



Candidate 8009
Alexandra Voronchikhina/Eduard Codó Cónsol
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University of South-Eastern Norway
Department of Natural Sciences
and Environmental Health

Influence on Alert Distance and Flight Reaction of Roe Deer



Abstract

As human development expands across the planet, there are fewer places where animals can find a safe refuge. This leads to animals encroaching on human settlements and an increase in animal-human interactions. As this increases nonlethal exposure to humans, some animals respond by decreasing vigilance and anti-predator behaviors. Vigilance is measured through alert distance, at which point the animal first reacts to the approaching threat and anti-predator behavior is measured through flight initiation distance, when the animal escapes from the area of the predator. This study measures the alert distance (AD) and flight initiation distance (FID) in roe deer (*Capreolus capreolus*) in response to human observer on foot in open agricultural fields in Midt-Telemark Norway to determine which variables influence AD and FID. A total of 119 observations were made over two seasons from August to December 2022 and 2023. Of the factors studied, FID was most affected by AD and AD was most affected by start distance and illumination. Start distance is the distance at which the human observer first starts to observe the roe deer, with our results showing an increase in start distance correlating to an increase in AD. Illumination indicates the amount of moonlight at the time of the observation, with our results showing an increase in illumination correlating to a decrease in AD, indicating that moon phases have an effect on roe deer vigilance. FID decreased with a decrease in AD as being alert sooner correlated to an escape sooner regardless of distance to forest or houses.

Introduction

More than 50% of the Earth's land surface has undergone changes in land use, primarily due to agriculture, leading to habitat fragmentation and land modification (Hooke *et al.*, 2012). This means there is a decrease in safe spaces for wild animals that have no human disturbance (Tucker *et al.*, 2018). Animals respond to human disturbance in the same manner as to predators; by avoiding disturbed areas or underusing them (Beale & Monaghan, 2004). Humans change the habitats of wild animals so quickly that behavioral adaptations aimed at predator risk and human disturbances can be insufficient (Leblond *et al.*, 2013). Large herbivores require a large space and are widely hunted; thus, they are especially vulnerable to the effects of human land use and disturbance (Carbillet *et al.*, 2020). Predation, from wildlife and human hunting, and non-lethal human disturbance can have the same trade-offs for wildlife, like putting energy into avoiding risk instead of activities that benefit fitness, like feeding, mating (Blumstein *et al.*, 2005) and desertion of preferred breeding sites (Robertson, 1997). Fernandex-Juricic and Telleria (2000) showed that the abundance of bird species adjacent to footpaths decreased with an increasing number of pedestrians. Gill *et al.* (1996) showed that pink-footed geese (*Anser brachyrhynchus*) reduced foraging of a crop that was closer to roads. These are examples of adapted behaviors in response to predator behavior or disturbance, i.e., a landscape of fear is created where prey changes their behavior due to the behavior of their perceived predator to increase their chances of survival (Laundré *et al.*, 2001).

Some animals are able to use an increase of human structures to their advantage, like the female moose (*Alces alces*) in Yellowstone giving birth closer to roads to avoid the increasing population of the brown bear (*Ursus arctos*) (Berger, 2007). They utilize human structures as defense against human-averse predators (Berger, 2007), which is an example of habituation. Habituation occurs through repeated low-risk exposure to potential predators, causing the animal to reduce its response over time as it learns there is no advantage to the stimulus (Rankin *et al.*, 2009), exhibiting a plastic behavioral response that has been demonstrated by many animals (Blumstein, 2016). Animals can learn through experiences with humans and adjust their anti-behavioral response (Bateman & Fleming, 2014). This kind of behavior often occurs to animals living near human settlements with repeated nonlethal human disturbances (Samia *et al.*, 2015). An increase in habituation by deer species is happening around the world in urban and urbanizing areas that prohibit human hunting and decrease the presence of predators (Honda *et al.*, 2018). It has also been found that wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) thrive in heavily human-dominated landscapes, even those with intensive recreational use and hunting (Wevers *et al.*, 2020). These two species have been known to thrive in human-dominated

landscapes, as their plasticity allows them to adjust and habituate to human presence (Linnell *et al.*, 2020).

To determine if habituation has occurred, researchers measure flight-initiation distance (FID), the distance from which an animal moves away from the approaching perceived threat (Ydenberg & Dill, 1986). This is studied as antipredator behavior, which the animals optimize to minimize the energy cost of escape by not moving away from the threat until necessary by balancing the cost of remaining in the area to the cost of escaping (Ydenberg & Dill, 1986). The behavioral response of an animal's decision to stay or leave an area is dependent on habitat quality, proximity to refuge, and relative availability of alternative habitats (Gill, 2007). FID represents risk assessment, which is related to habituation, as this reaction can be affected by continued nonlethal exposure to humans (Cooper & Blumstein, 2014; Uchida *et al.*, 2019). Individual experiences and reactions can also be seen as a result of habituation, where animals living near areas of high non-lethal human disturbance have a decrease in FID, as was found in impalas (*Aepyceros melampus*), where those exposed to hunting had higher FIDs than those inside a protected national park (Setsaas *et al.*, 2007). Animals are also able to adjust their escape speed due to risk and surroundings, where woodchucks (*Marmota monax*) (Bonenfont & Kramer, 1996) have bigger FIDs, and both woodchucks and golden marmots (*Marmota caudata aurea*) run faster when further from a habitat with refuge (Bonenfont & Kramer, 1996). Flight-initiation distance is commonly studied by having humans walk toward individual animals until they react (Burger & Gochfeld, 1991). This method is likely affected by the starting distance of the human, as animals detecting a person at a greater distance may flee at a greater distance. For example, Blumstein (2003) found a significant positive relationship between starting distance and FID in 64 bird species. There is concern that animals that become habituated to human presence will also have decreased vigilance, but these are two different reactions (Uchida *et al.*, 2019). Vigilance is related to alert distance (AD), which is the distance when the targeted individual first notices the approaching object (Cooper & Blumstein, 2014; Uchida *et al.*, 2019). The results of ADs and FIDs are useful for wildlife managers to determine the index of disturbance to set thresholds from which humans should not approach to minimize risk of disturbance to the wildlife (Rodgers & Smith, 1995).

