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Factors influencing flight behaviour and detection of wild ungulates on railways - a train-mounted video study

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Abstract

Wildlife-train collisions are a widespread issue, leading to significant costs to society, reduced animal welfare and potential impacts on species' population sizes. Understanding how ungulates respond to oncoming trains and what affects their detectability is crucial for developing effective mitigation strategies. Building upon the work of Bhardwaj et al. (2022), this study investigates how various factors influence flight behaviour in fallow deer (*Dama dama*), roe deer (*Capreolus capreolus)* and moose (*Alces alces*), as well as wildlife detection from the train driver's perspective. By utilizing films from driver-activated scare systems (DASS) mounted on the front windshield of trains on Norwegian and Swedish railways, this study offers insights into both wildlife reactions and the viewpoints of train drivers.

Based on approximately 1000 observations of ungulates, each individual encounter with trains was analysed in relation to railway features, train speed, the train driver's use of typhoon warning, the ungulates' location within the terrain and biotic and abiotic factors in the surrounding landscape of the railway. Detection distance and flight initiation distance (FID) was calculated based on the video footage. The results showed that with increasing distance from the railway tracks, ungulates in total were less likely to flee from an approaching train and more likely to increase their FID. Generally, there was a higher probability of flight when the typhoon was used to warn the ungulates, but the effect of this signal was not significant in any of the separate analyses on each species alone. There was also a higher likelihood of flight during dusk/dawn. Flight behaviour of fallow deer was significantly influenced by herd size, with a greater likelihood of flight in smaller groups separated from a large herd. In contrast to roe deer and fallow deer, moose were significantly affected by train speed, with flight likelihood and FID decreasing with increasing speed. All species showed a significantly higher probability of flight across track with closer distance to the track, and in areas where the rail embankment was covered by vegetation with exception of roe deer. Additionally, ungulates in total had a higher probability of an early flight, before detected by the train driver, when visibility was obstructed by vegetation, terrain and curvature of the railway. Lastly, detection distance from the train driver's perspective was significantly obstructed by vegetation along the railroad embankment.

Further studies are suggested on a warning system that could be activated before the animals are detected by the train driver to increase animals' FID, alongside the implementation of night vision cameras for improved detection of animals during nocturnal hours.

Sammendrag

Viltkollisjoner med tog er et utbredt problem som fører til betydelige kostnader for samfunnet, redusert dyrevelferd og kan potensielt reduserte populasjonsstørrelser. Det er derfor avgjørende å forstå hvordan hjortedyr responderer på tog som kommer kjørende, og hvilke faktorer som påvirker lokførers oppdagelse av dyrene. Dette for å utvikle effektive tiltak. Denne studien bygger på artikkelen til Bhardwaj et al. (2022), og ser på hvordan ulike faktorer påvirker fluktatferden hos dåhjort (*Dama dama*), rådyr (*Capreolus capreolus*) og elg (*Alces alces*), samt hva som påvirker tidlig og sen oppdagelse av dyrene. Ved å bruke opptak fra lokføreraktiverte skremmesystemer (DASS) montert på frontruten på tog som kjører på norske og svenske jernbanelinjer, gir denne studien innsikt i dyrenes respons fra lokførerens synsvinkel.

Basert på ca. 1000 observasjoner av hjortedyr, ble hvert individs respons på tog analysert i forhold til jernbanelinjens utforming, hastighet på toget, lokførers bruk av tyfon-signal, hjortedyrenes plassering i forhold til jernbanen, og andre biotiske og abiotiske faktorer i landskapet. Basert på innhentet videomateriale, regnet jeg ut oppdagelsesavstand og fluktavstand (FID). Resultatet for alle hjortedyr viste at både sannsynlighet for flukt og FID minket når dyrene var plassert med økende avstand fra jernbanesporet. Det var en økt sannsynlighet for flukt når tyfon-signalet ble tatt i bruk for å varsle dyrene, men effekten av signalet var ikke signifikant i noen av analysene gjort separat for hver art. Videre viste resultatet for alle hjortedyr en høyere sannsynlighet for flukt i skumringstiden. For dåhjort ble fluktatferden påvirket av flokkstørrelse, der det var høyest sannsynlighet for flukt i mindre grupper, i nærheten av sporet, adskilt fra en større flokk. Elg var den eneste arten som viste en signifikant forskjell i fluktrespons i forhold til hastighet på toget. Med togets økende fart hadde elg en lavere sannsynlighet for flukt og avtagende FID. Samlet viste hjortedyrene en signifikant høyere sannsynlighet for å flukte over jernbanesporet når de stod i nærhet til sporet, og på steder med vegetasjon langs jernbanelinjen. Unntaket var rådyr som i mindre grad ble påvirket av vegetasjonsdekket. Samlet hadde hjortedyrene en høyere sannsynlighet for å allerede være i flukt før de ble oppdaget av lokføreren, ved tett vegetasjon eller varierende terreng langs jernbanen, samt på bøyd spor. Disse faktorene kan potensielt hindre dyrenes oppdagelse av toget. For lokførere var vegetasjon langs jernbanelinjen en avgjørende faktor for oppdagelsesavstand.

Videre studier anbefales på et vasslingssystem som kan aktiveres før lokføreren oppdager dyrene for å kunne øke dyrenes FID, i tillegg til innstallering av et kamera utstyrt med infrarødt lys og varmedeteksjon, for å minske oppdagelsesavstanden nattestid.

