' include all individuals, which were part of a group with more than five fallow deer visible in the video. Horizontal lines and stars indicate significance values between categories (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1). See Table 13 in Appendix 5 for accurate statistical values.

3.4. Vigilance behaviour

The vigilance behaviour differed significantly between control and risk sounds ($p < 0.001$) (Table 14 Appendix 6). Ungulates, which were exposed to risk sounds spent in average about 18% of their time being vigilant (Figure 11). Also the individually tested risk sounds (dog, human, wolf) differed significantly from control sounds (Table 14 Appendix 6). Human sounds, however, had the lowest vigilance proportion ($p = 0.006$) among risk sounds compared to control sounds (Table 14 Appendix 6). Animals, which heard dog sounds, spent more time being vigilant ($p < 0.001$), but the highest proportion occurred for wolf sounds ($p < 0.001$) relative to control sounds (Figure 11, Table 14 Appendix 6). Furthermore, wolf sounds had also a significant higher vigilance proportion compared to the other risk sounds (Table 15 Appendix 6).
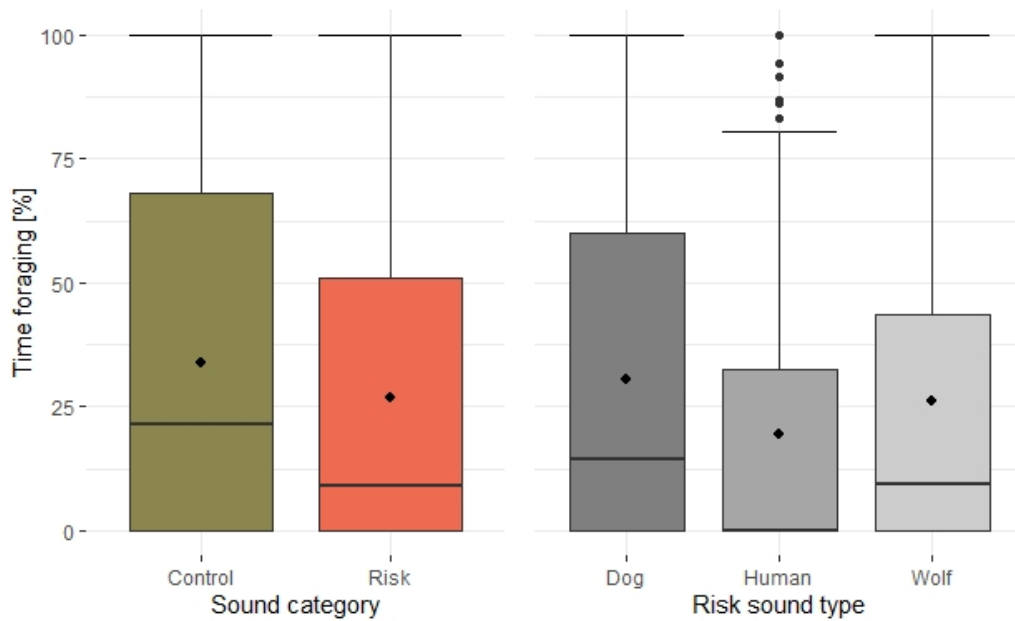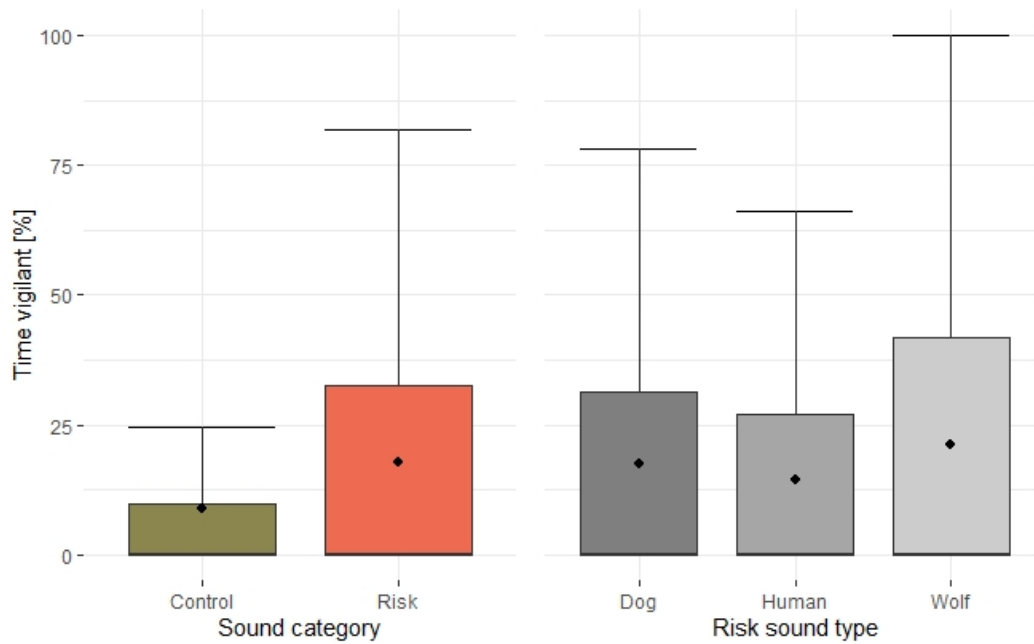
Figure 11: Proportion of time spent being vigilant in percent by an individual for control and risk sounds (pooled together) (left). The risk sound category is subdivided into the different risk sounds (dog, human, wolf) (right). The dot represents the mean per treatment category.

3.4.1. Distance effects

For all distance categories, control sounds had lower vigilance mean values than for risk sounds (Figure 12). For control sounds, the time being vigilant was slightly decreasing with increasing distance. So, animals which were situated more than 25 m from the ABR, used only 4% of their time for vigilance behaviour, whereas animals closer, at a distance between 5 to 10 m still spent 14% for this behaviour. Distance proved to have significant effects among those two distance categories for control sounds (Figure 12, Table 16 Appendix 6).