Gill *et al.* (2001) suggest that FID is not the most accurate indicator of human disturbance as populations differ in quality of the disturbance site as well as the availability of alternative sites. Thus, composite measures take into account multiple variables including AD, FID, distance to roads, and resource use levels by the animal of the desirable habitat (Gill *et al.*, 1996; Fernandez-Juricic *et al.*, 2001). When the walker, i.e. the person approaching an animal as part of an experiment, appears more threatening, faster and more direct, the prey had a greater escape

distance (Stankowich & Blumstein, 2005), indicating that animals look at the behavior of the walker and evaluate if there is an increased risk of attack. Stankowich (2008) found that there was a reduced flight response in roe deer in areas that had higher rates of human exposure, but areas that had hunting pressure produced a higher flight response than in areas without this pressure. They also found that ungulates pay attention to walker behavior and have higher perceptions of risk in open habitats (Stankowich, 2008). Habituation, leading to slower reaction times, can be attributed to a lack of alternative resources (Gill *et al.*, 2001) but the consistency of this effect suggests that ungulates do habituate in areas with large human populations. Habituation to even low impact stressors like hiking can take many years to happen and may even never happen (Fairbanks & Tullous, 2002) but many ungulate populations become habituated to the point of encroaching on human settlements (Stankowich, 2008).

Roe deer populations have thrived in human-dominated agricultural landscapes due to their behavioral and ecological plasticity (Hewison *et al.*, 2001) allowing them to benefit from the high-quality food resources provided by human agriculture activities (Abbas *et al.*, 2011) as well as safety from other predators. Their response to human activity is to use safe habitats during the daytime (Martin *et al.*, 2018), avoiding human-disturbed habitats (Padie *et al.*, 2015), shifting their spatial behavior by using woodland refuges during the day (Bonnet *et al.*, 2013), and using open field habitats during the night. The roe deer must make the tradeoff between high-quality habitats and habitats with increased safety (Hernandez & Laundre, 2005), and the use of each habitat involves a risk-reward assessment (Verdolin, 2006).

The main goal of this study is to use experimental approaches to evaluate the habituation and flight reactions of roe deer to humans. Wildlife can detect humans, as well as other predators through visual, auditory, and olfactory cues (Fernandez-Juricic *et al.*, 2002), thus wind direction was factored in to measure if there is an increased effect when a roe deer is downwind of the walker. Detection of humans is typically characterized by a quick reflex called the alert position, where the animal stops its current activity and focuses on the potential threat, increasing vigilance (Blix and Ursin, 1985). Weather conditions like rain or fog limit the ability of animals to detect predators as it decreases visibility, odor, and sound transmission (Martin, 2011). The visual acuity and color perception of the white-tailed deer (*Odocoileus virginianus*), which has a similar visual system to other ungulates, has been found to improve with light intensity (D'Angelo *et al.*, 2008), thus it is possible that with an increase of light from lunar illumination, roe deer will be able to see the approaching threat sooner and react faster compared to nights with lower illumination. There is conflicting information on whether moon light illumination has an effect on roe deer behavior, with some providing evidence that there is an increase in roe deer activity with an increase of illumination due to moon phases (Jasinka *et al.*, 2021), and others like Pagon *et al.* (2013) that

found no significant effect of moon light on roe deer activity in densely forested areas. Similar studies have found a positive relationship between illumination and FID, indicating that higher levels of illumination were associated with increased FID (Jolkkonen *et al.*, 2023) in wintering Eurasian curlew (*Numenius arquata*).

After detection of humans, the sensory response and alert reflex may be followed by a behavioral response (Blumstein, 2010) which may be passive or active depending on the threat, choosing to freeze and hide or actively escaping or fighting the threat (Bracha, 2004). For our purpose, we are looking for the active response after the alert reflex, where the animal spots the approaching human, which we label as first reaction and chooses to run, which we label as second reaction or escape reaction. This perceived risk increases when humans get closer and move and walk directly toward them (Stankowick & Coss, 2006). Wildlife with nearby habitats of refuge may feel safer and react slower than those that have to travel far to get to safety (Tadesse & Kotler, 2012). Some species are able to tolerate a closer approach with larger groups (spottail shiner *Notropis hudsonius*; Seghers, 1981), while others detect approaching threats from a longer distance and initiate flight sooner (house sparrow *Passer domesticus*; Barnard, 1980). Patch quality is an important factor, since an animal is less likely to leave a place with large food quantities, as it's unlikely to find this resource elsewhere (Cooper *et al.*, 2003). In places where there is a consistent, non-threatening human presence, animals generally have a lower flight initiation distance (Stankowich, 2005). There are many variables that can affect the behavior of wildlife. Our aim is to find the variables affecting the AD and FID of roe deer in the Midt-Telemark area.

In this study we investigated potential factors that influence alert distance (AD) and flight initiation distance (FID) of roe deer when approached by people in an experimental setting. We predicted 1) a lower AD and FID closer to houses and forest cover, and 2) increase of AD and FID with increased start distance, increased group size, wind direction pointed toward the deer, and initial deer behavior being observant, standing, walking, or running, as opposed to less vigilant behaviors where we predicted 3) a decrease in AD and FID for behaviors of laying and eating. We further predict 4) an increase in AD and FID with increased illumination. As AD can also influence FID, we predict 5) an increase of FID with increased AD.

Materials and Methods

Study area

Midt-Telemark Municipality was established on 1 January 2020 by merging the municipalities of Bø in Telemark and Sauherad (Mæhlum, 2024). The landscape comprises of 2 valleys, the wide main valley with the Bøelva, surrounded by wooded valley sides and mountains (Mæhlum, 2024). The forest line is close to 1,000 meters above sea level, due to good climate and high summer temperatures (Mæhlum, 2024). The highest mountain peak is on Lifjell, 1275m above sea level (Mæhlum, 2024). The area is a mix of agricultural fields in the valleys based on marine sediment and wooded hills (Mæhlum, 2024). Midt-Telemark had a population of 10,904 on 1/1/2024, a land area of 487 km² and a total area of 518 km² (Riiser, 2024). Midt-Telemark consists of 48,290 decares of agricultural land, 377,237 decares of forest, 13,597 decares of construction/ transportation and 79,386 decares of other types of land (Arealbarometer Nibio, 2023). The agricultural areas consist of grain (68%), roughage (21%), fruit/berries (9%), infield grazing (2%), and potatoes/vegetables (>0.05%) (Arealbarometer Nibio, 2023).

