Drivers of ungulate behavior in the context of human-wildlife conflicts

The effects of food, fear and temperature on ungulate landscape use and impacts

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Abstract

Ungulates inhabiting managed landscapes generate important ecosystem services. However, their landscape use may cause negative impacts on human land uses. Expanding ungulate populations in Europe lead to increased human-wildlife conflict, but is also perceived as positive by stakeholders that favor high ungulate numbers. Hence, there is a need for management strategies that consider both the positive and the negative impacts of ungulates, for example by managing their behavior in addition to numbers. In this thesis, I investigated how three key functional landscapes; the foodscape, the landscape of fear and the thermal landscape influenced ungulate landscape use and impacts. I also explored the role humans have in shaping these landscapes. I did this by using an array of methods: field inventories, landscape experiments, social data collection and GPS-data. I found that food, fear and temperature strongly influenced how ungulates used the landscape. In addition, I showed how humans shape the three functional landscapes, for example by changing the foodscape through crop planting or forestry activities, leading to consequences on ungulate impact on human land use. Finally, I found that crop damage was reduced by experimentally inducing fear. Hence, my thesis suggests that it is possible to steer ungulate behavior by managing these functional landscapes. My thesis highlights the importance of including behavioral drivers when managing ungulates and regarding the effects of humans on these drivers. I conclude that these drivers often interact with each other influencing ungulate behavior, and that there is a need for more holistic approaches looking across land use and landowner borders in order to efficiently manage ungulate communities in managed landscapes

Keywords: human-wildlife conflict, foodscape, landscape of fear, thermal landscape, crop damage, browsing pressure, ungulates, wildlife management

Faktorer som styr klövvilts beteende vid konflikter med människor - betydelsen av föda, rädsla och temperatur på klövviltets användning av landskapet

Sammanfattning

Klövvilt förser oss människor med flera viktiga ekosystemtjänster, men deras användning av resurser i ett av människor skött landskap kan leda till kostsamma skador. Ökande populationer av klövvilt kan leda till konflikt mellan vilt och människor, men kan också vara positivt för de människor som gynnas av höga tätheter. Därför behövs skötselstrategier som tar i beaktande både de positiva och negativa effekterna av varierande tätheter av klövvilt i landskapet. Med andra ord, förvalta klövvilts beteende, inte bara antal. Jag har undersökt hur tre funktionella landskap; foderlandskapet, rädslans landskap, och det termiska landskapet påverkar klövvilt och deras inverkan. Jag har också undersökt människans roll i att forma dessa landskap, och om det är möjligt att påverka landskapen för att minska klövviltets påverkan. Jag gjorde detta genom att använda en rad olika metoder: inventeringar, experiment, enkäter, och GPS-data. Jag fann att föda, rädsla och temperatur alla påverkar hur klövviltet använder landskapet, och i sin tur, djurens effekter på skog och jordbruk. Jag visar på den centrala roll människan har i att forma dessa funktionella landskap, till exempel genom att påverka födolandskapet som leder till konsekvenser för klövviltets effekter. Slutligen fann jag att man kan påverka hur svåra skador blir på gröda genom att skrämma bort djuren med ljud. Min avhandling understryker vikten av att inkludera beteende i skötseln av klövvilt och att beakta människans roll. Jag drar slutsatsen att det finns en potential i att påverka beteenden, och att det behövs ett mer holistiskt angreppssätt eftersom åtgärder i ett landskap kan ge konsekvenser för klövviltets påverkan på flera olika skalor och över landskapsgränser.

Nyckelord: foderlandskapet, fodertillgång, skrämsel, temperatur-relaterat beteende, viltskador, klövvilt, viltförvaltning

Dedication

To Olof – you bring me the greatest of joy

When you look at yourself from a universal standpoint, something inside always reminds or informs you that there are bigger and better things to worry about
Albert Einstein
(1879 -1955)

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Widén, A.*, Cromsigt, J.P.G.M., Dressel, S., Felton, A.M., Singh, N.J., Widemo, F. (2023). Direct and indirect effects of food, fear and management on crop damage by ungulates. *Ecological Solutions and Evidence*, 4, e12266.

II. Widén, A.*, Felton, A.M., Widemo, F., Singh, N.J., Cromsigt, J.P.G.M. Deer in the agriculture-forest matrix: interacting effects of land uses on browsing pressure on trees. (submitted)

III. Widén, A.*, Cromsigt, J.P.G.M., Felton, A.M., Widemo, F., Graf, L., Ericsson, G., Singh, N.J. Temperature mediated habitat selection in a multi-species ungulate system: thermal cover and forage availability as potential drivers. (manuscript)

IV. Widén, A.*, Clinchy, M., Felton, A.M., Hofmeester, T.R., Kuijper, D.P.J., Singh, N.J., Widemo, F., Zanette, L.Y., Cromsigt, J.P.G.M. (2022). Playbacks of predator vocalizations reduce crop damage by ungulates. *Agriculture, Ecosystems and Environment*, 328, 107853.

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The contribution of Anna Widén to the papers included in this thesis was as follows:

I. Main author. Designed the study together with all co-authors. Had main responsibility for planning and conducting field work and collection of data. Analysed the data with advice from co-authors. Wrote the manuscript with contributions from co-authors.

II. Main author. Designed the study together with all co-authors. Had main responsibility for planning and conducting field work and collection of data. Analysed the data with advice from co-authors. Wrote the manuscript with contributions from co-authors.

III. Main author. Designed the study with NS and JC. Analysed the data with advice from LG, NS and JC. Wrote the manuscript with contributions from co-authors.

IV. Main author. Designed the study with JC, MC, LZ, DK. Had main responsibility for conducting field work and collection of data. Analysed the data with advice from co-authors. Wrote the manuscript with contributions from co-authors.

Abbreviations

TNZ	Thermoneutral zone
ALS	Airborne laser scanning
ABR	Automated behavioral response system
CT	Camera trap
AROW	Aspen, rowan, oak and willow
PLS	Partial least squares
GLMM	Generalized mixed effect model
LMM	Linear mixed effect model
iSSF	Integrated step selection function

1. Introduction

1.1 Ungulates and humans

Ungulates and humans share the same landscapes (fig 1), both trying to fulfil their needs. In many cases these needs are overlapping and intersecting. For instance, ungulates need to forage to achieve their energy demands, while humans request high crop yields and high timber production in order to meet their needs (fig 1). Hence, both require resources from the same landscape, generating conflicts.

Ungulates contribute to biodiversity, are an important part of various ecosystems and provide several ecosystem services. They provide us with regulating ecosystem services such as keeping landscapes open by their browsing and grazing, thereby maintaining habitats for many plant and animal species (Apollonio *et al.*, 2017; Virtanen *et al.*, 2002) (fig 1). They influence seed dispersal, act as prey for large carnivores and carrion for scavengers (Linnell *et al.*, 2020; Widemo *et al.*, 2019). Furthermore, ungulates supply provisioning ecosystem services such as game meat, fur and hides (Widemo *et al.*, 2019). Finally, they also provide cultural ecosystem services such as recreational values from hunting and from wildlife tourism (Linnell *et al.*, 2020; Widemo *et al.*, 2019) (fig 1). Hence, ungulates are indeed essential for a well-functioning ecosystem.

Ungulates living in managed landscapes become largely dependent on human land use such as planted forests and agricultural lands for foraging and shelter (Linnell *et al.*, 2020; Valente *et al.*, 2020). In Sweden, as in many other countries, ungulates inhabit land where the majority of the area that is suitable for ungulates is owned and managed by someone with an economic interest and management goal (Nilsson *et al.*, 2022). Thus ungulates foraging, trampling and resting in these managed landscapes may generate negative impacts on these interests such as crop and timber production (Linnell *et al.*, 2020; Valente *et al.*, 2020; Reimoser & Putman, 2011).

Arable land generally provides high abundance of nutritious forage and is therefore often used by ungulates for feeding (Bleier *et al.*, 2012; Apollonio *et al.*, 2010; Conover, 2001) (fig 1). In Sweden in 2020, 54% of all farmers cultivating cereal and canola reported damage from wildlife (including damage from birds) and 17% of the total area cultivated with cereal was damaged by wildlife to some extent (Jordbruksverket, 2021). However, there are local differences and in some areas this number can reach up to 80% (Jordbruksverket, 2021). Hence, ungulates foraging and trampling in agricultural land is perceived as a significant problem for Swedish food production. However, due to the fact that also approximately 50% of all farmers in Sweden do not report any damage, it remains a challenge dealing with such a large variety of damage levels simultaneously.

In managed forests, ungulates may cause negative impact by browsing or bark stripping (Jarnemo *et al.*, 2014; Gerhardt *et al.*, 2013; Reimoser, 2003) (fig 1). In Sweden, one of the two dominant timber production tree species is Scots pine (*Pinus sylvestris*), which also constitutes a staple food for moose (*Alces alces*) during winter (Spitzer, 2019; Cederlund *et al.*, 1980). Pine is also being eaten in smaller proportions by the other deer species (red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*)) (Spitzer, 2019). The forestry sector thus regards browsing on pine as a significant problem leading to economic losses for forest owners since it may negatively affect regeneration and timber quality (through stem deformations and reduced growth) (Ramos *et al.*, 2006; Gill, 1992).

Figure 1. Illustration of how humans and ungulates share the same landscape. Ungulates inhabiting heavily managed landscapes fulfil their needs of energy intake by foraging on agricultural fields and production forests. The landscape is also inhabited by humans fulfilling their needs and interests, illustrated by agriculture, timber production and hunting/game keeping. Furthermore, ungulates provide a variety of ecosystem services where some are illustrated in this figure, maintaining habitats for many plant species, providing hunting opportunities as well as recreational activities and wildlife tourism.

As a result of improved conservation, management actions and increased availability of forage from agriculture and forestry, populations of ungulates are now increasing both in number and distribution across Europe (Linnell *et al.*, 2020; Presley *et al.*, 2019; Thulin *et al.*, 2015; Ferretti & Lovari, 2014; Apollonio *et al.*, 2010). These increasing populations lead to a growing conflict between wildlife and humans (Linnell *et al.*, 2020). At the same time, there are also many stakeholders that celebrate their revival/expansion because of the multiple positive impacts ungulates may have on the ecosystem they live in (Linnell *et al.*, 2020). Moreover, increasing ungulate populations may also benefit game management and hunting as an important part of the land use of some stakeholders, e.g., generating income from selling hunting opportunities.

Hence, ungulates range over areas involving several different human interests and conflicting goals (Redpath *et al.*, 2013; Bunnefeld *et al.*, 2011), e.g., between agriculture and game management, where farmers typically aim for high crop yields, while game keepers instead aim for a dense population of ungulates in areas where hunting is an important income source. Moreover, these conflicts may not only appear between stakeholders representing different land uses. Frequently, single landowners have an interest both in agriculture and game keeping, potentially leading to conflicting management goals within the same property (Mysterud, 2010; Mysterud, 2006; Gordon *et al.*, 2004). Managers and other stakeholders may thus face a challenge of maintaining the positive values of increasing ungulate populations, while minimizing their negative impacts on important human land uses.

Population control via culling is a well-established way of reducing negative impact on both forestry and agriculture and may be an efficient tool in some cases (Geisser & Reyer, 2004). However, previous research suggests that the relationship between ungulate densities and damage from foraging is not necessarily linear and not as strong as the relationship between forage availability and damage (e.g., (Pfeffer *et al.*, 2021; Bergqvist *et al.*, 2014). This implies that a reduction in ungulate densities does not necessarily lead to an equivalent reduction in damage, since there are multiple other factors influencing their impact, such as forage availability (Senft *et al.*, 1987). Furthermore, reducing ungulate population size may also prevent their contributions to ecosystem services and counteract other management interests aimed at hunting, recreation or wildlife tourism (Neumann *et al.*, 2022; Schröter *et al.*, 2014).

There is therefore a critical need for additional management approaches that take these multiple interests into account and aim for more variable ungulate densities across the landscape (e.g., lower densities in conflict-prone areas, and higher densities in either natural areas or where focus is on game keeping). One way of promoting more variable ungulate densities across the landscape is through managing the behavior of ungulates, in addition to managing their numbers (Cromsigt *et al.*, 2013). In order to steer the behavior and distribution of ungulates across the landscape we need to increase our understanding of drivers of ungulate behavior in human-managed landscapes, and how these drivers influence ungulate landscape use and ungulate impacts on important human land uses. In the following sections of the introduction, I will go through some of the key drivers of ungulate behavior and landscape use and how they may be important to consider in wildlife management.

1.2 Drivers behind ungulate behavior and landscape use

Animal behavior can be defined as responses of an animal to both internal and external stimuli (Dugatkin, 2020; Levitis *et al.*, 2009). In other words, how animals react and respond to their environment and internal needs. Ungulate behavior is thus influenced by different drivers tied to the internal needs, such as energy demands, and/or to external pressures such as reducing predation risk or avoiding unfavorable weather. This involves several decision processes where individuals will have to make compromises (i.e. trade-offs) (Hamel & Côté, 2008; Illius *et al.*, 2002; Sih, 1980). As an example, animals may alter their behavior to minimize predation risk at the expense of fulfilling their energy demands (Hamel & Côté, 2008; Sih, 1980). These behavioral compromises can influence how and where animals use the landscape, for example because of shifting their foraging behavior in response to external stimuli (Schmitz *et al.*, 1997). Hence, it is important to consider animal behavior when developing wildlife management strategies (Gaynor *et al.*, 2021; Martin, 1998; Burt, 1943).

In my thesis, I choose to focus on three key drivers of ungulate behavior, which I use to frame my objectives and predictions; food, fear and temperature. When discussing the effect of these drivers on animal space use and behavior, we often use the terms foodscape, landscape of fear and thermal landscape. I will use and describe these terms in detail in the following sections. I will also refer to them as "functional landscapes", in order to separate them from the physical landscape.

1.2.1 The foodscape and its influence on behavior, landscape use and impacts

Fulfilling nutritional demands is essential for maintaining or increasing fitness, and consequently feeding and searching for food are central parts of animal behavior (Parker *et al.*, 2009). Foraging decisions are complex and depend on several factors that vary over space and time (for review see: (Felton *et al.*, 2018). Two important factors that influence food selection are the availability of forage and the quality of the forage. At fine scales, food selection is also influenced by variables such as individual plant morphology, available bite sizes, the chemical content and nutritional value of a plant part (Simpson & Raubenheimer, 2012; Wam & Hjeljord, 2010; Stolter, 2008; Shipley *et al.*, 1998; Spalinger & Hobbs, 1992). Food selection patterns also vary with the nutritional status and demand of the animal (Felton *et al.*, 2018). For instance, one of these demands may be the need of nutritional balancing which is the altering of food intake to reach a nutritionally balanced diet (Raubenheimer & Simpson, 1997; Westoby, 1974). This hypothesis has been used to suggest that animals feeding on nutrient dense and energy rich forage may need to balance their diet by increasing their intake of fiber (Felton *et al.*, 2021; Felton *et al.*, 2016; Miranda *et al.*, 2015; Ando *et al.*, 2004). Hence, several factors on different scales influence foraging behavior and the 'foodscape' (Searle *et al.*, 2007) that ungulates inhabit, which I here define as the variation in forage availability and forage quality across a landscape for a specific ungulate species. Hence, both including availability and quality, as well as differences in nutritional demands of the animal.

Several studies have found that habitat selection is influenced by forage availability and forage quality (Merkle *et al.*, 2016; Van Beest *et al.*, 2010b; Anderson *et al.*, 2005; Fortin *et al.*, 2003). For instance, large herbivores in North America track and follow high-quality forage during spring green up, i.e they are surfing the "green wave" (Merkle *et al.*, 2016). Moreover, van Beest *et al.* 2010b found that both forage availability and forage quality influence habitat selection in moose, however, with varying selection patterns across spatiotemporal scales.

Moreover, the foodscape does not only have an influence on the distribution of animals and how they use the landscape, it can also have large effects on the degree of impact they have on their surroundings. For instance, several studies have found that variation in forage availability is important in predicting the impact ungulates have on their surroundings (Felton *et al.*, 2022; Pfeffer *et al.*, 2021; Herfindal *et al.*, 2015; Jarnemo *et al.*, 2014; Ball & Dahlgren, 2002). For instance, Jarnemo *et al.* 2014 show that in forest stands with high forage availability in the understory, bark stripping levels on Norway spruce (*Picea abies*) by red deer were lower than in stands with lower forage availability. A similar pattern for pine damage was reported by Pfeffer *et al.* 2021, where a higher density of pine (used as a proxy for forage availability) was associated with lower levels of pine damage. This implies that food is essential in determining both landscape use by ungulates, as well as the impact they have on their surroundings.

1.2.2 The landscape of fear and its influence on ungulate behavior, landscape use and impacts

Perceived predation risk plays an important role in shaping behavior of prey (LaManna & Martin, 2016; Brown, 1999). Even in the absence of direct mortality, the fear of predators may be powerful enough to induce behavioral antipredator responses (LaManna & Martin, 2016; Zanette *et al.*, 2011; Brown, 1999; McNamara & Houston, 1992; Lima & Dill, 1990). Such behavioral antipredator responses may have consequences on individual, population, community and ecosystem levels, a concept known as the "ecology of fear" (Brown *et al.*, 1999). These antipredator responses may involve changes in movement patterns (Suraci *et al.*, 2019) and habitat use (Blumstein & Daniel, 2002; Formanowicz Jr & Bobka, 1989; Bergerud *et al.*, 1983) and changes in vigilance and foraging behavior (Benhaiem *et al.*, 2008; Jayakody *et al.*, 2008; Verdolin, 2006; Hernández & Laundré, 2005). Hence, as animals navigate across the landscape they constantly adjust their behavior and their use of the landscape in response to changing levels of perceived predation risk (Laundré *et al.*, 2010). This spatial variation in perceived predation risk across a landscape is termed the "landscape of fear" (Laundré *et al.*, 2010). How animals move across a landscape of fear is influenced by different features of the landscape that may minimize or increase the perceived predation risk. One central feature is vegetation cover, influencing both visibility and detection for prey and predator (Gaynor *et al.*, 2019; Mysterud & Østbye, 1999). Creel *et al.* 2005, for example, reported that red deer in North America respond to the presence of wolves (*Canis lupus*) by selecting wooded habitats with protective cover and reduce their use of open habitats, which are preferred for foraging.

Fear-induced changes in habitat use/landscape use can affect the impacts that ungulates have on lower trophic levels and result in altered plant community structure by altered impact on vegetation (Beyer *et al.*, 2007; Ripple & Beschta, 2004; Smith *et al.*, 2003; Schmitz *et al.*, 1997; McLaren & Peterson, 1994). This is also known as a behaviorally mediated trophic cascade (Ripple & Beschta, 2012; Halofsky & Ripple, 2008; Schmitz *et al.*, 1997). As an example of such a cascade, studies have shown that high predation risk by wolves can result in reduced browsing pressure on trees in certain areas (Kuijper *et al.*, 2013; Ripple & Beschta, 2004). However, findings in Scandinavia have not found such a behavioral effect of predation risk on moose browsing (Ausilio *et al.*, 2021; Månsson *et al.*, 2017;

Wikenros *et al.*, 2016; Nicholson *et al.*, 2014). These studies explained this by suggesting that, in Scandinavia, human land-use practices such as forestry, agriculture and hunting are the main factors shaping the landscape structure, something that indeed will influence the effect of non-human predators, possibly being less important. However, studies have also suggested that ungulates in this region do respond to risk cues of predators, implying that predators still play an important role in the system (Sahlén *et al.*, 2016). The landscape of fear, by influencing how ungulates use landscapes, may shape where and when ungulates impact human land use, for example, the distance to cover has been shown to be an important feature in predicting damage by ungulates, with increasing damage closer to cover provided by e.g., nearby forest (Bleier *et al.*, 2012; DeVault *et al.*, 2007; Naughton-Treves, 1998).

1.2.3 The thermal landscape and its influence on ungulate behavior, landscape use and impacts

Maintaining a constant body temperature under varying ambient temperatures is physically demanding and the cost increases when an individual is outside its thermoneutral zone (TNZ) (Boyles *et al.*, 2011). The TNZ can be explained as the range of ambient temperatures where individuals can maintain their internal temperatures with minimal metabolic regulation (Gordon, 2012; Edition, 2001). When temperatures decrease below the TNZ, animals need to increase their heat production, for example by shivering (Gordon, 2012). When temperatures increase above the TNZ, temperature can be regulated by increased respiration, heart rate and/or metabolic rate (McCann *et al.*, 2013; Renecker & Hudson, 1990). However, such physiological responses can be very costly and animals can also manage their body temperature by thermoregulatory behavior (Veldhuis *et al.*, 2019), such as by modifying activity patterns (Bourgoin *et al.*, 2011; Aublet *et al.*, 2009) and/or by habitat selection (van Beest *et al.*, 2012; Bowyer & Kie, 2009; Dussault *et al.*, 2004). Changing the behavior as a response to unfavorable temperatures costs less energy than physiological responses, and is therefore often preferred (Maloney *et al.*, 2005).

Several different ungulate species have been observed to modify their habitat selection as a function of temperature. For example, ungulates may react to increasing temperatures by moving into dense cover providing shade (i.e., thermal shelter) (Alston *et al.*, 2020; Montgomery *et al.*, 2019; Melin *et* *al.*, 2014; van Beest *et al.*, 2012; Bowyer & Kie, 2009; Dussault *et al.*, 2004), or by migrating to higher altitudes in alpine habitats (Semenzato *et al.*, 2021; Aublet *et al.*, 2009). Seeking thermal shelter may be especially important for heat sensitive animals such as moose, with upper critical temperature thresholds at 14 °C (where they react with increased respiration rates) and 20°C (causing open-mouth panting) in summer, and -5°C and 0°C in winter (Renecker & Hudson, 1990). The influence of temperature on behavior may differ between species based on different TNZ limits, something that can be influenced by body size, but also thermal properties of animals pelage as well (Parker & Robbins, 2018). Larger species have less body surface per unit body mass making it easier for large animals to retain heat when it is cold, but more difficult to loose heat when it is warm (Jessen, 2012; Porter & Kearney, 2009; Cain *et al.*, 2006). Hence, larger animals are generally more susceptible to heat stress, while smaller animals are more susceptible to cold-stress (Owen-Smith & Goodall, 2014; Gardner *et al.*, 2011; Aublet *et al.*, 2009; du Toit & Yetman, 2005).

Since the thermal landscape has such an important influence on habitat selection and how ungulates use the landscape, it most likely also determines how ungulates interact with human land use and where they cause impact. For instance, seeking thermal cover during warm temperatures may result in a higher pressure on that forest patch, potentially increasing the impact on vegetation in that area.

1.2.4 Interactions between the foodscape, the landscape of fear and the thermal landscape

Most studies investigating how fear, food and temperature influence landscape use of wildlife explore these functional landscapes as single isolated landscapes. For example, studies may investigate the influence of landscape of fear separately from analyzing the influence of the foodscape. However, in reality, wildlife perceive all of these three landscapes simultaneously by, for example, responding to their internal needs of finding food and maintaining their body temperature while simultaneously responding to perceived predation risk. Hence, one can visualize the three landscapes as overlapping and interacting landscapes that ungulates perceive in the physical landscape. In other words, one can see them as three different layers of the physical landscape (fig 2) to which ungulates need to respond, including the trade-offs they face when responding to the different landscapes.

As an example, prey must balance predator avoidance with acquiring food (Brown, 1999; Sih, 1980). Prey thus navigate the landscape trying to avoid predation while at the same time gaining resources necessary for survival and reproduction (Bonnot *et al.*, 2013; Laundré *et al.*, 2010; Jayakody *et al.*, 2008; Creel *et al.*, 2005; Lima & Dill, 1990). This is something that will lead to a cost-benefit trade-off between food acquisition and staying safe. For instance, the perception of predation risk may lead to habitat displacement towards habitats that are perceived as safer, but result in selection for habitats with poorer food quality (Lehman *et al.*, 2019; Morgantini & Hudson, 1985), for instance, red deer in North America shift their habitats from open grass meadows to forests to reduce wolf predation risk, and thus lower their diet quality (Hernández & Laundré, 2005). Moreover, habitats with high canopy cover may provide thermal shelter against solar radiation and/or harsh weather but may not contain as much forage as habitats with a lower canopy cover (Schmitz, 1991) (fig 2). Thus, when selecting for these habitats ungulates may reduce their exposure to heat, but also reduce foraging opportunities, experiencing a food-cover trade off (van Beest *et al.*, 2012).

In my thesis, I elucidate the interactions between all three landscapes simultaneously, by combining observational and experimental approaches

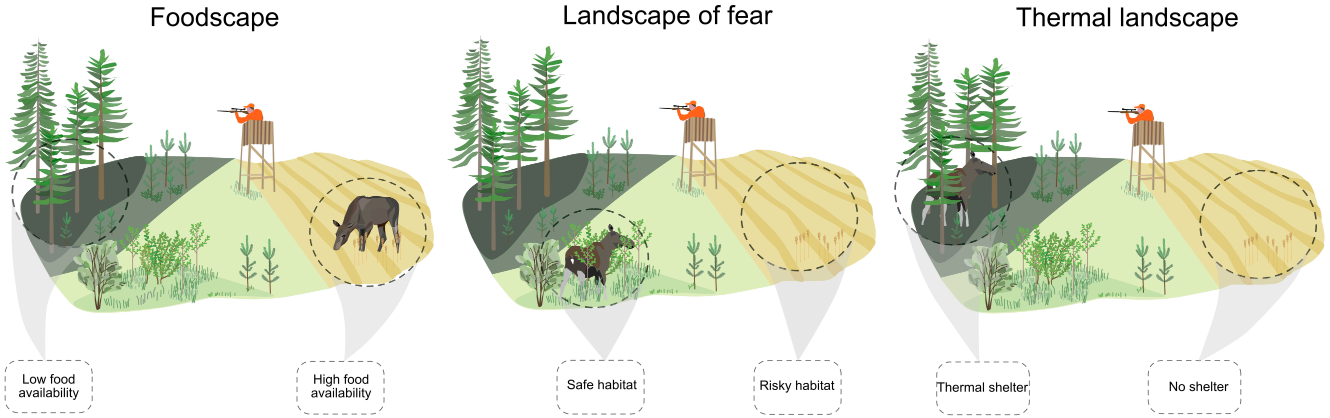


Figure 2. Layered landscapes. Illustration over the three functional landscapes coexisting in one single physical landscape. This involves how various features of the physical landscape can have different implications for ungulate use of the functional landscapes. For example, a forest in the foodscape may imply low food availability, while in the thermal landscape it provides thermal shelter. The moose is placed according to predictions of how it would respond to each functional landscape separately.

1.2.5 Human influence and how to manage ungulate behavior in a managed setting

We have now established that ungulates simultaneously face and navigate a landscape of fear, foodscape and thermal landscape. But, what role do humans play in shaping these landscapes? Is it possible to manage the animals' behavior by shaping these three landscapes in such a way that you distribute ungulates in ways that minimize conflict with humans?

Humans influence these landscapes both directly and indirectly. Through land use, humans change features of the landscape of fear, foodscape and thermal landscape that ungulates perceive. For instance, humans directly influence the foodscape by decreasing or increasing food availability and quality. Production forests are intensively managed with actions such as thinning, clear-cutting and reforestation (Gauthier *et al.*, 2015; Kuuluvainen *et al.*, 2012). These actions influence forage availability and quality, where clear cuts and young forest stands usually offer large amounts of forage (Edenius *et al.*, 2015; Kuijper *et al.*, 2009). At the same time, increasing stem density and reducing average forest age can negatively affect important forest floor vegetation, such as *Vaccinium* spp (Hedwall *et al.*, 2013), which provides important food for ungulates (Spitzer, 2019). In agriculture, the cultivation of crops strongly influences the food availability, providing high abundances of nutritious forage used by ungulates (Bleier *et al.*, 2012; Apollonio *et al.*, 2010; Conover, 2001). Forage availability and quality are also influenced by supplementary feeding of energy rich food across the landscape, conducted for several different reasons, such as reducing damage ("diversionary feeding") (Milner *et al.*, 2014), increasing winter survival and reproduction (Schwartz & Hundertmark, 1993), or increasing hunting opportunities (Smith, 2001). Additionally, it is also important to note that actions influencing the food availability in one habitat (e.g. in forests) may influence the foraging behavior in adjacent habitats (e.g. arable fields), since ungulates show transitional use between land use types (Månsson *et al.*, 2021; Allen *et al.*, 2014).