Risk sounds had a peak at '5 to 10 m', where ungulates spent in average 31% of their time being vigilant (Figure 12). Animals which were more than 25 m away from the ABR had also the lowest value, and spent just slightly more time being vigilant than for control sounds. Also for risk sounds the distance effect was significant among several distance categories (Table 16 Appendix 6). Nevertheless both, control and risk sounds, had significant differences among distance categories, the decrease of time spent being vigilant over distance is stronger for risk sounds than for control sounds (Figure 12).
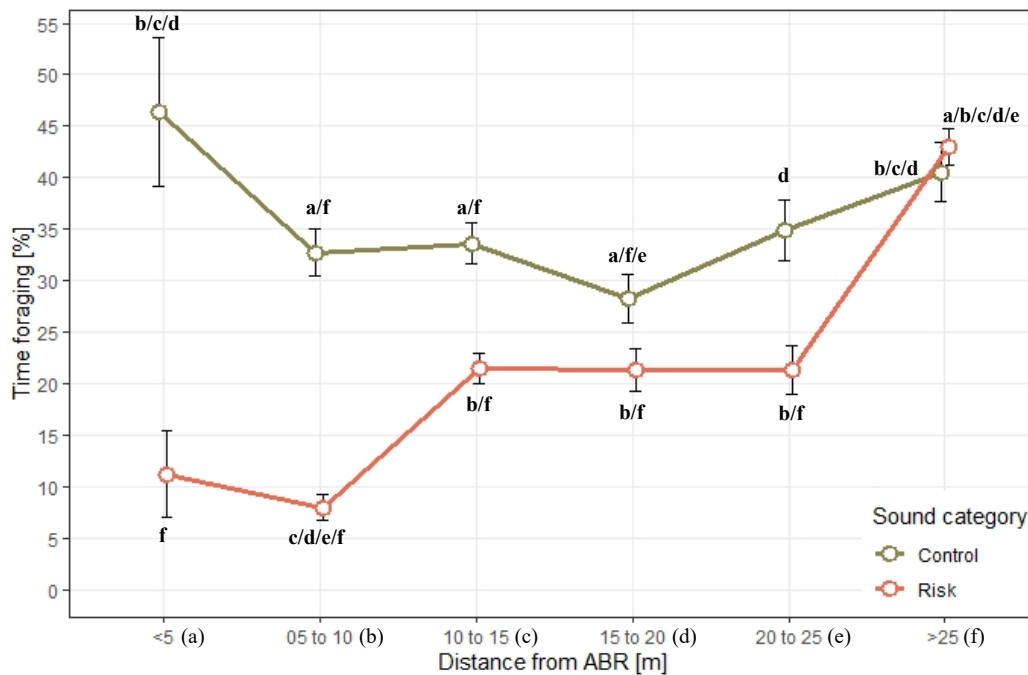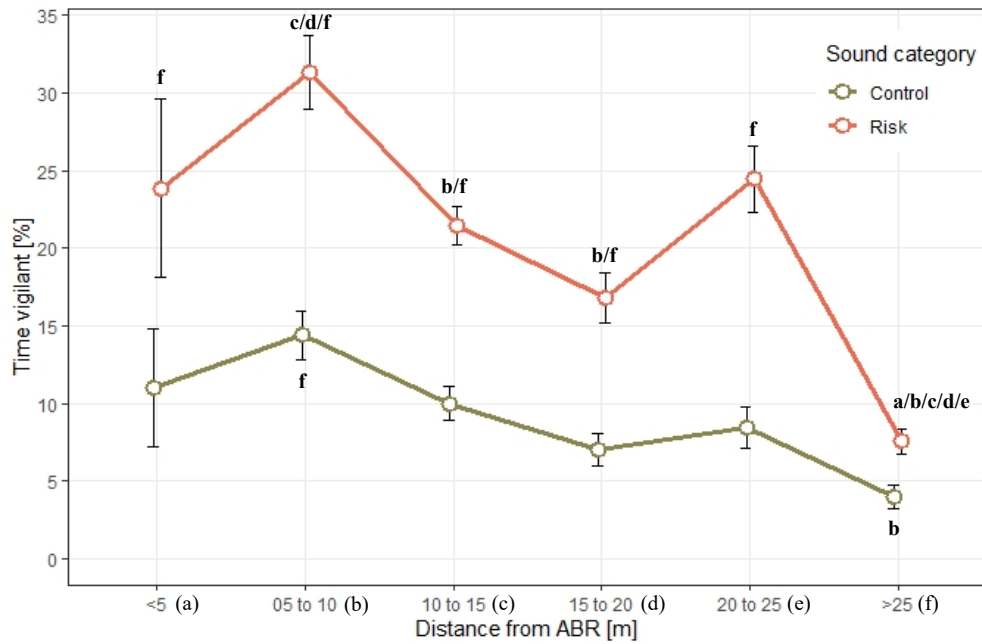
Figure 12:Mean proportion of time spent being vigilant in percent compared to the total behavioural time divided into control and risk sounds (pooled together) over distance to the ABR system. The dot represents the mean and the lines the according standard error per category. Significant effects (p<0.05) for the treatments among the distance categories are indicated by small letters. See Table 16 in Appendix 6 for accurate statistical values.

3.4.2. Group size effects

All different group size categories for risk sounds had a higher proportion of vigilance behaviour than the according groups for control sounds (Figure 13). Among group size categories for risk sounds, there was a significant difference between 'large groups' to 'small groups' (Figure 13, Table 17 Appendix 6). However, single fallow deer spent on average more time being vigilant than small and large groups. This pattern is also visible for control sounds, but there was also a statistically significant difference for large groups to 'single' individuals and 'small groups' (Figure 13, Table 17 Appendix 6). Large groups, which were exposed to control sounds spent overall the least time being vigilant.
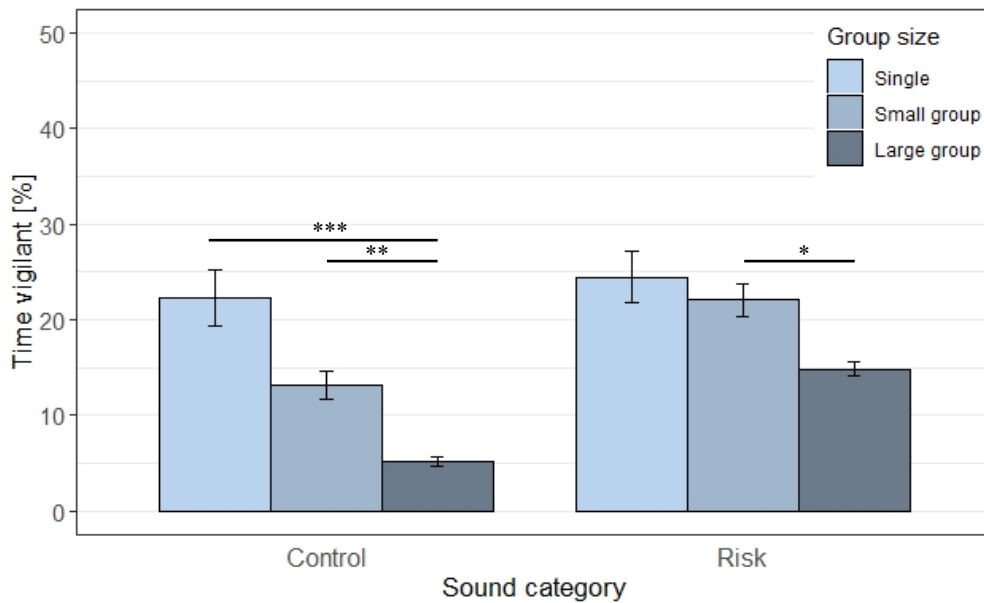
*Figure 13: Mean proportion of time spent being vigilant (+/- standard error) in percent for fallow deer divided into control and risk sounds (pooled together) for different group size categories. 'Single' individuals represent fallow deer, which were alone in the video frame, 'Small group' represent individuals, which were part of a group of two to five animals, and 'large group' include all individuals, which were part of a group with more than five fallow deer visible in the video. Horizontal lines and stars indicate significance values between categories (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1). See Table 17in Appendix 6 for accurate statistical values.*

4. Discussion

My results showed that ungulates exposed to risk sounds abandoned the sites significantly more often than when they heard a non-risky sound. Among risk sounds, human sounds had the highest impact, whereas dog sounds did not lead to a higher abandoning rate compared to non-risky sounds. Furthermore, there was a strong indication that the fleeing response to wolf sounds was stronger than to control sounds. Individuals moreover decreased their foraging time and increased the time being vigilant for risky sounds. Human sounds had for the behavioural response 'Foraging' the strongest impact, whereas for 'Vigilance' wolf sounds led to the highest proportion of time spent for this behaviour.