32,900 roe deer were killed by hunting in Norway in the year 2022-2023, of which 130 deer were killed by hunting in the Midt-Telemark Municipality (Statistisk sentralbyrå, 2024). 59 roe deer were killed by causes other than hunting including hit by a car (44), hit by a train (3), and died of other causes (12) (Statistisk sentralbyrå, 2024). There are 1,340 registered hunters in this municipality (Statistisk sentralbyrå, 2024). Roe deer are the third most popular game to hunt in this municipality after moose (*Alces alces*) and red deer (*Cervus elaphus*) (Statistisk sentralbyrå, 2024). The hunting season for roe deer in Norway is from the 25th of September to the 23rd of December and from 10th of August to the 23rd of December for adult roe buck (Lovdata, 2024). Experimental encounters with deer were conducted in both open and semi-open agricultural areas around Bø in Telemark (59°24'46"N, 9°4'9"E), Midt-Telemark Municipality (Figure 1).

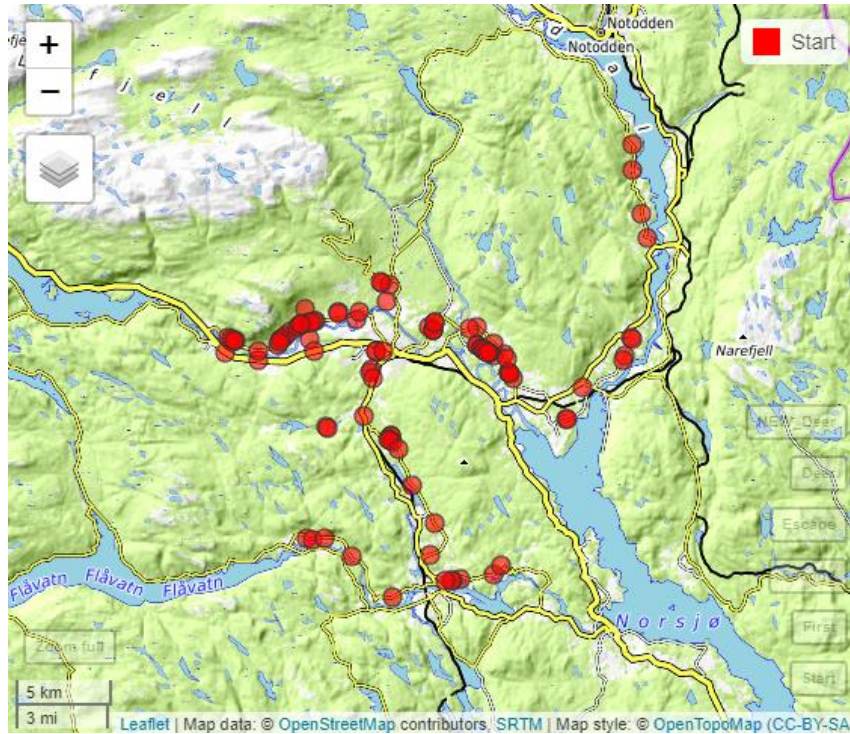


Figure 1. Map of Midt-Telemark area showing locations of experimental approach of roe deer in Midt-Telemark Municipality, Norway, during fall/winter 2022 and 2023. Red points are the start points of every recorded roe deer encounter based on GPS coordinates collected at the time of observation. Made in RStudio (R Core Team, 2022).

Experimental approaches

Ungulates generally exhibit activity mainly during crepuscular hours in human dominated areas, especially during the hunting season (Bonnot *et al.*, 2020). We only observed reactions of roe deer to experimental approaches in the late evening/night when typically, the roe deer are used to a low level of disturbance (Bonnot *et al.*, 2013) to attempt to find AD and FID. These experimental approaches were begun in the previous year by Venås *et al.* 2023, who provided the data from fall/winter 2022.

To study the FID of roe deer near human inhabited areas, we drove around the Telemark area between the hours 20:00 and 01:00. As one person drove at a safe speed, the other used thermal binoculars (Pulsar Accolade 2 LRF XP50 Pro, with built-in rangefinder) to observe the surrounding area. As we were aware that more activity happens in open agricultural fields, we primarily drove around areas with more fields. To be able to see the entirety of the animals' reactions, we only experimentally approached the roe deer that were less than 300 meters away at the starting point. As a roe deer is spotted, the car is stopped in a safe area and first observations are taken before leaving the car. These observations are the time, the compass

direction of the roe deer from the starting point, the number of animals, and the behavior of the roe deer. If there is more than one animal at the start, the closest and largest is chosen as the subject of observation (Figure 2).