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1. Introduction

There is a large increase in the establishment of railway lines globally (Newman et al., 2013) This is reflected through the need for more sustainable, climate-friendly and efficient systems for citizens, as well as economic benefits (Newman et al., 2013). Despite the benefits railways provide for the population, they have considerable consequences for wildlife, with collisions between ungulates and trains emerging as a major problem. In Norway 2022/2023, there were 982 registered ungulate collisions with trains. This includes species such as moose (*Alces alces*), roe deer (*Capreolus capreolus)*, and red deer (*Cervus elaphus*), and is an increase of over 16% from the previous year (Statistics Norway, 2023). Sweden faces an even greater challenge with ungulate-train collisions, with 4512 registered incidents of ungulate-train accidents in 2023, including moose, roe deer, red deer, fallow deer (*Dama dama*) and wild boar (*Sus scrofa)* (Nationella Viltolycksrådet, 2024a). Unlike collisions between cars, collisions with trains do not result in injury or death to humans but can lead to significant damage to trains and delays in railway traffic (Seiler & Olsson, 2017). In addition, it is also a stress factor to the train driver, passengers and others involved (Bhardwaj et al., 2022). Collisions with trains may also reduce the population size of some species (Jasińska et al., 2019). Studies in Sweden show that the railway appears to be a greater source of mortality in ungulates per kilometre than roads (Seiler & Olsson, 2017). The costs are also high: the Norwegian Public Roads Administration has estimated the annual socio-economic costs of wildlife collisions to be 600 million NOK (equivalent to 50 million EUR) (Muskhaug et al., 2010; Norges Bank, 2024). In Sweden, the socio-economic cost of ungulate collisions with trains is estimated to be between 100 to 150 million EUR per year (Seiler & Olsson, 2017).

To minimize the risk of a collision through mitigations it is important to increase knowledge about the flight behaviour of ungulates. While numerous factors may influence flight behaviour, we understand it is primarily motivated by fear. The 'landscape of fear' conceptual framework defines fear as the strategic manifestation of evaluating the trade-offs between food and safety through cost-benefit analyses (Bleicher, 2017), and drives the actions of prey in response to predation risk from predators (Laundré et al., 2010). Even though trains and vehicles can cause fatal outcomes for ungulates that are hit, the animals are much less evocative for these kinds of threats than for the appearance of a predator or a human on foot (Stankowich, 2008).

Because ungulates do not fear traffic enough to completely avoid it, highways in Norway and Sweden are often surrounded by large fences in addition to wildlife crossings, to prevent wildlife-collisions that can cause injuries or death to humans. Nevertheless, there are still several regions where there are no wildlife fences alongside the roads, resulting in numerous wildlife collisions (Hjorteviltregisteret, 2024; Nationella Viltolycksrådet, 2024b; Statens Vegvesen, 2024). Since collisions between ungulates and trains do not harm humans, railways are in general less protected from wildlife crossing (Seiler & Olsson, 2017). Additionally, train traffic along the railways occurs much less frequently compared to cars on the road. That means that there is a long interval of time during the day where the wildlife can stay at or cross the railway undisturbed by train traffic. Installing wildlife fences, along with designated wildlife crossings, is thereby not cost-effective enough to be implemented over long distances. An examination of what affects flight behaviour of ungulates and detection, both from an ungulates' and a train driver's perspective, can therefore be crucial for making affordable and effective measures to prevent ungulate-train collisions.

It is important to delve into specific factors that can affect flight response and detectability. One such factor is the positioning of ungulates relative to the railway tracks. Bhardwaj et al. (2022) found that ungulates tend to flee from an oncoming train, rather than remaining on the spot, when staying near or on the railway tracks. Furthermore, the numbers of individuals fleeing were significantly reduced when positioned outside the railway corridor. To prevent collisions, it is desirable that the ungulates exhibit fear towards an approaching train, even when they are standing at a greater distance from the tracks, to avoid the risk of them moving onto the tracks.

The speed of the train is also an important factor. An approaching train at high speed can be intimidating even for humans, and one might assume that a high-speed railway would scare away the ungulates. However, Bhardwaj et al. (2022) explained that increased train speed had a negative impact on flight with that the ungulates might not have enough time to react when the train approaches at high speed. Detecting wildlife also becomes more challenging at high speed. Since trains are not able to quickly slow down, the only option available to the train driver is to sound the horn in an attempt to scare away ungulates positioned on or near the railway track. The use of typhoon warning (horn) seemed to have a slightly positive effect on flight initiation distances (Backs et al., 2020; Bhardwaj et al., 2022), but the effect on reducing collision can be miniscule (Bhardwaj et al., 2022). Previous research has reported, through controlled experiments at feeding stations, that the use of natural sound stimuli such

as human voices and dog barking, increased flight responses in moose and red deer (Almås, 2021; Eilertsen et al., 2021).

Compared to roads, railways are narrower and often surrounded by natural landscapes and vegetation which wildlife uses as part of their habitat (Bhardwaj et al., 2022). According to train drivers, poor visibility, thick vegetation and poor light conditions, are some of the main causes for wildlife-collisions (Seiler & Olsson, 2017). These conditions simply make it harder for the animals to detect the oncoming train in time to escape, and harder for the train driver to detect animals in time to use warning signals.

According to Seiler and Olsson (2017) the presence of snow is also an important reason for ungulate-train collisions. Ungulates have a more energy-saving behaviour during winter (Græsli et al., 2020; Mysterud et al., 1997; Richard et al., 2014), and use the railway as an easier travel route because of great snow depths (St. Clair et al., 2020). Ungulate mortality due to train collisions is therefore higher during winter because the ungulates often choose to use the railway as an escape route from an oncoming train instead of moving away from the railway corridor (Rolandsen et al., 2005; Seiler & Olsson, 2017; St. Clair et al., 2020).