When animals were exposed to the different treatments, the distance to the ABR seemed to have an impact on the strength of the behavioural responses. As expected, increasing distance led, especially for risk sounds, to decreased abandoning rates of the site, increased foraging, and decreased vigilance. Furthermore, the size of the fallow deer groups showed to influence their behavioural responses as well. Larger groups left proportionally fewer times the site, increased their foraging time and decreased their time being vigilant for both, control and risk sounds. For a more detailed comparison of hypothesis and results see Table 18 in Appendix 7.

My results give novel insights into ungulates behaviour in response to different predator vocalisations within a human-modified landscape.

4.1. Perceived risk levels of ungulates

My results suggest that it is possible to create a landscape of fear for ungulates with an experimental induced risk in form of sound playbacks, as it has been shown for other species and in other environments (Smith et al. 2017; Suraci et al. 2019a; Suraci et al. 2019b; Gambra Caravantes 2020). As humans seemed to be perceived as a significant risk source and were most effective in steering animals to leave the site as well as to decrease foraging time, the other considered risk sounds could not show such clear patterns in all three studied behavioural responses (Figure 5, Figure 8 & Figure 11). Especially the dog sound had almost no influence on ungulates leaving and foraging behaviour, implying that ungulates do not perceive dogs, or at least dog vocalisations, as a potential threat per se. The effect of dog sounds has

also been proven unsignificant for pumas in California (Suraci et al. 2019b). Suraci et al. (2019b) suggested that dogs are neither seen as a predator nor as a direct hint for human presence. I would, based on the results presented here, follow this assumption to be applicable for my Swedish ungulates as well. It is unlikely that ungulates are not familiar with dogs, both as co-occurrence sign of humans, but also as a potential threat itself. Dogs are commonly used in different hunting practices, such as driven hunts, which should be perceived as a direct threat to ungulates itself, since it is directly associated with hunting and therefore also with humans. Feral or free-ranging dogs may not be very common in both study areas, and additionally during 1 March and 20 August it is not allowed to have dogs off-leash in Sweden. This potentially results in minimized encounters by them, which in turn might contribute to a possible explanation that ungulates do not change behavioural responses based on dog sounds. However, besides the assumption that it is unlikely that all dog-owners are acting according to this law, dogs still should serve as a proxy sign for humans as Suraci et al. (2019b) also assumed. And since humans has been proven to be seen as a major threat, similar effects should be caused by dog sounds. However, Clinchy et al. (2016) also found no correlation between wildlife responses to dogs as a human cue, highlighting that dogs might not be seen as an indicant for humans and the potential threat of them. Similar conclusions are drawn by Parsons et al. (2016) for several wildlife species, which showed significantly higher perceived risk behaviour to humans than to dogs itself.

Since dogs are the most common carnivore (Vanak & Gompper 2009) and abundant all across Sweden (Jordbruksverket 2021), it simply might also be that ungulates are too accustomed with frequent dog barks, and might have adapted their behaviour according to that. This would assume that the species' cost-benefit balance is more effective when ungulates are not altering their behaviour to dog vocalisations, since they are too abundant and frequent through space and time across the landscape. Ungulates might instead rely on other cues of dogs, such as visual or olfactory hints, to perceive dogs as present in the area and evaluate dogs as a potential risk, as it has been shown for other predator-prey interactions (Kuijper et al. 2014; Wikenros et al. 2015). Furthermore, ungulates might also be able to distinguish between different types of dog barks, which carry various context- and individual-specific information (Yin & McCowan 2004; Maros et al. 2008; Molnár et al. 2009). The particular dog playbacks used in this study might not have represented a vocalisation of a for instance hunting dog, which would might have had a higher threat implication.

Additionally, ungulates seem to be able to distinguish between dog – as the domesticated form of the wolf - and wolf sounds, since wolf sounds had clearly more risk impact on ungulates than dog sounds (Figure 5, Figure 8 & Figure 11). Therefore, I conclude that dogs are not seen as a cue of human presence, nor as a

predator itself, and have also not a comparable impact as the natural wild predator, the wolf.

Nevertheless, it still remains speculation why dogs might not be perceived as potential threat. Humans on the other hand had by far the highest impact, which is corresponding to results of other wildlife species studies (Theuerkauf & Rouys 2008; Suraci et al. 2019b). So, my results go along with those studies and support the human 'super predator' theory (Ciuti et al. 2012; Darimont et al. 2015; Clinchy et al. 2016; Smith et al. 2017). This can lead to the assumption that ungulates might have adapted to the different risk levels of predators and it might be most effective to alter behaviour mainly for the highest predation risk source. For ungulates in those areas, this would be the human presence, since they represent the highest mortality rate, compared to wolves and dogs. Also, Theuerkauf & Rouys (2008) concluded that hunting by humans influenced ungulates density distribution much more than wolves did. The reason for that might be that also wild carnivores, as the wolf, are highly influenced by humans and human activity and have to adapt their behaviour (Theuerkauf 2009; Kuijper et al. 2016; Smith et al. 2017), resulting in potentially less 'effective' behavioural changes on their natural prey.

However, it has been shown for some prey species that wolves were able to alter their movement patterns (Mao et al. 2005), foraging patterns (Churski et al. 2021), vigilance levels (Halofsky & Ripple 2008), group size (Creel & Winnie 2005), and having even impacts on vegetation level, reflected by diet shifts of e.g. red deer (Churski et al. 2021). Here, ungulates in both study areas were considered to have not encountered the natural predator wolf, since wolves occur only very sporadically in both study sites. Therefore I assumed that ungulates might have become naïve, less vigilant, and in conclusion more vulnerable to predation as it has been suggested in other studies (Bøving & Post 1997; Berger 1999; Berger et al. 2001). My results showed however that ungulates reacted to the wolf sound with increased abandoning rate of the site, decreased foraging behaviour and especially increased vigilance as a direct response (Figure 5, Figure 8 & Figure 11). This suggests that ungulates did not become naïve to this predator, but instead retained recognition capabilities and altered their behaviour according to it. This might be due to the comparable short time frame wolves have been absent from those areas. However, Berger (1999) showed that already ten generations of predator absence can be enough to lose those recognition capabilities. Nevertheless, other studies showed that species are even able to recognize also an unfamiliar, but native predator and alter their behaviour according to that (Hettena et al. 2014; Dalerum & Belton 2015). To understand this issue better, it might have been useful to compare the behavioural responses between the study sites, since it cannot be assured that ungulates have not perceived wolf occurrence in the study site in Öster Malma (see Figure 2). However, this comparison was not possible, based on the relatively low sample size in Nordmaling. Overall, it is noteworthy that the sounds

of a natural, but most likely unfamiliar predator had higher impacts than the very abundant domesticated form of the wolf, the dog, had.