Humans also influence the landscape of fear. They do this by hunting or scaring, usually with the aim of reducing negative impacts of ungulates on human interests (Pęksa & Ciach, 2018; Setsaas *et al.*, 2018; Bonnot *et al.*, 2013; Vistnes & Nellemann, 2007; Geisser & Reyer, 2004), or by their mere presence, sometimes referred to as humans being a "super-predator" (Zanette & Clinchy, 2020; Darimont *et al.*, 2015). Studies show that humans may induce strong reactions and antipredator responses in ungulates similar to those caused by other predators (Zanette & Clinchy, 2020). Furthermore, humans also influence the landscape of fear by affecting landscape structures on different scales (Gaynor *et al.*, 2019). For example, humans may create open habitats that are perceived as risky or create vegetation structures that can function as protective cover, and by this setting the stage for spatial variation in perceived predation risk (Gaynor *et al.*, 2019).

Intense management of the landscape also influences the thermal landscape that ungulates perceive, i.e., their possibility of seeking thermal shelter during times of unfavorable temperatures. For instance, thermal shelter is usually found in mature forests with a dense canopy cover (Melin *et al.*, 2014; van Beest *et al.*, 2012; Dussault *et al.*, 2004), suggesting that forestry measures that influence stem density and canopy cover will influence the thermal landscape. For example, Norway spruce has a very high shade-casting ability (Díaz-Calafat *et al.*, 2023) and may thus provide good thermal shelter.

These diverse ways through which humans shape the physical and perceived functional landscapes may create opportunities to manage and steer ungulate behavior. Several of the important landscape features that influence how ungulates navigate in these three functional landscapes are already managed by humans, thus it would be possible to more pro-actively manage them with the aim of steering behavior in order to minimize human-wildlife conflict. Trying to steer animal behavior by proactively manipulating the landscape of fear through scaring animals is something that has been done for a long time, although it has usually been conducted on a smaller scale by private landowners where effects of their efforts have not been measured sufficiently. Similarly, although a number of scientific studies have shown that it is possible to impact/steer wildlife behavior via inducing fear (Crawford *et al.*, 2022; Suraci *et al.*, 2019; Smith *et al.*, 2017; Hettena *et al.*, 2014; Zanette *et al.*, 2011), we lack knowledge on the consequences this could have for the impacts of ungulates on human land use. Additionally, very few of these studies are performed in an actual management setting, where the human-wildlife conflict occurs (Smith *et al.*, 2020). In order to efficiently steer the behavior of ungulates through management, more knowledge is therefore needed on how fear, food and temperature influence behavior and landscape use in a human managed setting.

1.3 Objectives

With this thesis, I aim to contribute knowledge regarding how the three functional landscapes - the landscape of fear, the foodscape, and the thermal landscape - influence the landscape use and impact of ungulates within a managed environment. Furthermore, I aim to investigate how humans shape these functional landscapes and the potential of managing these landscapes to steer ungulate behavior.

Specifically, the objectives of my thesis were to:

1. Investigate how the foodscape, the landscape of fear and the thermal landscape influence landscape use and impacts by ungulates in a managed setting (*Paper I, II and III*)

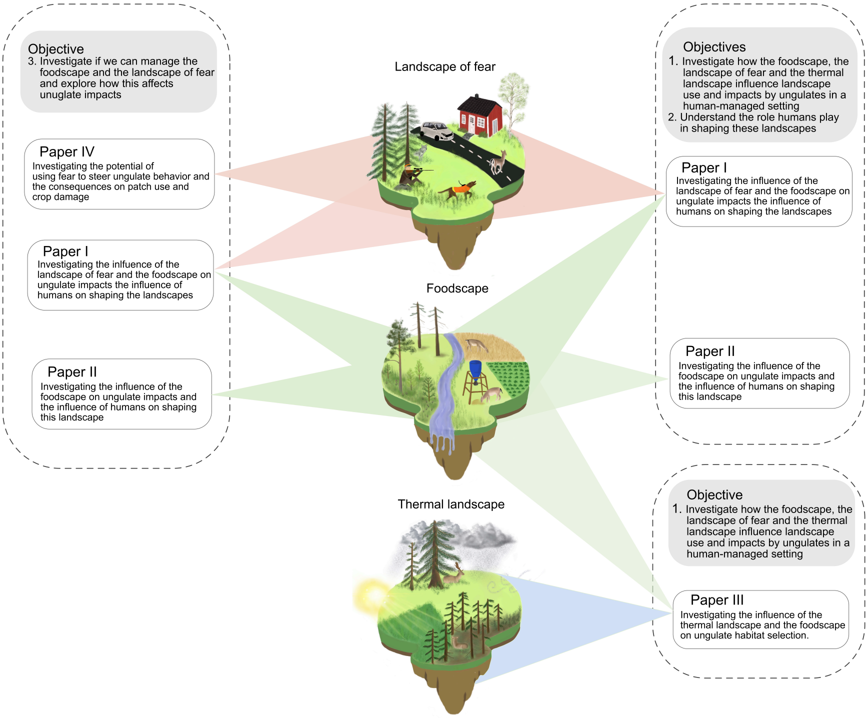
2. Understand the role humans play in shaping these three functional landscapes (*Paper I and II*)

3. Investigate if we can manage the foodscape and the landscape of fear and explore how this affects ungulate impacts (*Paper I, paper II and paper IV*)

To address these objectives, my research is centered on four ungulate species of high ecological and economic interest in Sweden and other parts of Europe: moose, red deer, roe deer and fallow deer (*Dama dama*). Note that in *paper I* and *IV* I also include wild boar *(Sus scrofa)*. The study is conducted in regions characterized by diverse land use and conflicting human interests, providing a unique opportunity to study these objectives in areas where the human-wildlife conflict occurs.

It is my hope that these findings will serve as an important stepping stone towards managing ungulates in a way that considers diverse interests of humans, while simultaneously regarding the values of thriving ungulate populations. My vision is that ungulates and humans can continue to share the same landscape, while encountering fewer conflicts.

The four papers attached to this thesis overlap in their coverage of addressing my three objectives and figure 3 provides an overview of how the different objectives are addressed by my four papers, as well as how the different functional landscapes are addressed and explored in the different papers.



Objective
3. Investigate if we can manage the foodscape and the landscape of fear and explore how this affects unuglate impacts

Paper IV
Investigating the potential of using fear to steer ungulate behavior and the consequences on patch use and crop damage

Paper I
Investigating the inlfuence of the landscape of fear and the foodscape on ungulate impacts the influence of humans on shaping the landscapes

Paper II
Investigating the influence of the foodscape on ungulate impacts and the influence of humans on shaping this landscape

Objectives
1. Investigate how the foodscape, the landscape of fear and the thermal landscape influence landscape use and impacts by ungulates in a human-managed setting
2. Understand the role humans play in shaping these landscapes

Paper I
Investigating the influence of the landscape of fear and the foodscape on ungulate impacts the influence of humans on shaping the landscapes

Paper II
Investigating the influence of the foodscape on ungulate impacts and the influence of humans on shaping this landscape

Objective
1. Investigate how the foodscape, the landscape of fear and the thermal landscape influence landscape use and impacts by ungulates in a human-managed setting

Paper III
Investigating the influence of the thermal landscape and the foodscape on ungulate habitat selection.

Figure 3. Conceptual overview outlining how the three different objectives of my thesis is addressed by the four papers. Illustrated is also how the landscape of fear, the foodscape and the thermal landscape are included and explored in the four papers.

2. Methods

2.1 Study area and study species

The data for this thesis originated from two study sites in Sweden, one in south central Sweden and one in northern Sweden. Data for paper I, II and IV was collected in the county of Södermanland in southern Sweden (study area 1) (fig 4), while data for paper III was collected in the county of Västerbotten (study area 2) (fig 4). Study area 2 (the northern site) is situated in the boreal forest zone, while study area 1 (the southern site) is located in the transitional boreo-nemoral zone with mixed broadleaf and coniferous forests (Moen, 1998). Both areas are heavily influenced by human management and contain a mosaic of forests, agricultural land and wetlands. Agriculture is more common in the southern study area, comprising 20-39% of the total land area (with local differences between municipalities), while only comprising between 5 – 11% of the total area in the northern study area (Jordbruksverket, 2020a).

The composition of agricultural land also differs, with the southern area being a mix of crops with cereals (wheat, barley and oat), grass (leys) and rape seed (canola) being the three most common crops (Jordbruksverket 2020b). This area also includes cattle farms and a number of estates that obtain income from selling hunting rights or hunting opportunities for several ungulate species. These estates usually maintain ungulate populations at high densities through supplementary feeding. Agriculture in the northern study area is dominated by grass production and dairy farms, with some cereal production aimed at fodder for livestock (Jordbruksverket 2015)

The forests in both areas are intensively managed using a system of clear-cutting and reforestation by planting of mostly Scot's pine and Norway spruce. Common tree species in both study areas are Scots pine, Norway spruce, birch (*Betula spp*.), poplar (*Populus spp*.), willows (*Salix spp*.) and alder (*Alnus spp*.). The vegetation in the forest field and shrub layer is composed of different shrubs like bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*), but also various forbs, grasses and mosses.

Moose, roe deer, red deer and fallow deer coexist in both study areas, while wild boar is common in the southern area. Semi-domesticated reindeer (*Rangifer tarandus*) occur in the northern study area during winter. The southern study area hosts one of the highest ungulate densities in Sweden (Cromsigt *et al.*, 2023) and the ungulate populations in both areas are managed via annual regulated hunting.

Hunting for the deer species is seasonal, while wild boar is hunted year-round. Carnivores in the areas are lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) at both sites and brown bear (*Ursus arctos*) in the northern site. During recent years observations of single wolves have increased in the southern study area and since 2015 a wolf pack established a territory in the area with one confirmed reproduction in 2021. In 2023, the numbers had increased to five reproducing and three territory holding pairs in the vicinity.

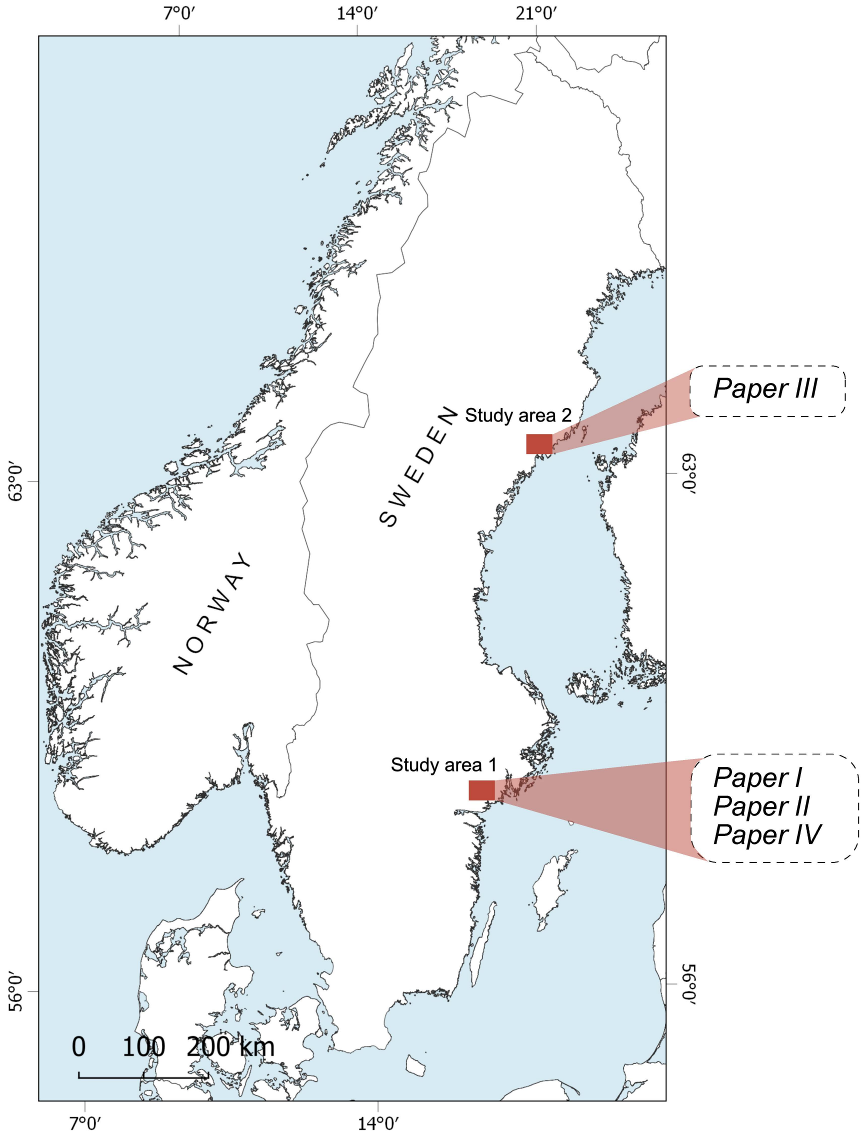


Figure 4. Locations of the two different study areas used in my thesis and from what areas data for each of the four papers are collected.

2.2 Study design

2.2.1 Influence of the foodscape and the landscape of fear on ungulate impacts on agriculture and the role of humans in shaping these functional landscapes (*paper I*)

To assess the influence of the foodscape and the landscape of fear on ungulate impact on agricultural fields, I used a combination of a landscape experiment, field inventories and social science data collection. I designed a landscape experiment in the southern study area consisting of 16 oat fields and 32 grass fields, thereby simulating a foodscape with varying forage quality containing both attractive nutrient dense crops (oat) and less attractive crops (grass) (fig 5a). To do this, I approached farmers and financially compensated them to grow oats. This was necessary because the high densities of ungulates in the study area has led farmers to switch to the production of grass, instead of oats (Åberg, 2017). I aimed to get a balanced experiment with the same number of oat fields and grass fields, but we only managed to convince farmers to grow oats on 16 of our fields.

The fields were placed in a systematic manner with a distance of approximately 3km between them, aiming for fields that were not used by the same fallow deer, being the most common species in the study area. In order to measure crop damage on the fields, I placed three exclosures (2.3 x 2.3m) on each field to exclude ungulates from grazing (fig 5b). Each exclosure was paired with an unfenced grazed plot with a 5m distance between them. Forage availability was estimated both on the fields and along transects placed in each cardinal direction starting at the field edge (fig 5c). Furthermore, to gain information about the role of humans in shaping the foodscape and the landscape of fear I sent out questionnaires to each landowner.

2.2.2 Influence of the foodscape on ungulate impacts in forests, and the role of humans in shaping this functional landscape (*paper II*)

To investigate the influence of the foodscape on ungulate impacts in forests I used parts of the experimental set up described above for *paper I* (2.2.1). I used 24 of the 48 fields (14 oat fields, 14 grass fields) as a proxy for difference in food quality in the agricultural landscape and then measured ungulate impact in the forests surrounding these fields. I only chose fields that had a direct connection with surrounding forests. Further, I aimed for a balanced study design, with an even number of oat fields and grass fields in order to compare impacts between crop types of different quality. Hence, in *paper I* where I investigated the impact on agriculture I used the 48 fields in order to measure crop damage on them. While in *paper II* I used 24 of these fields as a proxy for forage quality in the agricultural landscape and then measured how variation in the quality of agricultural fields affected ungulate impact in the forests surrounding the fields. Impact in forests was measured as browsing pressure on trees in 100m2 plots distributed at 12.5, 25, 50, 100 and 200m along 200m long transects surrounding the fields (fig 5d). Since I was interested in impact in forests, I only included transects where forest covered the entire length of the transect. Hence, and since forest cover varied across the area, the number of transects differed depending on the landscape structure with a minimum of 4 and a maximum of 8 (fig 5d and e). I also measured food availability in the forest patches along the same transects. Hence the study contained information about food in the agricultural landscape as well as the forest landscape. Plots along the transects consisted of a nested design, where I measured different things at whole-plot and sub-plot level (fig 6).

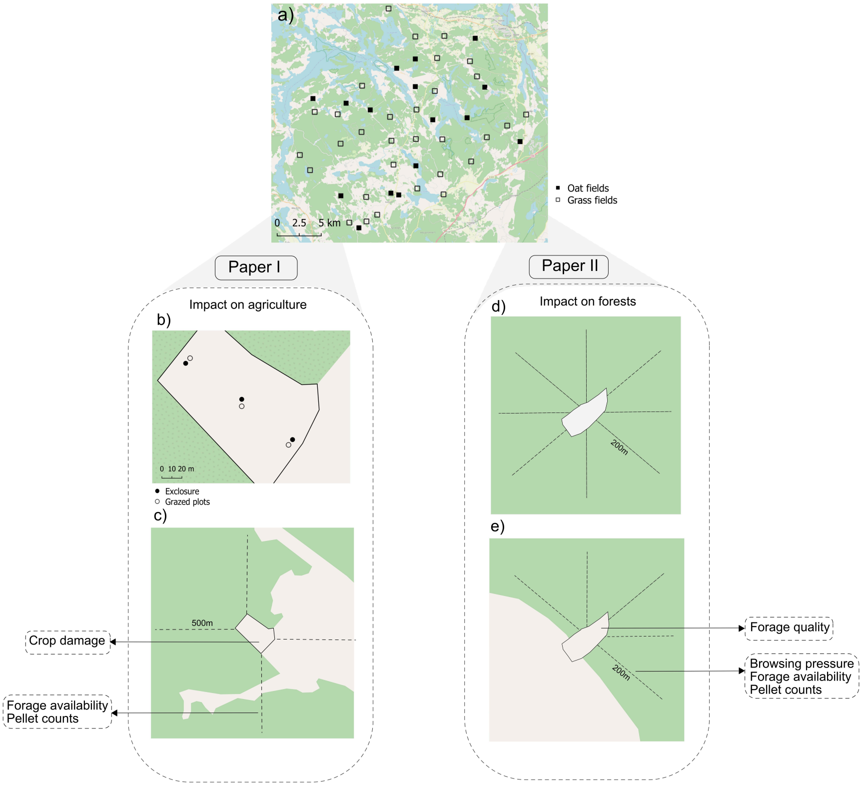


Figure 5. a) Placement of the 48 fields used in the experimental set up to measure impact by ungulates on agricultural fields (*paper I*). 24 of these fields were also used as forage quality "proxies" in order to investigate impact by food on browsing damage in forests (*paper II*). The study design for paper I is illustrated by showing placement of (b) the pairs of exclosure and grazed plots on one of the fields, and (c) the four transects where forage availability and pellet counts were measured. The study design for paper II is illustrated in panel d by the placement of transects where browsing damage as well as forage availability and pellet counts was measured. Note that all transects contained forest throughout the entire 200m. A minimum of 45 degrees between transects at their starting point were accepted, generating a maximum of 8 transects. Under some circumstances only 5 of 8 transects were covered by forest throughout the entire transect length (200m). *(figure is modified from paper I and II)*.

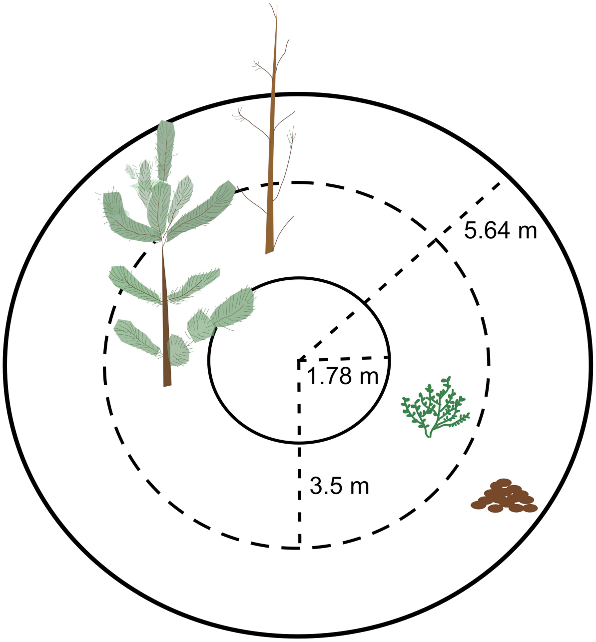


Figure 6. Plots with a total area 100m^2 were distributed along the 200m long transects to measure browsing pressure, forage availability and pellet counts. The plot was divided into the three different radiuses used for collecting browsing pressure (r=3.5), tree availability (r=3.5), bilberry shoot height r = (3.5), and pellet counts (moose and red deer r=5.64), (roe deer and fallow deer r = 1.78). (*The figure is modified from the original version in paper II*).

2.2.3 Influence of the thermal landscape and the foodscape on habitat selection (*paper III*)

To investigate how the thermal landscape and the foodscape influence ungulate habitat use and habitat selection I used data from 57 animals (27 moose, 7 red deer and 23 roe deer) marked with GPS collars in the northern study area (fig 4). To evaluate habitat selection as a function of temperature, I used a combination of two raster layers; (1) the National land cover data from the Swedish Environmental Protection Agency (2018) (Naturvårdsverket, 2020), which maps land cover types at a spatial resolution of 10 m and (2) canopy cover models derived from Airborne Laser Scanning (ALS) data from the Swedish National Land Survey (2020) (Lantmäteriet, 2023).

2.2.4 Managing the landscape of fear and the related effects of ungulates on agriculture (*paper IV*)

To explore if wildlife management can induce a landscape of fear and thus steer ungulate behavior and resulting impacts on agriculture, I experimentally induced fear on agricultural fields in the southern study area (*paper IV*). To do this, I selected seven independent wheat fields 4km apart in the southern study area. I increased perceived predation risk on each field by broadcasting predator playbacks using Automated behavioral response systems (ABRs) (Suraci *et al.*, 2017). These systems consist of a camera trap, which records videos, connected to a playback speaker system, which broadcasts a playback whenever the camera trap is triggered by a passing animal. In order to decide where to place the ABRs I searched for ungulate "hotspots" along field edges, such as well-used game trails and/or a high abundance of tracks or dung. I confirmed that these places were indeed highly used by deploying regular camera traps (CTs) at these places for one week. Subsequently, I placed ABRs and CTs on these hotspots for a six week long experiment. During the first two weeks of the experiment, the ABRs did not broadcast any sounds to explore potential differences in deer use between areas in front of CTs and ABRs before starting the playbacks. After these two weeks, I turned on the sound system of the ABRs and the playback treatment phase started. During this period each field had two ABRs and four CTs along the field edges.

To be able to determine if the response of the broadcasted playback was generated by any type of sound or if it was induced by fear from a potential predator, the ABRs broadcasted different playback types. The ABRs broadcasted three predator playbacks (dog, wolf, human) and three non-predator playbacks (goose, owl, raven). Each ABR broadcasted playbacks following a predefined playlist. I used 10 exemplars of each playback type (i.e. 10 human, 10 dog, 10 raven etc.). The playlists consisted of 24 h divided into 15 min intervals containing one playback type each (i.e. one species vocalization). When an ABR was triggered, it randomly broadcasted a selected exemplar from that playback type within the 15 min interval, but then switched to a different playback type for the next 15 min interval. As an example, if an animal triggered the ABR between 10:00 and 10:15, the speaker selected a playback from the playlist, e.g., dog, and randomly picked an exemplar of dog. If the animals remained close by, and came back within this 15 min interval, another random exemplar of dog was broadcasted.

However, if the animal came back at 10:20, the ABR would broadcast a different playback type, e.g. raven.

Furthermore, the two ABRs on each field were programmed to broadcast different intensities of predator playbacks, giving me the possibility to investigate differences between low-predator level and high-predator level on crop damage and patch use in front of the ABRs. The high predator level ABRs were programmed so that during a 2 hour period animals triggering the ABR would be twice as likely to hear predator vocalizations compared to when triggering a low-predator level ABR (for details about ABR programming please see paper IV).In order to investigate the influence on crop damage, I placed two 25m long transects in front of each ABR and CT. One transect faced the same direction as the ABR/CT and the other faced 45 degrees away.

2.3 Data collection

2.3.1 Assessing the foodscape

Features of the foodscape, such as food availability and quality, were measured in different ways to answer the question of the different papers. For paper I, where the aim was to investigate the influence of the foodscape (amongst other things) on impact on agriculture, I used the crop type of the 48 different fields as a proxy for food quality, where oat represented a nutrient dense crop, and grass a less nutrient dense. Forage availability was estimated both on the fields and in the surrounding area. I measured forage availability on the fields by converting the biomass inside the exclosures into biomass in gram per m^2 and further into total biomass in grams per field. In the surrounding area, I recorded the presence of ungulate forage species that touched a 3m high pole (representing browsing height of moose) at every 5 meter along the 500m long transects surrounding the fields (fig 5c). I identified five key forage groups that previous work identified as important for all ungulate species in the study area (Spitzer, 2019); Ericaceous shrubs: (bilberry, lingonberry and heather), birches: ((downy birch (*Betula pubescens)* and silver birch (*Betula pendula*)), other deciduous trees: ((oak (*Quercus robur)*, rowan (*Sorbus aucuparia)*, aspen (*Populus tremula)* and willow)), graminoids and forbs. For further analysis, I calculated the proportion of the key forage groups per transect and then an average of the four transects. Furthermore, since oak, rowan, aspen and willow are relatively rare species in the area (Felton *et al.*, 2022; Bergqvist *et al.*, 2014) I grouped them into a group named AROW for further analysis.

Additionally, I collected information about supplementary feeding (as such activity also influences forage availability and quality) in the close vicinity of the fields by using questionnaires sent out to all landowners and/or farmers. I asked respondents if they had conducted supplementary feeding on the fields (or in close vicinity) and at what intensity this had been done (sporadic feeding throughout the growing season, feeding for half of the growing season or feeding for the entire growing season). To further address the objective of the role of humans in influencing the foodscape, I also asked each respondent what their dominant land use type on their farm was, giving them six answer alternatives (crop production, meat production, dairy production, equine husbandry, hunting/game keeping or forestry). This gave an idea of the overarching management goal with their farm, something that may influence management practices that are conducted on their land.

For paper II, which aimed at investigating the influence of the foodscape on ungulate impacts in forests, I used the different crop types of the 24 fields originating from the same experimental design as paper I (fig 5a) as a proxy for forage quality in the fields. Additionally, I measured forage availability in the forests surrounding the fields, hence in the same forest patches as where I measured browsing pressure (described further below). As a measurement of forage availability I counted the number of available trees from scots pine, birch and AROW within moose browsing height within a 3.5m radius (i.e. 38.5m2) of the entire 100m2 plots that were distributed along the 200m long transects (fig 6) (see section 2.2.2 for study design explaining the distribution of transects and plots). I also measured the shoot height of 4 random bilberry bushes in the same plot, as a measure of availability of an important food item for all deer species (fig 6).

In paper III, where GPS data on animals was used to investigate habitat selection in relation to the thermal landscape and the foodscape I used ALS data from the Swedish national land survey collected in 2020 to calculate a shrub cover model as a proxy for forage availability. The shrub cover was calculated representing the browsing height of the different ungulate species in the study. For moose, shrub cover was calculated below 3m, for red deer and roe deer it was calculated below 2m. The shrub cover model was calculated using the number of first radar returns/hits below the different browsing height limits divided by the total number of returns/hits (e.g., (Bohlin *et al.*, 2021; Melin *et al.*, 2016). This generated pixel values ranging between 0-100 % as the percentage (%) of echoes/hits below the different browsing height limits.

2.3.2 Assessing the landscape of fear

Questionnaire

In order to investigate the influence of the landscape of fear on impact by ungulates on agriculture (*paper I*), I asked questions about conducted practices tied to the landscape of fear in the questionnaire. I asked respondents if they had conducted any type of scaring practices as well as if any hunting had been conducted on the field. Questions about hunting were also asked on a larger scale, 500m surrounding the field, in order to find out of if hunting pressure around the field could have an impact on crop damage on the field. Each response option had three intensity alternatives: sporadic hunting/scaring throughout the growing season, hunting/scaring for half of the growing season or hunting/scaring for the entire growing season.