Herd dynamics can also affect flight behaviour. According to a study on ungulate behaviour next to a road, ungulates are more reactive in smaller herds and when they are dispersed (Brown et al., 2012). Deer species like roe deer, moose and red deer are solitary animals, but can occur in small groups of related individuals (Hjeljord, 2008). During winter and in areas with high densities, roe deer can form small herds (ibid.). Fallow deer on the other hand are social animals and live in groups all year (Feldhamer et al., 1998).

Perhaps the most crucial factor in promoting survival among ungulates when encountering a train is the timing of their flight. Flight Initiation Distance (FID) is the distance at which the ungulate flees from the approaching train. FID is strongly affected by detection distance (Blumstein, 2003; Bonnot et al., 2017), as early detection of trains promotes early opportunities for flight. Further investigation of factors affecting FID is therefore essential for mitigation interventions.

To be able to analyse ungulates' response to an oncoming train, driver-activated scare systems (DASS) have been placed on the front windshield of trains, recording every event of ungulate encounters. This enables an analysis of flight behaviour and detectability from the train driver's perspective. Previous research by Bhardwaj et al. (2022) investigated the flight response of moose and roe deer to trains, as well as factors influencing detectability using the

same method. This study is a continuation of this article and will focus on the following species: moose, roe deer, and fallow deer. In accordance with the research by Bhardwaj et al. (2022) I aim to investigate the flight behaviour and detectability of ungulates that managed to escape from an approaching train. The objective is to explore if ungulates respond differently depending on factors such as the train driver's use of typhoon warning, speed of the train, the ungulates' location within the terrain, railway features and other biotic and abiotic factors in the surrounding landscape of the railway. To explore these objectives, I investigated the likelihood of flight from an oncoming train, their direction of flight, variation in FID, probability of flight before detection by train driver, and the detection distance of animals from the train driver's perspective. In addition, my study will also examine herd size and the presence of snow on the ground as factors influencing flight behaviour. Based on these research objectives, I identify the following research questions:

1: What factors influence the likelihood of ungulates fleeing from an oncoming train?

2: How do various factors affect the flight direction of ungulates?

3: What are the variations in flight initiation distance (FID) among ungulates, and what factors influence these variations?

4: What factors increase the likelihood of flight of ungulates before detection by the train driver?

5: How do surrounding factors affect the detection distance of ungulates from the train driver's perspective?

2. Materials and methods

2.1 Study area

This study was conducted on Norwegian and Swedish railways where video cameras have been attached to trains on different passenger rail networks. I first analysed all video material from year 2022-2023 collected from Kinnekullebanan, Gjøvikbanen and Rørosbanen railways, which included 915 individual observations of wildlife. Unfortunately, the amount of data was not sufficient to conduct robust statistical analyses. Therefore, I was provided with video material from 2015-2018 from several different Swedish railways including Kinnekullebanan, Ostkustbanan, Vänerbanan, Västra stambanan, Berglandsbanan, Mälarbanan, Södra stambanan, Ådalsbanan, Kolbäck-Oxelösund, Mittbanan, Värmlandsbanan, Botniabanan, Svealandsbanan, Dalabanan, and Norra stambanan, from which I utilized 149 individual observations of roe deer and moose. Most of the data was collected from Kinnekulle railway in Sweden, which is a railway where exceptionally many wildlife-train collisions occur in Sweden (up to 2.5 accidents with ungulates per km and year during 2017-2021) (Håkansson et al., 2023). Although the railway line has low traffic intensity, it has a high frequency of collisions with wild ungulates, especially roe deer and fallow deer. Collisions with moose on the other hand, do not happen very frequently along this railroad.

2.2 Experimental design

All cameras were programmable DASS (Driver Activated Scare System)-units (Seiler et al., 2022b). We used different types of DASS-units to collect the data. The original DASS-unit (figure 1 and 2) consisted of a manual alarm trigger, a manual on-off switch, Wi-Fi link for automatic image transfer, USB-C connection and a single-board computer. For the single-board computer we used a Raspberry Pi 4 model B. This computer included a monitor, a real time clock, internal sound cards, Wi-Fi and Bluetooth communication, USB connections for output to SD cards, a microphone input, and a Raspberry Pi Camera Module 2 to film the events. The Bluetooth adapter was installed with the purpose of later connecting it to an external speaker capable of playing various sound signals. The speakers were first fully installed in March 2024 and will become part of ongoing research projects.

A Nextbase 522GW dashboard camera has also been used for filming (figure 3). This camera has principally the same functions as the original DASS-unit, but with a higher image resolution, continuous sound recording and a GPS speedometer function. The manual alarm

trigger-button was located directly on the dashboard camera, unlike the original DASS-units where the alarm trigger was an easily accessible pressure switch attached with an extended cable. Therefore, the Nextbase camera could only be used on trains where the windshield was no further away than an arm's length from where the train driver was seated.
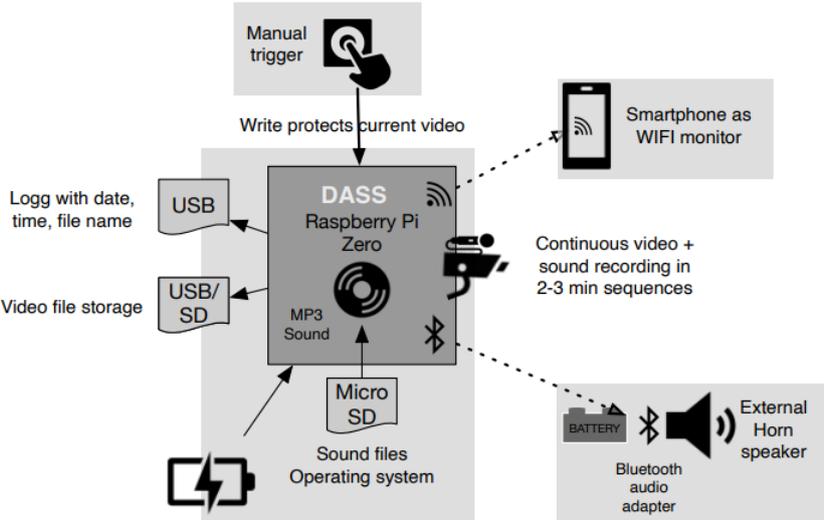
Figure 1: DASS original concept from (Seiler et al., 2022b)

Figure 2: DASS-unit mounted on the front shied of a train, filming a dead fallow deer on the railway track (foto by Mathias Olsson).