4.2. Group size and distance effects

The overall assumption of the group size effect is that there is reduced individual vigilance necessary when animals are being a part of a large group (Lima & Dill 1990; Roberts 1996; Beauchamp 2014). My results also show that leaving rate of the site, foraging behaviour, as well as vigilance behaviour differed among group size classes for fallow deer. There is an overall pattern of reduced abandoning rates, increased foraging time and decreased vigilance time when group size increases visible (Figure 7, Figure 10 & Figure 13). This correlates to the theory and findings of others studies (Lipetz & Bekoff 1982; Lima 1995; Shi et al. 2011). However, this pattern was not only visible for ungulates which were exposed to risk sounds, but also for ungulates which were exposed to control sounds. For latter, I hypothesized that the behavioural responses would not change with group size. Even though the effect might not have been so noticeable for the abandoning rate (Figure 7), for foraging (Figure 10) and vigilance behaviour (Figure 13) the differences among group sizes for control sounds were obvious. It has not been statistically tested here, if the effect of group size is significant for each sound treatment, but the figures suggest that group size is explaining differences in behaviour in general, and not only a direct response to current perceived risk. So, the advantageous effects of grouping behaviour seem to be omnipresent, regardless of direct perceived risks, even though the difference of control and risk treatments are also visible among the group size classes.

An actual change in group sizes, as an adaptive, proactive behavioural response strategy to risk, might be more seen in the long-term and also dependent of the particular area and habitat types (Creel et al. 2014). However, this might be useful to investigate further, since this would also affect the foraging and vigilance behaviour in return. A smaller group size might be advantageous, since there is a general higher detectability rate if the herd size of prey increases and accordingly also an increased attack rate by predators (Delm 1990; Hebblewhite & Pletscher 2002; Beauchamp 2014). However, it seems that the positive effects of flocking behaviour, involving the delusion effect, which states a decreased probability for the single individual to be killed (Delm 1990) and also the 'many eyes' theory (Roberts 1996), where more eyes are available to scan the environment for potential predators, might exceed the negative implications of large herd sizes.

As it also has been shown here, single individuals spent for both, control and risk sounds the highest proportion of time being vigilant, whereas large groups spent the least time being vigilant and scanning for potential predators (Figure 13). So group size, as the theory suggests, leads to a decreased time an individual has to

spend being vigilant. For wolf-prey interactions it has been studied that vigilance decreased with increasing group size for elk in wolf areas (Eisenberg et al. 2014) as the theory would predict. The same study however found also that vigilance increased as elk group size increased for areas with high wolf predation, suggesting that this behavioural effect might be predation risk level dependent (Eisenberg et al. 2014). Other studies found no correlation at all for group size and behavioural responses of predation risk (Laundré et al. 2001; Wolff & van Horn 2003). This might be based on other co-occurring effects of larger group sizes, such as interspecies competition. Hebblewhite &Pletscher (2002) detected two different grouping strategies: Living in small herds which were rarely encountered by wolves, or forming large herds with reduced predation risk through the dilution effect. For each species in the certain environment might be an optimal group size, which maximise the advantageous effects, whereby keeping the negative effects on a minimum level (Markham et al. 2015).

The same overall pattern is visible for the foraging behaviour, where for risk sounds single individuals foraged the least proportion of their time and large groups foraged proportionally more. This correlates to the assumption that individuals can increase their time allocation for other activities, such as foraging, as a consequence of decreased vigilance behaviour. For single individuals the time they spent being vigilant exceeds the time spent foraging, for large groups foraging time exceeds vigilance time (Figure 10 & Figure 13).

Also the distance of the animal to the ABR, seemed to have an impact on the behavioural response, respectively the intensity of this response. Whereas there was no clear difference between abandoning rates for control sounds (Figure 6), risk sounds showed especially for the two closest distance categories a strikingly proportional higher abandoning rate than for the following distance categories. This suggests that the risk sounds are most effective in altering behaviour up to a distance of ten meters. The same pattern was shown for the foraging behaviour, where the distance between zero and ten meter led by far to the least foraging proportion for risk sounds (Figure 9). Animals located between ten and 25 meter showed almost no difference in foraging proportion for risk sounds, whereas animals further than 25 meters away showed similar foraging behaviour than ungulates which were exposed to control sounds. In general, there was no clear increase of foraging time over distance visible for control sounds, as hypothesized. However, this shows that risk treatments could not decrease foraging time for animals, which were further than 25 meters away, relative to control sounds.

The vigilance behaviour showed a slightly different pattern, having highest vigilance mean values for five to ten meters and 20 to 25 meters for risk sounds (Figure 12). This might correlate with other combined factors for those distance categories, as e.g. group size, which might have influenced those results. However, it is visible that the impact of distance on vigilance behaviour was higher for risk

sounds than it was for control sounds, and therefore supporting the initial hypothesis.

Overall, both distance and group size seem to influence the intensity of the behavioural response, especially for risk sounds.

4.3. Management implications

To tackle the ongoing and in future probably even intensifying human-ungulate conflicts, the management has to go beyond population control, especially since stakeholders have controversially goals (Linnell et al. 2020). Novel approaches, such as the 'hunting for fear' might contribute to a possible solution (Cromsigt et al. 2013). The use of scaring devices itself, such as visual, olfactory, or auditory measures are not a new development, but the effectiveness of those methods is questionable, with studies providing evidence for (Kuijper et al. 2014; Wikenros et al. 2015; Bíl et al. 2018; Conti et al. 2018) and against (Andreassen et al. 2005; Elmeros et al. 2011; Schlageter & Haag-Wackernagel 2012; Mpemba et al. 2019; van Ginkel et al. 2019) their utility. Howery (2013) reviews how those human-manipulated cues can be used to manage effectively the behaviour and spatial distribution of rangeland livestock. And also the results presented here show that vocalisations can alter ungulates behaviour in a direction, which would be favoured by management goals. However, especially ungulates, which can adapt their behaviour according to human presence, a more advanced method with a combination of several cues might be necessary to sustain those results. Particularly also since species perception and also group size and distance, as well as potential habituation, might influence the success of such measures. Nevertheless, it has also to be mentioned that this management approach -in this extent- is a very local measure and probably just shifting the problem to another property.

Besides those management preferred changes in behaviour based on fear, the methods might also negatively influence individual performance and fitness (Zanette et al. 2011), since animals have to move more, spend more time being vigilant and need more time to get their necessary food intake. Researchers argued that the landscape of fear induced by wolves in the Yellowstone national park had impacts on the individual performance, implying inferior body condition and lower pregnancy rates (Creel et al. 2007; Christianson & Creel 2014). However, even though other studies revealed those results (Cook et al. 2004; White et al. 2011; Proffitt et al. 2014) this points to a conclusion that effects of the landscape of fear might go beyond the intended alterations and therefore have to be considered with caution. More knowledge is needed to successfully develop a potential new management solution.