Playback experiment

I also assessed the landscape of fear by inducing fear on the seven wheat fields in my playback experiment. I simulated a landscape of fear using the ABR and CT experimental set up that is explained in section 2.2.4

2.3.3 Assessing the thermal landscape

To estimate the thermal landscape in order to investigate its influence on habitat use and selection, I used land cover maps and canopy cover models derived from ALS data. The original land cover map consisted of 26 land cover classes and I reclassified these into 4 new land cover categories in order to decrease the factorial levels in further analysis: arable land, clear cut: non-vegetated open land or temporarily non-forest forest where trees are below 5m, forest: vegetated land with trees above 5m and other: being all other open land such as urban, water and wetland. Canopy cover was generated using the ALS data by using the number of first radar returns/hits above 3m for moose, and 2m for red deer and roe deer / the total number of first returns. This generated pixel values ranging between 0-100 % being the percentage of echoes above 3m and/or 2m. E.g. a canopy of 100% means that 100% of the echoes were above 3m and/or 2m i.e. no echoes from lower strata. For more detailed information about how ALS data was surveyed see paper III. I chose 3 and 2 meters respectively to represent canopy cover that was above each species browsing height, i.e. not serving as food and also being high enough to be above each species head while standing up.

2.3.4 Assessing ungulate densities

To account for possible effects of ungulate density on impact on both agriculture (*paper I*) and forests (*paper II*), I counted pellet groups in $100m^2$ plots distributed along the transects used in each study respectively. For paper I, pellet groups were counted in plots along the four 500m long transects distributed in each cardinal direction (fig 5c), and for paper II pellet groups were counted in plots along the 200m transects (fig 5d). The method of counting pellets was the same in both studies. Moose and red deer pellet groups were counted within a 5.64m radius ($100m^2$), while fallow deer and roe deer were counted within a 1.78m radius ($10m^2$) (fig 6). I only counted pellet groups that were deposited above the leaf litter. Because I was interested in the overall influence of ungulate species on browsing pressure, we combined the pellet counts into one combined ungulate pellet count.

2.3.5 Assessing impacts by ungulates

Impact on agriculture (paper I and paper IV)

In order to investigate impact on agriculture as a function of the foodscape and landscape of fear, I measured crop damage by comparing the biomass inside the exclosures with the paired grazed plot. On grass fields, I harvested the biomass inside the exclosure and in the grazed plot using electric scissors just before the farmer would harvest the field. On oat fields, I collected the panicles and straws above 5cm and weighed them. All samples were later dried at 65°C in drying cabinets for 48h. I then calculated the difference in dry weight biomass between exclosures and grazed plots as % biomass loss. For further analysis, I used an average of the three exclosures and the three grazed plots.

Grass fields were harvested multiple times by farmers and I thus took measurements both before the first harvest and after the second harvest. The exclosures were removed just before harvest and replaced immediately after each harvest occasion, at the exact same position as before.

As a measurement of the impact of the playback experiment on agriculture, I measured crop damage along the two transects in front of each ABR and CT on the fields. Along the transects I measured crop damage in 1m^2 squared plots placed at 5, 10, 15, 20 and 25 m distances. In each plot, I counted the number of grazed wheat stalks and the number of ungrazed wheat stalks, resulting in a proportion of grazed wheat stalks per plot. I ended up with 10 crop damage measurements per ABR and CT, respectively.

I used a patch use metric to investigate possible difference in ungulate use of areas in front of ABRs and CTs. This was generated using images from CTs and videos from ABRs and was calculated by multiplying the length of a photo/video sequence in seconds (i.e. the difference between start time and end time of a sequence) with the maximum number of individuals per species in the sequence. This generated a measure of how many individuals per species had used the patch and for how long (please see paper IV for a detailed explanation of the classification and calculation). I also calculated total bout duration as a measure of relative fearfulness of the different playback types, giving an idea of how long animals stayed and how long it took for them to come back after hearing different playbacks. This metric was generated from categorizing videos from the ABRs into bouts, where a bout is independent and treatment-specific if > 60 min has elapsed since the last time the same species heard the same playback treatment at that site. I then categorized videos into "first exposure videos" (i.e., the first time ever the animals heard a certain playback type or when > 60 min had elapsed since the last exposure to that playback type) and non-independent "repeat exposure video" (i.e., when an animal hears the same playback treatment <60 min since the last time they heard it, cause by an animal retriggering the camera or coming back within the same 15min interval). The total bout duration is the sum of the intervals between a first exposure video and all subsequent repeat videos in a bout. This generates a measure of how frightening the playbacks are. Hence, if there was just one video in a bout, it is likely that the broadcasted playback was very frightening because the animals immediately left the area after the playback. While, if the playback was not that frightening, animals might stay and retrigger the ABR, hence creating several repeated exposure videos and thus increasing the total bout duration. (Please see detailed description on total bout duration in paper IV).

Impact on forests (paper II)

To investigate impact on forests as a function of the foodscape, I measured browsing pressure in plots along the 200m long transects on the following species: Scots pine, silver birch, downy birch, AROW. Browsing pressure was measured on one individual tree of each species closest to the center of a 3.5 radius (38,5m^2) of the entire 100m^2 plot (fig 6). On each individual, I counted the number of shoots and number of browsed shoots. I only recorded recent summer browsing, determined by the color of the bite surface (Öhmark *et al.*, 2015). Thus, winter browsing was not recorded or included, while pre-summer browsing (from May-June) was included depending on the color of the bite surface. In cases where the number of shoots were too high ~ > 150 on one individual tree, I instead counted the shoots on a randomly selected primary branch and extrapolated this to the whole plant by multiplying it with the number of primary branches. I averaged the browsing pressure of all plots per distance class and transect (i.e. average browsing pressure on 12.5, 25, 50, 100 and 200m for each field). Furthermore, I also pooled the two birch species in to the same group since they are relatively rare in the area.

2.3.6 Assessing habitat use and habitat selection

To estimate habitat use and habitat selection in relation to the thermal landscape and the foodscape, I used GPS data from 57 animals (27 moose, 23 roe deer and 7 red deer) generated between 2017-2019. The immobilization procedure has been described elsewhere (Græsli *et al.*, 2020; Lian *et al.*, 2014; Evans *et al.*, 2012). In addition, all GPS collars were equipped with a sensor measuring ambient temperature. All GPS readings were stored and quality controlled in the WRAM database (Wireless Remote Animal Monitoring plat-form) (Dettki *et al.*, 2014). To account for the period with maximum forage availability and warmer temperatures, we used data from 1 May-30 September for our analyses.

2.4 Statistical analyses

2.4.1 Influence of the foodscape and the landscape of fear on ungulate impacts on agriculture and the role of humans in shaping these functional landscapes (*paper I*)

I used partial least squares (PLS) path analysis to investigate how food, fear, humans and ungulate density influenced the impact ungulates had on agriculture (*paper I*). With this multivariate analysis, I was able to explore direct and indirect effects of different foodscape and landscape of fear variables as well as ungulate density on crop damage. Furthermore, I could also explore how human management directly influenced the foodscape and the landscape of fear. We constructed the PLS model according to the conceptual framework in figure 7, illustrating the different paths we investigated in the model.

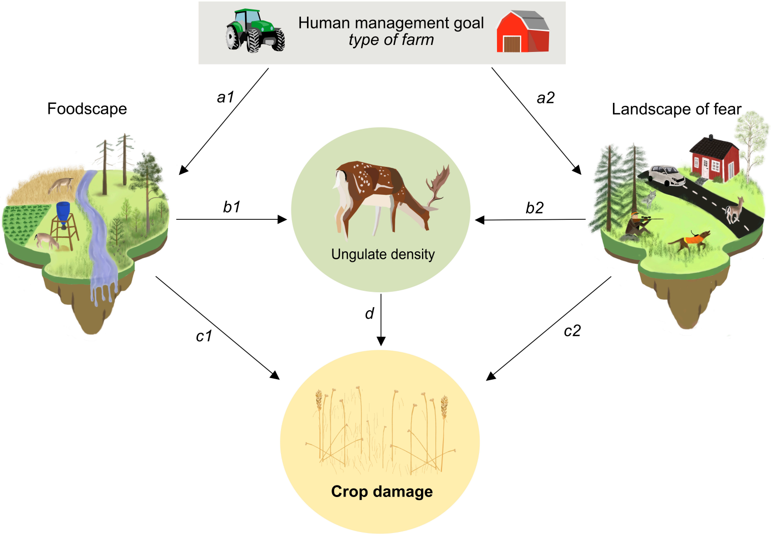


Figure 7. The conceptual model which was the basis for the PLS model investigating the influence of the foodscape and the landscape of fear on crop damage by ungulates, as well as the role of humans in shaping these functional landscapes. The figure illustrates the difference paths that were tested in the PLS model, being he direct effect of human management goal on the two functional landscapes (a1 and a2), the direct effect of these landscapes on crop damage (c1 and c2), as well as the influence of ungulate density on crop damage (d). Additionally, indirect effects of humans on crop damage was also tested (e.g. a1+c1) as well as indirect effects of humans on ungulate density (e.g. a1 + b1). (*from paper I*)

PLS path models, in contrast to normal path analysis, are more flexible when it comes to sample sizes, residual distribution and measurements scales (Mateos-Aparicio, 2011) while still allowing for a complex model for relatively small number of independent observations. The analysis was conducted in the program SmartPLS3 (Ringle *et al.*, 2015).

2.4.2 Influence of the foodscape on ungulate impacts in forests, and the role of humans in shaping this functional landscape (*paper II*)

To analyze the influence of the foodscape as well as ungulate density on ungulate impact (browsing pressure) on forests, I used generalized mixed effect models (GLMMs function glmer in lme4 package; (Bates *et al.*, 2014)) with a binomial distribution. The response variable was the proportion of browsed shoots. I made one model looking at browsing pressure on all tree species pooled together as the response variable, and three additional separate models investigating browsing pressure on pine, birch and AROW separately. The explanatory variables were crop type (oat or grass), availability of trees within browsing height, bilberry shrub height, ungulate density (all deer species pooled together) and the distance from each measuring plot to the field edge. I also added an interaction between crop type and ungulate density in order to test if the influence of crop type on browsing pressure was driven by an increase in the abundance of deer or increased intake by individual deer. Additionally, I included the interaction between distance and crop type to test whether the effect of distance from field edge on browsing pressure would depend on crop type. Furthermore, the field ID was included as a random effect.

2.4.3 Influence of the thermal landscape and the foodscape on habitat selection (*paper III*)

Habitat selection was analyzed using Integrated Step Selection Function (iSSF) (Avgar *et al.*, 2016). iSSFs models the probability of an animal stepping into a particular habitat instead of stepping into another available habitat, by for every observed step generating a set of available steps (Thurfjell *et al.*, 2014), in our case 10 available steps. Furthermore, iSSFs simultaneously accounts for movement related parameters by including step lengths and turning angles in the model.

In my case, I investigated the probability of selecting a certain habitat depending on the ambient temperature at the particular location and time, together with information of land cover type, shrub cover, canopy cover and their interactions. iSSFs were fitted using the amt package in R (Signer *et al.*, 2019). For more details about the iSSF modeling approach, please see paper IV.

2.4.4 Managing the landscape of fear and the effects on ungulate impacts on agriculture (*paper IV*)

To investigate the influence of induced fear on ungulate patch use, I first compared patch use between periods when ABR sound systems were disabled (i.e. no playback broadcasted) and the period when they did broadcast playbacks. For this, I used a Linear mixed effect model (LMM) using the lme4 package in R (Bates *et al.*, 2014) with patch use in front of ABRs and in front of CTs as response variable. I used treatment (CTs and ABRs) and period (before and during playback treatment) as explanatory variables. I also included the interaction between treatment and period to test whether the difference in patch use between ABRs and CTs depended on the playback treatment being active or not. Field ID was added as random intercept to account for potential dependence within fields.

I also tested the difference in patch use between the three risk-levels (only during the playback treatment period) by fitting a LMM. Patch use was again used as response variables and treatment (regular CTs as no-sound treatment, high-predator level ABR and low-predator level ABR) was used as explanatory variable. Field ID was added as random intercept to account for potential dependence within fields.

To estimate difference in crop damage between the three risk levels I used a GLMM with a binomial distribution using the lme4 package. The response variable was the proportion of damaged wheat straws. Treatment (no-sound control CT, high-predator level ABR and low-predator level ABR) was added as an explanatory factor and a random intercept with transect nested within location nested within field was added to correct for hierarchical structure of the crop damage measurements.

Finally, to investigate the relative fearfulness using the total bout duration metric, I tested if there was a difference in total bout duration among the four different playback treatments (bird control, dog, wolf, and human). I did this using a GLMM with zero truncated negative binomial distribution using the glmmTMB package in R (Brooks *et al.*, 2017). ABR ID nested within Field ID was added as a random factor. Furthermore, I tested if there was a difference in the number of predator vocalization videos between the two predator level ABRs (low-predator level and high-predator level) with a Wilcoxon Matched Pairs tests.

3. Results

3.1 Influence of the foodscape and the landscape of fear on ungulate impacts and the role of humans in shaping these functional landscapes (*paper I*)

Crop type, being a proxy for forage quality in the agricultural landscape, strongly and significantly influenced crop damage (PLS results: $\beta = -0.886$, $p = 0.008$; $f2 = 0.207$), where biomass loss was higher on oat fields compare to grass fields. This was the only variable that directly influenced crop damage. I found no evidence that the other variables representing the landscape of fear or the foodscape had a direct effect on crop damage. However, supplementary feeding had a positive effect on ungulate density ($\beta = 0.406$, $p = 0.044$; $f2 = 0.205$), suggesting that the ungulate density on fields where supplementary feeding had been conducted was higher compared to other fields.

I found that human management goals significantly influenced the foodscape and the landscape of fear. Fields where landowners had an agricultural management goal had a higher vegetation biomass compared to other fields ($\beta = 0.346$, $p = 0.007$, $f2 = 0.136$). Moreover, these landowners also conducted more scaring practices on the fields compared to other landowners ($\beta = 0.235$, $p = 0.022$, $f2 = 0.058$).

3.2 Influence of the foodscape on ungulate impacts and the role of humans in shaping this functional landscape (*paper II*)

Crop type had a significant effect on browsing pressure in surrounding forests, with higher browsing pressure surrounding oat fields compared to grass fields ($p<0.01$, $z = 2.66$, est = 0.89) (fig 8). Note that these results represent browsing pressure on all tree species pooled together, please see *paper II* for further details about species differences.

Browsing pressure was higher in areas with high ungulate density ($p<0.01$, $z = 2.77$, est = 0.15) (fig 9a). Furthermore, forage availability in the forests also played an important role in determining browsing pressure, with lower browsing pressure in forests with higher tree availability ($p = 1.01e\text{-}05$, $z = -4.41$, est = -0.11) (fig 9b) The interaction between ungulate density and crop type showed that browsing pressure was higher in areas with high ungulate densities around grass fields, but the opposite was true around oat fields ($p = 0.01$, $z = -2.39$, est = -0.21) (fig 9c). Furthermore, the interaction between crop type and distance to field edge was significant ($p<0.01$, $z = -2.71$, est = -0.19), where the influence of distance from field edge was stronger around oat fields compared to around grass fields (fig 9d).

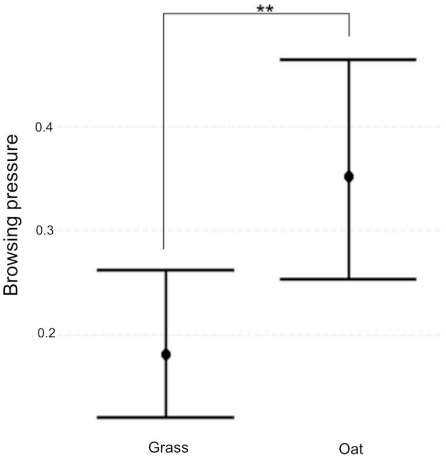


Figure 8) Difference in browsing pressure on all tree species combined in forest patches surrounding grass fields and oat fields. Bars represent 95% CI interval, * represent significant differences.

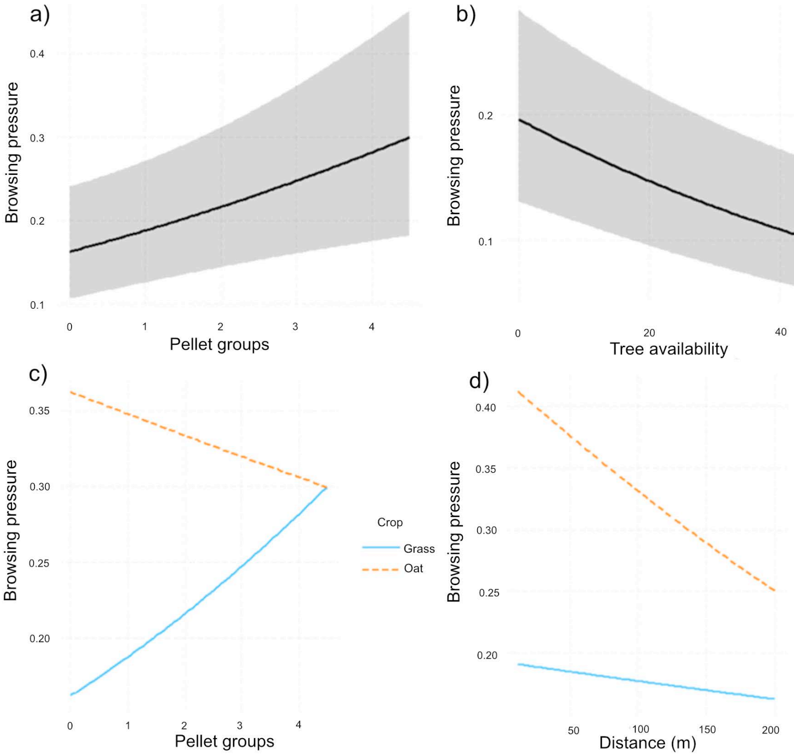


Figure 9). Result from the study investigating influence of food and ungulate density on browsing pressure in forests (*paper II*): a) the influence of pellet groups on browsing pressure and b) the influence of forage availability (tree availability) on browsing pressure, c) the interaction between pellet groups and crop type on browsing pressure, d) the interaction between distance from field edge and crop type on browsing pressure

3.3 Influence of the thermal landscape and the foodscape on habitat selection (*paper III*)

3.3.1 Moose

Moose avoided arable land compared to forests regardless of temperatures during day and night, although this was not significant regarding the coldest night time temperatures (fig 10a and 11a). They selected clear cuts compared to forests regardless of temperatures both during day and night (fig 10a and 11a). Temperature had no influence on selection for the habitat category “other”, regardless of time of day. Temperature strongly influenced moose selection of areas with canopy cover both during day and night, where they selected for areas with more canopy cover during warm temperatures, and avoided them during cold temperatures (fig 10b and 11b). Moose selected for areas with more shrub cover during warm temperatures and avoided them during colder temperatures during the day (fig 10c).

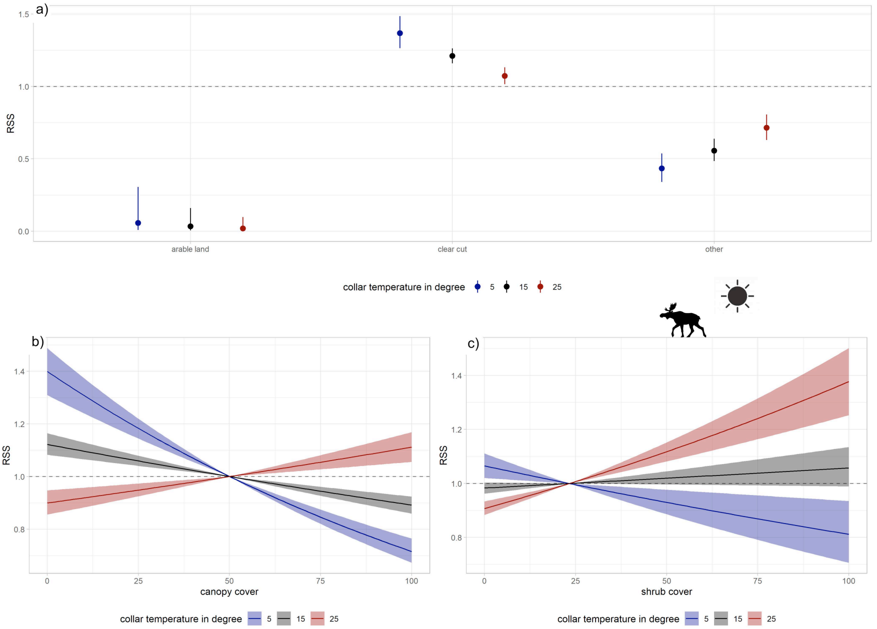


Figure 10) Plots showing the influence of the interaction between temperature and a) land cover types b) canopy cover and c) shrub cover, on the predicted probability of habitat selection in moose (population level estimates) during day. Temperature is set to three constants, 5, 15 and 25 represented by blue, grey and red. The y-axis represents the relative selection strength (RSS) where in panel a, this illustrates how much more or less likely moose are to select for that habitat in comparison to forests, indicated by the dashed line. In panels a and b this represents how much more likely or less likely moose are to select for that habitat in comparison to the average b) canopy and c) shrub cover. The dashed line indicates no preference or avoidance. Error bars and bands represents 95% confidence intervals around the population level estimates. Significant results are expressed when bars and bands are not overlapping the dashed line.

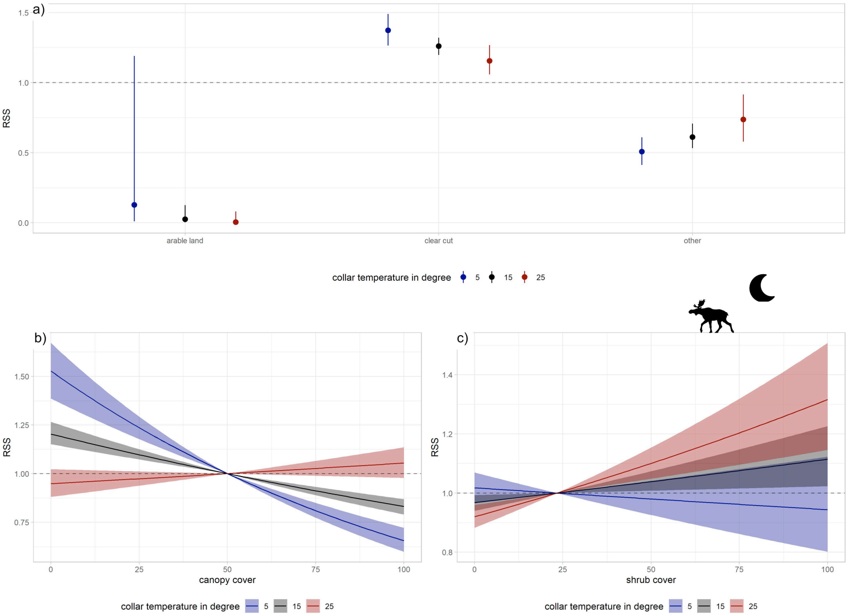


Figure 11) Plots showing the influence of the interaction between temperature and a) land cover types b) canopy cover and c) shrub cover, on the predicted probability of habitat selection in moose (population level estimates) during night. Temperature is set to three constants, 5, 15 and 25 represented by blue, grey and red. The y-axis represents the relative selection strength (RSS) where in panel a, this illustrates how much more or less likely moose are to select for that habitat in comparison to forests, indicated by the dashed line. In panels a and b this represents how much more likely or less likely moose are to select for that habitat in comparison to the average b) canopy and c) shrub cover. The dashed line indicates no preference or avoidance. Error bars and bands represents 95% confidence intervals around the population level estimates. Significant results are expressed when bars and bands are not overlapping the dashed line.

3.3.2 Red deer

Red deer selected arable land compared to forests during colder temperatures during the day, while selecting it during warm temperatures at night (fig 12a and 13a). They selected clear cuts during warmer temperatures during the day and night (fig 12a and 13a). Moreover, just as for moose, temperature influenced their selection of areas with canopy cover both during night and day, where they selected for areas with more canopy cover during warm temperatures, and avoided them during cold temperatures, both during day and night (fig 12b and 13b). Furthermore, they selected for areas with more shrub cover with increasing temperatures, and avoided them during colder temperatures, however only during the day (fig 12c).

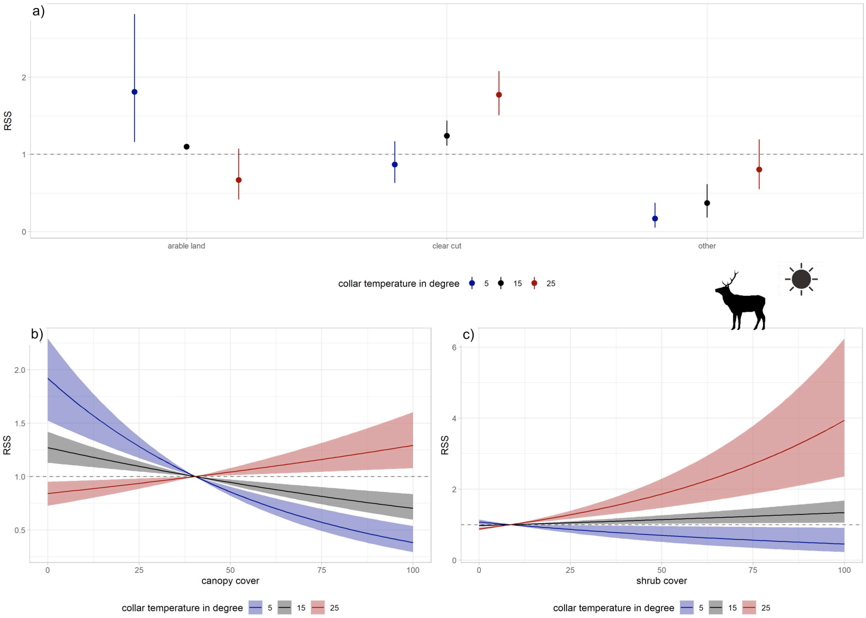


Figure 12) Plots showing the influence of the interaction between temperature and a) land cover types b) canopy cover and c) shrub cover, on the predicted probability of habitat selection in red deer (population level estimates) during day. Temperature is set to three constants, 5, 15 and 25 represented by blue, grey and red. The y-axis represents the relative selection strength (RSS) where in panel a, this illustrates how much more or less likely red deer are to select for that habitat in comparison to forests, indicated by the dashed line. In panels a and b this represents how much more likely or less likely red deer are to select for that habitat in comparison to the average b) canopy and c) shrub cover. The dashed line indicates no preference or avoidance. Error bars and bands represents 95% confidence intervals around the population level estimates. Significant results are expressed when bars and bands are not overlapping the dashed line.

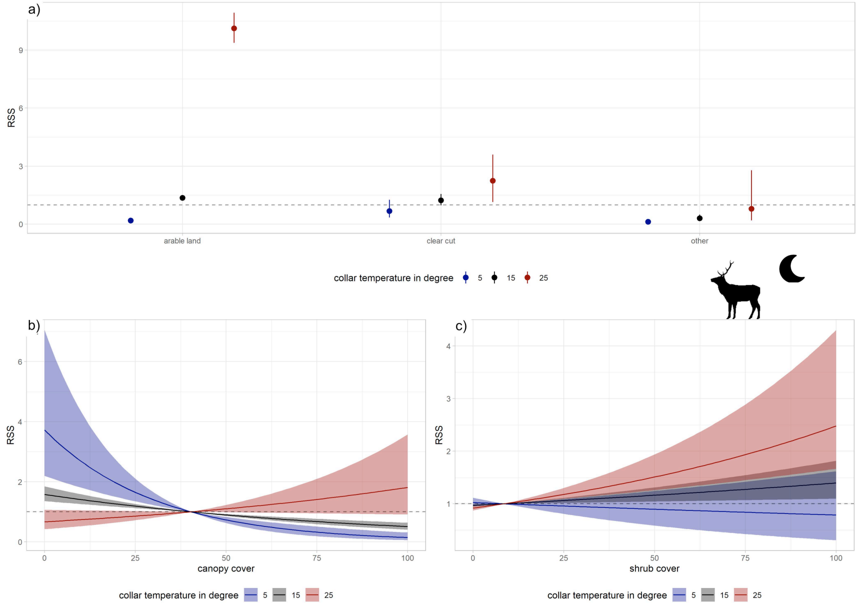


Figure 13) Plots showing the influence of the interaction between temperature and a) land cover types b) canopy cover and c) shrub cover, on the predicted probability of habitat selection in red deer (population level estimates) during night. Temperature is set to three constants, 5, 15 and 25 represented by blue, grey and red. The y-axis represents the relative selection strength (RSS) where in panel a, this illustrates how much more or less likely red deer are to select for that habitat in comparison to forests, indicated by the dashed line. In panels a and b this represents how much more likely or less likely red deer are to select for that habitat in comparison to the average b) canopy and c) shrub cover. The dashed line indicates no preference or avoidance. Error bars and bands represents 95% confidence intervals around the population level estimates. Significant results are expressed when bars and bands are not overlapping the dashed line.