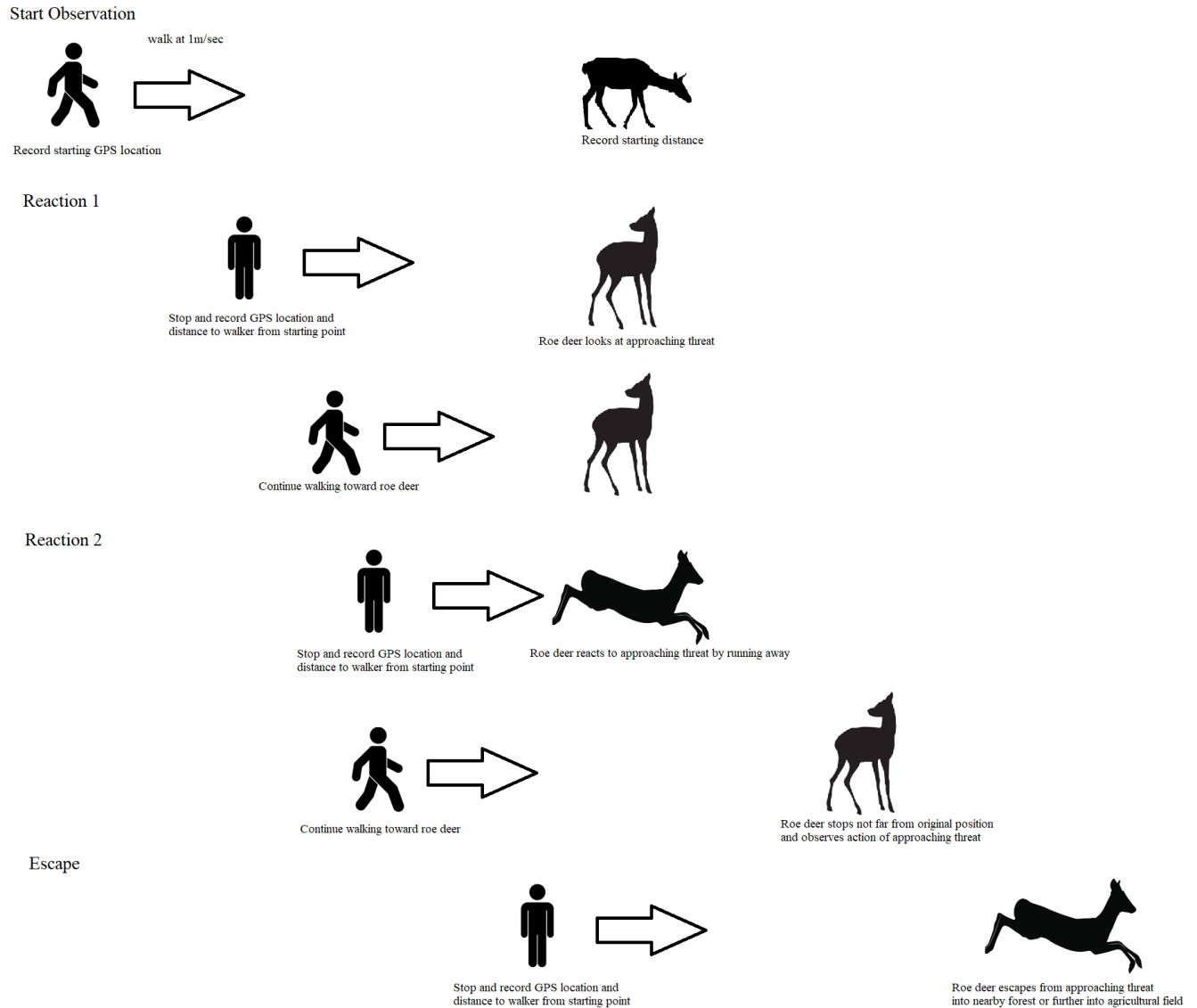


Figure 2. Illustration of the method used to observe the alert distance and flight initiation distance of roe deer during experimental approaches in Midt-Telemark Municipality, Norway, 2022-2023.

Two people are required for an experimental approach, a walker and a watcher (Figure 2). The start distance is recorded as the distance from the starting point to the initial location of the roe deer using thermal binoculars. The walker takes the GPS coordinates of the starting point using a GPS (GARMIN) and walks directly toward the roe deer at a steady pace of approximately

1 m/sec. The watcher stays at the starting point and uses the binoculars and a phone and earpods to communicate directions to the walker as the walker is unable to see the target due to the darkness. The watcher looks for reactions in the roe deer in response to the walker and proceeds with the observation (Figure 2). The first reaction, or alert distance (AD), is defined as a roe deer looking directly at the walker, which indicates alert. At this point the watcher communicates to the walker to stop walking and records the distance from the starting point to the walker. This is also when the walker uses the GPS to record their current coordinates. Then the watcher communicates to the walker to continue walking. The walker will be instructed to stop at the second reaction, or flight initiation distance (FID), which is defined as the roe deer moving away from the walker. Typically, roe deer stop running away after 20 to 50 meters and look back at the walker to see if he/she will continue their approach. The walker records their coordinates, and the watcher records the distance of the walker from the starting point as well as the new distance of the roe deer, then instructs the walker to continue the approach, adjusting their direction as needed. The final reaction is the escape reaction, defined as a roe deer running away completely either into a nearby forest or several hundred meters away. It is also possible that there is no reaction 2 and the roe deer goes directly from reaction 1 to escape reaction, as seen in Figure 3. An example of all points is shown in Figure 4, where the roe deer observed gave a first reaction, second reaction and an escape.

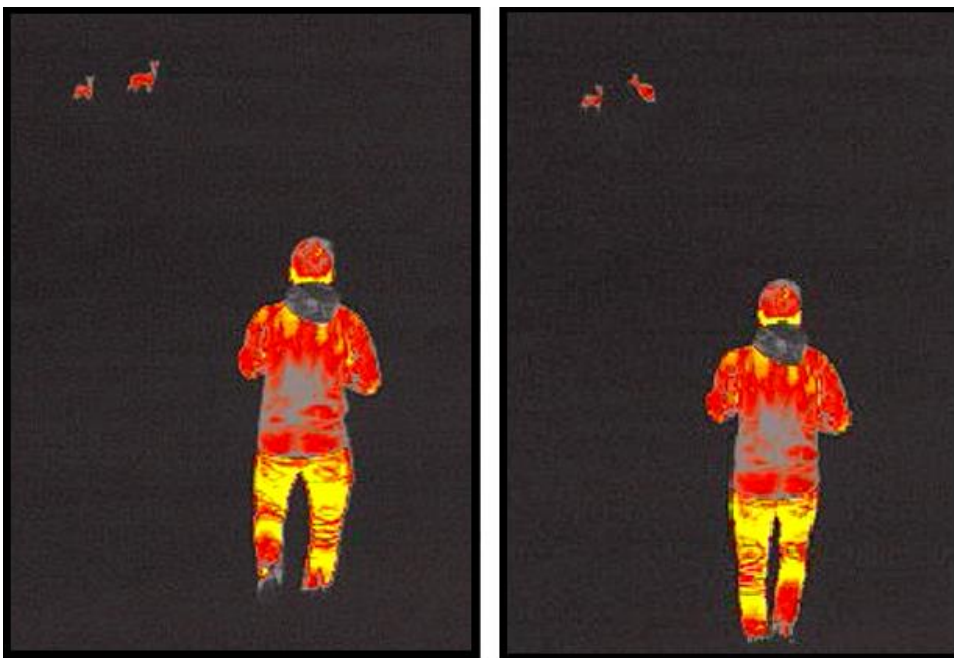


Figure 3. Thermal photos of roe deer experimental approach. On the left, the roe deer can be seen looking directly at the walker, which is recorded as the first reaction. On the right, the roe deer react to the walker

continuing walking toward them by running away. Captured by Thermal binoculars (Pulsar Accolade 2 LRF XP50 Pro, with built-in rangefinder).