4.4. Limitations of conclusions and further research

Despite the overall results of this study, there are also limitations in drawing conclusions from them. Most data entries were collected of fallow deer (Table 4 Appendix 2), which might lead to an overrepresentation of fallow deer behavioural responses compared to the other ungulate species. That is why I suggest for further studies to focus also on other ungulate species and species comparisons. Other ungulate species might perceive the risk sounds in a different way and therefore behave significantly differently.

When creating a landscape of fear to e.g. protect agricultural fields from ungulate damage, it has to be considered that the distance seem to have a high impact, partly also flattening out the difference of control and risk sounds at some point (see Figure 9 & Figure 12). Furthermore, the installation of ABRs are a very locally method. In this study it was not possible to analyse the effect on behaviour over a longer time period. So, ungulates might habituate to the exact location of the sound system and avoid those particular areas with also altering their crossing routes. But, if they shift their crossing routes and therefore their whereabouts just about 25 m, the camera will not be triggered and no sound will be played, leading in conclusion, to no behavioural changes. Ungulates, might in fact be able to habituate to the systems itself rather fast, resulting in less or no possible impact, respectively change in behaviour. This study was carried out in a relatively short time frame, so animals might not only habituate to the local source of risk, but also be able to habituate over time to the same sound treatments, in conclusion also leading to a minimized impact of them. Unfortunately it was not possible here to analyse the returning rate, and therefore another important factor of the effectiveness of the risk sounds, of ungulates to the sites. To understand the dimension of ungulate's altered movement, a tracing of the exact whereabouts after the treatment would be preferable. Here, it was only possible to consider if animals left the camera's sight of view, leaving uncertainty if they left the agricultural field (respectively bait site) itself.

Also, there might be a difference in risk perception between day and night time, either resulting in stronger responses during night based on the limited visual ungulates' ability, or contrary in a less strong response based on the animals increased security feeling. This might also be species and sound dependent, since ungulate species are prioritising different senses based on their natural capacities. Wild boar for example, have a limited visual ability and therefore would react maybe stronger to auditive cues than other species, which would maybe prioritize visual cues over auditive cues.

For moose it has been shown that they are also sensitive to the vocalisations of ravens (*Corvus corax*), where Berger (1999) suggested that moose perceive them as cues of predator occurrence and might alter their behaviour accordingly to avoid predation. Therefore, the here used raven sound potentially did not have functioned as a real control sound. Thus, a comparison of non-sound behaviour to control and

risk sounds would be preferable and might give more insights into the effect of an unexpected sound itself.

Other factors might also influence those behavioural responses, such as distance to other human infrastructure, social class, or surrounding landscape structure. The inclusion of those factors were beyond the scope of this study, and other studies found also no correlation of those factors to behavioural responses (Eisenberg et al. 2014). However, the risk perception of ungulates in homogenous landscapes may be different to those in heterogenous landscapes, where the possibility of finding other habitats and food resources are manifoldly and no resource shortness is occurring (Schmidt & Kuijper 2015). In heterogenous landscapes, individuals are able to switch to other food resources in more safe habitat patches easily and the effects of risk sounds might be significantly different to animals living in more homogenous landscapes. Also, social class might have an impact on vigilance levels (Eisenberg et al. 2014), where cows with calves might be most vigilant compared to other social classes (Wolff & van Horn 2003; Halofsky & Ripple 2008). In this study, mainly male adults were analysed, resulting in potentially - according to the previously stated findings –comparable lower vigilance rates.

In summary, the landscape of fear and the perception of risks is a complex framework, altered by various factors which might influence the results. To successfully be able to alter ungulates behaviour and predict behavioural responses, more knowledge is needed.

5. Conclusions

My results show that it is possible to alter ungulates behaviour with an experimentally created landscape of fear through sound systems. The fear of the human 'super predator' exceeds by far the fear of wolf and dog, and led to the hypothesized behavioural changes of abandoning the site, as well as altered foraging and vigilance behaviour.

The solution of the ongoing human-wildlife conflict, caused by overabundance and damages of herbivores, requires more than population control. Fear can contribute to conserving biodiversity and preserving healthy ecosystems, as well as be potentially used as a management method to prevent agricultural fields from damages. Several studies emphasize the existence and preservation of large carnivores, respectively large carnivore populations, to create a landscape of fear and to gain the beneficial ecosystem services resulting of it (Ripple & Beschta 2004; Ripple et al. 2014; Suraci et al. 2016). Here, it has been shown that the fear of wolves is altering ungulates behaviour, including suppressed foraging behaviour. This supports the importance of large carnivores across the landscape as playing an influencing role on lower cascading levels, since they can affect ungulates' consumption of vegetation. Nevertheless, the strong response of ungulates to human sounds also highlights the unique role humans play in affecting and altering species' behaviour, maybe even beyond presumed dimensions. A high human occurrence, especially in foraging, resting, or reproductive areas of ungulates might therefore has major consequences for species' performance.

However, perceived predation risk is a complex function of several factors, such as species (Kitchen et al. 2010; Kuijper et al. 2014), group size (Creel et al. 2014), individual fitness (Bleicher 2017), sex (Laundré et al. 2001), age (Eisenberg et al. 2014), evolutionary history (Berger et al. 2001), season (Wolff & van Horn 2003), time of day (Kohl et al. 2018), resource shortness and potential gain from the food source (McArthur et al. 2014), community composition (Ashby et al. 2020), landscape factors (Kauffman et al. 2007; Creel et al. 2014), and more, resulting in highly individually perceived landscapes of fear. This makes predictions of behavioural responses and management implications difficult to forecast.

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Acknowledgements

Appendix

Appendix 1

*Figure 14: Example snapshots of videos showing different coded behaviour types: **top left** – Roe deer (Nordmaling) showing "Standing – Head-up" behaviour; **top right** – Roe deer (Öster Malma) showing "Standing – Chewing" behaviour; **middle left** – Fallow deer (Öster Malma) showing "Standing – Foraging" behaviour; **middle right** – Fallow deer (Öster Malma) showing "Running – Head-up" behaviour; **bottom left** – Moose (Öster Malma) showing "Approaching – Look at camera" behaviour; **bottom right** – Moose (Öster Malma) showing "Fleeing – Head-up" behaviour.*

Appendix 2

Table 4: Data entries (videos times individuals) per study site, species, and sound type.

Study site	Species	Sound type				
		Control	**Human**	**Dog**	**Wolf**	**Total**
		All entries				
Öster Malma	Moose	6	2	4	3	15
	Roe deer	42	12	15	12	81
	Red deer	15	0	2	5	22
	Fallow deer	870	223	533	276	1902
	Wild boar	30	2	0	2	34
	Sum	*963*	*239*	*554*	*298*	***2054***
Nord-maling	Moose	2	0	8	4	14
	Roe deer	15	5	5	6	31
	Red deer	12	14	34	12	72
	Fallow deer	38	48	62	25	173
	Sum	*67*	*67*	*109*	*47*	***290***
	Total	**1030**	**306**	**663**	**345**	**2344**

Table 5: Number of videos per sound type and study site divided into full-risk and half-risk ABR sites (see section 'Automated Behavioural Response (ABR) System' for explanation).