3.3.3 Roe deer

Roe deer selected arable land to a similar degree as forests regardless of temperatures, both during day and night, however with an exception during warm daily temperatures (fig 14a and 15a). They selected clear cuts compared to forests during warmer temperatures, both during day and night, and selected it to a similar degree as forests during colder temperatures (fig 14a and 15a). They avoided the habitat category “other”, during day and night with an exception during colder temperatures at night where they selected for it to a similar degree as forests (fig 14a and 15a).

Temperature did not influence their selection of areas with canopy cover during day or night (fig 14b and 15b). Instead roe deer strongly selected for areas with more shrub cover during warm temperatures, and avoided them during colder temperatures at day-time (fig 14c).

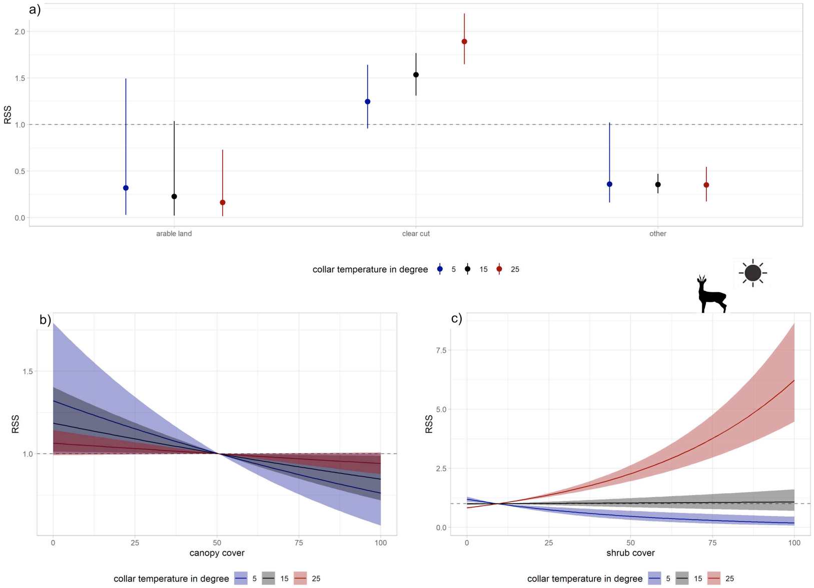


Figure 14) Plots showing the influence of the interaction between temperature and a) land cover types b) canopy cover and c) shrub cover, on the predicted probability of habitat selection in roe deer (population level estimates) during day. Temperature is set to three constants, 5, 15 and 25 represented by blue, grey and red. The y-axis represents the relative selection strength (RSS) where in panel a, this illustrates how much more or less likely roe deer are to select for that habitat in comparison to forests, indicated by the dashed line. In panels a and b this represents how much more likely or less likely roe deer are to select for that habitat in comparison to the average b) canopy and c) shrub cover. The dashed line indicates no preference or avoidance. Error bars and bands represents 95% confidence intervals around the population level estimates. Significant results are expressed when bars and bands are not overlapping the dashed line.

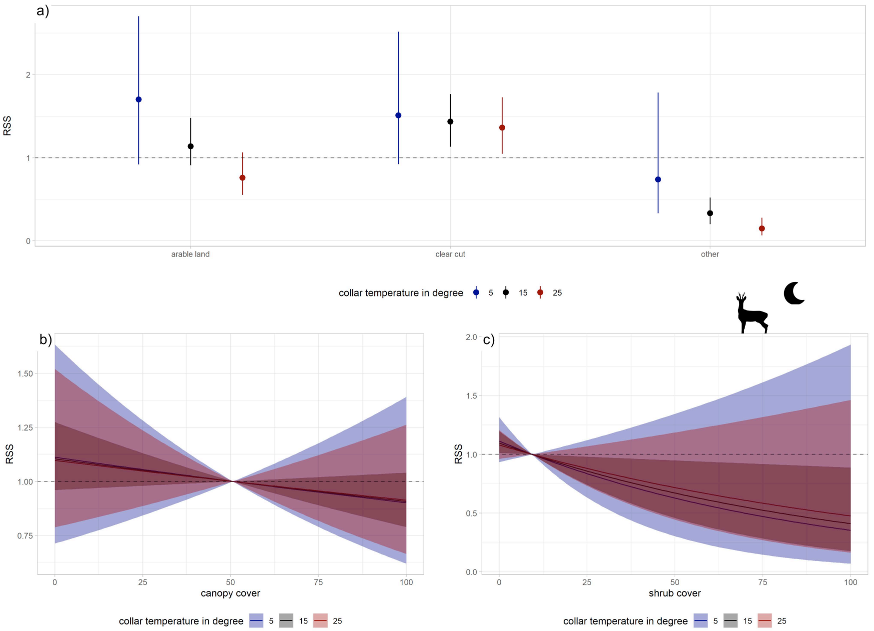


Figure 15) Plots showing the influence of the interaction between temperature and a) land cover types b) canopy cover and c) shrub cover, on the predicted probability of habitat selection in roe deer (population level estimates) during night. Temperature is set to three constants, 5, 15 and 25 represented by blue, grey and red. The y-axis represents the relative selection strength (RSS) where in panel a, this illustrates how much more or less likely roe deer are to select for that habitat in comparison to forests, indicated by the dashed line. In panels a and b this represents how much more likely or less likely roe deer are to select for that habitat in comparison to the average b) canopy and c) shrub cover. The dashed line indicates no preference or avoidance. Error bars and bands represents 95% confidence intervals around the population level estimates. Significant results are expressed when bars and bands are not overlapping the dashed line.

3.4 Managing the landscape of fear and the effects on ungulate impacts on agriculture (*paper IV*)

I found a strong influence of fear on both patch use and crop damage on agricultural fields. Patch use in front of ABRs and CTs did not differ during the pre-playback period (when sound system was disabled), (t-value= 0.50, p = 0.618). However, during the playback treatment period there was a significant difference in patch use between ABR locations and CT locations with higher patch use at CT locations (t-value=3.05, p = 0.003). Furthermore, the patch use also increased in front of CTs during the playback treatment period (t-value = 2.06, p = 0.04) which was not the case for patch use in front of ABRs (t-value = -0.57, p = 0.5).

During the playback-treatment period, patch use was lower at high predator risk ABR locations compared to CTs (t-value = 2.17, p = 0.03). Furthermore, patch use was lower at low-predator level ABRs compared with CTs, although this was not significant (t-value = -1.92, p = 0.07). I found no difference in patch use between high-predator level and low-predator level ABRs (t-value= 0.31, p = 0.76).

Crop damage was significantly lower at ABR locations than CTs (Chisq = 28.38, pr (>Chisq) = <0.001) (fig 16). There was no significant difference in crop damage between low-predator level and high-predator level, however, there was a tendency of lower damage at high-predator level ABR sites compared to low-predator level ABR sites (t = 1.76, p = 0.08) (fig 16). Additionally, I found that the total bout duration was significantly different between the playback treatments (control, dog, wolf, human) (Chisq = 49.559, pr>Chisq= <0.001). Ungulates reacted strongest to human vocalizations and the bout durations after hearing human sounds were shorter compared to after hearing other vocalizations (human vs. control Z-value = 6.85, p = <0.001; human vs. dog Z-value= 4.61, p = <0.001; human vs. wolf Z-value = 3.09, p = 0.002) (fig 17).

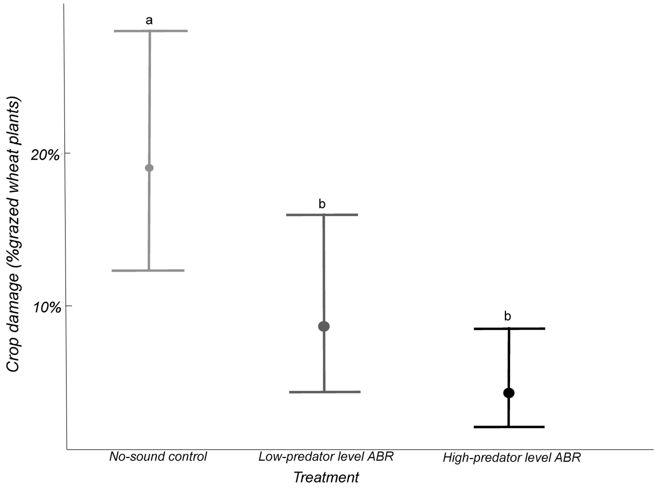


Figure 16. Result from the experimental study inducing fear on agricultural fields using playbacks. a) Patch use between the ABRs and CTs both during and before manipulation of predator playbacks, b) difference in patch use between the CTs (no-sound control) and the two different risk-level ABRs. c) difference in crop damage between CTs and ABRs. Bars represent 95% confidence interval. * denotes significant differences between the treatments. (*from paper IV*)

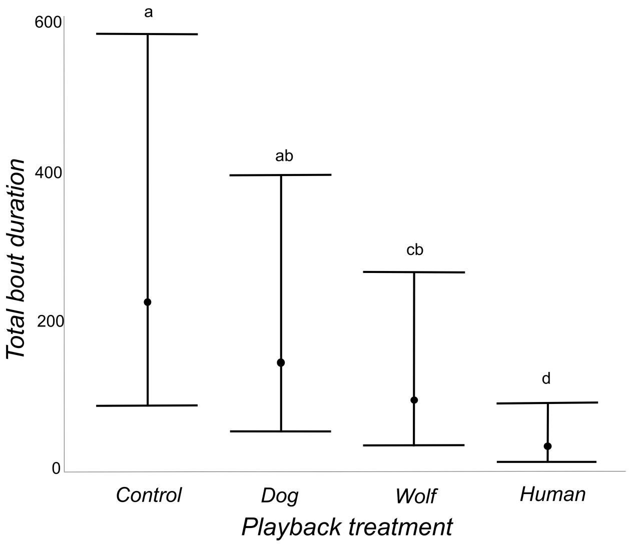


Figure 17. Difference in total bout duration (in seconds) between the four different playback types used in the experimental playback study. Bars represent 95% CI. Different letters denote significant differences. (*from paper IV*)

4. Discussion

With this thesis, I aimed to provide knowledge on how the three functional landscapes (the foodscape, the landscape of fear and the thermal landscape) influence how ungulates use the physical landscape and the impact they have on human land use. Furthermore, I also aimed to explore the role of humans in shaping these functional landscapes and whether they can be managed. I addressed this by applying a variety of methods across scales, such as GPS data on larger spatial scales, field inventories, social data collection and landscape experiments – all within a human-wildlife conflict context. My results show that all three functional landscapes significantly influence the impact that ungulates have on important human land uses. Additionally, I also show that humans play an important role in shaping these landscapes. In the following sections, I will discuss the role of the different functional landscapes as well as the role of humans in more detail.

4.1 The foodscape and humans

The foodscape is known to be an important driver of ungulate behavior (Parker *et al.*, 2009), as it influences both how animals are distributed in the landscape but also where they cause impact (Felton *et al.*, 2022; Merkle *et al.*, 2016; Herfindal *et al.*, 2015; van Beest *et al.*, 2010a; Van Beest *et al.*, 2010b). My studies confirm this and showed that it is variation in the availability and quality of food that determine impact by ungulates. I demonstrate that crop damage was significantly higher on oat fields compared to grass fields (*paper I*), and additionally that crop type was the only variable that turned out to have a significant effect on crop damage. This suggests that, in my study area, quality of forage may “overshadow” other factors, such as fear, the availability of forage and ungulate density, in determining variation in crop damage. I found that increased perceived predation risk, such as scaring or hunting on fields, had no effect on crop damage, suggesting that the benefit of feeding on such attractive crops may be higher than the cost of responding to fear. This highlights that antipredator behavior and strategies resulting from perceived risk sometimes don't correlate perfectly with the landscape of fear, due to trade-offs and animals needing to conduct other activities for example foraging (Gaynor *et al.*, 2019). Gaynor et al. 2019 also discuss the fact that in high quality forage patches, the cost of antipredator behavior, such as not feeding there and instead seeking cover, may outweigh the benefit of feeding in that patch. This theory originates from the risk allocation hypothesis (Lima & Bednekoff, 1999), which states that prey has to trade-off the time spent on antipredator behavior with other essential activities, such as finding food and foraging. Furthermore, one reason for the lack of effect of hunting and scaring on crop damage could be that the strength of antipredator responses depends on the predictability of risk, both in time and space (Ferrari *et al.*, 2009). When risk is predictable in time and space, which is usually the case with hunting and scaring practices, prey may respond strongly and avoid those areas when they are risky, however, they will most likely return when risk has decreased, continuing foraging (Cromsigt *et al.*, 2013).

This highlights that these functional landscapes interact with each other, which is important to consider in wildlife management, since some management practices aiming for reducing negative impact may not function as expected due to animals also responding to other functional landscapes. In other words, there may be mismatches between risk and prey response since prey also need to conduct other essential activities. Additionally, it is also possible that we, using the questionnaire did not manage to measure the scaring conducted well enough, i.e I did not include information about exactly where the scaring had been conducted or exactly how it had been conducted, potentially making it difficult to put it in to relation to the resulting crop damage on fields.

Crop type also had a strong influence on browsing pressure in forests surrounding the fields, with higher browsing pressure surrounding oat fields compared to grass fields. This suggests that features of the foodscape are important across land use borders and that food quality in one land use may influence the impact on adjacent land use types.

This emphasizes the powerful role humans have in shaping the foodscape and the consequences this may have on ungulate impact. By cultivating different crops, humans may influence the impact ungulates have both on that particular field, but also in the surrounding areas. Moreover, I showed how human management choices also influence the forage availability on the fields, where landowners aiming for agricultural production generated fields with a higher biomass compared to fields owned by other landowners. This goes in line with earlier findings where crop performance and biomass production differed between types of farms (Nkurunziza *et al.*, 2020). Accordingly, human practices directly influence two of the most important features of the foodscape, food availability and food quality, which is of great importance to understand how negative impacts by ungulates can be mitigated.

The majority of studies investigating ungulate impact focused on different land use types separately (Pfeffer *et al.*, 2021; Jarnemo *et al.*, 2014; Bleier *et al.*, 2012; DeVault *et al.*, 2007). I show that actions in one land use type have consequences in other land use types. Thus my findings serve as an important addition to this literature, pointing towards a more holistic management spanning across land uses and landowners' borders. Additionally, the use of experimental manipulation of crop types, allowed me to tease apart cause and effect of crop damage and to study patterns that wouldn't be possible to study in settings where farmers had already adapted to high crop damage levels.

Moreover, my findings suggest that the mechanisms behind ungulate impact may be complex and driven by nutritional demands and strategies. For example, I showed how the influence of ungulate density on browsing pressure surrounding fields differed depending on crop type, where browsing pressure increased with increasing ungulate density around grass fields, but not around oat fields. Additionally, the browsing pressure around oat fields was high even at relatively low ungulate densities. This suggests that browsing pressure around oat fields was not necessarily driven by a high number of ungulates being attracted to the area for feeding (and spilling over to nearby forests), but rather by nutritional demands. According to the nutritional balancing hypothesis (Simpson & Raubenheimer, 2012), ungulates feeding on nutrient rich crops may need to increase their intake of fibrous plants (Felton *et al.*, 2016). Similar findings have been reported by (Jarnemo *et al.*, 2022), showing that bark stripping by red deer on spruce was higher in forest patches close to a nutrient dense crop and that the effect of proximity of crops was not due to an increased red deer density in those forest patches. The influence of nutritional demands may also explain how crop type shaped the effect of distance from the field on browsing pressure, where browsing pressure declined more strongly with increasing distance around oat fields compared to grass fields. Hence, ungulates feeding on energy rich oat may fulfill their needs of feeding on fibrous woody plants in the close vicinity of the fields. This emphasizes that foraging behavior is indeed complex with foraging decisions being highly context dependent (Felton *et al.*, 2018).

Furthermore, forage availability inside the forest patch itself was also important in determining damage, with decreasing browsing pressure in areas with a high availability of tree saplings that are known to be important forage items for all cervid species (Spitzer, 2019). This result goes in line with several other studies (Jarnemo *et al.*, 2022; Pfeffer *et al.*, 2021; Jarnemo *et al.*, 2014; Ball & Dahlgren, 2002) and lends further support to the findings regarding the importance of alternative forage in production forests to mitigate negative impact by ungulates. Furthermore, it suggests that features of the foodscape are important on different scales, both in the surrounding landscape across land use borders, as well on a more local scale inside the patch where damage is occurring (Felton *et al.*, 2022).

The foodscape did not only influence the impact of ungulates, but also the number of ungulates in an area, where areas with supplementary feeding had a higher number of ungulates compared to areas without supplementary feeding. This is likely a result of humans aiming to maintain high populations using supplementary feeding (Smith, 2001). Once again, this underlines the role humans have in shaping the foodscape: not only influencing the impact ungulates have, but also their densities. Even so, there was no direct effect of supplementary feeding, or indirect effects through increasing ungulate densities, on levels of damage.

4.2 The thermal landscape

My study on habitat selection as a function of temperature highlights that moose, red deer and roe deer are all strongly influenced by temperature when they navigate the landscape, however, with some divergent patterns.

Moose and red deer strongly selected for areas with a high % canopy cover when temperatures increased both during day and night, and especially so when temperatures reached 25°C. This result suggests that they choose to move into areas providing thermal shelter in order to stay within their thermal limits, something that has been found in earlier studies, however mainly focused on moose (Alston *et al.*, 2020; Melin *et al.*, 2014; van Beest *et al.*, 2012; Merrill, 1991). By showing that red deer also use areas providing thermal shelter I add important knowledge in how different cervid species use the thermal landscape.

Areas with a high % canopy cover was avoided by moose and red deer during colder temperatures, implying that these habitats are mainly preferred for their provision of thermal shelter. This is most likely because areas with denser canopies, provide relatively low amount of forage (Juvany *et al.*, 2023; Petersson *et al.*, 2019; Hedwall *et al.*, 2013). This result could imply that moose and red deer experience a food-cover trade-off, however, they also strongly selected for areas with more shrub cover during increasing daily temperatures, while avoiding them during colder temperatures. Suggesting that they actually do use areas with high forage availability when warm, but that this selection is not necessarily driven by forage availability alone, but most likely by temperature.

Their strong selection for shrub cover with increasing temperatures is most likely explained by the fact that shrub cover may function as thermal shelter for moose and red deer when bedded down during warm days. Hence, during summer, both moose and red deer spend a relatively large proportion of each day (24h) bedded while ruminating and resting (Adrados *et al.*, 2008; Moen *et al.*, 1997; Renecker & Hudson, 1990).Moose and red deer usually bed down under thermal cover (McCann *et al.*, 2016; Millspaugh *et al.*, 1998), which indeed could be provided by cover below 3 and 2m when they lay down.

However, proximity to forage and predator concealment are also two important factors influencing bed site selection (McCann *et al.*, 2016; Pitman *et al.*, 2014; Patthey, 2003; Gebert & Verheyden-Tixier, 2001; Mysterud & Østbye, 1999; Roloff & Kernohan, 1999; Millspaugh *et al.*, 1998), especially so during spring and summer when food intake is increased (Renecker & Hudson, 1986) and predator concealment is extra important for hiding and protecting offspring (Geist & Walther, 1974; Espmark, 1969; Altmann, 1956). Hence, shrub cover may by itself provide thermal shelter for bed site locations, but will also serve other important purposes in combination with canopy cover.

Moose and red deer diverged in their selection of clear cuts, where moose selected for clear cuts compared to forests regardless of temperatures both during day and night, however being less likely to select these habitats during the warmest temperature, especially during the day. Red deer on the other hand, were instead more likely to select clear cuts during warmer temperatures, both during day and night. The fact that clear cuts are preferred is most likely because clear cuts and early successional forests (from shortly after clear cutting to when trees grow out of browsing height) host large amounts of forage (Edenius *et al.*, 2015; Olsson *et al.*, 2011; Kuijper *et al.*, 2009). Furthermore, why this habitat is also selected at warmer temperatures is most likely explained by that planted clear cuts may also provide shrub cover and lower canopy cover, as well as local canopy cover by a few mature trees left after harvest. Hence it is important to remember that clear cut is here defined as any forest land with vegetation below 5m. Indeed implying that these habitats may provide local thermal shelter for red deer and moose.

Moose avoided arable land regardless of temperatures, while red deer selected for it during colder temperatures during the day and warm temperatures at night. This suggests that arable land is a more preferred habitat for red deer compared to moose, something that is supported by studies showing that red deer frequently use meadows and arable land for foraging (Månsson *et al.*, 2021; Allen *et al.*, 2014; Godvik *et al.*, 2009; Biro *et al.*, 2006) and also has a higher proportion of grass in their diet compared to moose (Spitzer, 2019; Krojerová-Prokešová *et al.*, 2010; Kerridge & Bullock, 1991). The fact that red deer decreased their selection of arable land during warm temperatures suggest that they move into more shaded habitats when temperatures increase. Seeking cooler habitats may also be an explanation for why red deer selected arable land during the warmest temperatures at night, since open land is colder that more dense forests that trap heat during night (Díaz-Calafat *et al.*, 2023; De Frenne *et al.*, 2019).

In contrast to moose and red deer, roe deer did not select for areas with more canopy cover with increasing temperatures, instead they selected areas with more shrub cover, however only during the day. This result is perhaps suggesting that roe deer are less heat sensitive that the other two deer species, but may also be because shrub cover (below 2m) is sufficient for acting as thermal shelter for this smaller species during warm temperatures, especially so when roe deer are bedded. Just as for moose and red deer, roe deer prefer to bed down below dense canopy cover, measured with lower heights than our canopy cover measurement (Mysterud, 1996).

Furthermore, as for moose and red deer, shrub cover may serve other important purposes, where concealment from predators may be extra important for roe deer during spring and summer. Roe deer fawns are extra vulnerable to fox predation (Jarnemo *et al.*, 2004) and are hidden for as long as four weeks (Jarnemo *et al.*, 2004; Lent, 1974). Jarnemo et al., 2004; Lent, 1974), usually in areas that decrease predation risk, i.e in areas with a high understory cover (Van Moorter *et al.*, 2009; Jarnemo *et al.*, 2004; Linnell *et al.*, 1999). Hence, this could further explain roe deer's strong selection for habitats with more shrub cover. However, because of the strong differences in selection between temperatures, it is most likely that temperature plays the most important role in selection of these type of areas.

Based on my results that moose and red deer selected areas with more canopy cover, but also areas with more shrub cover during warm temperatures, suggests that they in fact do not experience such a strong trade-off between thermal cover and food. Furthermore, the same might be true for roe deer, that selected areas with more shrub cover during warm temperatures, hence providing both forage, but potentially also sufficient thermal shelter.

Furthermore, my results highlights that areas with shrub cover seem to be important for all three species during warm temperatures. These habitats also provide forage for all three species and it is therefore likely that with increasing temperatures due to climate change, the pressure on these types of habitats may increase, potentially with competition over common resources and thermal shelter as an outcome. Moreover, my findings suggest that management actions that influence both canopy cover and shrub cover will directly influence important features of the thermal landscape and the foodscape, hence, influencing ungulates ability to respond to increasing temperatures and internal needs.

4.3 The landscape of fear and humans

The landscape of fear plays an essential role in influencing ungulate landscape use and impacts, and humans play a central role in shaping this functional landscape. My study confirmed that humans may shape the landscape of fear in different ways and on different scales. By their management goals and practices landowners may influence the level of risk in the landscape via conducting scaring practices, with different intensity depending on the goal they have with their land. However, the influence that risk will have on ungulate impact may vary depending on mismatches between risk and responses, since ungulates also need to conduct other essential activities such as foraging. This is in line with the fact that we did not see an effect of these scaring activities on crop damage. Additionally, humans may also induce fear in ungulates by their mere presence.

In my experimental study where I induced fear on agricultural fields, I showed that both the patch use and crop damage were significantly influenced by perceived predation risk. Thus, I found a behaviorally mediated trophic cascade in a human managed landscape, something that until now has been rarely reported (Smith *et al.*, 2020). Furthermore, I found that hearing human voices gave the strongest fear response, lending further support to the fact that humans can be regarded as a human super predator and coinciding with other studies where human induced fear outweigh those of other predators (Crawford *et al.*, 2022; Zanette & Clinchy, 2020; Suraci *et al.*, 2019; Smith *et al.*, 2017). The fact that manipulating fear in a human management setting significantly reduced the impact by ungulates on wheat provides important knowledge regarding the process of applying the "ecology of fear" as a management tool and more broadly, to manage behavior in ungulates. It can be seen as an important first step towards implementing non-lethal management tools that effectively mitigate negative impacts.

4.4 Managing behavior

The three functional landscapes considered in this thesis are already to a strong degree affected by humans, but often not pro-actively aimed at managing human-wildlife interactions and also with limited thinking about what consequences different actions might have. Some actions, such as scaring, hunting or supplementary feeding, are often done with an aim to either reduce or increase the number of animals or their impact (Linnell *et al.*, 2020; Milner *et al.*, 2014; Smith, 2001). Nevertheless, when it comes to management actions on a larger scale, such as managing the agricultural landscape by cultivating different crops or enhancing biomass production, these actions usually do not thoroughly consider their potential influence on the foodscape, the landscape of fear and the thermal landscapes of ungulates, nor the subsequent consequences for ungulate impacts on larger scales.

My thesis stresses that management actions actually do influence the foodscape, the landscape of fear and the thermal landscape that ungulates inhabit. Using experimental manipulation I show how actions in the foodscape and the landscape of fear have important effects on damage on relatively large scales. Moreover, even though I did not experimentally test the influence of management actions on the thermal landscape I found that vegetation structures like shrub cover played an essential role in driving habitat selection in moose, red deer and roe deer, and these are structures that are highly influenced by different forestry practices. Hence, I believe there is a large potential in managing behavior through managing these landscapes, by increasing the consideration of potential consequences across land use types and adopting a more pro-active approach with clear goals. It is important to stress that a more holistic approach where goals are set across land uses and landowners' property borders may be important in order to manage behavior successfully in a managed landscape. For example, when trying to steer ungulate distributions by inducing fear, animals may move to a different part of the landscape, hence, potentially increasing conflicts between wildlife and human land use in this area. Therefore, it is crucial that all of these functional landscapes are managed in a way that allows animals to be steered away from areas where they can cause damage into areas where they can be safe and are "allowed" to be. In order to achieve this, a collective aim across larger areas and among several landowners is likely needed. By visualizing the physical landscape as layers of a foodscape, a landscape of fear and a thermal landscape (fig 2), as well as considering how one action in the physical landscape may influence ungulate behavior and impact, I believe we are on the right path towards minimizing human-wildlife conflicts.

4.5 Management suggestions

4.5.1 The foodscape

Forage availability has been shown to be important in influencing damage by ungulates in several different studies. It is therefore important to manage the landscape taking into account how different actions influence forage availability and with the aim of increasing the availability of food items that are important for ungulates. My thesis highlights that it is important to focus on enhancing forage availability in several land use types simultaneously in a mixed landscape. For example, forage in the agricultural landscape will not only influence impact by ungulates on the agricultural fields but also in the surrounding forests. Therefore, the managed landscape needs to be regarded as one integrated landscape and actions influencing forage availability needs to be taken on several scales and across land use borders. Furthermore, it is important to point out that even though my results show that attractive crops like oat lead to higher crop damage on fields and higher levels of browsing pressure in forests. The landscape scale effect of more and more people shifting away from these attractive crops due to the risk of damage, will most likely lead to that the few individual landowners who remain with attractive crops will get a worse situation.