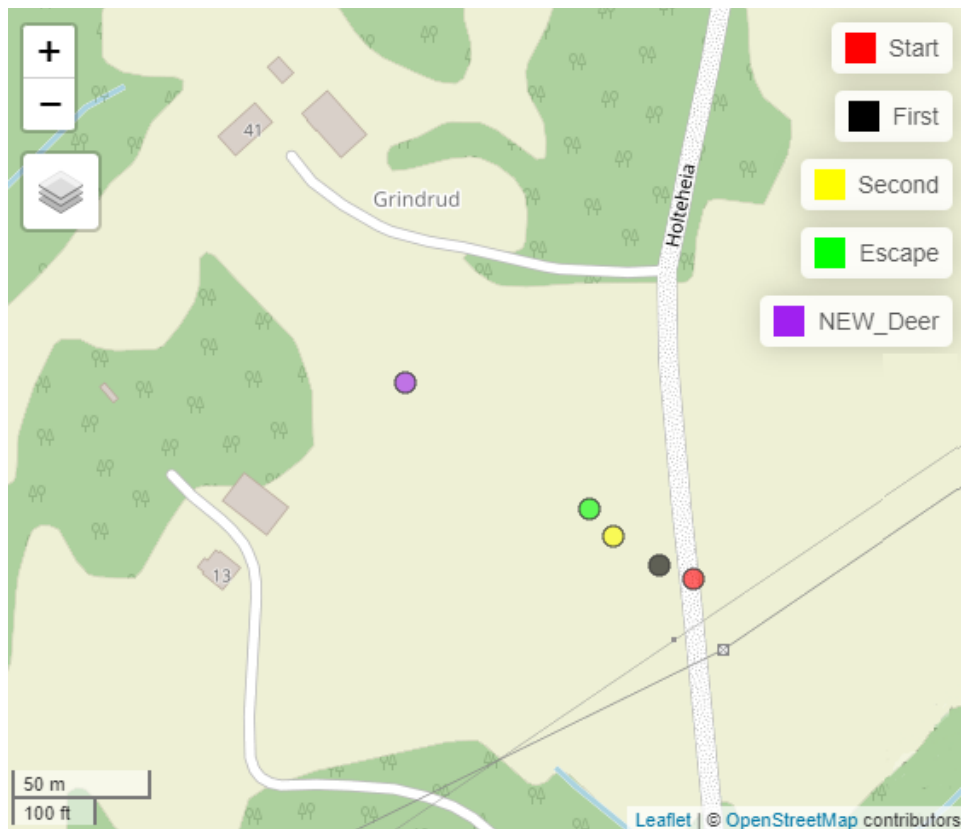


Figure 4. Example of an observation with all reactions of roe deer during experimental approach in Mid-Telemark Municipality, Norway, during fall/winter 2022 and 2023. New_Deer labeled by purple dot is the position of the deer at the start. The other points; start, second, and escape are the position of the walker when the corresponding reaction was observed. These points are used to find the alert distance (AD) and flight initiation distance (FID).

Approach no:	Observer:	Date:				
Compass Direction:	Time:	No animals:				
Behavior:						
<input type="checkbox"/> Lying	<input type="checkbox"/> Walking	<input type="checkbox"/> Feeding	<input type="checkbox"/> Standing	<input type="checkbox"/> Running	<input type="checkbox"/> Observant	
Distance:						
Start:	Reaction 1:	Reaction 2:	New Distance:	Escape:		
Weather:						
<input type="checkbox"/> Overcast	<input type="checkbox"/> Partly overcast	<input type="checkbox"/> Fog	<input type="checkbox"/> Rain	<input type="checkbox"/> Snow on ground	<input type="checkbox"/> Snowing	<input type="checkbox"/> Clear
Wind: Direction:						
<input type="checkbox"/> Calm	<input type="checkbox"/> Light Breeze	<input type="checkbox"/> Moderate Breeze	<input type="checkbox"/> Strong Breeze	<input type="checkbox"/> Storm		
Habitat:						
<input type="checkbox"/> Agricultural field		<input type="checkbox"/> Partly forested		<input type="checkbox"/> Pasture		

Figure 5. Field protocol used during experimental approach of roe deer in Midt-Telemark Municipality, Norway, during fall/winter 2022 and 2023.

At this point the experimental approach is finished, and other variables are recorded in the field protocol (Figure 5), including wind direction, weather condition, and habitat type. Habitat type was removed from analyses and results as all observations were recorded in the same habitat type of agricultural field. The wind direction is recorded using powder to see where it was blown and using a compass to determine the direction. In order to not increase possibility of habituation or increase stress, locations where roe deer were approached were given a minimum resting time of one week.

Alert distance is measured using starting distance and first reaction ($AD = \text{Start distance} - \text{first reaction distance}$). FID is measured using starting distance, second reaction if there was one, and escape distance; no second reaction ($FID = \text{Start distance} - \text{escape reaction distance}$), includes second reaction ($FID = \text{New Distance} - \text{escape reaction distance}$).

Behavior was recorded before the start of the approach and classified as “Lying”, “Walking”, “Feeding”, “Standing”, or “Running”. Deer observance at start was recorded based on whether the roe deer were clearly observing us during setup before the experimental approach began, which begins at recording of starting point and start distance. Deer observance at start is classified as “Y” for observant and “N” for nonobservant. Weather conditions are divided into “Overcast”, “Partly overcast”, “Clear”, “Rain”, “Fog”, “Snowing”, and “Snow on Ground”. Wind was

recorded as “Calm”, “Light Breeze”, “Moderate Breeze”, “Strong Breeze”, and “Storm”. This was collected in conjuncture with wind direction to determine the strength of odor toward the animal. Compass direction which was procured using a compass app (Compass & Altimeter PixelProse SARL) and powder was later replaced by data obtained using the Bearing function from the *Geosphere* (v1.5.18; Hijmans, 2022) package.

One negative value was removed from the FID model as an outlier when the walker passed the roe deer and it had not run away as the negative value was not able to be used in the model. We had behaviors such as lying, standing, eating, running, and walking but due to low numbers of running and walking, those were combined into moving to get more accurate data. This still gave a small number for moving; thus, those values were labeled as NA for 5 data points. Wind type was removed as the distribution of the variable was extremely skewed, as there was little variation within.