Figure 3: Nextbase 522GW dashboard camera mounted on the front shield of a train at Kinnekullebanan railway (foto by Elise Lyng Monssen).

Both the Raspberry Pi unit and Nextbase dashboard camera were attached inside the windshield of the trains with a suction cup. Before the trains started their routes, the train drivers started the DASS-units which then recorded continuously video sequences of 1-3 minutes in length. Every time the train drivers detected an animal, they manually triggered the alarm function on the camera. The camera then saved a 30 second video sequence that started 10 seconds before the alarm was activated. The complete sequence of events was thereby recorded. On the Raspberry Pi unit, the sound recording started when the alarm was activated, while the Nextbase camera recorded audio continuously. Video sequences were stored in two different folders. One folder with the continuous video sequences of 3 minutes in length, and one folder with the 30 second saved video sequences triggered by the alarm. The 30 second saved video sequences with the recorded animal observations were later uploaded on the image management platform Capture.slu.se (Seiler et al., 2022a).

2.3 Video analysis

I analysed video sequences after they had been uploaded on Capture. I used Capture and VLC Media Player (VideoLan, 2024) to watch the videos. Each encounter between trains and ungulates was analysed. All variables that were used are listed with a short description in table 1.

2.3.1 Uncertain species

Identifying individual species on videos from a moving train can be challenging. For example, under poor light conditions, when individuals are observed from a long distance, when video quality is poor, or vegetation or typography only allows for a brief glimpse of the animal, the species can be hard to determine. Roe deer and fallow deer are species that can easily be confused with each other. Moose is much easier to identify but can sometimes be confused with red deer. Species uncertainty was therefore defined as factor "yes" or "no" for each individual observation.

2.3.2 Obstructions

There were several variables intended to describe factors that could potentially impede the detection of the animal by the train driver. Figure 4 demonstrates some of the variables. Among these, 'day period', 'curvature', 'railside vegetation' and 'terrain' were included, along with a separate variable called 'obstruction' which was created to indicate the primary factors obstructing early detection of animals. By incorporating the 'obstruction'-variable, I was able to exclude video footage where detection was primarily hindered by poor video quality or by other man-made objects (passing trains, hay bales in a field, etc.), which would counteract the effect of the other obstructions.

Figure 4: Screenshots of films from Capture that shows variables that influence detection of animals. Top left: Obstruction by trees. Top right: obstruction by terrain. Bottom left: cleared vegetation that do not obstruct visibility of animals. Bottom right: obstruction by low light conditions on a curved railway during dusk.

2.3.3 Analysing herds

When there were multiple individuals featured in one video sequence, each individual was analysed separately with focus on the individual's response to the oncoming train. For herds of more than 15 individuals, I analysed the 5-10 individuals standing closer to the railway, or those that provided a representative sample of response. In the videos I analysed, fallow deer that occurred in large herds of more than 30 individuals, often in a clearing, tended to form smaller groups where some of them stayed close to the railway, while the rest of the herd was standing further away. A representative sample of response was thereby hard to accomplish and only the 5-10 individuals standing closest to the railway were analysed.

2.3.4 Flight direction

Flight direction was initially categorized as flight away from track, across track, and along track. Unfortunately, there was not enough video material to include thorough analyses of individuals running along track. Therefore, a binary variable was created for individuals either running across or away from track. These did not include individuals that were already in flight from start of the video.

2.3.5 In flight at start

'In flight at start' is a binary variable created for analysing animals that were already in flight when first visible on the video. When an animal is in flight from start, we assume it has already detected the train before the train driver has detected the animal. When the train driver has detected the animal from a long distance, we infer that the animal has likely detected the train from a similar distance or longer, because ungulates are able to hear an approaching train and are in a better position to visually detect trains through vegetation than a train driver is to perceive an animal amidst bushes and trees.

2.3.6 Calculating detection distance and flight initiation distance

An important part of the analyses was to measure the distance from the train where the animals were detected and their FID. I calculated detection distance from when the animal was first visible on the video and counted seconds until the train reached the spot where the animal was first standing. When calculating distance in meters, I multiplied the speed of the train in m/s with time in seconds.

When calculating the FID I counted the seconds from when the animal initiated its flight until the train reached the spot where the animals were standing before initiating flight. I calculated the distance in meters the same way as for detection distance.

The Nextbase 522GW dashboard cameras came with a GPS speedometer-function which made it possible to track the speed of the train in km/h on the video uptakes. Thereby I converted km/h to m/s and multiplied it with the time in seconds and got the distance in meters in result.

$$\frac{km/h}{3.6} \times s = m$$

The original DASS-units that were used did not have a speedometer-function on the GPS. Speed of the train were thereby measured by counting seconds the train used between electric poles along the railway with a regular distance in between (Norway; 50m on a straight track, 30-40m on curved tracks. Sweden; 60m on a straight track, 40-50m on curved tracks). I then calculated the speed in meters per second by dividing distance per second.