Hence, if we increase the amount of attractive forage in the landscape, the impact on single fields will most likely be lower, due to a dilution effect. Because of this is it also important to aim for a more holistic approach where some areas of the landscape are managed to yield high availability of attractive forage, where ungulates are allowed to feed in safety and then simultaneously more pro-actively aiming for protecting fields and forest patches that are vulnerable to damage. I believe, actions enhancing the foodscape on several scales should be incorporated in different steps of wildlife management in combination with different actions connected to the landscape of fear.

4.5.2 The landscape of fear

In order to reach strong fear responses that have consequences on impact, management should attempt to create variation in fear across time and space that reduce habituation and the chances of animals returning to the area when risk is over. Such variation should reduce the chance that animals can predict when risk will appear on a certain crop field. This can be done by conducting scaring practices that appear on varying times and in varying places using different scaring techniques and tools. However, in order to shape the landscape of fear these actions need to be done closely together with management actions in the foodscape, all with one collective aim. I believe scaring actions will be effective in the long term if people also allow ungulates to be safe in the areas where they are scared to and/or areas where they are not actively scared from, and also provide forage in this area that have similar value to the forage in the area that they are scared from. Furthermore, I believe that manipulating risk by using playbacks can be regarded as a potentially strong method to reduce damage for a shorter amount of time on vulnerable crops and creating high risk areas. It is once again important that these methods do not become predictable and that animals do not become habituated, as this would weaken the effect. Additionally, these actions should be combined with enhanced forage availability in combination with low risk areas in other parts of the landscape.

4.5.3 The thermal landscape

Managing temperature is difficult but humans have a strong influence on creating and changing different landscape structures that are important as thermal shelter. I showed that both canopy cover and shrub cover were important for ungulates when navigating the thermal landscape, cover that also serves other important purposes. Shrub cover in different areas of the landscape appears to serve as an important thermal shelter during warm temperatures when ungulate are bedded, but also serve as predator concealment and forage. It would therefore be beneficial to create multilayered forests that offer both local shading opportunities, forage and concealment for ungulates, as this may reduce some of the trade-offs animals experience when navigating the thermal landscape. In similarity to the management recommendations of the foodscape and the landscape of fear, the thermal landscape would also likely be best managed across borders.

4.6 Conclusion

With my thesis I conclude that it is of high importance to account for behavioral drivers when it comes to understanding how ungulates use the physical landscape and where they cause negative impact. I show that ungulate habitat selection and impact is influenced by all three functional landscapes addressed in this study jointly. Hence, these landscapes interact and overlap with each other, influencing the response of ungulates to each behavioral driver respectively.

Furthermore, my thesis emphasizes the central role humans have in shaping these functional landscapes, and the importance they have in influencing the impact by ungulates. Humans' influence on the foodscape spans across different scales and has consequences for ungulate impacts on both agriculture and forestry. Moreover, I show that humans' influence on the foodscape has effects on ungulate damage across the borders of land use types, suggesting that it is important to include humans and human practices when assessing what drives ungulate landscape use.

The fact that humans play such an important role in shaping these functional landscapes may enable a more forward-thinking management, with the aim of steering ungulate behavior in order to minimize conflict. By reducing crop damage via the manipulation of fear, I show that steering ungulate behavior to reduce their impact is possible. This suggests that there is a potential to influence the impact by ungulates in a setting that is heavily managed by humans, by using the knowledge of behavioral drivers.

Additionally, my findings show that humans generated the strongest fear response among a range of potential predators, adding further support to the important role of humans. I believe my findings are of high importance when developing additional strategies that aim for managing behavior, reducing negative impacts and mitigating human-wildlife conflict - so that humans and ungulates can continue to share the same spaces.

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Popular science summary

Ungulates and humans coexist in the same landscape. Ungulates contribute to several ecosystem services, such as creating habitats for plants and animals and thus improving biodiversity, providing hunting opportunities and game meat, as well as providing opportunities for recreation and wildlife tourism. However, ungulates may also cause damage in areas managed by humans such as agriculture and production forests by foraging, resting and trampling. This can lead to conflicts between ungulates and humans.

As ungulate populations are expanding both in numbers and distribution across Europe, this conflict is increasing. However, some stakeholders who depend on game keeping or hunting for their livelihoods are favored by this expansion. In other words, some are negatively affected by increased ungulate populations, while some are gained. Because of this, there is a need to manage these ungulate populations with both interests in mind, i.e. to both minimize their negative impact, but also consider their positive impacts.

A common method to reduce ungulate impact is to decrease their numbers by hunting. However, a linear relationship between a reduced number of animals and reduced damage is not always present, since there are also many other factors influencing damage levels simultaneously, for instance forage availability. There is therefore a need for an additional management approach, that takes other factors into account and that aims for variable ungulate densities across the landscapes. In order to manage and steer ungulate populations, we need to know more about what factors drive their behavior and how they may be important in influencing ungulate impact on human land use.

In this thesis I focus on factors influencing behavior in ungulates, and I regard these factors as functional landscapes; namely the foodscape, the landscape of fear and the thermal landscape. These landscapes illustrate how animals perceive the physical landscape based on food availability and quality, predation risk and temperatures. I investigated how these functional landscapes influence habitat selection but also damage on crops and forests. Furthermore, I explored what role humans have in influencing these functional landscapes, i.e. if they influence any features such as food quality or availability for example and if these landscapes could be manipulated. I did this by using a large variety of methods, such as field inventories, landscape experiments, questionnaires and also large scale GPS data.

I found that all of these three functional landscapes influenced how ungulates select habitats as well as where and to what degree they cause damage on agriculture and forests. For example, both food quality and food availability influenced the damage on crops and forests. This influence spanned across land use types, where food quality in the agricultural landscape influenced the impact in forests. I observed that ungulates respond to all of these functional landscapes at the same time, which can result in a variety of responses to each individual functional landscape. For instance, ungulates must respond to increasing temperatures, while also considering predation risk and the needs to find food.

Furthermore, I found that humans play an important role in influencing the foodscape and the landscape of fear, by changing features in both of these landscapes in different ways. Humans influence food quality by growing different crops and food availability by enhancing field biomass as well as conducting supplementary feeding. They also influence the level of fear on fields via management actions such as scaring and hunting but also by their mere presence. I found that by experimentally manipulate fear by broadcasting different sounds crop damage was reduced, and ungulates reacted most fearful to human voices compared to other sounds. All of this emphasizes that humans and their actions need to be incorporated in future management since they play such a central role in shaping ungulate impact on the landscape.

Furthermore, my study suggests that we should incorporate knowledge of ungulate behavior in order to develop more effective management strategies to reduce the human wildlife conflict. There is great potential in managing ungulate behavior by conducting actions that influence these functional landscapes and thus also influence ungulate impact. However, there is a need for a more “holistic“ approach, looking across land use and landowner borders taking into account that actions in one land use type may influence impact in another land use type. It may be fruitful to visualize the physical landscape as layers of foodscape, landscape of fear and thermal landscape, and realize that actions conducted in the physical landscape will also influence how ungulates perceive these functional landscapes.

Populärvetenskaplig sammanfattning

Klövvilt och människor lever i samma landskap. Klövvilt bidrar med många ekosystemtjänster, som att skapa habitat för flertalet växt- och djurarter och därigenom öka biologisk mångfald, skapa jaktmöjligheter och viltkött, samt bidra med rekreation och vilturism. Men klövvilt som lever i landskap som är förvaltade och påverkade av människan, som jordbruksmark eller produktionsskogar, kan dock orsaka skada genom att de betar, trampar eller vilar där. Detta kan leda till konflikter mellan människa och vilda klövdjur.

I takt med att klövviltspopulationerna expanderar i Europa så blir även konflikten mellan människa och vilt mer påtaglig. En ökande klövviltsstam gynnar dock de markägare och intressenter som sysslar med viltvård och jakt. Alltså är en stor del markägare negativt påverkade av en ökad klövviltspopulation, medan några gynnas av den. På grund av detta finns det ett ökat behov av att förvalta klövvilt med hänsyn till båda intressen, alltså med en målsättning att minska skador på grödor och skog, men samtidigt ta hänsyn till de intressenter som gynnas och de positiva faktorerna som klövvilt för med sig.

En vanlig metod för att minska klövviltets skador i ett område är att minska antalet djur genom jakt. Det finns dock inte alltid ett linjärt samband mellan ett minskat antal djur och minskad skadenivå, eftersom det även finns en mängd andra faktorer som påverkar hur svåra skadorna blir, där fodertillgången i landskapet är ett sådant exempel. Det finns därför ett behov av kompletterande förvaltningsmetoder där andra faktorer tas in i beräkningen, med ett mål att skapa varierande klövviltstätheter i landskapet. För att etablera sådana metoder behövs mer kunskap om vad som påverkar djurens beteende och hur detta i sin tur påverkar deras effekter på landskapet.

I denna avhandling fokuserar jag på hur tre funktionella landskap påverkar viltets beteende, nämligen födolandskapet, rädslans landskap och det termiska landskapet. Dessa tre landskap belyser hur klövvilt uppfattar och reagerar på fodertillgång och kvalitet, rädsla, samt temperaturer. Jag undersökte hur dessa tre landskap påverkar habitatval hos klövvilt samt skador på grödor och skog. Vidare undersökte jag människans roll i att påverka dessa funktionella landskap, exempelvis om människan har någon effekt på födolandskapet genom att ändra födokvalitet eller mängden föda i landskapet. Jag studerade även möjligheterna att påverka dessa funktionella landskap och vilken effekt detta i så fall kan ha på skador av klövvilt. Allt detta undersöktes genom en rad olika metoder så som fältinventeringar, landskapsexperiment, enkäter och analyser av GPS-data.

Mina resultat visar att alla dessa tre funktionella landskap påverkar hur klövvilt väljer habitat och magnituden av den skada de orsakar på grödor och skog. Till exempel så påverkar både foderkvalitet och fodermängd mängden skada på grödor och skog, och visar sig därför vara en viktig faktor i att avgöra skademönster.

Vidare så kan jag visa att födolandskapet har en stark influens på klövviltets effekter som sträcker sig över markanvändningsgränser.Jag fann att klövvilt reagerar på alla dessa tre funktionella landskap samtidigt. Exempelvis måste klövvilt svara på ökande temperaturer, samtidigt som de också måste beakta behovet av föda.

Jag kunde också visa att människan spelar en central roll i att påverka såväl födolandskapet som rädslans landskap, dels genom att påverka foderkvalitet och fodertillgång på olika sätt, men även genom att bidra till en ökad rädsla genom jakt och skrämsel. Mina resultat visar att skador på grödor kunde minskas genom att experimentellt manipulera rädsla genom att spela upp olika sorters ljud och att klövvilt reagerade starkast på människoröster jämfört med andra ljud. Detta understryker att man måste ta hänsyn till människans handlingar i framtida förvaltning. Vidare visar jag att vi bör inkludera kunskap om klövvilts beteende för att kunna utforma nya mer effektiva förvaltningsmetoder med en målsättning att reducera konflikten mellan människa och vilt. Det finns en stor potential i att förvalta klövvilts beteende, dock måste det till ett mer holistiskt angreppsätt, där man förvaltar klövvilt över markanvändnings och markägargränser och tar hänsyn till att en åtgärd i jordbruket också i sin tur påverkar klövviltets inverkan på skogsbruket. Det finns därför ett behov av att på en större skala visualisera det fysiska landskapet som lager av födolandskap, landskap av rädsla och landskap av temperatur, där handlingar i det fysiska landskapet påverkar hur klövvilt reagerar på de funktionella landskapen.

Personal reflections

Apart from gaining substantial amount of knowledge on my research topic I have also gained extensive insight in human-wildlife conflicts, communication and trust-building processes.

Throughout my years as a PhD student I had the opportunity to establish collaborations with several landowners, something that has been a rewarding process and over several chats I have gained insights and perspectives on how the conflict looks like on grass root level. I have had the chance to examine the conflict from different angles and perspectives, something that has deepened my understanding of the topic. Furthermore, these people have also taught me valuable things about their land, the wildlife that inhabit their land and how they manage their land. For this I am grateful.

These collaborations have also taught me the importance of communication, respect and trust. A large part of my time has been spent communicating with stakeholders, building up trust and showing respect towards their knowledge and interests. I have learnt the importance of providing time for this, and I believe that without the trust and respect from stakeholders, there is little chance our research actually will be implemented.

Finally, I have gained insights in the importance of collaboration among different interests when striving for a viable ungulate population while simultaneously minimizing negative impacts and conflicts. Instead of focusing on motives or objectives behind a management action, it could be more effective to concentrate on the potential outcome of the action. Since this may result in a win-win situation for multiple interests.

This part of the journey has been challenging, but also rewarding. I am thankful that I had the opportunity to view this topic from different perspectives and levels, enhancing my belief in the importance of regarding various viewpoints of this conflict in order to solve future issues.

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RESEARCH ARTICLE

Direct and indirect effects of food, fear and management on crop damage by ungulates

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Abstract

1. Foraging on crops by wild ungulates may create human–wildlife conflicts through reducing crop production. Ungulates interact with and within complex socio-ecological systems, making the reduction of crop damage a challenging task. Aside from ungulate densities, crop damage is influenced by different drivers affecting ungulate foraging behaviour: food availability and food quality in the landscape (i.e. the foodscape) as well as fear from hunting and scaring actions (i.e. the landscape of fear) may together affect the degree of damage via both direct and indirect effects. A better understanding of the individual effects of these potential drivers behind crop damage is needed, as is an appreciation of whether the effects are dependent on ungulate density.
2. We investigated this by applying path analysis to test indirect and direct links between ungulate density, foodscape, landscape of fear and human management goals on crop damage of oats and grass, respectively.
3. Our results suggest that crop type is the major driver behind crop damage, with more damage to oats than to leys, implying that human decisions (i.e. changing crop type) influence the level of crop damage.
4. We found that management goals and actions influenced the foodscape and the landscape of fear, by affecting the amount of forage produced in the agricultural landscape and the amount of scaring actions. Additionally, we found that supplementary feeding influenced the local ungulate densities in the area.
5. Our results highlight the importance of including human actions on multiple levels when assessing drivers behind damage by ungulates in managed landscapes. We suggest that more studies using path analysis on multiple scales are needed in order to tackle complex issues, such as crop damage and other human–wildlife conflicts.

KEYWORDS
agriculture, crop damage, deer management, path analysis, ungulate

1 | INTRODUCTION

Wild ungulates interact with and within complex socio-ecological systems (Reimoser & Putman, 2011) and many of these systems are heavily influenced by multiple human interests and different types of land use (Dressel et al., 2018). While such ungulates (e.g. different deer species and wild boar) may benefit from certain human land use practices (e.g. agriculture and/or forestry) through increased foraging opportunities and shelter (Ferretti & Lovari, 2014; Presley et al., 2019), their foraging and trampling may also create human–wildlife conflicts, for example, through reducing crop production and increasing associated economic losses (Reimoser & Putman, 2011). The cost of grazing and browsing from wild ungulates can be extensive, varying widely among continents and countries, with Europe having the highest number of wildlife-damage compensation schemes and the highest amount of compensation paid (Ravenelle & Nyhus, 2017). However, the costs are often unclear since data on wildlife-related crop damage are unavailable or limited due to the lack of monitoring programs (Linnell et al., 2020; Reimoser & Putman, 2011). In some European countries, however, documented compensation payments for crop damage by wild ungulates reaches >10 million euro in certain years (Linnell et al., 2020).

High risk of crop damage can lead to farmers adjusting their crop choice to reduce grazing pressure by wild ungulates. For example, in areas with high ungulate densities in Sweden, farmers may switch to crops that are less attractive to ungulates and less prone to damage (Åberg, 2017; Statens Offentliga Utredningar, 2014). Thus, the risk of crop damage may be preventing farmers from choosing the most profitable crop, and from producing a mix of roughage (e.g. silage) and concentrates (e.g. cereals) necessary in raising livestock. With ungulates increasing both in numbers and distribution throughout Europe (Apollonio et al., 2010; Linnell et al., 2020; Thulin et al., 2015), there is a growing need to understand the drivers behind the damage they cause on farmland. Successful ways to reduce this damage will ultimately depend on a better understanding of the dynamic interactions between the use of agricultural lands by ungulates and farmers. In this article we developed and tested a detailed conceptual model of these interactions and the direct and indirect drivers of crop damage to address these knowledge gaps.

1.1 | Conceptual model of crop damage

Ungulate densities have been suggested to be an important direct driver in determining the intensity and distribution of crop damage (Bleier et al., 2012, 2016; Kupferschmid et al., 2020) (path d in Figure 1). However, behavioural responses of the ungulates may result in additional density independent damages, or alter the degree of density dependence. Thus, it is important to include factors that can influence ungulate behaviour and potentially act as indirect drivers of crop damage when aiming for mitigating damage.

The availability and quality of forage across the landscape, here referred to as the foodscape [Searle et al., 2007], are important drivers of foraging behaviour, influencing ungulate habitat selection and space use across spatial and temporal scales (Senft et al., 1987) as well as influencing densities, by determining the carrying capacity (Allen et al., 2017). Forage availability importantly influences how ungulates affect human land use, with lower damage levels in areas with high availability of natural forage (Herfindal et al., 2015; Jarnemo et al., 2014; Kupferschmid et al., 2020; Månsson, 2009; Pfeffer et al., 2021). Thus, the effect of the foodscape on variation in crop damage within a landscape can be: (1) direct—(i.e. density independent) the foodscape influences foraging behaviour by steering ungulates spatio-temporal use of the landscape, including crop fields (path c1 in Figure 1) and (2) indirect—through the foodscape influencing ungulate densities (i.e. density dependent; path b1 + d in Figure 1).

Moreover, animals also face trade-offs between finding food and reducing predation risk (Brown et al., 1999). Prey can respond to predation risk by altering their behaviour, including foraging in less risky habitats or changing time allocation to feeding (Bergerud et al., 1983; Blumstein & Daniel, 2002; Creel et al., 2005; Lima & Dill, 1990; Thaker et al., 2011). The term landscape of fear is used when prey respond to spatial variation in predation risk, for example, by adjusting their foraging-site selection (Laundré et al., 2010). Thus, fear-inducing practices to mitigate crop damage, such as hunting and scaring, may drive variation in animals' spatial and temporal use within the landscape as it influences their perception of predation risk (Gaynor et al., 2019). However, these practices may also influence ungulate densities across the landscape through reducing the total number of animals in the landscape via killing or scaring (path b2 + d in Figure 1). Fear has been shown to have strong community level effects and may influence population abundance and fecundity partly due to the consequences of the reduction in time spent foraging, resulting in fewer offspring (Zanette & Clinchy, 2020). Thus, we assume that the landscape of fear, similar to the foodscape, will have both a direct (i.e. density independent; path c2 in Figure 1) and an indirect effect (Path b2 + d in Figure 1) on crop damage.

The foodscape and the landscape of fear are under constant influence by diverse human management practices and interests. Diverse, and sometimes conflicting, human interests determine the tolerated population densities of wildlife (Gordon et al., 2004; Menichetti et al., 2019), as wildlife deliver ecosystem services such as hunting and wildlife tourism, and limit others such as food production (Widemo et al., 2019). Landowners aiming for recreational hunting or ecotourism (Gordon et al., 2004; Menichetti et al., 2019) often maintain high ungulate densities by increasing food availability via supplementary feeding or habitat management (e.g. sowing dedicated game crops) (Cooper et al., 2006; Smith, 2001), thus intentionally changing the foodscape to benefit game. Likewise, landowners aiming for agricultural profit may manipulate the foodscape for increasing crop yield, crop performance and productivity (Nkurunziza et al., 2020). Human goals and management strategies, thus directly influence both forage availability and forage quality in agricultural fields and the surrounding landscape (path a1 in Figure 1). Similarly, land owners may intentionally or unintentionally

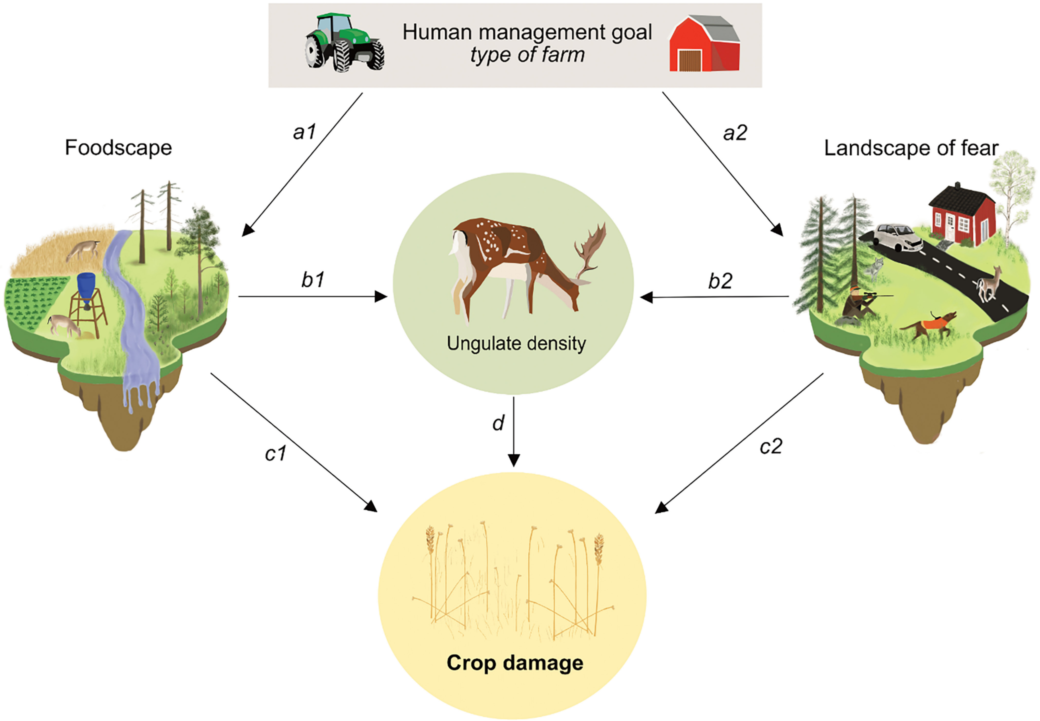

FIGURE 1 Conceptual model illustrating direct and indirect effects between human management goals, foodscape, landscape of fear and ungulate density on crop damage. Human management goals (the type of farm) can directly influence the foodscape and the landscape of fear (paths a1 and a2). The foodscape and landscape of fear can directly influence ungulate density (path b1 and b2) and also crop damage (path c1 and c2). Ungulate density can directly influence crop damage (path d), meaning that there is an indirect link from the foodscape and landscape of fear to crop damage via ungulate density (path b1 + d and b2 + d), as well as indirect links from management goal on crop damage via foodscape and landscape of fear (path a1 and a2 + c1 and c2), and ultimately from management goal via foodscape and landscape of fear, via ungulate density (path a1 and a2 + b1 and b2 + d).

shape the landscape of fear depending on their management goal and strategies. Specifically, farmers aiming for high crop yields often conduct different actions to reduce negative impact of wildlife by increasing the hunting pressure or using scaring practices to reduce damage on fields (Bonnot et al., 2013; Geisser & Reyer, 2004; Pęksa & Ciach, 2018; Setsaas et al., 2018; Vistnes & Nellemann, 2007). Hence, farmers' practices directly influence the landscape of fear depending on their management goals (path a2 in Figure 1).

A major limitation of previous studies is that they have not managed to disentangle individual effects of the drivers of crop damage, such as foodscape versus landscape of fear and whether the effects are density dependent or independent (i.e. direct or indirect) since many studies assess them separately (Corgatelli et al., 2019; DeVault et al., 2007; Naughton-Treves, 1998; Retamosa et al., 2008).

Moreover, we lack an understanding of the dynamic interaction between ungulate and human behaviour. In such dynamic interactions, ungulates respond to foodscapes and landscapes of fear that are (un)intentionally shaped by human land use, but human land use also responds to the behaviour of the ungulates. Understanding these interactions between human behaviour (in terms of their management goals and practices), and ungulate behaviour and their effects on crop damage calls for an alternative type of data collection as it deals with people's motivation as well as animal behaviour. In this study, we approach this challenge by applying an interdisciplinary approach that combines social survey data to quantify the human management goals and behaviours with ecological experimental field data on ungulate densities, foodscape and crop damage. We then use a path analysis to investigate direct and indirect effects on crop damage according to the above-described conceptual framework (Figure 1). Multivariate modelling approaches such as path analysis can provide useful insights in complex systems like these. They allow researchers to simultaneously test complex direct and indirect links between several dependent and independent variables and thereby identify if mediation occurs (Ahn, 2002; Lam & Maguire, 2012).

Unfortunately, the fact that agriculture in many areas, including our study area in southern Sweden, has been adapted to minimize ungulate damage by switching to less attractive crops, particularly in areas with high ungulate density, limits the potential to study the full extent of the foodscape (i.e. strong contrasts in crop quality) in existing agricultural landscape. Therefore, we manipulated the agricultural foodscape experimentally, by contracting farmers to sow crops (oat) they normally would have avoided due to the risk of high levels of crop damage. Thus, we created a strong experimental variation in the foodscape in the form of fields planted with crops that are very attractive to ungulates versus crops that are much less attractive. On top of this, we included a large number of farmers that varied widely in their main management goals (intensive crop production versus strong focus on wildlife use and situations in between) and, therefore, their potential management practices. Using questionnaires we collected detailed information about these management goals and practices. The combination of our interdisciplinary approach with experimentally manipulating the foodscape on a large scale, allowed us to investigate how human management goals and practices influence the foodscape and landscape of fear and ultimately ungulate densities, and crop damage on fields.

2 | MATERIALS AND METHODS

2.1 | Study area and study design

The study was performed in the county of Södermanland, in the hemiboreal climate zone of southern central Sweden (58.96° N, 17.15° E). The mean monthly temperature ranged between 5 and 20°C during the study period (April–August 2020) and mean monthly precipitation ranged between 25 and100 mm from April to August 2020 (Swedish Meteorological and Hydrological Institute [SMHI], 2021). The region is composed of a mix of boreal forests and agriculture with 20%–39% of the total land area being agricultural land (Jordbruksverket, 2020a). The agricultural land is comprised of leys (hereafter grass), cereals and rape seed (*Brassica napus*) as the three most common crop types. The three dominating cereal crops are wheat (*Triticum* spp.), barley (*Hordeum vulgare*) and oat (*Avena sativa*) (Jordbruksverket, 2020b). The average annual yields in 2020 in the county were 7240 ± 65 kg winter wheat/ha (mean ± SD), 4230 ± 140 kg barley/ha, 4510 ± 131 kg oats/ha, 2680 ± 383 kg grass/ha and 3470 ± 38 kg rape seed/ha (Jordbruksverket, 2020c). In addition to crop fields, the area consists of cattle farms and a relatively large number of estates where game management and hunting is an important part of the land use, including those who sell hunting opportunities. The diversity in land use and management is creating conflict in the area, where farmers are concerned about crop damage by the high population densities of wild ungulates (Åberg, 2017).

Moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) coexist in the study area. The populations of these ungulates are managed through regulated annual hunting, and harvest statistics can be seen as indices of relative abundance. During the hunting season 2019/2020, the following number of ungulates were harvested per 1000 ha in the study area: ~69 fallow deer, ~14 wild boar, ~5 roe deer, ~2 Moose and ~2 red deer (moose data: Länsstyrelserna (2021); other ungulates: Svenska Jägareförbundet (2021)). As an important objective of this study, we wanted to test how the type of crop, that is, quality or palatability to ungulates, affects crop damage. For this purpose, we selected oat as an attractive nutrient-dense crop (to ungulates) and grass as a less nutrient-dense crop (Felton et al., 2021). Due to the high densities of ungulates in the study area, most farmers had already switched to the production of grass at the time of our study, as they perceived high damage on oats (Åberg, 2017). We, therefore, specifically approached farmers and financially compensated them to grow oats. Our aim with this was to set up a balanced experimental design with a similar number of oat and grass fields, diversifying quality of crops and simulating a foodscape consisting of both attractive, nutrient dense (oat fields) areas and less attractive, less nutrient dense (grass fields) areas. However, we only managed to convince farmers to grow oats on 16 fields and thus ended up with 16 oat fields and 32 grass fields. The fields were spaced in a systematic manner with approximately 3 km between each other aiming for independent fields not being used by the same ungulate individual. Five of the fields had a shorter distance between each other due to logistical and natural circumstances, with a minimum distance of 1 km.