Statistical Analysis

All our data work, including organizing, obtaining variables, statistical analyzing, making graphs and data modelling was done using RStudio (v2023.9.0.463; Posit team, 2023). We estimated the coordinates of a deer’s positions before and during approaches based on the location of the starting points of the approaches, the compass directions a walker walked, and the start distances with the *SP* package (v1.5.1; Bivand & Pebesma, 2005). Another feature obtained through the *Geosphere* package's functions was the roe deer's compass directions from the starting observation points.

The distances of roe deer to the nearest forest patch and nearest house were obtained using the bearing function from the *Geosphere* package (v1.5.18; Hijmans, R., 2022). The spatial data for the forests were obtained from the AR50 from NIBIO (Nedlasting Av kartdata, n.d) and the houses were from the FKB-Bygning from GeoNorge (Kartkatalogen, n.d). Illumination refers to the amount of moonlight due to the lunar phase that was present during the experimental approach, which was obtained with the *Moonlit* package (v0.1; Smielak, 2024) using the starting point coordinates, time, and date of each approach. Variables collected during field observations included FID, AD, start distance, deer behavior at start, group size, and deer observance at the start. To assess the directional influence of wind on deer movement, a binary variable was derived from wind directions, starting positions, and deer locations, indicating whether the wind was blowing from the starting point towards the deer or not, with a tolerance angle of 45° from the *Geosphere* package (v1.5.18; Hijmans, R., 2022).

We used Generalized Linear Models with Gamma distribution to evaluate the effect of several variables on AD and FID (Table 1) to determine the values that explain the variance in

AD and FID, after stepwise regression using a significance level of > 0.05 to remove non-significant variables until only significant variables remained. All models analyzing FID included also AD as additional variable. A process of variable selection and validation was conducted before running the modelling, variable's potential correlations were tested through correlation tests.

Table 1: Variables used to evaluate the factors affecting alert distance (AD) and flight initiation distance (FID) of roe deer during experimental approach in Midt-Telemark Municipality, Norway, in fall/winter 2022 and 2023.

AD	Start distance from watcher to roe deer
	Distance to nearest house
	Distance to nearest forest
	Deer behavior at start of approach
	Group size
	Deer observance at start Y/N
	Illumination
	Wind direction, blowing toward deer Y/N
FID	AD
	Start distance from watcher to roe deer
	Distance to nearest house
	Distance to nearest forest
	Deer behavior at start of approach
	Group size
	Deer observance at start Y/N
	Illumination
Wind direction, blowing toward deer Y/N	

Results

A total of 119 experimental approaches were made. 30 observations were made from September to December 2022 (Venås *et al.* 2023), and 89 observations were made from September to December 2023.

AD significantly increased with increasing starting distance and decreased with increasing illumination (Table 2; Figure 6, Figure 7). All other variables were removed as non-significant from the models. FID significantly increased with increasing alert distance (AD) (Table 3, Figure 8). All other variables were removed as non-significant from the models.

Table 2: Generalized linear model results for prediction of alert distance of 119 roe deer experimental approaches after stepwise regression using scaled predictors.

Variable	Estimate	SE	t	p
Intercept	8.038	2.834	2.837	0.005
Start distance	0.784	0.029	27.133	<0.001
Illumination	-0.003	0.001	-2.727	0.007

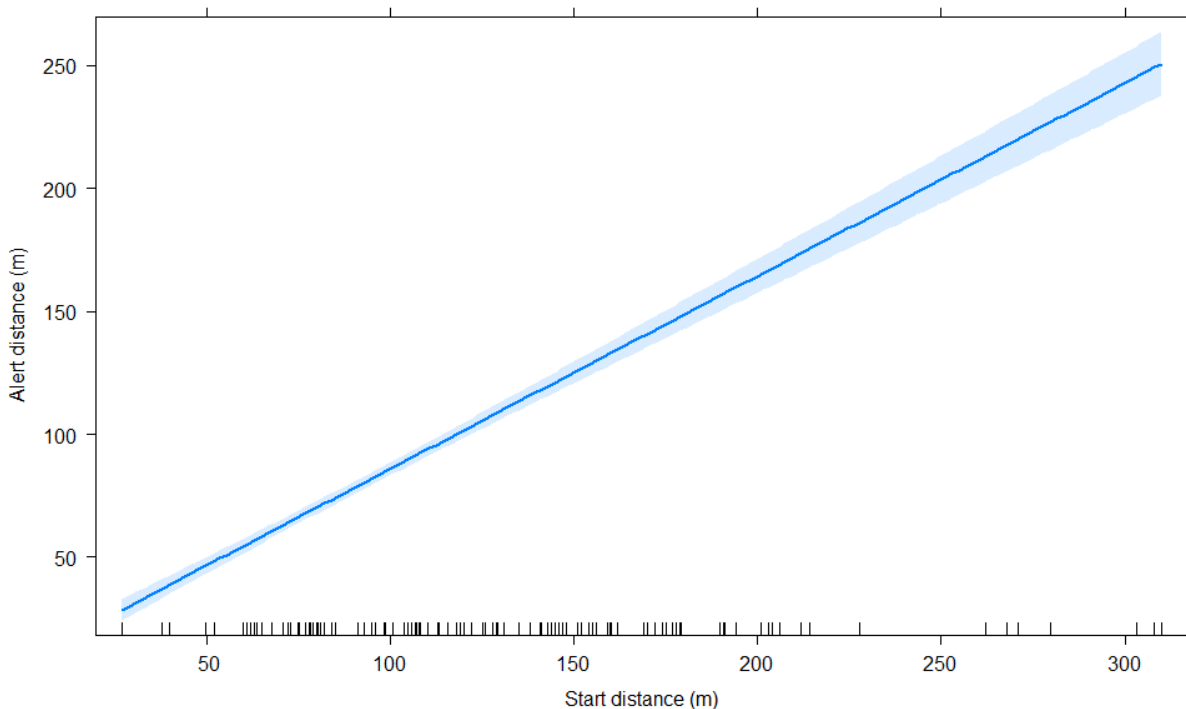


Figure 6. Effect plot between start distance and alert distance (in meters) during 119 experimental approaches of roe deer in Midt-Telemark, Norway. The 95% confidence interval is indicated by the light blue area. The tick marks on the x axis indicate the position of the data points.