	Sound type					
	Control	**Risk**	Human	Dog	Wolf	**Total**
No. of videos	264	381	112	169	100	**645**
	Öster Malma					
Total	*212*	*218*	*65*	*94*	*59*	**430**
Full risk	37	121	40	47	34	*158*
Half risk	175	97	25	47	25	*272*
	Nordmaling					
Total (Full risk)	*52*	*163*	*47*	*75*	*41*	**215**

Appendix 3
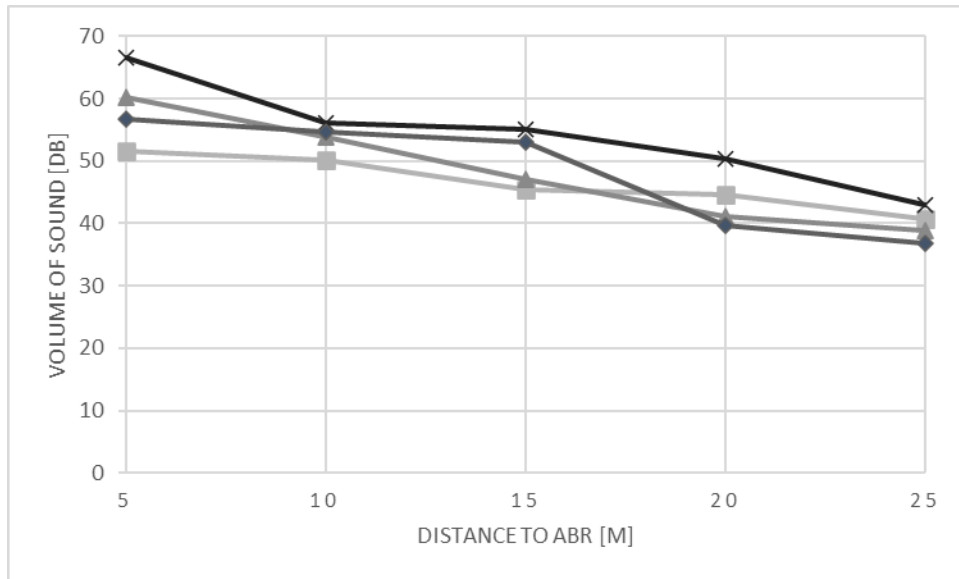
Figure 15: Measured sound volume (in decibel) of the ABR system in the field (study site Öster Malma). Exemplarily for four different ABRs. Measured mean value with App: Decibel X (SkvPaw Co. Ltd).

Appendix 4

Table 6: Generalized Linear Mixed Model results for behavioural response 'leaving the site within the video time' (binary response, yes/no). Tested between control and risk treatment (risk sounds pooled together) (left), and for treatments itself (right). Intercept represents the control, respectively bird sounds.

Predictors	Leaving yes/no Control-Risk				Leaving yes/no Treatments			
	Log-Odds	*std. Error*	*Statistic*	*p*	*Log-Odds*	*std. Error*	*Statistic*	*p*
(Intercept)	-2.20	0.71	-3.10	**0.002**	-2.59	0.91	-2.86	**0.004**
Risk	1.36	0.56	2.46	**0.014**				
Dog					-0.76	0.71	-1.08	0.280
Human					5.21	1.20	4.36	**<0.001**
Wolf					1.97	1.03	1.91	0.056

Table 7: Multiple comparisons of means (Tukey post hoc test) of the GLMM for the behavioural response 'leaving the site within the video time' (binary response, yes/no) among the different sound treatments.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Dog - Bird	-0.7625	0.7063	-1.080	0.6898	
Human - Bird	5.2071	1.1950	4.357	<0.001	***
Wolf - Bird	1.9697	1.0323	1.908	0.2135	
Human - Dog	5.9696	1.2872	4.638	<0.001	***
Wolf - Dog	2.7322	1.0971	2.490	0.0573	.
Wolf - Human	-3.2374	1.0021	-3.231	0.0064	**
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					

Table 8: Multiple comparisons of means (Tukey post hoc test) of the GLMMs for the behavioural response 'leaving the site within the video time' (binary response, yes/no) among the distance categories (Distance of animal to ABR in m) for control and risk sound data subsets.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Control sounds					
>25 - <5	-0.42942	0.55799	-0.770	0.9704	
05 to 10 - <5	-0.07956	0.52706	-0.151	1.0000	
10 to 15 - <5	-0.51462	0.52921	-0.972	0.9216	
15 to 20 - <5	0.57830	0.52072	1.111	0.8693	
20 to 25 - <5	-0.71507	0.55535	-1.288	0.7803	
05 to 10 - >25	0.34986	0.33225	1.053	0.8930	
10 to 15 - >25	-0.08520	0.32717	-0.260	0.9998	
15 to 20 - >25	1.00772	0.30502	3.304	0.0111	*
20 to 25 - >25	-0.28565	0.34803	-0.821	0.9610	
10 to 15 - 05 to 10	-0.43506	0.27521	-1.581	0.5947	
15 to 20 - 05 to 10	0.65786	0.26095	2.521	0.1095	
20 to 25 - 05 to 10	-0.63551	0.32586	-1.950	0.3549	
15 to 20 - 10 to 15	1.09292	0.25731	4.248	<0.001	***
20 to 25 - 10 to 15	-0.20045	0.31771	-0.631	0.9878	
20 to 25 - 15 to 20	-1.29337	0.30026	-4.307	<0.001	***
Risk sounds					
>25 - <5	-3.5620	0.7534	-4.728	< 0.001	***
05 to 10 - <5	-1.1439	0.7264	-1.575	0.58730	
10 to 15 - <5	-2.0977	0.7228	-2.902	0.03729	*
15 to 20 - <5	-1.8281	0.7319	-2.498	0.11038	
20 to 25 - <5	-2.8803	0.7599	-3.790	0.00183	**
05 to 10 - >25	2.4181	0.3219	7.512	< 0.001	***
10 to 15 - >25	1.4643	0.2778	5.272	< 0.001	***
15 to 20 - >25	1.7339	0.3085	5.621	< 0.001	***
20 to 25 - >25	0.6817	0.3277	2.080	0.27246	
10 to 15 - 05 to 10	-0.9538	0.2387	-3.996	< 0.001	***
15 to 20 - 05 to 10	-0.6842	0.2773	-2.467	0.11911	
20 to 25 - 05 to 10	-1.7364	0.3434	-5.057	< 0.001	***
15 to 20 - 10 to 15	0.2696	0.2383	1.132	0.85392	
20 to 25 - 10 to 15	-0.7826	0.3103	-2.522	0.10419	
20 to 25 - 15 to 20	-1.0522	0.3296	-3.192	0.01530	*

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 9: Multiple comparisons of means (Tukey post hoc test) of the GLMMs for the behavioural response 'leaving the site within the video time' (binary response, yes/no) among the different group size categories (only applied for fallow deer) for control and risk sound data subsets.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Control sounds					
Single - Large group	0.8007	0.3811	2.101	0.08705	.
Small group - Large group	0.9130	0.2569	3.555	0.00106	**
Small group - Single	0.1123	0.3742	0.300	0.95068	
Risk sounds					
Single - Large group	0.9041	0.3258	2.775	0.0147	*
Small group - Large group	0.3895	0.2203	1.768	0.1759	
Small group - Single	-0.5146	0.3000	-1.715	0.1947	
*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*					

Appendix 5

Table 10: Generalized Linear Mixed Model results for behavioural response 'proportion of time spent foraging'. Tested between control and risk treatment (risk sounds pooled together) (left), and for treatments itself (right). Intercept represents the control, respectively bird sounds.