We measured crop damage by ungulates on these 48 agricultural fields (Figure 2b) by comparing crop biomass between 2.3 × 2.3 m fenced exclosure plots (with a 1.6 m tall metal net to prevent ungulate grazing) and unfenced paired grazed plots. Within each field, we placed three pairs of exclosures and grazed plots with 5 m distance between paired plots and each pair situated at the same distance to (i.e. parallel to) the field edge. Per field, we placed one pair in the centre of the field (furthest distance to any field edge), one pair 10 m from a forest edge and one pair 10 m from a non-forest edge (Figure 2c). Forest was mapped using the national ground cover data in QGIS (QGIS Development Team, 2021). In total, we thus had 144 pairs of exclosures and grazed plots on 48 agricultural fields. We erected the exclosures on all fields (oat and grass) around 20 April 2020, coinciding with the sowing of the oat fields.

2.2 | Ecological data collection

2.2.1 | Crop damage

To estimate biomass loss (crop damage) on fields caused by ungulates, we took biomass measurements manually by harvesting the exclosures and the grazed plots using electric scissors just before the farmer would harvest the field. A buffer zone of 0.65 m was applied in the control plots and the exclosures to account for potential edge effects, thus biomass was only collected from a 1 m^2 plot in each control and exclosure. In addition, in the fields with oats, we collected the panicles and the straws above 5 cm separately and weighed them. Samples were stored in paper bags and frozen. All samples were dried at 65°C in drying cabinets for 48 h. Farmers harvested all grass fields, except one, multiple times. On these fields,

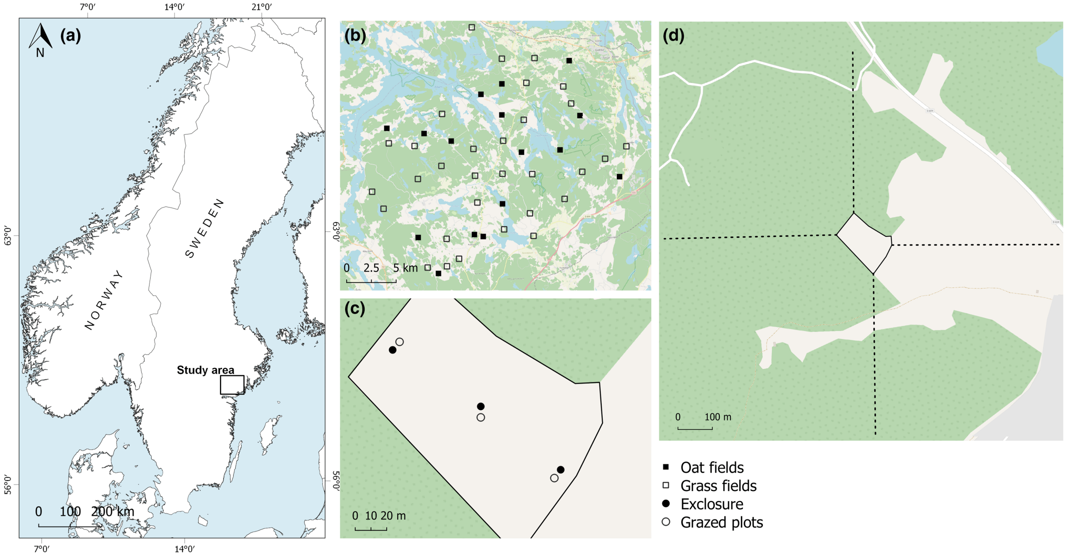

FIGURE 2 (a) Location of the study area within Sweden, (b) map of the study area with distribution of experimental fields (oat fields as black squares, grass fields as white squares, green colour indicates forest and white/cream colour represents non forest), (c) the placement of pairs of exclosures (black circles) and grazed (white circles) plots and (d) the distribution of the four 500 m transects in each cardinal direction from the field edge.

we took biomass measurements both before the first harvest in late May to early June 2020, and after the second harvest by the end of July to early August 2020. For grass fields, the exclosures were removed prior to harvest and replaced immediately after each harvest at the exact same position using the already existing holes from the poles.

Based on the biomass measurements in dry weight, we calculated difference in biomass between exclosure and grazed plots, which was later calculated into % biomass loss. The precision of the balance measured to the nearest 0.1 g. An average of the three exclosures and three grazed plots per field was used in the analyses.

2.2.2 | Biomass production on fields

To get an estimate of how much biomass the field would have produced without ungulate grazing, as part of the foodscape, we calculated biomass produced per field. For this, biomass in dry weight inside the exclosures was converted into biomass in gram per m^2 and further into biomass in gram per field. The area of the field was estimated using the function $area in the field calculator in QGIS.

2.2.3 | Alternative forage availability

We measured alternative forage availability surrounding the fields along 500 m transects in each cardinal direction from the field edge in July 2020 (Figure 2d). We used a modification of the step-point method (Evans & Love, 1957). The step-point method allows for quantification of food items (vegetation) at different foraging heights. For this we used a 3 m wooden pole (3 m representing the maximum browsing height for the largest ungulate, moose) (Spitzer et al., 2021). We took measurements every fifth metre along the transects (see Appendix for species list) resulting in 100 measurements per transect, 400 per field. At every fifth metre, the pole was placed at the tip of the boot and all species that touched the pole were recorded as present in each of the height classes. Based on the forage availability data and on previous work on diet use of the ungulates in this system (Spitzer et al., 2020), we identified five key forage groups comprising food items being important for all four ungulate species; Ericaceous shrubs: (bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*)), birch: (downy birch (*Betula pubescens*) and silver birch (*Betula pendula*)), other deciduous trees: (oak (*Quercus robur*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willow (*Salix* spp.)), graminoids and forbs. Based on this, we calculated the proportion of the key forage species groups per transect. An average of the four transects was calculated to give us one alternative forage availability index per field.

2.2.4 | Ungulate density

To get an estimation of ungulate density of the surrounding area, we conducted a pellet count survey in June 2020 during the early growing season. We were not able to measure pellet counts on the fields due to high vegetation and thus used the pellet counts in the surrounding area as a proxy for ungulate density in the local area, including the fields. We measured pellets as number of pellet groups in 100 m^2 circular plots distributed at 0, 100, 200, 300, 400 and 500 m along the above-mentioned transects starting from the field edge (Figure 2d) making 24 pellet count plots per field. Pellet groups were defined as a group, if consisting of ≥20 pellets for moose and ≥10 pellets for all other ungulates. Moose and red deer were estimated within a 5.64 m radius (100 m^2), fallow and roe within a 1.78 m radius (10 m^2). We counted only pellet groups that had been deposited after the leaf-fall of the previous autumn; that is, pellet groups that were deposited above the leaf litter and not heavily decomposed. Because we were interested in the overall influence of ungulate species on crop damage, and not species specific effects on crop damage, we combined the pellet counts into one ungulate index. Another reason for combining pellet counts of individual species into one index is that pellets of several of the species in our study area (specifically roe, fallow and red deer) are very difficult to differentiate (Spitzer et al., 2019). We divided the number of pellet groups along transects by the total area sampled for all transects (around the field), thus only considering the actual area sampled. We thus ended up with one ungulate index per field.

2.3 | Social data collection

We developed a questionnaire to collect information on management goals and practices conducted at three different levels: the whole farm, the surrounding area (500 m area surrounding the field) and on the specific field included in the study. To identify the human management goal on each farm (farm level), we asked respondents to specify 'what is the dominant land use type on your farm' giving them six answer alternatives (crop production, meat productions, dairy production, equine husbandry, hunting/game keeping and forestry). With respect to management practices on field level, respondents were asked 'which of the following management options did you carry out on your field in order to decrease damage', giving them nine answers alternatives (supplementary feeding, fencing, extended hunting during regular hunting season, protective hunting outside regular hunting season, fear-inducing measures using: scarecrow, sound, human presence or dog; and none of the above). Each response option also included three alternatives related to the frequency of implementation: sporadic implementation throughout the growing season, implementation for half of the growing season or implementation for the entire growing season.

Note that a 'Yes' answer for supplementary feeding could imply that supplementary feeding was conducted on the field or in close vicinity of the field, that is, field edge. Furthermore, with respect to management practices conducted in the surrounding area, a map of the field with a marked area of 500 m surrounding the field was attached to the survey. Respondents were asked 'which of the following management options were carried out inside the marked area', given the same nine answer alternatives stated above.

We sent the questionnaire to all involved farmers in our study. Several of the 48 fields were used by the same farmer and, as a result, the survey was sent to a total of 35 respondents. Of those, 31 farmers representing 44 fields responded, which corresponds to a response rate of 88%. Due to restriction in the number of variables that could be used in the analysis, based on sample size, we could not include management practices on both the field level and in the surrounding area in the model. Because of our ultimate question being what influences crop damage on the fields, and because uncertainty increases in answers on the surrounding area (e.g. the respondent might not own all of the land in the 500 m surrounding area), we chose to include management practices on field level for further analysis. However, to better estimate the direct impact from hunting on ungulate density, we included answers about hunting in the surrounding area in the analysis, but this variable was not linked with human management goal due to the above-mentioned uncertainty. Management practices in order to decrease damage at the field level were grouped into three separate variables: hunting (including extended hunting during regular hunting season and/or protective hunting outside regular hunting season), the answers were assigned scores ranging from 0 to 3. A score of 0 indicated no hunting conducted, a score of 1 represented sporadic hunting during the growing season, a score of 2 indicated hunting during half the growing season and a score of 3 represented hunting during the entire growing season. The scores were then summed, and the resulting sum was utilized in subsequent analyses. Fear-inducing actions/scaring (including presence of scarecrows, use of sounds, human presence, and/or dog presence, the answers assigned scores ranging from 0 to 3. A score of 0 indicated no scaring conducted, a score of 1 represented sporadic scaring during the growing season, a score of 2 indicated scaring during half the growing season and a score of 3 represented scaring during the entire growing season. The scores were then summed, and the resulting sum was utilized in subsequent analyses) and supplementary feeding where the answers similarly were assigned scores ranging from 0 to 3. A score of 0 indicated no supplementary feeding conducted, a score of 1 represented sporadic supplementary feeding during the growing season, a score of 2 indicated supplementary feeding during half the growing season and a score of 3 represented supplementary feeding during the entire growing season. The scores were then summed, and the resulting sum was utilized in subsequent analyses. Fencing was excluded in the analysis since none of the landowners used this method. Management goal at the farm level was pooled into one variable and labelled '−1' for hunting/game keeping, '1' for agriculture and '0' for both, with agriculture being comprised of crop production, meat production and equine husbandry. Forestry was excluded from the analysis due to low sample size, that is, very few landowners had forestry as their main goal.

2.4 | Statistical analysis—PLS application

We used partial least squares (PLS) path analysis to investigate indirect and direct effects of ungulate density, foodscape, landscape of fear and human management goal on crop damage and to test the hypothesized conceptual model shown in Figure 1. PLS is a specialized form of path analysis that tries to maximize the explained variance in the model (Eriksson et al., 2006; Vinzi et al., 2010). PLS path models, in contrast to normal path analysis, are less conservative regarding sample sizes, residual distribution and measurements scales (Mateos-Aparicio, 2011) while still allowing for a complex model for relatively small number of independent observations. Analysis was conducted in the program SmartPLS3 (Ringle et al., 2015). Before fitting the model, all variables were checked for multicollinearity (Pearson's $r \geq +0.7$ or ≤ -0.7). We used language of evidence according to Muff et al. (2022), using the p-values as cut-off values accordingly: little or no evidence of effect, $p = 1–0.1$; weak evidence, $p = 0.1–0.05$; moderate evidence, $p = 0.05–0.01$; strong evidence, $p = 0.01–0.001$; and very strong evidence $p = 0.001–0.0001$ (Muff et al., 2022).

3 | RESULTS

Twenty-seven percent of the total variation in crop damage (i.e. percentage reduction in yield in controls as compared to exclosures) was explained by all predictors together (Figure 3). The average biomass on fields was 1349.7 kg (SE: 306.83, min: 112.48 kg, max: 12,510 kg). The biomass loss on fields caused by grazing ungulates (i.e. crop damage) averaged 41% (SE: 0.04) with a maximum of 99% and min of 0. The average alternative forage availability surrounding fields represented as an average proportion of four transects per field was 36% (SE: 0.02, min: 0, max: 76%). The average ungulate density represented as pellets per square meter was 0.08 (SE: 0.01, min: 0, max: 0.53). Thirty-one percent of the total variation in ungulate density was explained by variables representing the foodscape, landscape of fear and human management goals (Figure 3).

3.1 | Variables (other than management goal) influencing crop damage

We found strong evidence for the choice of crop type influencing crop damage ($\beta = -0.886$, $p = 0.008$; $f2 = 0.207$, Figure 2), with higher biomass loss on oats (54% on average and standard error of 9%) than on grass fields (34% on average and standard error of 4%). We found no evidence for any other direct effect between foodscape or landscape of fear variables and crop damage.

3.2 | Variables (other than management goal) influencing ungulate density in the landscape

We found moderate evidence that supplementary feeding had a positive effect on ungulate density ($\beta = 0.406$, $p = 0.044$; $f2 = 0.205$, Figure 2). The mean ungulate density on fields with supplementary feeding was 0.14 pellets/m^2 (SE: 0.05), while mean ungulate density

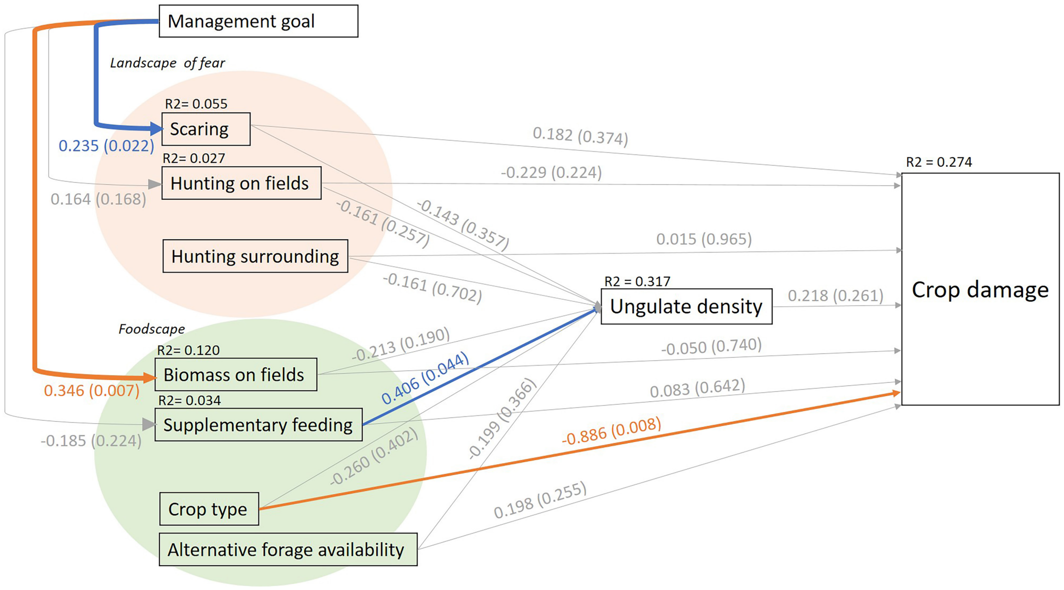

FIGURE 3 Path analysis/PLS results showing direct effects of foodscape, landscape of fear, human management goals and ungulate index on crop damage. Values in the figure are path coefficients (direct effects) and p-values. Positive path coefficients from the management goal box implies positive effect from farms with agricultural goal. Colours of arrows represents the strength of evidence based on p-value. Orange = strong evidence of effect ($p = 0.01–0.001$). Blue = moderate evidence of effect ($p = 0.05–0.01$), according to Muff et al. (2022).

on fields without supplementary feeding was 0.06 pellets/m^2 (SE: 0.008). Besides that, none of the other foodscape and landscape of fear-related variables had a direct effect on ungulate density.

3.3 | Influence of human management goal on crop damage and ungulate density

The management goal of the farm had significant influence on the management practices performed. We found moderate evidence that the management goal determined scaring practices ($\beta=0.235$, $p=0.022$, $f2=0.058$). Expectedly, landowners having agriculture as their main goal were more likely to scare ungulates than landowners having hunting/game keeping as their main goal. We found that strong evidence suggested that landowners with agriculture as their main management goal had significantly higher biomass on their fields compared to landowners with a hunting/game keeping goal ($\beta=0.346$, $p=0.007$, $f2=0.136$). We found no evidence of management goal affecting the presence of supplementary feeding on fields ($\beta=-0.185$, $p=0.224$, $f2=0.035$) or hunting on fields ($\beta=0.164$, $p=0.168$, $f2=0.028$). We found moderate evidence for a negative total indirect effect of management goal on ungulate density ($\beta=-0.209$, $p=0.011$, Table S1), meaning the results of all indirect effects of management goal on ungulate density (via supplementary feeding, scaring, hunting on fields and biomass on fields). This implies that practices conducted by agricultural farms led to lower ungulate densities. Estimates for all indirect and total effects can be found in Table S1.

4 | DISCUSSION

We found that management goals such as agriculture and game keeping directly influenced the foodscape and the landscape of fear for ungulates, by influencing the production biomass on fields, and by influencing the amount of scaring practices conducted on the fields. The crop type influenced crop damage, with higher levels of damage on oats compared to leys, showing the importance of the food quality. Overall, we show that a simple decision such as crop choice can greatly influence ungulates' impact on agriculture, and that none of the other foodscape and landscape of fear measures came even close to having this direct effect.

One reason for the strong effect of crop type and the lack of influence from the other variables may be due to a frequency-dependent selection, that is, that selectivity of a food item will increase if its availability is low at landscape level (Greenwood & Elton, 1979). High ungulate densities in the study area (fallow deer in particular) have led to farmers adapting their management by growing less attractive crops, in order to decrease ungulate damage. Therefore, nutrient-dense palatable cereal crops like oats are relatively rare in the area. The fact that we increased the number of cereal fields in a landscape, where these fields are rare, might have led to a strong selection of oat fields, and thus potentially overshadowing the effects of surrounding foodscape and landscape of fear. This frequency-dependent selection has been seen also in forest ecosystems where a higher number of available stems of the highly selected food item, the scots pine (*Pinus sylvestris*), results in a lower relative level of browsing damage on pine due to a dilution effect (Bergqvist et al., 2014; Díaz-Yáñez et al., 2017; Pfeffer et al., 2021). Furthermore, as in the agricultural landscape (with farmers switching to less palatable grass fields instead of cereals), forest owners are taking action in order to decrease browsing damage, currently regenerating forests with less palatable spruce on sites more suitable for pine (Felton et al., 2020; Lodin et al., 2017). Moreover, similar actions in the agricultural landscape will thus most likely lead to increased grazing on the remaining fields of palatable crops, possibly influencing damage patterns in the landscape in opposite direction of what is desired. However, we can only speculate as to why the strong selection for oat would lead to a lack of strong influence from the other landscape variables. This is because our sample size limited our possibilities of investigating the relative effect of the explanatory variables on crop damage on the two different crops separately.

Surprisingly, we did not find any evidence for an effect of ungulate density on crop damage, something that has been suggested to be an important variable explaining crop damage in other studies (Bleier et al., 2012; Corgatelli et al., 2019). One explanation may be that the ungulate densities in our study area are generally high everywhere and even the relatively low densities within our study area are high compared to densities elsewhere. As a result, even comparatively low densities (for our area) likely caused high levels of damage. Furthermore, since we were not able to measure pellet counts on the fields due to high vegetation, the pellet counts we performed in the surrounding landscape potentially underestimated field use and actual grazing pressure on the fields. However, it is reasonable to believe that ungulate density in the close vicinity of the field reflects the use of the field as well. We thus assumed that a high ungulate density in the area surrounding the field also means a high use of the fields. Furthermore, studies have showed that the effect of ungulate density can be overshadowed by other factors in the surrounding landscape (Felton et al., 2022; Jarnemo et al., 2014). For example, food availability can show higher significance than ungulate density in explaining damage (Felton et al., 2022; Jarnemo et al., 2014). Our results show a similar pattern, since the effects of features of the foodscape (i.e. crop type) show a stronger influence on crop damage than ungulate density. Supplementary feeding had a positive influence on ungulate density. This implies that in the areas with frequent supplementary feeding, local ungulate density is higher. The manipulation of the foodscape seems not only to have an influence on crop damage (by crop type), but also on ungulate density. Moreover, our result shows that the major influence of supplementary feeding is on ungulate density and not on crop damage on fields.

4.1 | Influence of human management

Both the foodscape and the landscape of fear were influenced by the human management goal and the resulting management practices. Biomass on fields, being a proxy of forage productivity on the fields, was higher on farms with an agricultural goal compared to farms with a game keeping/hunting goal, implying that important features of the foodscape are driven by how the farm is managed. This is further supported by Nkurunziza et al. (2020) who found that the productivity on crop fields was largely driven by differences in farming practices guided by the category of farm. Thus, depending on how landowners decide to manage their farm, ungulates navigating in that landscape will experience differences in the foodscape. Furthermore, our study shows that scaring practices were more often conducted on farms with an agricultural goal. This makes sense since farmers that aim for high agricultural yields and production (i.e. agricultural management goal) have a greater need to invest in scaring practices to reduce negative impacts by wildlife, that is, directly influencing the landscape of fear. Therefore, human management goals direct what management practices will take place in a particular area, which in turn influences different features of the foodscape and landscape of fear. Moreover, when comparing the standardized ß coefficients, we can conclude that human management goals have a stronger effect on the foodscape than the landscape of fear, with a higher ß coefficient for biomass (0.392) than for scaring (0.149). Furthermore, the fact that we found strong evidence for a total indirect effect of human management goal on ungulate density implies that the actions conducted depending on the type of farm not only influence the landscape ungulates navigate in but also the ungulate density in the landscape. However, more studies are needed in order to disentangle specific indirect effects of human management goal on ungulate density.

4.2 | Limitations of study and future research needs

In this study, we were restricted to a fairly low sample size (for this type of complex system), reducing the statistical power of the model and making it difficult to disentangle relative impacts. One possible reason for the lack of relatively strong effect sizes in our model is also that our measurement of crop damage may have been insufficient in capturing the possible variation in damage caused by our explanatory variables. We were restricted to biomass measurements from three exclosures and three grazed plots per field (three pairs). Thus, only investigating grazing impacts in a relatively small area of the field.

In our study, we examined a complex system characterized by multiple factors that influence ungulate density and impact. It is important to acknowledge that we may have inadvertently overlooked and excluded variables that likely play an important role in determining ungulate density and their landscape impact. This may be an important explanation for the fact that our model only explained 27% of the variation in crop damage. For instance, landscape features such as the proportion of surrounding forest and the distance to forest cover, which provide safe shelter, have been recognized as important determinants of ungulate landscape use (Bleier et al., 2012, 2016; DeVault et al., 2007). Similarly, other variables representing the landscape of fear, such as settlements, roads hiking trails and human presence, are known to influence how ungulates distribute across the landscape (Menichetti et al., 2019; Pęksa & Ciach, 2018). However, due to the limitations of our sample size, we were constrained in the number of variables we could include in our model. Therefore, future research should consider incorporating these additional features to gain a better understanding of the factors that determine crop damage. Moreover, possible scaling issues and spatial resolution could have impacted the power of our model. The effects of management actions on ungulate density and crop damage might vary across different scales, including within-fields, between-fields and in the larger landscape. However, due to logistical reasons, we were limited in measured the potential response at various scales. Consequently, we may not have adequately accounted for the influence management actions on ungulate density and crop damage. All together, these factors likely contributed to the relatively low explanatory power of our model and may also explain why some management actions did not yield the expected results (e.g. the lack of effect of hunting on ungulate density). By taking these limitations into account, future studies may provide a more comprehensive picture of the underlying factors influencing ungulate impact.

5 | CONCLUSIONS

To conclude, crop damage by ungulates is part of a complex web of multiple influencing factors with indirect and direct relationships across several spatial levels. By tackling this complex system using a novel interdisciplinary approach, and incorporating ecological drivers as well as human practices, we were able to show that depending on how humans manage their land, they will directly influence the landscape ungulates navigate in by modifying the foodscape and the landscape of fear, consequently influencing ungulate density in the area and the impact ungulates have on the landscape. Moreover, we can conclude that crop type was the strongest driver of crop damage. Implying that farmers can influence damage levels by adapting choice of crop, as indicated in our study area with the reduced levels of cereal crops as a result of high ungulate levels. This pattern may in the long run influence damage patterns in the landscape in opposite direction of what is desired, with high levels of damage on remaining cereal fields, something that of course is of high societal relevance knowing the large economic impact crop damage may have.

Furthermore, the understanding that crop type plays an important role in determining crop damage can offer valuable insights for management recommendations aimed at influencing animal behaviour and mitigating negative impacts. For example, by strategically providing attractive forage in specific locations and designating these areas for ungulate grazing, it may be possible to influence damage patterns in the landscape by diverting animals away from areas where their impacts are unwanted. However, it is important to consider that the intensity of ungulate use will likely be higher in the close proximity of such sacrificial areas, potentially resulting in increased impact in such nearby areas (Gundersen et al., 2004; Månsson, 2009; van Beest et al., 2010).

There is a need for a management approach that involves the foodscape on a larger scale, beyond property borders of land owners and a need for collective action in order to decrease individual risk. We suggest that more studies are needed using this type of path analysis on larger scales and using larger sample sizes, to tackle complex issues such as wildlife damage to crop production and human–wildlife conflicts. Our findings highlight that it is important to incorporate human actions on multiple levels when assessing the potential drivers behind damage caused by free-ranging ungulates in managed landscapes.

AUTHOR CONTRIBUTIONS

Anna Widén, Fredrik Widemo, Joris P. G. M. Cromsigt, Annika M. Felton, Sabrina Dressel and Navinder Singh conceived the idea and designed the study; Anna Widén collected the data; Anna Widén analysed the data with contributions from Sabrina Dressel, who especially contributed with knowledge on path analysis methodology as well as collecting and treating social data. Anna Widén led the writing of the manuscript, but all authors contributed to drafts and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.nk98sf7xw (Widén et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Parameter estimates (est), standard deviations (STDEV), *T*, *p* values and F2 values, and 97.5% confidence interval of path analysis model, showing direct effects, specific indirect effects, total indirect effects and total effects. *p*-values showing strong evidence of effect ($p=0.01$–0.001) are marked in orange and *p*-values showing moderate evidence of effect ($p=0.05$–0.01) according to Muff et al. (2022), are marked in blue.

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Appendix

Table 1. Parameter estimates (est), standard deviations (STDEV), T, p values and F2 values, and 97,5% confidence interval of path analysis model, showing direct effects, specific indirect effects, total indirect effects and total effects. P-values showing strong evidence of effect (p =0.01 - 0.001) are marked in orange and P-values showing moderate evidence of effect (p = 0.05 – 0.01) according to Muff et al. 2022, are marked in blue.