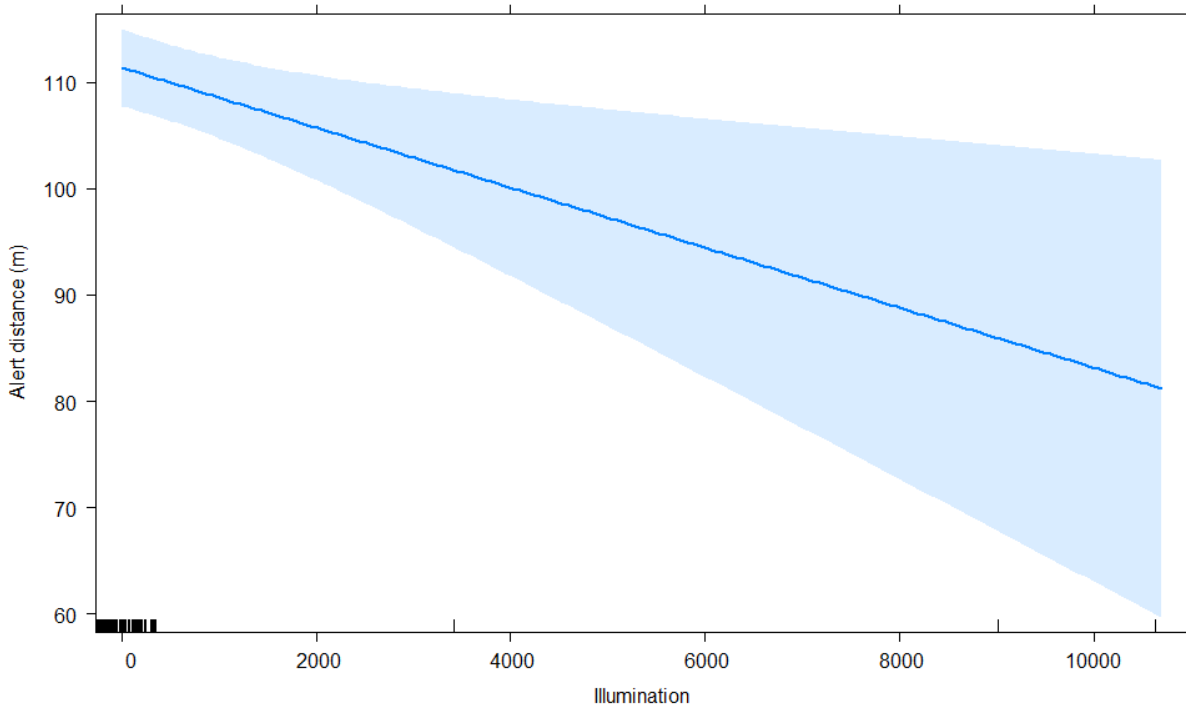


Figure 7. Effect plot between illumination and alert distance (in meters) during 119 experimental approaches of roe deer in Midt-Telemark, Norway. The 95% confidence interval is indicated by the light blue area. The tick marks at the x axis indicate the intensity of illumination at the data points.

Table 3: Generalized linear model results for prediction of flight initiation distance of 119 roe deer experimental approaches after stepwise regression using scaled predictors.

Variable	Estimate	SE	t	p
Intercept	28.052	7.327	3.829	0.0002
AD	0.492	0.077	6.361	<0.001

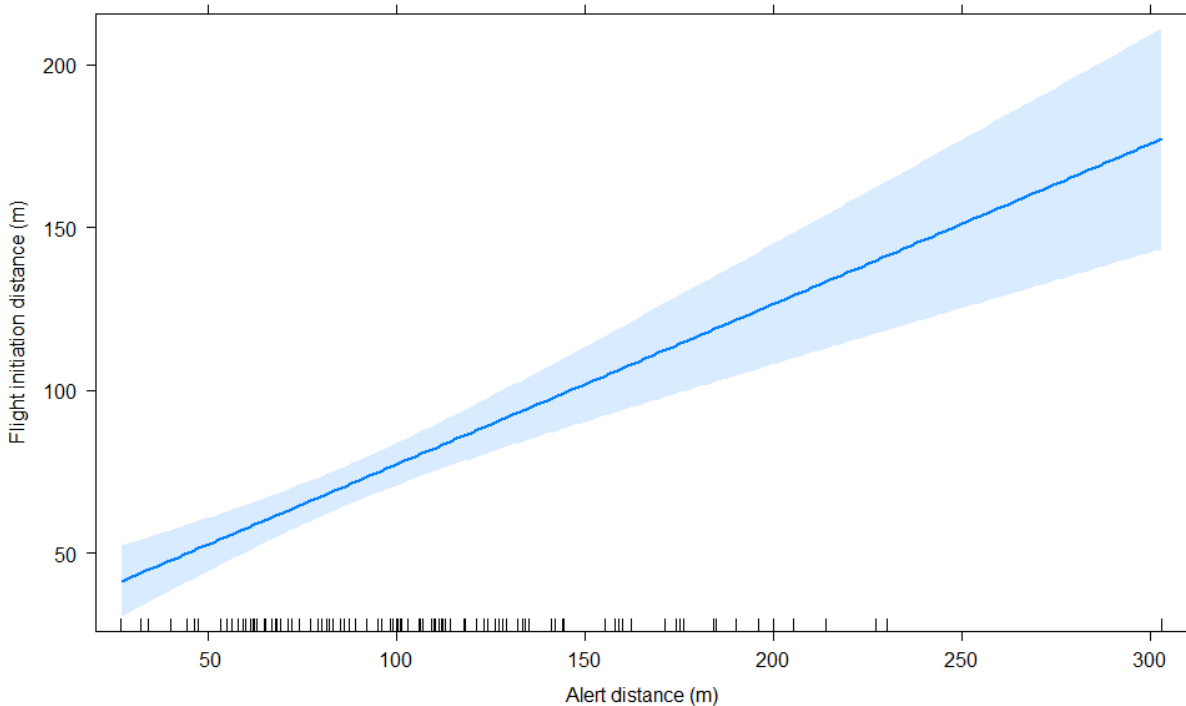


Figure 8. Effect plot between alert distance and flight initiation distance in meters during 119 experimental approaches of roe deer in Midt-Telemark, Norway. The 95% confidence interval is indicated by the light blue area. The tick marks at the x axis indicate the position of the data points.