Table 1: List of response variables and explanatory variables used in the analysis.

Variable	Description
Response Variables	
Flight	Binary variable quantifying if the animal flees or not; yes (1) or no (0).
Flight across or away from track	Binary variable describing if the animal flees across track or away from track; across track (1) and away from track (0).
In flight at start	Binary variable quantifying if the animal is already in flight when it is first visible on the video; a) yes, b) no.
Detection distance	Continuous variable measuring the distance from the train at which the animal is first visible on the video.
FID (Flight Initiation Distance)	Continuous variable measuring the distance from the train at which the animal initiates its flight.
Explanatory Variables	
Railway	Categorical variable describing at which railway the animal was observed.
Start position	Where the animal was positioned when first visible on the video. Categorized as a) on track, b) near track (between the rail-side verges, but not on the tracks), c) 25 meters or less outside corridor, and d) more than 25 meters outside corridor.
Time of day	Describing different day periods. Categorized as a) day, b) dusk/dawn, and c) night.
Snow	Binary variable quantifying if snow was present where the animal was standing; a) yes, b) no.
Curvature	Describes the curvature of the track where the animal was first observed. Categorized as a) straight, b) bend.
Railside vegetation	Describes the type of vegetation surrounding the railway where the animal is observed. Categorized as a) clear, b) low shrub, c) trees and d) unknown. "Clear" is described as newly cut or trimmed vegetation, or simply grass.
Terrain	A binary variable describing if terrain obstructs visibility of the animal. Categorized as a) yes, and b) no.
Obstruction	What mainly obstructs visibility of animals on the video. Categorized as a) curvature, b) terrain, c) vegetation, d) low light, e) weather, f) video quality, g) none.
Warning	Binary variable quantifying if there was any use of typhoon warning when observing an animal; a) typhoon, b) no warning.
Species	Describes the specie observed. Categorized as a) moose, b) roe deer, c) fallow deer.
Uncertain species	Binary variable quantifying if there is any uncertainty regarding the type of specie; a) yes, b) no.

Herd size	Describes different group sizes of individuals of the same species. Categorized as a) 1-5 individuals, b) 6-15 individuals, c) 15-30 individuals, d) >30 individuals.
Visible at start	Binary variable quantifying if the animal is visible during the start of the video; a) yes, b) no.
Train speed	Speed of the train measured in km/h

2.3.7 Analysing flight behaviour

When analysing flight behaviour of the animals, I used the following explanatory variables: 1) start position, 2) day period, 3) train speed, 4) use of warning signal, 5) snow, 6) railside vegetation and 7) heard size. To explain flight behaviour, I did four separate analyses.

First, I conducted a logistic regression for flight based on 'start position', 'day period', 'train speed', 'heard size' and 'warning'. 'Flight' was measured as a binary variable: flight (1) or no flight (0). In this analysis I combined 'on track' and 'near track' into the factor 'inside corridor', because individuals positioned on the track will normally always have to flee to prevent getting hit by the train.

Secondly, I conducted a logistic regression analysis on flight direction to determine the probability of flight across track compared to flight away from track. 'Flight direction' was also measured as a binary variable: flight across track (1) and flight away from track (0). The analysis was based on the explanatory variables 'start position', 'train speed', 'snow', 'railside vegetation' and 'heard size'. I combined the factors 'outside corridor (<25m)' and 'outside corridor (>>25m)' into the factor 'outside corridor' because animals far away from railway corridor would normally never run across track, and to obtain results that are easier to interpret.

A linear regression analysis on FID was fit based on the explanatory variables 'start position', 'day period' and 'train speed'. I also calculated the average FID. The analysis on FID only includes individuals first observed on the track and near track because FID of individuals outside the railway corridor could not be measured accurately. I did not include individuals that were already in flight from start of the video because FID could not be measured. Individuals observed at night were also excluded from this analysis since FID was uncertain because of low visibility.

Lastly, I conducted a logistic regression analysis on the probability of individuals flight from start of the video based on the explanatory obstruction-variables, 'day period', 'curvature',

'railside vegetation', 'terrain' and 'detection distance'. This analysis did not include individuals that were already visible at start of the video.

All analyses were initially conducted collectively for the overall observation of ungulates, including observations where species identification was uncertain, and then conducted separately for fallow deer, roe deer and moose. Since observations of roe deer and moose occurred at different railways, I included 'railway' as a random effect in the analyses on total observations of ungulates and in the analysis on roe deer. Unfortunately, moose were observed at many different railways with only a few observations at each, and the results would therefore be difficult to interpret if I were to include the random factor. In the analysis on flight direction on roe deer, 'snow' was included as a covariate with 'railway' as a random effect. 'Herd size' was only included in the analyses on total observations of ungulates and the separate analyses on fallow deer since there were only three videos of roe deer and one video of moose with including a group of more than 6 individuals. In the analysis on flight direction in moose, I combined 'outside corridor (>25)' and '– (>>25)' into the factor 'outside corridor'. I also excluded the variables 'start position' and 'day period' in the analysis on FID in moose because of few observations on the track and during dusk/dawn.

2.3.8 Analysing detection distance
I based the analysis of detection distance on the following explanatory variables; 1) start position, 2) railside vegetation, 3) curvature, 4) day period and 5) terrain.

To be able to explain detection distance, I did a linear regression based on type of obstruction of visibility. Observations of animals obstructed by bad video quality were removed because detection distance could not be measured properly.