Variable	est	STDEV	T-value	p-value	97,5% CI	F2
Direct effects						
Crop type → Crop damage	-0.671	0.338	1.985	**0.047**	0.028	0.114
Biomass on fields → Crop damage	0.018	0.152	0.118	0.906	0.304	0.000
Forage availability → Crop damage	0.132	0.177	0.744	0.457	0.480	0.020
Supplementary feeding → Crop damage	0.209	0.182	1.150	0.250	0.528	0.043
Scaring → Crop damage	-0.551	0.429	1.284	0.199	0.362	0.055
Ungulate density → Crop damage	0.132	0.193	0.684	0.494	0.479	0.015
Hunting on fields → Crop damage	-0.027	0.164	0.166	0868	0.276	0.001
Hunting in the surrounding → Crop damage	-0.417	0.329	1.268	0.205	0.250	0.047
Crop type → Ungulate density	-0.409	0.320	1.278	0.201	0.317	0.050
Biomass on fields → Ungulate density	-0.253	0.164	1.543	0.123	0.013	0.078
Forage availability → Ungulate density	-0.132	0.193	0.684	0.494	0.361	0.024
Supplementary feeding → Ungulate density	0.398	0.190	2.089	**0.037**	0708	0.213
Scaring → Ungulate density	-0.438	0.336	1.303	0.193	0.306	0.042
Hunting on fields → Ungulate density	-0.172	0.133	1.294	0.196	0.084	0.034
Hunting in the surrounding → Ungulate density	-0.109	0.388	0.282	0.778	0.771	0.004

Human management goal → Biomass on fields	0.392	0.389	3.027	0.002	0.612	0.182
Human management goal → Supp. feeding	-0.161	0.154	1.049	0.294	0.138	0.027
Human management goal → Scaring	0.149	0.047	3.161	0.002	0.237	0.125
Human management goal → Hunting on fields	0.143	0.128	1.121	0.262	0.357	0.021
Specific indirect effects						
Human management goal → biomass on fields → crop damage	0.007	0.064	0.101	0.913	0.168	
Human management goal → hunting on fields → crop damage	-0.004	0.032	0.122	0.903	0.040	
Human management goal → supp. feeding → crop damage	-0.034	0.051	0.656	0.512	0.022	
Human management goal → scaring → crop damage	-0.082	0.069	1.1896	0.235	0.023	
Human management goal → biomass on fields → ungulate density → crop damage	-0.013	0.025	0.518	0.605	0.019	
Human management goal → supp. feeding → ungulate density → crop damage	-0.008	0.027	0.315	0.753	0.007	
Human management goal → scaring → ungulate density → crop damage	-0.009	0.018	0.469	0.639	0.009	
Human management goal → hunting on fields → ungulate density → crop damage	-0.003	0.009	0.360	0.718	0.004	
Biomass on fields → ungulate density → crop damage	-0.033	0.059	0.562	0.574	0.060	
Supp. feeding → ungulate density → crop damage	0.052	0.087	0.602	0.547	0.294	
Hunting on fields → ungulate density → crop damage	-0.023	0.045	0.499	0.618	0.041	

Hunting in the surrounding → ungulate density → crop damage	-0.014	0.081	0.178	0.859	0.126	
Forage availability → ungulate density → crop damage	-0.017	0.025	0.044	0.392	0.039	
Crop type → ungulate density → crop damage	-0.054	0.098	0.594	0.583	0.059	
Human management goal → biomass on fields → ungulate density	-0.099	0.084	1.181	0.238	0.007	
Human management goal → supp. feeding → ungulate density	-0.064	0.082	0.780	0.436	0.023	
Human management goal → scaring → ungulate density	-0.065	0.056	1.157	0.247	0.018	
Human management goal → hunting on fields → ungulate density	-0.025	0.034	0.720	0.472	0.020	
Total indirect effects						
Biomass on fields → crop damage	-0.033	0.059	0.562	0.574	0.060	
Crop type → crop damage	-0.054	0.098	0.594	0.583	0.059	
Forage availability → crop damage	-0.017	0.044	0.392	0.695	0.039	
Hunting on fields → crop damage	-0.023	0.046	0.499	0.618	0.041	
Hunting in the surrounding → crop damage	-0.014	0.081	0.178	0.859	0.126	
Human management goal → crop damage	-0.146	0.100	1.459	0.145	0.034	
Scaring → crop damage	-0.058	0.114	0.508	0.612	0.072	
Supp. feeding → crop damage	0.052	0.087	0.602	0.547	0.294	
Human management goal → ungulate density	-0.253	0.081	3.112	**0.002**	-0.055	
Total effects						
Biomass on fields → crop damage	-0.015	0.145	0.106	0.915	0.268	
Crop type → crop damage	-0.725	0.326	2.222	**0.026**	-0.040	
Forage availability → crop damage	0.114	0.177	0.646	0.519	0.448	

Hunting on fields → crop damage	-0.050	0.156	0.321	0.748	0.252	
Hunting in the surrounding → crop damage	-0.431	0.313	1.379	0.168	0.172	
Scaring on fields → crop damage	-0.609	0.403	1.513	0.130	0.106	
Supp. feeding → crop damage	0.261	0.166	1.579	0.114	0.543	
Ungulate density → crop damage	0.132	0.193	0.684	0.494	0.497	
Biomass on fields → ungulate density	-0.253	0.164	1.543	0.123	0.041	
Crop type → ungulate density	-0.409	0.320	1.278	0.201	0.214	
Forage availability → ungulate density	-0132	0.193	0.684	0.494	0.3294	
Hunting on fields → ungulate density	-0.172	0.133	1.294	0.196	0.124	
Hunting in the surrounding → ungulate density	-0.109	0.388	0.282	0.778	0.695	
Scaring → ungulate density	-0.438	0.336	1.303	0.193	0.248	
Supp. feeding → ungulate density	0.398	0.190	2.089	**0.037**	0.690	
Human management goal → ungulate density	-0.253	0.081	3.112	**0.002**	-0.055	
Human management goal → biomass on fields	0.392	0.130	3.027	**0.002**	0.602	

Species list

Spruce
Pine
Other conifer
Birch
Rowan
Aspen
Alder
Salix
Oak
Other deciduous
Bilberry
Cowberry
Calluna
Juniper
Raspberry
Labrador tea
Other shrub
Forb
Fern
Moss
Other vegetation

IV

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Playbacks of predator vocalizations reduce crop damage by ungulates

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ABSTRACT

Wild ungulates are a major consumer of agricultural crops in human dominated landscapes. Across Europe, ungulate populations are leading to intensified human-wildlife conflicts. At the same time, ungulates play a vital role in the structuring and functioning of ecosystems, and are highly appreciated for recreational hunting. Thus, managers often face the challenge of maintaining the benefits of having thriving ungulate populations while simultaneously minimizing their negative impacts. Broadcasting playbacks of predator vocalizations (e.g. dogs barking, wolves howling or humans talking) could potentially be used to induce fear and thereby displace or steer behavior of ungulates from conflict-prone sites resulting in reduced visitation and foraging time and consumption. Predator playback experiments in wilderness areas have repeatedly demonstrated to reduce the preys′ resource use and impacts on the surrounding landscape, but this has not been tested in agricultural fields where human-ungulate conflicts are most pronounced. We responded to this need by conducting a predator playback experiment in multiple crop fields in southern Sweden, where multiple ungulate species (fallow deer, roe deer, red deer, moose, wild boar) coexist, using a novel integrated camera trap – speaker system (ABRs) that broadcasts sounds of choice when a camera is triggered by an ungulate. Predator playbacks (wolf, dog, human) reduced deer patch use and crop damage on wheat fields more than playbacks of control sounds (owl, goose, raven). Our results confirm findings from previous studies in wilderness areas, and demonstrate that broadcasting predator playbacks using ABRs may provide an effective tool to reduce crop damage at the scale and duration of our study.

1. Introduction

Wild ungulates can have strong effects on their environment, and in human-dominated landscapes this may lead to conflicts with human land use such as agriculture (Reimoser and Putman, 2014). Ungulate numbers and distribution are increasing across Europe (Apollonio et al., 2010b; Linnell et al., 2020; Thulin et al., 2015) due to better conservation practices, wildlife management actions and increased availability of forage arising from agriculture and forestry practices (Ferretti and Lovari, 2014; Presley et al., 2019). Across Europe, these increasing populations lead to increased crop damage, affecting production and incomes in agriculture (Reimoser and Putman, 2014). Estimating the cost of wild ungulate grazing on agriculture is difficult because many countries lack national monitoring programs (Linnell et al., 2020; Reimoser and Putman, 2014). However, compensation for crop damage by wildlife represents 35% of the total global agricultural compensation (Ravenelle and Nyhus, 2017) and in some European countries reaches up to 13 million euro annually (Linnell et al., 2020). Agricultural impacts of ungulates, such as wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and red deer (*Cervus elaphus*) are thus seen as an increasing problem (e.g. Apollonio et al., 2010a; Bleier et al., 2017; Marchiori et al., 2012; Menichetti et al., 2019; Schley and Roper, 2003).

Although expanding ungulate populations in Europe lead to increasing conflicts with human land use, they also play crucial roles in the functioning of Europe's ecosystems (Linnell et al., 2020). In fact, many stakeholders celebrate the ungulate comeback in Europe and

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emphasize diverse positive impacts of increased ungulate populations (e.g. prey for large carnivores, carrion for scavengers and ecosystem engineers) and as a resource for hunters or wildlife tourism (see Linnell et al., 2020 for a detailed review). Managers thus face the challenge of maintaining and/or promoting these perceived positive values of increased ungulate populations while minimizing their negative impacts. Hence, while population control may in some cases be an efficient management tool to reduce crop damage (Geisser and Reyer, 2004) this may also counteract other management goals aimed at improving hunting, recreational value or conservation. There is thus an urgent need for management approaches that create/aim for variable ungulate densities across the landscape (low in conflict-prone areas, high in natural habitats or where focus is on wildlife use). One such management approach, which is receiving increasing interest, is the use of tools and methods to induce fear (anti-predator responses) to steer the behavior and distribution of wildlife across the landscape (Cromsigt et al., 2013; Garvey et al., 2020; Gaynor et al., 2020). In addition to creating variable densities across landscapes, this approach is also of interest for species that are difficult to control numerically (e.g., wild boar) and because society is increasingly asking for non-lethal tools to reduce conflicts (Blumstein, 2016; Cromsigt et al., 2013; Garvey et al., 2020; Gaynor et al., 2020; Reimoser and Putman, 2014; Shivik, 2006).

The science behind using fear as a tool to influence behavior is based on the so-called “ecology of fear” (Brown et al., 1999). The ‘ecology of fear’ posits that anti-predator behavior is powerful enough to have population-, community- and ecosystem-level impacts (Brown et al., 1999; Lima and Dill, 1990; McNamara and Houston, 1992), as corroborated in a growing number of experiments on free-living wildlife (reviewed in Zanette and Clinchy, 2020). Prey should respond strongly and consistently to the perceived presence of predators (Smith et al., 2017; Zanette and Clinchy, 2020), because the cost of failing to avoid a predator is almost certain death (Lima and Dill, 1990; Bouskila and Blumstein, 1992; Johnson et al., 2013). Consequently, compared to deterrents (e.g. scare crows or lines of flags along fence lines; Shivik, 2006) that do not simulate predator cues using fear as a tool in wildlife management may be more effective (Cromsigt et al., 2013; Garvey et al., 2020; Gaynor et al., 2020; Zanette and Clinchy, 2020). Animals may perceive the presence of predators using visual, olfactory and/or auditory signals (Creel and Christianson, 2008) and respond by either leaving or avoiding the risky area or increasing their vigilance, resulting in reduced time spent foraging (Brown et al., 1999; Lima and Dill, 1990; Kuijper et al., 2014; Gaynor et al., 2020; Zanette and Clinchy, 2020). Broadcasting auditory predator cues has proven to be a particularly effective means of inducing fear responses in wildlife (e.g. Zanette et al., 2011; Hettena et al., 2014; Suraci et al., 2016; Smith et al., 2017; Suraci et al., 2019b).

To develop effective acoustic tools that manipulate fear, one needs to know what auditory cues lead to the strongest anti-predator responses (Garvey et al., 2020; Gaynor et al., 2020; Smith et al., 2020). Prey may perceive and respond to different predators in very different ways due to differences in their vulnerability and/or their anti-predator strategies (Clinchy et al., 2016; Durant, 2000; Zanette and Clinchy, 2020; van Beeck Calkoen et al., 2021; Epperly et al., 2021). Recent worldwide analyses, however, have established that humans may be “super predators” (Darimont et al., 2015; Zanette and Clinchy, 2020) eliciting similarly strong antipredator responses in a wide range of ungulate and carnivore species (Zanette and Clinchy, 2020). Correspondingly, multiple recent predator playback experiments have demonstrated that ungulates and carnivores in Europe, Africa and North America fear hearing the human ‘super predator’ far more than non-human predators (Clinchy et al., 2016; Suraci et al., 2019b; Zanette and Clinchy, 2020).

The effective use of fear as a tool in wildlife management depends on minimizing habituation (Shivik, 2006; Blumstein, 2016; Zanette and Clinchy, 2020). Habituation is governed in part by the time between exposures to an aversive stimulus; irregularity and infrequency lessen the likelihood of habituation (Blumstein, 2016; Zanette and Clinchy, 2020). One should thus be able to minimize habituation by maximizing variation in the characteristics of the aversive stimulus and ensuring exposure is intermittent rather than continuous (Zanette et al., 2011; Garvey et al., 2020; Shivik, 2006). The Automated Behavioral Response system (ABR) represents a newly-developed tool that could be used in an applied setting to implement auditory fear cues while minimizing the chance of habituation at the scale of weeks (e.g. 4 weeks, Suraci et al., 2016; 5 weeks, Suraci et al., 2019b) and even entire breeding/growing seasons (e.g. 4 months, Zanette et al., 2011). This integrated camera trap – speaker system only broadcasts a sound when animal movement activates the camera sensor, thereby ensuring exposure is intermittent. The ABR can moreover be programmed to broadcast any sound in any order, ensuring variation is maximized, thereby further ensuring habituation is avoided (Suraci et al., 2017; Smith et al., 2020).

Systems, such as the ABR, may offer novel ways of applying the ecology of fear to mitigate human-wildlife conflicts. However, most studies using ABRs or similar systems have focused on changes in animal behavior and have not measured the consequences of these behavioral changes on the wildlife’s landscape use and forage resources. Moreover, few have performed studies in the actual management setting where human-wildlife conflicts occur (Smith et al., 2020) but see (Thuppil and Coss, 2016) for the use of playbacks to reduce crop raiding by elephants (*Elephas maximus)* in India. A recent review of the use of frightening devices to protect crops found no examples of the broadcast of predator vocalizations as a measure to protect crops (Enos et al., 2021). Hence, we urgently need more studies that experimentally test these fear-manipulating tools, such as ABRs, in an actual management context and link behavioral responses to the ungulate impacts on the landscape, such as crop damage. In this study, we used ABRs to broadcast predator vocalizations, and thus manipulate fear, to test whether inducing fear can reduce crop damage. In addition, we had two sets of ABRs programmed with different frequencies at which predator and control vocalizations were triggered; a set of ABRs with high frequency of predator playbacks (“high-predator level”) and a set of ABRs with lower frequency of predator playbacks (“low-predator level”). We then compared patch use by ungulates and crop damage between regular camera traps sites (no-sound controls), “high-predator level” ABR sites and “low-predator level” ABR sites.

2. Methods

2.1. Study area description

The study was performed in the county of Södermanland, in the hemiboreal climate zone of southern Sweden (58.963899 N, 17.156465 E, Fig. 1a). The climate is mild with a monthly mean temperature of 16–20 degrees in May-July and mean precipitation of 75–100 mm, (Swedish Meteorological and Hydrological Institute (SMHI), 2021). A mosaic of boreal forests and agriculture characterizes the county with 20–39% of the total land area being used as agricultural land (Jordbruksverket, 2020a). The agricultural land comprises a mixture of crops with cereals (wheat, barley and oat being the three dominant species), grass (leys) and rape seed (canola) (*Brassica napus*) being the three most common crops (Jordbruksverket, 2020b). The average annual yields in the county are 7240 kg/ha (winter wheat), 4230 kg/ha (barley), 4510 kg/ha (oat), 2680 kg/ha (grass) and 3470 kg/ha (rape seed) (Jordbruksverket, 2020c). In addition to crop fields, the area consists of cattle farms and a relatively large number of estates that obtain income from selling hunting rights on several wild ungulate species. These estates maintain high densities of ungulates through supplementary feeding during winter and other forms of wildlife habitat management (e.g., sowing game crops). This diversity in land use is creating conflict in the area, where farmers are increasingly concerned about crop damage by the high-density populations of wild ungulates. Moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) coexist in the study area. The

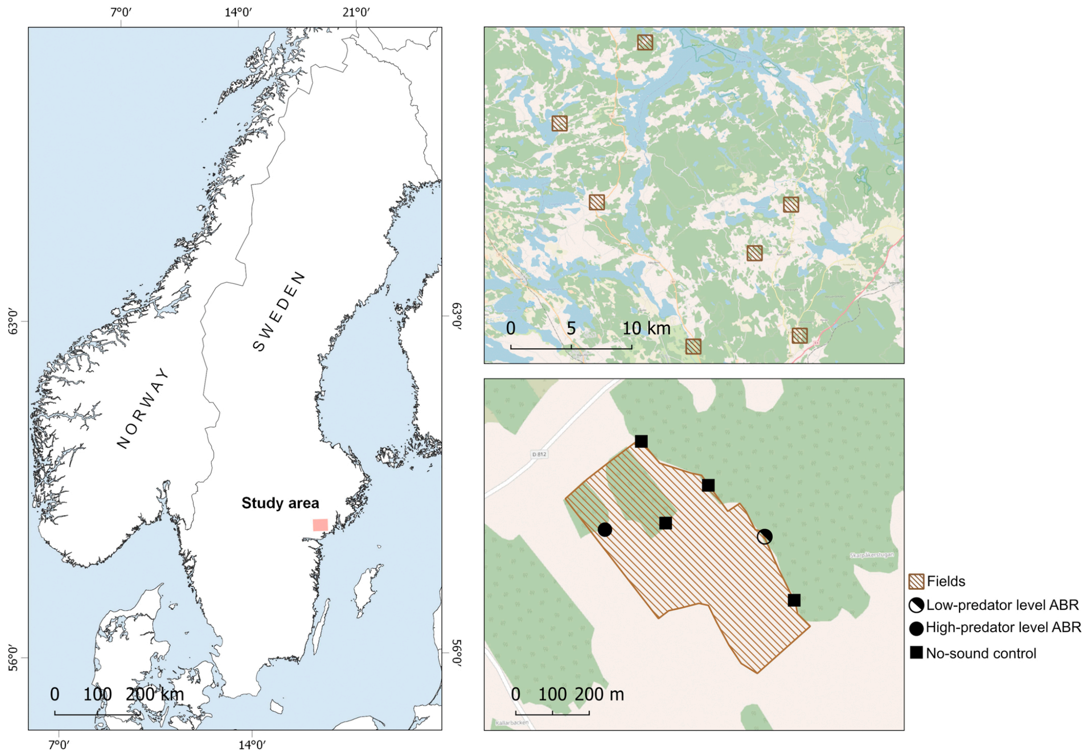

Fig. 1. a) Map representing the placement of study area in Sweden, b) distribution of the 7 fields in the study area and c) placement of 4 camera traps (no-sound controls) and ABRs on one example field. (For color please see online figure)

populations of these ungulates are managed through regulated annual hunting. The main form of hunting is with baying dogs, but sit and wait hunting and stalking occur as well. Hunting is seasonal for the deer species, but is allowed year-round for wild boar. However, baying dogs cannot be used during February-July. During the hunting season 2019/2020, ungulates were harvested at the following rates within the hunting district, indicative of their relative abundances: ~69 fallow deer per 1000 ha, ~14 wild boar per 1000 ha, ~2 Moose per 1000 ha, ~5 roe deer per 1000 ha and ~2 red deer per 1000 ha and (moose data: (Länsstyrelserna, 2021) other ungulates: (Svenska Jägareförbundet, 2021)).

Wolves were absent in the study area and locally extinct since the late 19th century (Ekman, 2010). However, during recent years, observations of single wolves have increased in the area and since 2015 a wolf pack established a territory in the area with 1 confirmed reproduction in 2021. Lynx occur sporadically in the area, but no permanent family groups have been confirmed to date.

2.2. *Experimental design*

Within our study area, we selected seven independent crop fields (Fig. 1b), ranging between 15 and 28 ha in size, sown with winter wheat *(Triticum aestivum)*. We selected fields that were at least 4 km apart, which reflects the average home range size of fallow deer (Borkowski and Pudelko, 2007; Ciuti et al., 2003; Davini et al., 2004). Fallow deer is the most common ungulate in the study area (see above) and responsible for a considerable proportion of the crop damage in the region (personal communication with local landowners). By keeping the 4 km distance, we assumed that our fields were visited by different fallow deer herds. Furthermore, the fields were situated next to country roads, except for one, which was 100 m away from a larger road. Distance to settlements and housing ranged from 100 m to 284 m with an exception of one field having a settlement 50 m from the field edge. All fields had at least one field edge covered by forest.

We experimentally broadcasted predator vocalizations with the objective of increasing perceived predation risk in certain locations of our crop fields. Instead of continuously broadcasting sounds, we used Automated Behavioral Response systems (ABRs) (Suraci et al., 2017), consisting of a video-enabled camera trap (BTC-8FHD-PX; Browning Trail Cameras, Morgan, UT) linked to a playback speaker unit triggered by the camera's activation. The CT activates the speaker unit as soon as a passing animal triggers the passive infrared sensor of the camera. Before the start of the experiment, we searched for locations which were intensively used by ungulates along the edges of all fields (e.g., well-used game trails coming out of the forest into the field, high abundance of dung or tracks). We then confirmed this initial assessment by deploying four camera traps capturing images (HC500; Reconyx Inc., Holmen, WI; from here on referred to as "regular CTs") in the identified spots per field (two fields had five camera traps). We ran those CTs for one week starting 4th of June 2020. Based on this information, we then placed CTs and ABRs on the most highly used parts of each field's forest edges for a six-week long study (Fig. 2). During the first two weeks, we disabled the sound system of the ABRs to allow us to record "pre-playback treatment" differences in ungulate patch use in front of regular CTs and ABRs and contrast ungulate patch use between pre-treatment and during treatment. During these first two pre-treatment weeks, each field thus had six

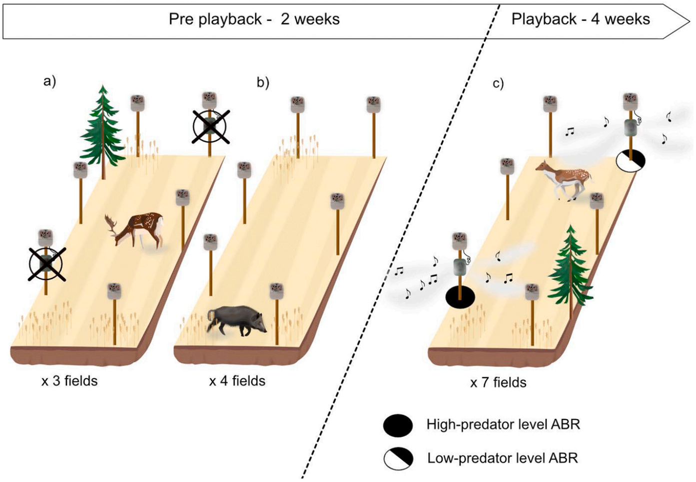

Fig. 2. Explanation of the different study phases and study design. a) Three fields were deployed with 4 camera traps (regular CTs) and 2 ABRs with disabled sound systems during the pre-playback period. B) 4 fields were deployed with 6 regular CTs (2 of them on ABR locations) during the pre-playback period. C) During the playback period, all 7 fields were deployed with 4 regular CTs and 2 ABRs, one with high frequency of predator vocalizations (high-predator level) and one with low frequency of predator vocalizations (low-predator level). During these playback weeks, ABRs and CTs were placed on the exact same spots as during the pre-playback weeks. (For color please see online figure)

cameras, where on four fields these were all regular CTs and on three fields two were ABRs and four were regular CTs. ABRs and regular CTs used different camera trap models (Browning vs. Reconyx) and ABRs recorded videos whereas regular CTs captured images. We used the pre-treatment data to test if this led to detection differences between ABRs and regular CTs.

During the next four weeks, starting June 29 2020, we started the actual playback experiment and placed ABRs on all seven fields at the same locations with activated playback systems. Each field had four CTs and two ABRs at the same locations as we used during the first two weeks (Fig. 2c). During this playback experiment, we broadcasted predator (dog, wolf, human) and non-predator control vocalizations (goose, owl, raven, see below for more details). We refer to the locations of the two ABRs in each field as “experimental plots” whereas the regular CTs in each field served as “no-sound control plots”. On each field, the two ABRs were deployed at least 400 m from each other to ensure that the playbacks broadcasted at one ABR location were not audible at the other. In the field, we could no longer hear the ABRs at a distance of ~150 m, however, as ungulates have better hearing than humans, we decided to place ABRs at least 400 m apart. We also aimed for at least 200 m distance between regular CTs and ABRs, and between regular CTs. On four fields this distance was not possible due to the size of fields and other practical restrictions such as keeping the surrounding habitat similar. In these cases, the distance between regular CTs (the ones without sound playbacks) were a minimum of 100 m. We placed ABRs and regular CTs on 1.5 m high poles, facing a parallel direction along the forest edge. The poles were placed on the field edge in immediate connection to the planted crop and thus also adjacent to the forest edge.

2.3. ABR settings

When an animal triggered the ABR camera’s sensor, the camera started recording a video and the attached speaker started broadcasting a playback from unique pre-determined playlists (see Supplementary Materials for the playlists). These playlists were made up of the vocalizations of different predator and non-predator control (bird) playback types (Hettena et al., 2014; Crawford et al., 2022; Epperly et al., 2021). All of the species whose vocalizations we used were naturally occurring in our study area. The predator vocalizations comprised of dogs (barking), wolves (barking and howling) and humans (talking). As controls, we used the vocalizations of different bird species, similar to previous ABR experiments on the fear responses of ungulates (Crawford et al., 2022; Epperly et al., 2021). In our experiment, we used Barnacle goose (*Branta leucopsis*), Common raven (*Corvux corax*) and Tawny owl (*Strix aluco*), which are all common in our study area and have comparable sound characteristics (e.g. pitch and interval) to those of the predators. By choosing non-predator control vocalizations with similar sound characteristics to the predator vocalizations, we aimed to ensure that any difference in response to predator vocalizations was attributable to perceived predation risk, and not to differences in sound characteristics (e.g. lower vs. higher pitch; Zanette et al., 2011; Hettena et al., 2014; Suraci et al., 2016; Zanette and Clinchy, 2020). We broadcasted different bird species according to the appropriate times in the diel cycle (i.e., goose and raven during the day, owl at night). Note that the species of birds used were not of interest to the study. The objective was to compose a single class of vocalizations, i.e. controls, and hence, as in previous ABR experiments, no analyses were conducted of differences in responses to the different birds.

We used 10 exemplars of each playback type (i.e., species vocalization). The 10 human exemplars consisted of recordings of ten different individuals, 5 females and 5 males, speaking conversationally in Swedish (i.e., reading different texts in a neutral fashion not conveying alarm or threat; following Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019a, 2019b; Crawford et al., 2022). Sound files of dogs and wolves originated from online audio and video databases, and library archives, and bird playbacks were downloaded from https://www.xeno-canto.org. Dog exemplars included recordings of multiple breeds, e.g. Alsatians, Dobermans and hunting hounds. We edited all sound files for consistency in amplitude and quality using Audacity® (www.audacityteam.org) and broadcasted the playbacks at a consistent mean sound pressure level of 80 dB at 1 m, to ensure responses to the playbacks were unrelated to variability in sound intensity across or within treatments and loud enough to be audible within the 15 m detection range of the camera’s motion sensor (Smith et al., 2017; Suraci et al., 2019b; Zanette and Clinchy, 2020; Crawford et al., 2022; Epperly et al., 2021).

Each playlist consisted of 24 h divided into 15-minute intervals, each of which contained one playback type (i.e., one species vocalization). We pre-determined the order of playback types in each playlist, balancing and randomizing predator and control playback types across the 24 h and avoiding order effects. In the end, we had 4 different playlists (two for the High-predator, and 2 for the Low-predator treatment, see further below), which were used in our ABRs (please see the Supplementary Materials for each playlist). This set-up follows an established protocol from previous ABR experiments (see Crawford et al., 2022 for a detailed explanation of the reasoning behind this set-up). The set-up determines that the playback type changed every 15 min (if camera was triggered), broadcasting randomly-selected exemplars from that playback type within the 15 min, but switching to a different playback type for the next 15-minute interval (if the camera was triggered). To illustrate this, if an animal triggered the ABR between, e.g., 12:00 and 12:15, the speaker would select a playback from the pre-determined playlist, e.g. Tawny owl, and start playing a random exemplar of Tawny owl. If the animal remained in the vicinity and re-triggered the ABR within this interval, the ABR would broadcast a different, randomly selected, exemplar of Tawny owl. If the animal left the vicinity and returned during the next 15 min interval, 12:15 and 12:30 (or a later time), the ABR would broadcast a different playback type, e.g. humans.