Predictors	Foraging Proportion Control-Risk				Foraging Proportion Treatments			
	Log-Odds	std. Error	Statistic	p	Log-Odds	std. Error	Statistic	p
(Intercept)	-1.82	0.30	-6.08	**<0.001**	-1.78	0.30	-5.96	**<0.001**
Risk	-0.39	0.11	-3.58	**<0.001**				
Dog					-0.11	0.12	-0.87	0.383
Human					-0.94	0.18	-5.11	**<0.001**
Wolf					-0.68	0.16	-4.24	**<0.001**

Table 11: Multiple comparisons of means (Tukey post hoc test) of the GLMM for the behavioural response 'Foraging proportion' among the different sound treatments.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Dog - Bird	-0.1051	0.1206	-0.872	0.81499	
Human - Bird	-0.9429	0.1844	-5.112	< 0.001	***
Wolf - Bird	-0.6798	0.1603	-4.241	< 0.001	***
Human - Dog	-0.8378	0.1824	-4.592	< 0.001	***
Wolf - Dog	-0.5747	0.1624	-3.539	0.00219	**
Wolf - Human	0.2631	0.2050	1.283	0.56601	
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					

Table 12: Multiple comparisons of means (Tukey post hoc test) of the GLMMs for the behavioural response 'Foraging proportion' among the distance categories (Distance of animal to ABR in m) for control and risk sound data subsets.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Control sounds					
05 to 10 - <5	-1.37979	0.47868	-2.882	0.04100	*
10 to 15 - <5	-1.42135	0.47546	-2.989	0.02993	*
15 to 20 - <5	-1.61741	0.47770	-3.386	0.00825	**
20 to 25 - <5	-0.81766	0.48995	-1.669	0.53231	
>25 - <5	-0.51403	0.50600	-1.016	0.90578	
10 to 15 - 05 to 10	-0.04156	0.20817	-0.200	0.99995	
15 to 20 - 05 to 10	-0.23763	0.21806	-1.090	0.87687	
20 to 25 - 05 to 10	0.56212	0.24760	2.270	0.19160	

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
>25 - 05 to 10	0.86576	0.28175	3.073	0.02316	*
15 to 20 - 10 to 15	-0.19607	0.20690	-0.948	0.92843	
20 to 25 - 10 to 15	0.60368	0.23662	2.551	0.10031	
>25 - 10 to 15	0.90732	0.27281	3.326	0.01012	*
20 to 25 - 15 to 20	0.79975	0.24251	3.298	0.01112	*
>25 - 15 to 20	1.10338	0.27451	4.019	< 0.001	***
>25 - 20 to 25	0.30364	0.28753	1.056	0.89062	
Risk sounds					
05 to 10 - <5	-0.49434	1.16357	-0.425	0.99784	
10 to 15 - <5	1.28970	1.08059	1.194	0.81569	
15 to 20 - <5	1.25684	1.08636	1.157	0.83470	
20 to 25 - <5	1.44772	1.09446	1.323	0.74144	
>25 - <5	3.58603	1.09864	3.264	0.01102	*
10 to 15 - 05 to 10	1.78404	0.48148	3.705	0.00228	**
15 to 20 - 05 to 10	1.75118	0.50110	3.495	0.00492	**
20 to 25 - 05 to 10	1.94205	0.51938	3.739	0.00191	**
>25 - 05 to 10	4.08037	0.52566	7.762	< 0.001	***
15 to 20 - 10 to 15	-0.03286	0.23321	-0.141	0.99999	
20 to 25 - 10 to 15	0.15802	0.27118	0.583	0.99047	
>25 - 10 to 15	2.29633	0.28971	7.926	< 0.001	***
20 to 25 - 15 to 20	0.19087	0.29592	0.645	0.98487	
>25 - 15 to 20	2.32919	0.31913	7.299	< 0.001	***
>25 - 20 to 25	2.13832	0.33013	6.477	< 0.001	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 13: Multiple comparisons of means (Tukey post hoc test) of the GLMMs for the behavioural response 'Foraging proportion' among the different group size categories (only applied for fallow deer) for control and risk sound data subsets.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Control sounds					
Small group - Single	-0.3872	0.4530	-0.855	0.66206	
Large group - Single	1.4599	0.4331	3.371	0.00205	**
Large group - Small group	1.8471	0.2768	6.672	< 1e-04	***
Risk sounds					
Small group - Single	0.8678	0.3829	2.266	0.057494	.
Large group - Single	1.6438	0.3977	4.134	0.000101	***
Large group - Small group	0.7760	0.2299	3.375	0.001993	**

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Appendix 6

Table 14: Generalized Linear Mixed Model results for behavioural response 'proportion of time spent being vigilant'. Tested between control and risk treatment (risk sounds pooled together) (left), and for treatments itself (right). Intercept represents the control, respectively bird sounds.

| Predictors | Vigilance Proportion Control-Risk | | | | Vigilance Proportion Treatments | | | |
	Log-Odds	std. Error	Statistic	p	Log-Odds	std. Error	Statistic	p
(Intercept)	-2.82	0.13	-21.4	**<0.001**	-2.82	0.13	-21.4	**<0.001**
Risk	0.97	0.15	6.29	**<0.001**				
Dog					0.86	0.18	4.91	**<0.001**
Human					0.62	0.23	2.73	**0.006**
Wolf					1.36	0.19	7.24	**<0.001**

Table 15: Multiple comparisons of means (Tukey post hoc test) of the GLMM for the behavioural response 'Vigilance proportion' among the different sound treatments

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Dog - Bird	0.8645	0.1759	4.914	< 0.001	***
Human - Bird	0.6234	0.2282	2.731	0.03125	*
Wolf - Bird	1.3633	0.1884	7.236	< 0.001	***
Human - Dog	-0.2412	0.2198	-1.097	0.68835	
Wolf - Dog	0.4988	0.1781	2.80	0.02533	*
Wolf - Human	0.7400	0.2299	3.219	0.00695	**
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					

Table 16: Multiple comparisons of means (Tukey post hoc test) of the GLMMs for the behavioural response 'Vigilance proportion' among the distance categories (Distance of animal to ABR in m) for control and risk sound data subsets.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
Control sounds					
05 to 10 - <5	-0.0759	0.6538	-0.116	1.0000	
10 to 15 - <5	-0.5108	0.6569	-0.778	0.9686	
15 to 20 - <5	-1.0594	0.6983	-1.517	0.6345	
20 to 25 - <5	-0.7915	0.7097	-1.115	0.8656	
>25 - <5	-1.8952	0.8433	-2.247	0.2011	
10 to 15 - 05 to 10	-0.4349	0.3387	-1.284	0.7800	
15 to 20 - 05 to 10	-0.9835	0.4134	-2.379	0.1516	
20 to 25 - 05 to 10	-0.7156	0.4323	-1.655	0.5413	