Like in the analysis on flight behaviour, all analyses were done for the overall observation of ungulates, and separately for fallow deer, roe deer and moose. 'Railway' was included as a random factor in the analysis on the total observations of ungulates, and in the analyses on roe deer. In both analyses I only included individuals that was first observed on the track and near the track, because detection distance measured for animals outside the railway corridor were not reliable. For the same reason I excluded observations where individuals were visible at the start of the video and when vision of the animals were obstructed by bad video quality. Visibility obstructed by human made objects were also excluded to not interrupt with the other more natural obstructions. 'Terrain' was excluded from all analyses, and 'day period' excluded from the separate analysis on roe deer because of too few observations.

2.3.9 Statistics

Processing the data from the videos were done in Microsoft Excel (v.2403)(Microsoft Corporation, 2024) where detection distance and flight initiation distance were calculated. The statistical analyses were done in the software R Studio (v.4.3.1)(R Core Team, 2023).

Logistic regression analyses on fallow deer were fit using the 'glm()' function that belongs to generalized linear models (GLM). There were only observations of fallow deer on Kinnekullebanan railway, and there was no need to consider any additional variance. Roe deer and moose on the other hand, were observed at different railways. Logistic regression analyses for these species were therefore fit using the 'glmer()' function that belongs to the generalised linear mixed model (GLMM) and is part of the 'lm4' package (Bates et al., 2015). GLMM allows for the incorporation of random effects to account for repeated observations on different railways.

In the same way, linear regression analyses were fit using the 'lm()' function for fallow deer and the 'lme()' function for roe deer and moose. The 'lme()' function belongs to the linear mixed-effects model (LME) and is part of the 'nlme' package (Pinheiro & Bates, 2000). The LME model also incorporate random effects.

I used 'dredge()' function, which is part of the 'MuMIn' package (Barton, 2023), to generate and compare all possible models from my set of candidate models. To identify the best fitting model, I used the AIC (Akaike Information Criterion) method. The model with the lowest AIC-value among all models, is considered as the best fitting model (Mazerolle, 2006), but all models with a ΔAIC under 2 are considered as valid models to use. In those cases, were there were several models with a ΔAIC under 2, the models with lower degrees of freedom were chosen as the most parsimonious model (Zhang et al., 2012).

When I ran the logistic regression analysis on probability of flight in roe deer, I got complete separation of the factor 'outside corridor (>>25)'. To solve the issue, I used 'bglmer()' from the 'blme' package (Chung et al., 2013), instead of using 'glmer()'.

For visualizing my data, I used the 'ggpredict()' function from the 'ggeffects' package (Lüdecke, 2018) to calculate predicted values and confidence intervals for specified terms in my models. I used the 'ggplot()' function from the 'ggplot2' package (Wickham, 2016) to create the plots.

3. Results

In the analysis I included a total of 384 videos, which accounted for 1019 individual observations of wildlife. These observations comprised 568 instances of fallow deer, 179 of roe deer, 126 of moose and 146 individuals with uncertain species identification. A significant portion of my data, encompassing a total of 820 observations of the specified species, was collected from Kinnekullebanan railway area. The rest of the observations were collected from Ostkustbanan (n = 51), Gjøvikbanen (n = 48), Vänerbanan (n = 22), Västra stambanan (n = 19), Berglandsbanan (n = 11), Rørosbanan (n = 10), Mälarbanan (n = 7), Södra stambanan (n = 7), Ådalsbanan (n = 6), Kolbäck-Oxelösund (n = 5), Mittbanan (n = 5), Värmlandsbanan (n = 3), Botniabanan (n = 2), Svealandsbanan (n = 1), Dalabanan (n = 1) and Norra stambanan (n = 1). Furthermore, the typhoon warning signal was used on a total of 164 individuals across the observed species (table 2).

Table 2: Number of individuals recorded with and without use of typhoon warning.

Warning signal	n individuals of fallow deer	n individuals of roe deer	n individuals of moose
No warning	502	123	107
Typhoon	66	56	19

3.1 Probability of flight
3.1.1 Wild ungulates in total
In the analysis examining the probability of flight in wild ungulates, model 24 was considered as the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. Model 24 included the variables 'day period', 'herd size', 'start position' and 'warning' (table 3).

Table 3: AIC model selection table for the total of observed ungulates, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	Day_period	Herd_size	Start_pos	Train_speed	Warning	df	logLik	AICc	delta	weight
24	3.319	+	+	+		+	10	-449.3	918.9	0.00	0.414
32	3.516	+	+	+	-0.00420	+	11	-448.5	919.4	0.44	0.332
8	3.342	+	+	+			9	-451.7	921.6	2.65	0.110
22	3.307	+		+		+	7	-454.1	922.4	3.46	0.073
30	3.541	+		+	-0.00489	+	8	-453.2	922.5	3.54	0.071

Table 4 and figure 5 show a significant higher probability of flight for individuals positioned inside corridor (n = 267 out of 275). Similarly, the probability of flight for individuals less than 25 meters from corridor (n = 388 out of 573) was significantly higher than for individuals positioned more than 25 meters from corridor (n = 23 out of 171). During

dusk/dawn the probability of flight was significantly higher (n = 210 out of 279) than during daytime (n = 439 out of 708). During night-time there was a lot of variation in standard error with an overall high probability of flight (n = 29 out of 32), and there was no significant difference compared to daytime and dusk/dawn. With the use of typhoon warning, individuals were significantly more likely flee (n = 142 out of 162) than with no use of warning (n = 536 out of 857). Figure 5 shows that individuals were less likely to flee when they occurred in medium sized groups (6-15 individuals: n = 144 out of 255. 15-30 individuals: n = 55 out of 113) rather than small groups (1-5 individuals: n = 413 out of 563). A herd size of more than 30 individuals, had a significantly higher likelihood of flight (n = 66 out of 88) compared to a herd size of 15-30 individuals.