When programming the ABRs, we also needed to set the delay and the duration of the playback vocalization (Suraci et al., 2017). To ensure that one captures the response of the animal to the broadcast vocalization, one needs to select a delay between the start of the video recording and the start of the sound broadcasting so that the animal is in full view in the video when the broadcast starts. If this delay is too short, then the video may not capture the immediate response of the animal to the sound, if the delay is too long, the animal may be out of sight. The optimal delay varies among species and systems (Suraci et al., 2017). We, therefore, determined the optimal delay through a separate two-week trial (starting 9th June 2020) with six ABRs deployed in a fallow deer enclosure and on grass fields. Based on this trial, we set the system such that the playback started three seconds after the camera was triggered. Following a well-established protocol used in previous ABR experiments, we set the duration of all different playback types to 10 s and set the camera to record 30 second videos (Crawford et al., 2022; Epperly et al., 2021). Hence, during each 30 s video, there was 3 s of silence, followed by 10 s of the playback sound and then another 17 s of silence (Crawford et al., 2022).

2.3.1. ABR Programs “high-predator level” and “low-predator level”

In addition to comparing the patch use and crop damage between ABR locations and no-sound control locations (regular CTs), we compared ungulate visitation between the two ABRs on each field, which were programmed to broadcast predator vocalizations at two different intensities; one ABR being programmed with the aim of inducing a high level of predator-induced fear and the other a low level. The low-predator level ABRs were programmed such that, during each 2-hour period, there were five 15-min intervals during which animals would hear controls (birds) if the ABR was triggered, one 15-min interval during which they would hear dogs, one during which they would hear wolves and one during which they would hear humans. The high-predator level ABRs were programmed such that, during each 2-hour period, there were two 15-min intervals during which animals would hear controls (birds) if the ABR was triggered, two 15-min intervals during which they would hear dogs, two during which they would hear wolves and two during which they would hear humans. Hence, during any given 2-hour period animals would be twice as likely to hear predator vocalizations when passing by high-predator level ABRs compared to when passing low-predator level ABRs (Crawford et al., 2022).

2.4. Crop damage measurements

We measured crop damage by ungulates on the fields at the end of the playback experiment, starting the 1st of August 2020, using two 25 m long transects starting at the location of each ABR and regular CT unit (Fig. 3). To cover a larger area in front of the ABR and regular CT one transect faced the same direction as the ABR and regular CT, and the other one faced 45 degrees away from the direction the ABR/regular CT were facing. On each transect, we laid out 1 m^2 square plots at 5, 10, 15, 20 and 25 m distances along the transect. In each of these plots, we determined damage as the proportion of wheat stalks where the top culm had been entirely or partly grazed, relative to all stalks in the plot (Fig. 3). We thus ended up with 10 crop damage measurements per ABR or regular CT unit, leading to 60 crop damage measurements per field.

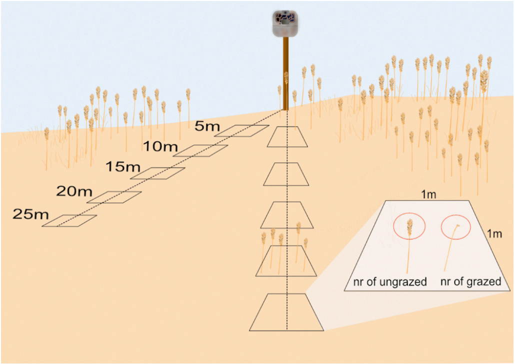

Fig. 3. Outline of crop damage measurements. Crop damage was measured along two transects of 25 m, one facing in the same direction as the camera trap/ABR and the other one in a 45 degree angle. Along the transects, 5 1 m2 square plots were distributed in which the number of grazed and ungrazed wheat straws were counted. (For color please see online figure)

2.5. Processing of camera trap data

Images from regular CTs and videos from ABRs of fallow deer, red deer, roe deer, moose and wild boar were identified and classified in the camera trap data management platform TRAPPER (Bubnicki et al., 2016). Before classification, sequences with 5 min interval were generated (following Bubnicki et al., 2019), where photos/videos that were captured within 5 min from each other belonged to the same sequence, i.e. one sequence could consist of a visit of a single individual or group of individuals. We recorded the species present in that sequence and the maximum number of individuals per species on a photo/video in that sequence and we converted the camera trap data into a measure of patch use by multiplying the length of each sequence in seconds (as the difference between start time and end time of a sequence) with the maximum number of individuals in the sequence. In this study, we were ultimately interested in testing if broadcasting risk cues can reduce crop damage. Because of this crop damage perspective, our main analysis did not focus on changes in ungulate individual behavior, but on changes in the overall use of, or pressure on, the plot by ungulates (i.e., independent of whether this use was by the same individual or different individuals).

As explained in the Introduction, animals should leave areas they perceive as fearful; and leave more rapidly the greater the perceived fear (e.g. when more frightening predators are heard; Brown et al., 1999; Zanette and Clinchy, 2020). Correspondingly, the rate at which animals leave or return to a food patch has been used to estimate the relative fearfulness of different predator vocalizations in most previous ABR experiments (Smith et al., 2017; Suraci et al., 2019b; Crawford et al., 2022). Accordingly, we quantified the relative fearfulness of the different playback treatments in our experiments based on ‘total bout duration’, defined as follows. Adhering to an established protocol from previous ABR experiments (Crawford et al., 2022; Epperly et al., 2021), we categorized videos into independent treatment-specific bouts if > 60 min elapsed since the last time the same species heard the same sound treatment at that site. The first video of a given species at a given site hearing a given treatment, if either, there were no prior exposures to that treatment, or > 60 min had elapsed since the last exposure to that treatment, we term a ‘first’ exposure video. If the vocalization heard is not frightening (e.g. birds), the animal may remain and feed on the crop, in which case it would re-trigger the ABR within the same 15 min interval, and hear the same playback type (e.g. birds), Videos of the same species at the same site, hearing the same treatment < 60 min since the last time they did, cannot be considered independent and we term these ‘repeat’ exposure videos. An independent treatment-specific ‘bout’ thus comprises a ‘first’ video and any and all ‘repeat’ videos. The ‘total bout duration’ is the sum of the intervals between the first exposure video and all subsequent repeat exposure videos in a bout. If there was just one video, i.e., just one first exposure alone, as is likely when the vocalization heard is very frightening and the animals flee the vicinity, the total bout duration is 30 ss (the length of the video).

2.6. Statistical analysis

All analyses on patch use were carried out in R 4.0.0 (R Core Team, 2013). To test for a possible detection difference between the different camera models and recording types (video vs image) of the ABRs and regular CTs, we compared patch use between ABRs and regular CTs using the data from pre-playback weeks with a Linear mixed effect model (LMM). Here we compared three fields, since we only had ABRs on three fields during this initial pre-treatment trial. In this model, the response variable was patch use and fixed factor was camera type with two levels (regular CTs vs ABRs), field ID was added as random intercept.

2.6.1. Patch use and crop damage

All analyses on patch use were carried out using LMM with a Gaussian error distribution or generalized linear mixed effect models (GLMM) with a Binomial error distribution as implemented in the lme4 package (Bates et al., 2015). When modeling patch use, we included the log10 transformed number of days the camera/ABR had been out in the field as an offset, to correct for differences in camera functioning. Furthermore, we added Field ID as a random intercept to correct for potential dependence of patch use estimates within fields. When modeling crop damage, we added a random intercept for each transect nested within location nested within field ID to correct for the hierarchical structure of the crop damage measurements.

We performed several analyses to look at differences in patch use between the CTs and the two ABR programs. We performed these analyses on the patch use of the combined patch use of all ungulate species and of each species separately, for the species with sufficiently high sample size.

We first ran a LMM to compare patch use between the pre-treatment weeks and the treatment weeks. Here, we grouped the two ABR programs (High-predator level and low-predator level) per field to test if the patch use was lower in front of ABRs than in front of regular CTs during the playback treatment weeks. Here, patch use index was log transformed. *Treatment* with two levels (regular CT versus ABR) and *Period* with two levels (before versus during playback treatment) were included as fixed effects. We included the interaction between treatment and period to test whether the difference in visitation in front of regular CTs versus ABRs depended on the playback treatment being active or not.

To test how patch use varied among the three overall sound treatments (regular CTs as no-sound treatment, high-predator level ABR and low-predator-level ABR), we fitted LMM for only the treatment weeks. The response variable in this model was again patch use, which was log transformed. Camera type was included as a fixed factor with three levels (no-sound control CT, Low-predator level ABR and High-predator level ABR).

Finally, we tested if crop damage on fields varied among the plots with regular CTs, high-predator level ABRs and low-predator-level ABRs using a GLMM. In this model, the response variable was the proportion of damaged wheat straws within each 1-m^2 measuring plot and camera type was again included as a fixed factor with three levels (no-sound control CT, high-predator level ABR and low-predator level ABR).

2.6.2. Total bout duration

To test whether there was a difference in total bout duration among the four vocalization treatments (bird control, dog, wolf, human) we conducted a GLMM with zero truncated negative binomial distribution using the glmmTMB package. We added ABR ID nested within Field ID as a random intercept to account for the hierarchical structure of the bout duration measurements.

To test whether there was a difference in predator vocalization videos between the high-predator level ABR and the low-predator level ABR, we conducted Wilcoxon Matched Pairs tests, comparing predator vocalization videos in total, and dog, wolf and human vocalization videos considered separately.

3. Results

Average trapping rates (number of sequences/number of regular CTs/ABRs) and coefficient of variation across all locations used in the study were 14.6 (CV = 0.79) for fallow deer (no-sound control = 17.1, CV = 0.75; low-predator level = 9.6, CV = 0.62; high-predator level = 8.6, CV = 0.67), 14.5 (CV = 1.14) for roe deer (no-sound control = 18.6, CV = 0.97; low-predator level = 6.2, CV = 1.39; high-predator level = 4.5, CV = 0.78), 5.25 (CV = 1.45) for red deer (no-sound control = 5.1, CV = 1.54; low-predator level = 8, CV = 0; high-predator level = 2.5, CV = 0.28), 4.07 (CV = 1.35) for moose (no-sound control = 4.5, CV = 1.36; low-predator level = 2, CV = 0.7; high-predator level = 3, CV = 0), 4.9 (CV = 0.93) for wild boar (no-sound control = 5.2, CV = 0.93; low- predator level = 7, CV = 0.60; high-predator level = 2, CV = 0), and Overall ungulate patch use did not significantly differ between ABRs and regular CTs during the pre-treatment trial, when ABRs were not broadcasting sounds (F-value: 0.71, p-value: 0.41).

The total number of videos recorded at the two differently programmed ABRs were 166 at high-predator level ABR (predator vocalization videos = 129, control vocalization videos = 37) and 289 at low-predator level ABR (predator vocalization videos = 98, control vocalization videos = 191).

3.1. Patch use and crop damage

3.1.1. Differences in patch use before and during the playback treatment

We found no difference in patch use between regular camera trap locations and ABR locations during the pre-treatment period (t-value = 0.50, p = 0.618) (Fig. 4), During treatment there was a significant difference in patch use between ABR locations and CT locations with higher patch use at CT locations (t-value = 3.05, p = 0.003). Patch use increased at regular CT locations during treatment (t-value = 2.06, p = 0.04) (Fig. 4), patch use at ABRs did not change significantly during treatment (t-value = −0.57, p = 0.5) (Fig. 4).

3.1.2. Influence of different levels of predator-induced fear on patch use

During the treatment weeks, patch use differed between the no-sound controls, low-predator level ABRs and high-predator level ABRs (F-value = 3.47, p = 0.04; Fig. 5). Patch use was lower at high-predator risk ABR locations compared to no-sound control locations (t-value = 2.17, p = 0.03) and at low-predator level ABRs compared with no-sound controls, although this latter difference was only marginally significant (t-value = −1.92, p = 0.07). There was no difference in patch use between high-predator level and low-predator level ABRs (t-value = 0.31, p = 0.76; Fig. 5). Notably, although the high-predator ABRs were programmed to broadcast predator vocalizations at a higher intensity, the actual number of predator vocalization videos recorded at high-predator ABRs was not substantially greater than at low-predator ABRs (129 vs. 98 respectively), and the difference was not statistically significant (Wilcoxon Matched Pairs tests, all $p > 0.500$).

Patch use of red deer, moose and wild boar could not be analyzed separately due to low sample sizes for these species. Patch use of fallow

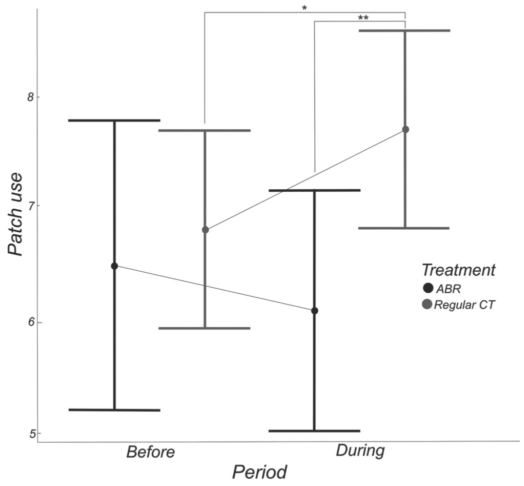

Fig. 4. Model prediction plot from a linear mixed effect model showing the difference in patch use (log transformed) between the two treatments ABR and regular CTs as well as between the two periods before manipulation of predator vocalizations and during manipulation of predator vocalizations. Bars represent predictions +95% confidence interval. * denotes significant differences between the treatments.

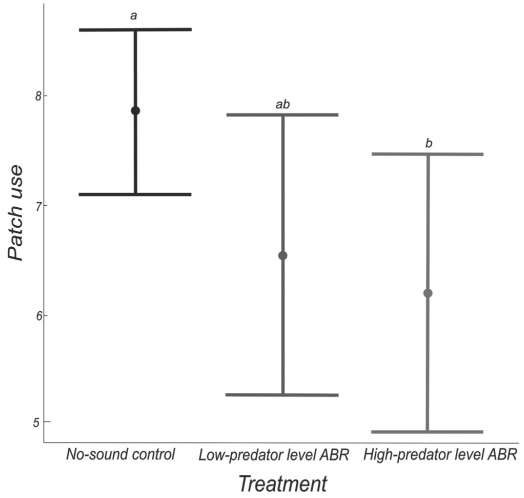

Fig. 5. Model prediction plot from a linear mixed effect model showing the difference in patch use (log transformed) between the three treatments during manipulation of predator vocalizations; no-sound control, low-predator level and high-predator level ABRs. Bars represent predictions +95% confidence interval. Shared letters denote non-significant differences.

deer and roe deer differed among the three treatments (Fig. 6; fallow deer, F-value = 3.25, p = 0.04; and roe deer, F-value = 14.78, p = <0.001). Fallow deer patch use was lower at high-predator level than at no-sound control sites, (t-value = −2.17, p = 0.03), and tended to be lower in low-predator level ABRs than no-sound controls (t-value = −1.71, p = 0.09). Roe deer patch use was lower at both high-predator level (t-value = −2.52 p = 0.01) and low-predator level (t-value = −5.19, p = <0.001) ABR sites compared to the no-sound control sites. We did not find any difference in patch use between high-predator level and low-predator level ABRs for either fallow deer (t-value = 0.56, p = 0.58) or roe deer (t-value = −1.58, p = 0.13).

3.1.3. *Influence of different levels of predator-induced fear on crop damage*

Crop damage was lower at ABR locations than no-sound control locations (Chisq = 28.38, pr (>Chisq) = <0.001). Furthermore, crop damage tended to be lower at high-predator level ABR sites compared to low-predator level ABR sites (t = 1.76, p = 0.08) (Fig. 7).

3.2. *Total bout duration*

Total bout duration significantly differed among the vocalization treatments (control, dog, wolf, human) (Chisq = 49.559, pr (>Chisq) = <0.001). Human vocalizations triggered the strongest responses (Fig. 8), where bout durations following human sounds were consistently shorter compared to durations following other vocalizations (human vs. control Z-value = 6.85, p = <0.001; human vs. dog Z-value = 4.61, p = <0.001; human vs. wolf Z-value = 3.09, p = 0.002). Compared to non-predator controls (Fig. 8), ungulates significantly reduced their bout duration in response to hearing wolves (Z-value = −3.18, p = 0.001), and they tended to reduce their bout duration in response to hearing dogs (Z-value = −1.78, p = 0.075).

4. Discussion

Overall ungulate patch use and crop damage were much lower in plots in front of ABRs than in plots in front of regular CTs (no-sound control). Moreover, the difference between ABRs and no-sound control plots in patch use (Fig. 5) and crop damage (Fig. 7) was stronger for the high-predator level ABRs than for the low-predator-level ABRs. Our behavioral analysis of total bout duration confirmed that predator vocalizations induced stronger fear responses than non-predator vocalizations. Ungulates more quickly left a plot (shorter bout duration) after hearing predator vocalizations than after control bird vocalizations (Fig. 8). With regards to wildlife management, we demonstrate that experimentally broadcasting predator vocalizations, using systems such as ABRs, has potential as a tool to mitigate human-wildlife conflicts and can effectively reduce wildlife use and crop damage, at least at the scale, and for the duration, of our study.

Before we began broadcasting vocalizations (i.e. during the 2 weeks the ABRs were muted), there was no significant difference in patch use between ABR locations and regular camera trap locations (Fig. 4). Interestingly, during the playback treatment period, patch use increased in locations in front of the regular CTs (no-sound control), while it decreased at ABR locations (albeit not significantly so) (Fig. 4). This increase in patch use of the no-sound control locations might reflect an increase in overall field use due to a ripening of the crop and/or redistribution of the use within the field away from the ABRs towards the no-sound control locations. Observational studies similarly found that fear may lead to a redistribution of prey moving to safer areas (Blumstein and Daniel, 1995; Creel et al., 2008; Creel and Winnie, 2005). Recently, Suraci et al. (2019b) experimentally demonstrated that mountain lions (*Puma concolor*) altered their movement and space use in response to hearing playbacks of the human 'super predator' speaking, broadcast using systems similar to the one we used here.

Although the high-predator ABRs were programmed to broadcast predator vocalizations twice as often (i.e., 100% more) as the low-predator ABRs, the actual number of videos with predator vocalizations recorded at high predator ABRs was only 32% greater than at low-predator ABRs, most likely explaining the modest difference observed in patch use between the low-predator level and high-predator level. One possible explanation for this lies in the total bout duration results; i.e., animals left plots more quickly following a predator vocalization than following a control vocalization, so there are consequently fewer

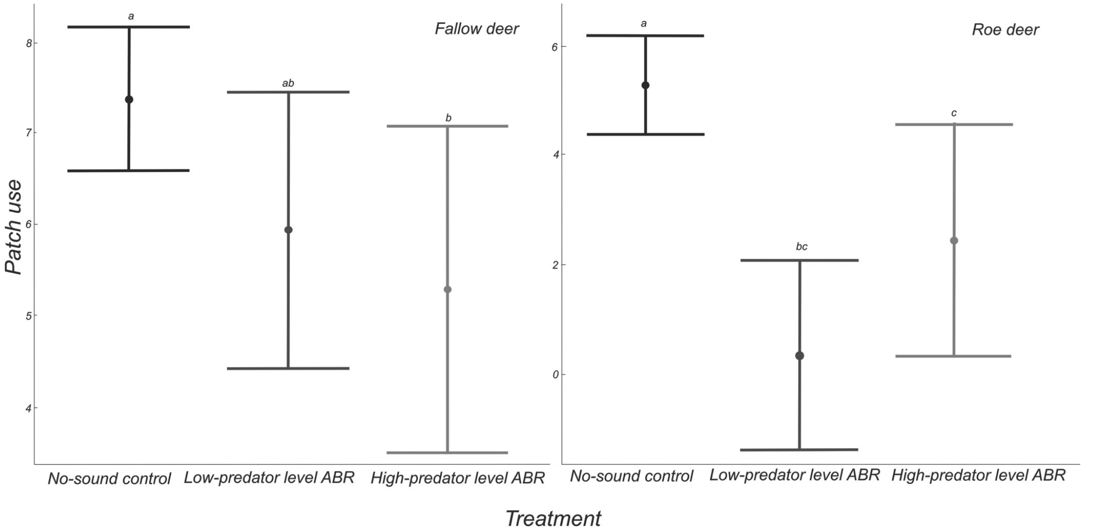

Fig. 6. Model prediction plots from linear mixed models showing the difference in the two ungulate species' patch use (log transformed) between the three treatments during manipulation of predator vocalizations; no-sound control, low-predator level and high-predator level ABRs. Bars represent predictions +95% confidence interval. Shared letters denote non-significant differences.

'repeat' predator videos. The actual number of videos with predator vocalizations is thus a function of both how ungulates behave after hearing a vocalization and the difference in programming between the ABRs. The total bout duration results further demonstrate that which specific predators were heard can be expected to affect patch use, with patches being abandoned more when humans were heard (Fig. 8). This helps explain why patch use by roe deer was lower at low-predator level ABRs than high-predator ABRs (Fig. 6), because roe deer actually heard four times as many human vocalization playbacks at low-predator ABR locations than high-predator ABR locations.

The pattern of our total bout duration response to the four vocalization treatments (control, dog, wolf, human; Fig. 8) corresponded precisely with that from a prior predator playback experiment on deer in the southeastern USA (Crawford et al., 2022). I.e., that bout duration responses were strongest to human vocalizations, then to wolf vocalizations, and with only a weak response to dog vocalizations. This suggests that the effects on patch use and crop damage observed in our study were likely attributable to predator-induced fear. Our results confirm those from previous experiments conducted on free-living wildlife demonstrating that predator-induced fear can cause cascading effects on the preys' resources and the surrounding landscape (Smith et al., 2017; Suraci et al., 2016, 2019a, 2019b; Zanette and Clinchy, 2020). Moreover, our total bout duration results, where the Swedish ungulates responded most strongly to human vocalizations, are in line with other studies that human-induced fear effects outweigh those of other predators (Zanette and Clinchy, 2020) (. In fact, several other playback experiments have demonstrated this effect of human vocalizations for carnivores in Europe and North America (Clinchy et al., 2016; Suraci et al., 2019b)), and diverse ungulates in South Africa (Zanette and Clinchy, 2020; Crawford et al., 2022) . This so-called human 'super predator' effect has been explained by recent analyses showing that, worldwide, humans kill herbivores and carnivores at greater rates than non-human predators (Darimont et al., 2015; Zanette and Clinchy, 2020).

Notably, previous experiments testing responses to dogs all demonstrate that hearing dogs barking either does not induce fear in wildlife (Suraci et al., 2019b), or has a very weak effect (Clinchy et al., 2016; Crawford et al., 2022; Epperly et al., 2021), as our results indicate (Fig. 8). This result is somewhat surprising, especially for our study area where barking dogs are frequently used in hunting. One explanation for our study may lie in the fact that we did not use playbacks of the hunting dog breeds used in our area. However, this does not explain the lack of response to dog playbacks in an increasing number of studies from a variety of systems. All of these experiments utilized multiple exemplars of dog vocalizations drawn from different breeds, and one experiment (Suraci et al., 2019b) directly tested and demonstrated that individual cougars (*Puma concolor*) that had themselves been hunted using dogs, did not respond fearfully to hearing either large or small dogs. We currently lack a clear explanation for the absent, or weak, responses to dog sounds, although part of the explanation may lie in saying "barking dogs seldom bite". I.e., that across the multiple types of dogs present in most landscapes (including many non-hunting dogs) the barking of dogs generally does not associate with increased predation.

The fact that manipulating fear (perceived predation risk) influenced patch use by ungulates and also significantly reduced their impact on highly valuable crops, provides important knowledge regarding the process of applying the 'ecology of fear' as a management tool. How effective the use of fear is in reducing crop damage depends on minimizing habituation (Blumstein, 2016; Shivik, 2006; Zanette and Clinchy, 2020). In our study we managed to reduce crop damage during an important time for the farmer, i.e., the 4 weeks just before harvest. Habituation has been successfully avoided in similar experiments in wilderness areas for longer time periods (e.g. 4 weeks, (Suraci et al., 2016); 5 weeks, Suraci et al., 2019b) or entire breeding/growing seasons (e.g. 4 months, Zanette et al., 2011). Thus, there is a potential of protecting crops from grazing by ungulates for a longer period of time than we could show in this study. Furthermore, it has also been shown that fear can have major impacts on much larger areas than the spatial scale in our study (1 square km blocks in a study by Suraci et al., 2019a in the USA), pointing to the potential to induce fear and mitigate habituation at the whole field-level. Based on this 5 week, 1 square km study by Suraci et al. (2019a), the costs of providing crop protection could be as low as $USD 15 (€ 13.5) per ha for equipment and $USD 3 (€ 2.7) per ha per week for operating costs. However, replication of this work, and

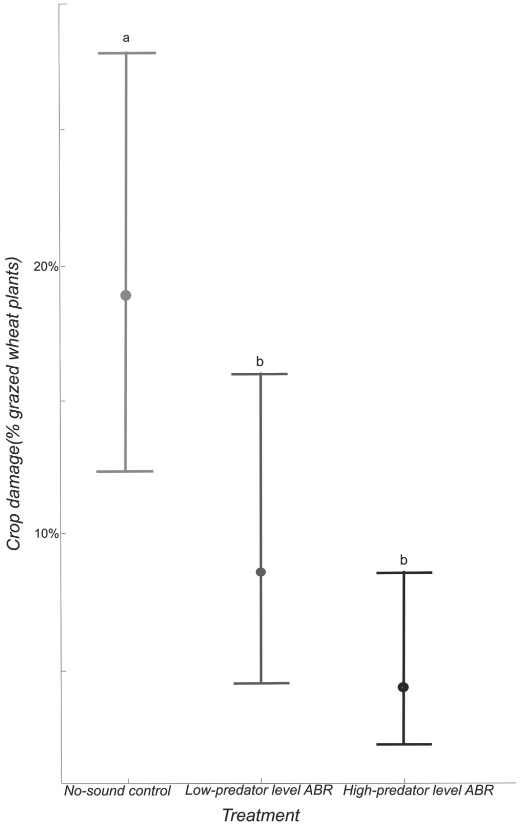

Fig. 7. Model prediction plot from a generalized linear mixed model showing the difference in crop damage between the three treatments during manipulation of predator vocalizations; no-sound control, low-predator level and high-predator level ABRs. Bars represent predictions +95% confidence interval. Shared letters denote non-significant differences.

more rigorous costing in actual agricultural applications remains essential and costs may vary widely among systems depending on local labor costs and costs for material such as batteries.

4.1. Conclusion and management recommendations

In conclusion, our results contribute novel knowledge on how fear influences not only wildlife behavior, but also can modify their impact on the landscape. Furthermore, it provides insight and valuable components in assessing the potential of applying the ‘ecology of fear’ as a tool to mitigate human-wildlife conflicts. Hearing the vocalizations of the human ‘super predator’ (people speaking) is especially fearful and should thus be used when aiming to reduce ungulate use and damage on agricultural land. We recommend using exclusively human vocalizations in situations where ungulate densities are low or moderate. Earlier studies suggests that this could be effective throughout the entire growing season (Suraci et al., 2016; Zanette et al., 2011) at a whole-field level (Suraci et al., 2019b). When ungulate densities are likely to be high, it may be advisable to increase variation by adding the vocalizations of other predators to increase variation and thus reduce the probability of habituation. Our results regarding the reactions to non-human predator vocalizations suggests that wolf vocalizations may be more efficient than dog vocalizations, however, we need more tests to provide solid recommendations regarding the most frightening non-human predator vocalizations to include with human vocalizations.

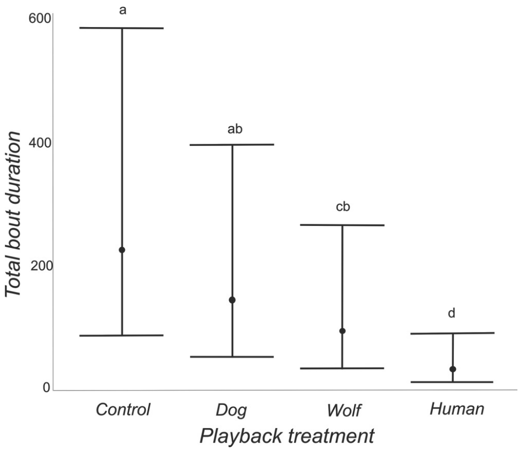

Fig. 8. Difference in total bout duration (seconds) of all ungulate species combined between the different playback treatments broadcasted by the ABRs. Squares in boxes represent mean value.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.107853.

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