Discussion

The results support our prediction of an increase in AD with an increase in start distance, but in contrast to our prediction we found that illumination resulted in a decrease in AD. The results also support our prediction of an increase in FID due to an increase in AD. We also predicted a lower AD and FID closer to houses and forest cover, and an increase of AD and FID with increased group size, wind direction pointed toward the deer, and initial deer behavior being observant, standing, walking, or running, as opposed to less vigilant behaviors where we predicted a decrease in AD and FID for behaviors of laying and eating. These predictions were found to not be supported by the results.

The distance at which a predator starts its approach, the start distance, and when the prey first detects them, i.e., the alert distance, are crucial in the decision of flight of the prey, as found by Blumstein (2003) where the flight behavior of many bird species was strongly affected by the start distance. The FEAR (flush early and avoid risk) hypothesis indicates that animals will flee soon after detecting an approaching threat in order to avoid the risk (Blumstein, 2010). Bonnot *et*

al (2015) found support for the FEAR hypothesis in roe deer, indicating a strong influence of alert on flight initiation distance. This supports our results, indicating that AD (and subsequently FID) is highly dependent on starting distance of the experimental approach.

A significant effect caused by distance to buildings would have indicated a lack of habituation by the roe deer if closer distance to buildings would result in an increased AD or FID as this would indicate an increase in fear closer to human settlements, but the variable was not found to be significant. This can indicate habituation as the deer in this area are not affected by distance to buildings. Some studies have found that human disturbances where there is a high density of human infrastructures have no effect on roe deer vigilance (Wevers *et al.*, 2020, Benhaiem *et al.*, 2008). Sönnichsen *et al.* (2013) also found vigilance in roe deer was not significantly affected by distance to houses.

The behavior of the roe deer prior to the start of the experimental approach had no effect on AD or FID. As there were few approaches that had the roe deer behavior as walking or running, the effect of this behavior could not be determined. The deer observance at the start, indicating vigilance, had no effect. This contradicts Stankowich and Coss (2006), who found that the Columbian black tailed deer (*Odocoileus hemionus*) spent more time assessing the threat when alert to the presence of the researchers during experimental setup. This led to a higher AD and FID, likely due to being able to receive more information of the threat prior to approach in a non-threatening way (Stankowich & Coss, 2006). This can also be used to explain no effect in standing, which can be considered as a more vigilant action than laying or eating. This may be explained by the deer's habituation to loud noises and humans, as the locations were all near active roads. Møller (2015) found that multiple bird species had longer FIDs when eating than when loafing (bird laying), while our results showed no effect of laying or eating on AD or FID. This may be explained by the roe deer's familiarity with local threats regardless of vigilant or nonvigilant behaviors. While Bonnot *et al.* (2017) found patterns with groups of roe deer reacting to approaching humans faster than solitary roe deer, Sönnichsen *et al.* (2013) found vigilance in roe deer declined with group size. Thus, as Stankowich (2008) hypothesized, group size effects on vigilance can be context dependent. It is also possible that delays in individual vigilance in larger groups due to perceived safety in numbers may cancel out effects of enhanced vigilance (Blackwell & Seamans, 2009). This may explain our results in which group size had no effect on AD or FID. Hayward *et al.* (2023) found that predator odor, indicated by wind direction, was not the fundamental determinant of distance of ungulate prey to lions (*Panthera leo*), though they expected a downwind position would cause the ungulate prey to situate themselves further, which supports our results of wind direction pointing toward the roe deer had no effect on AD or FID. They determine that by the time the odor has been detected, the ungulate prey would have

already detected them through other senses (Hayward *et al.*, 2023). Odor plays a stronger role in prey risk avoidance in more closed habitats, such as temperate mixed deciduous forests (Kuijper *et al.*, 2014) as opposed to the open agricultural fields in our experiment location. Ungulates have an excellent sense of smell, able to avoid predator location based on odor (Cara, 2005). They are also able to distinguish between odors of predator species like the blacktailed deer which can recognize the risk of wolves (*Canis lupus*) through avoiding urine odor and ignoring the less threatening black bear (*Ursus americanus*) scent (Chamaillé-Jammes *et al.*, 2014). Thus, it is possible that the roe deer in the study area are able to distinguish the non-threatening scent of humans as they live in close proximity.

Illumination indicates that with more light, the animal decreases its vigilance, resulting in a decreased alert distance. The result may be contributed to a decrease in antipredator behavior during an increase of moon illumination as there is evidence of increased roe deer vehicle collisions during full moon phases (Steiner *et al.*, 2021; Galinskaitė & Ignatavičius, 2023), which can be considered a decrease in antipredator behavior as roe deer have been found to react to vehicles in the same way as predators (Pfeiffer *et al.*, 2020). Lashley *et al.* (2014) had also hypothesized an increase in vigilance for white-tailed deer (*Odocoileus virginianus*) during the brightest parts of the day and night, full moon, but found the opposite. They presume this is due to being able to see predators better allowing a greater visual capability, allowing for reduced vigilance while foraging.

As all experimental approaches were made in autumn during hunting season (10th of August to 23rd of December), results may be affected as the presence of predators (i.e., hunters) forces ungulates to devote more time to vigilant behavior (Childress & Lung, 2003) which includes being more vigilant during hunting season (Benhaiem *et al.*, 2008).

Conclusion

Roe deer exhibit high levels of behavioral plasticity, allowing them to inhabit many different environments. This strategy comes with a cost of decreased vigilance, putting the animal at risk of predation from other animals, and an increase of human encounters. As distance to houses and distance to forest had no significant effect on either AD or FID, there is evidence that roe deer in this area have habituated to humans. It's possible that having the same reaction regardless of environment is one of the traits that has allowed the roe deer to succeed in surviving and thriving throughout Europe. While it is not confirmed whether moon illumination, and thus increased visibility, have a direct effect on roe deer behavior, our study shows an effect of increased moon illumination resulting in a decreased alert distance, thus decreased vigilance. Whether increased

moon illumination leads to decreased vigilance is something that can be researched in future studies.

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