Table 4: Parameter estimates from the most parsimonious model for probability of flight in total of observed ungulates.

	Estimate	Std. Error	z-value	p-value
Intercept (Inside corridor, day, no warning, herd size:1-6)	3.319	0.48	7.03	<0.001
Outside corridor <25	-2.534	0.38	-6.67	<0.001
Outside corridor >>25	-5.155	0.44	-11.71	<0.001
Dusk/dawn	0.712	0.2	3.57	<0.001
Night	0.736	0.72	1.03	0.305
Typhoon	0.801	0.36	2.25	0.025
Herd size: 15-30	-0.574	0.28	-2.08	0.038
Herd size: 6-15	-0.219	0.2	-1.08	0.280
Herd size: >30	0.511	0.33	1.58	0.116
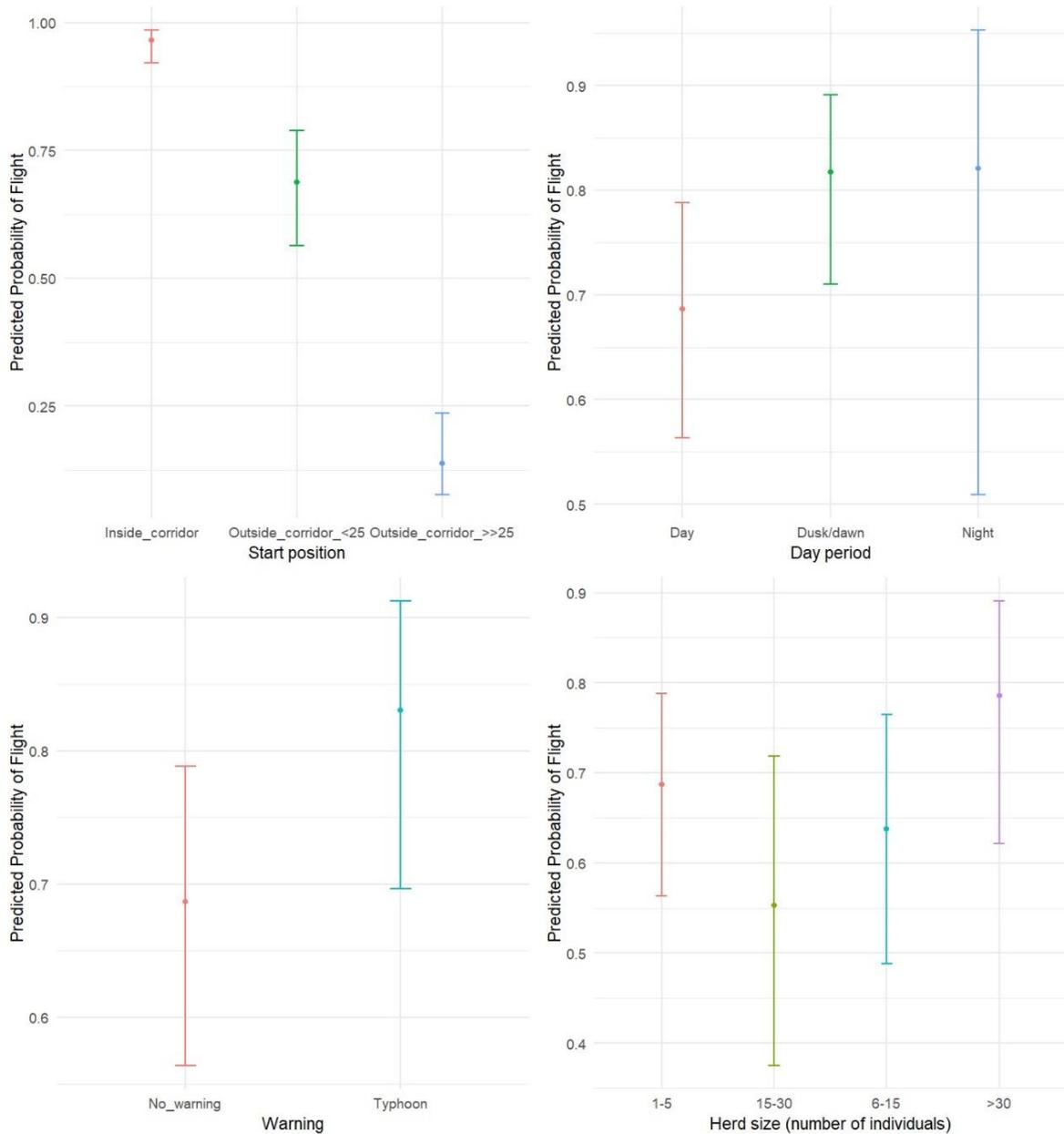
Figure 5: Predicted probability of flight in total of observed ungulates with 95% confidence intervals, based on the explanatory variables; 'start position', 'time of day', 'warning' and 'herd size'.

3.1.2 Fallow deer

In the analysis examining the probability of flight in fallow deer, I did not include 'warning' in my model because fallow deer fled in all cases when utilizing the typhoon warning. This resulted in model 8 being the most parsimonious model with a ΔAIC of less than 2. The model was characterised by the inclusion of the variables 'day period', 'start position' and 'herd size' (table 5).

Table 5: AIC model selection table for fallow deer, where the best fitting models are ranked from top.