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
>25 - 05 to 10	-1.8193	0.6281	-2.897	0.0397	*
15 to 20 - 10 to 15	-0.5485	0.4183	-1.311	0.7643	
20 to 25 - 10 to 15	-0.2807	0.4370	-0.642	0.9866	
>25 - 10 to 15	-1.3844	0.6313	-2.193	0.2250	
20 to 25 - 15 to 20	0.2678	0.4971	0.539	0.9940	
>25 - 15 to 20	-0.8359	0.6743	-1.240	0.8045	
>25 - 20 to 25	-1.1037	0.6860	-1.609	0.5724	
		Risk sounds			
05 to 10 - <5	0.33807	0.59005	0.573	0.99195	
10 to 15 - <5	-0.33876	0.57942	-0.585	0.99116	
15 to 20 - <5	-0.57532	0.59899	-0.960	0.92362	
20 to 25 - <5	-0.02333	0.59739	-0.039	1.00000	
>25 - <5	-1.83755	0.61167	-3.004	0.02830	*
10 to 15 - 05 to 10	-0.67682	0.22685	-2.984	0.03028	*
15 to 20 - 05 to 10	-0.91339	0.27303	-3.345	0.00945	**
20 to 25 - 05 to 10	-0.36140	0.26947	-1.341	0.74476	
>25 - 05 to 10	-2.17562	0.29977	-7.258	< 0.001	***
15 to 20 - 10 to 15	-0.23657	0.24920	-0.949	0.92710	
20 to 25 - 10 to 15	0.31542	0.24529	1.286	0.77723	
>25 - 10 to 15	-1.49879	0.27825	-5.387	< 0.001	***
20 to 25 - 15 to 20	0.55199	0.28853	1.913	0.37137	
>25 - 15 to 20	-1.26223	0.31703	-3.981	< 0.001	***
>25 - 20 to 25	-1.81422	0.31396	-5.778	< 0.001	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 17: Multiple comparisons of means (Tukey post hoc test) of the GLMMs for the behavioural response 'Vigilance proportion' among the different group size categories (only applied for fallow deer) for control and risk sound data subsets.

	Estimate	Std. Error	z value	Pr (>|z|)	Sign.
		Control sounds			
Small group - Single	-0.6635	0.4362	-1.521	0.2794	
Large group - Single	-1.8971	0.4178	-4.541	<1e-04	***
Large group - Small group	-1.2337	0.3602	-3.425	0.0018	**
		Risk sounds			
Small group - Single	-0.1375	0.3344	-0.411	0.9089	
Large group - Single	-0.6247	0.3247	-1.924	0.1275	
Large group - Small group	-0.4872	0.2089	-2.332	0.0493	*

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Appendix 7

Table 18: Overview of hypotheses, measures in this study, and presented results (Hypotheses, which were confirmed are highlighted in green).

Hypothesis		Sub-hypothesis	Measure	Result	Sign.
Risk sounds affect site choice of ungulates	**General**	Ungulates are spending less time at the site when exposed to risk sounds compared to control sounds	Leaving site within video time (y/n) among sound treatments	Ungulates were leaving the site approx. 10% more often when exposed to risk sounds	*
	Distance	**RS:** Less avoidance with increasing distance	Leaving site within video time (y/n) among distance categories for data subsets of CS and RS	Proportional higher abandoning rate when closer to the ABR	yes
		CS: No change in avoidance over distance		Relatively equal abandoning rate over distance	no
		RS- CS: Higher abandoning proportion among distance categories for RS compared to CS		RS had always higher abandoning rate except for distance category "15 to 20 m"	n.t.
	Group size	**RS:** Less avoidance for larger groups	Leaving site within video time (y/n) among group size categories for data subsets of CS and RS	The larger the group, the lower the abandoning rate	yes
		CS: No change in avoidance among group sizes		No difference for single individuals and small groups; large groups had the lowest abandoning rate	yes
		RS- CS: Higher abandoning proportion among group size categories for RS compared to CS		RS had for all group size categories higher abandoning rates	n.t.

Hypothesis		Sub-hypothesis	Measure	Result	Sign.
Risk sounds affect foraging behaviour II	General	Ungulates are spending less time foraging when exposed to risk sounds compared to control sounds	Proportion of foraging behaviour to non-foraging behaviour among sound treatments	Ungulates spent less time foraging for risk sounds than for control sounds	***
	Distance	RS: Higher foraging proportion with increasing distance	Proportion of foraging behaviour to non-foraging behaviour among distance categories for data subsets of CS and RS	Ungulates increased foraging time with increasing distance	yes
		CS: No change in foraging proportion over distance		No clear pattern over distance in foraging proportion	yes
		RS- CS: Less foraging proportion among distance classes for RS compared to CS		RS had always lower foraging proportions except for distance category ">25 m"	n.t.
	Group size	RS: Higher foraging proportion for larger groups	Proportion of foraging behaviour to non-foraging behaviour among group size categories for data subsets of CS and RS	Mean proportion spent foraging is increasing with increasing group size	Yes
		CS: No change in foraging proportion among group sizes		Mean proportion spent foraging is highest for large groups	Yes
		RS- CS: Less foraging proportion among group sizes for RS compared to CS		Less time foraging for single individuals and large groups, but not for small groups	n.t.
Risk sounds affect vigilance behaviour III	General	Ungulates are spending more time being vigilant when exposed to risk sounds compared to control sounds	Proportion of vigilance behaviour to non-vigilance behaviour among sound treatments	Ungulates spent more time being vigilant for risk sounds than for control sounds	***
	Dist	RS: Less time being vigilant with increasing distance	Proportion of vigilance behaviour to non-vigilance	Ungulates decreased proportion being vigilant with increasing distance	Yes

Hypothesis	Sub-hypothesis	Measure	Result	Sign.
	CS: No change in vigilance proportion over distance	behaviour among distance categories for data subsets of CS and RS	Slight decline in proportion being vigilant over distance	Yes
	RS- CS: Higher vigilance proportion among distance categories for RS compared to CS		Higher mean vigilance proportions among all distance classes for RS	n.t.
Group size	RS: Less time being vigilant for larger groups	Proportion of vigilance behaviour to non-vigilance behaviour among group size categories for data subsets of CS and RS	Mean proportion spent being vigilant is highest for single individuals and lowest for large groups	No
	CS: No change in vigilance proportion among group sizes		Mean proportion spent being vigilant is decreasing with increasing group size	Yes
	RS- CS: Higher vigilance proportion among all group size categories for RS compared to CS		Higher mean vigilance proportions for all group size categories for RS	n.t.

RS= risk sounds (human, dog & wolf), CS= control sounds (different bird species), n.t. = not statistically tested

Significance codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1 < ' ' < 1

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