	(Intercept)	Day_period	Herd_size	Start_pos	Train_speed	df	logLik	AICc	delta	weight
8	4.438	+	+	+		8	-261.7	539.7	0.00	0.661
16	4.293	+	+	+	0.0018157	9	-261.7	541.7	2.00	0.241
6	4.485	+		+		5	-267	544.1	4.40	0.072
14	4.625	+		+	-0.001678	6	-267	546.1	6.40	0.026

Results from table 6 and figure 6 indicates that fallow deer were significantly more likely to flee from an oncoming train when positioned inside corridor (n = 116 out of 117) and significantly less likely to flee when positioned outside corridor. When positioned less than 25 meters from corridor, predicted probability of flight was approximately 50% (n = 220 out of 349). When positioned more than 25 meters from corridor the predicted probability was significantly lower (n = 14 out of 102). Fallow deer were also significantly more likely to flee by dusk/dawn (n = 123 out of 151) compared to day- (n = 221 out of 408) and night-time (n = 6 out of 9). In large herds of more than 30 fallow deer, individuals were significantly more likely to flee (n = 66 out of 88) compared to individuals in smaller groups (1-5 individuals: n = 105 out of 152, 6-15 individuals: n = 125 out of 220, 15-30 individuals: n = 54 out of 108).

Table 6: Parameter estimates from the most parsimonious model for probability of flight in fallow deer.

	Estimate	Std. Error	z-value	p-value
Intercept(inside corridor. day. herd size: 1-5)	4.438	1.011	4.391	<0.001
Outside corridor <25	-4.292	1.016	-4.224	<0.001
Outside corridor >>25	-6.488	1.054	-6.156	<0.001
Dusk/dawn	1.154	0.271	4.257	<0.001
Night	0.501	0.775	0.646	0.518
Herd size: 15-30	-0.131	0.338	-0.386	0.699
Herd size: 6-15	-0.072	0.282	-0.255	0.799
Herd size: >30	0.897	0.363	2.472	0.013
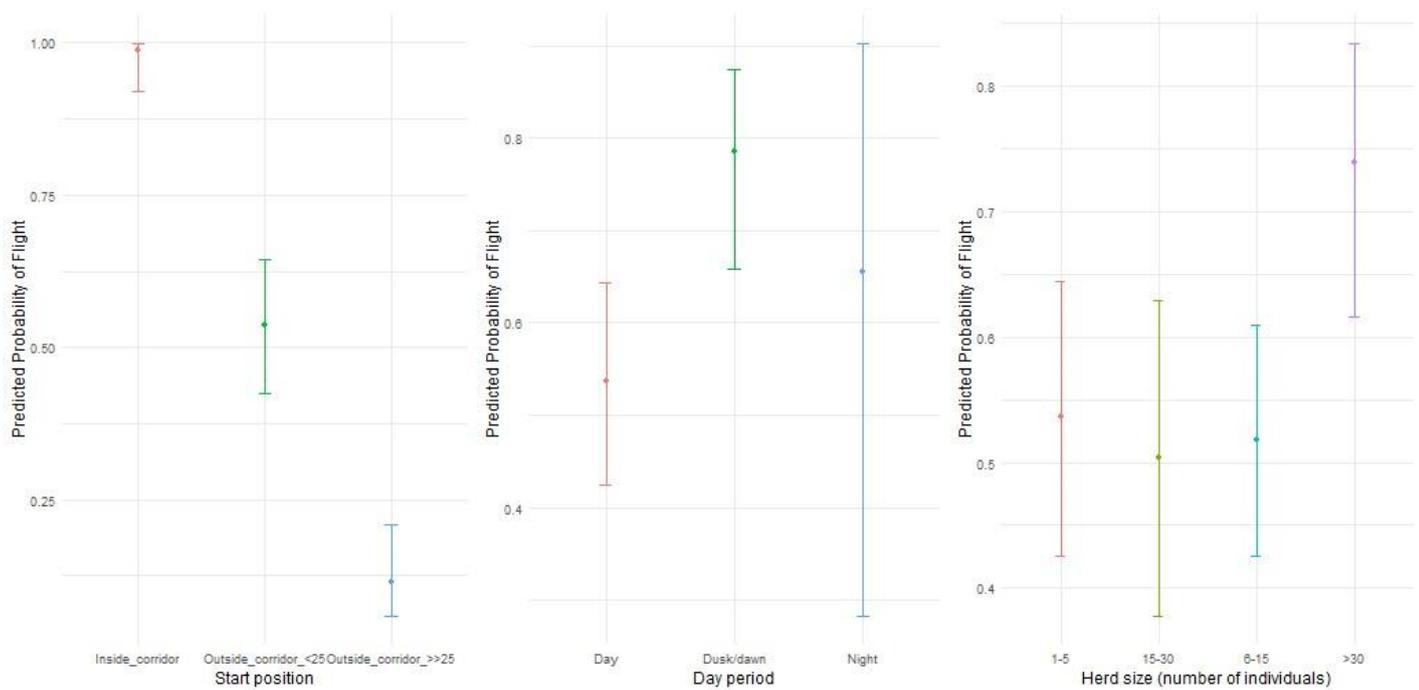
Figure 6: Predicted probability of flight in fallow deer with 95% confidence intervals, based on the explanatory variables; 'start position', 'day period' and 'herd size'.

3.1.3 Roe deer

In the analysis examining the probability of flight in roe deer, model 3 was the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. Model 3 included the variable; 'start position' (table 7).

Table 7: AIC model selection table for roe deer, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	*Day_period*	*Start_pos*	*Train_speed*	*Warning*	*df*	*logLik*	*AICc*	*delta*	*weight*
3	2.567		+			4	-67.15	142.5	0	0.369
4	2.316	+	+			6	-65.82	144.1	1.59	0.166
7	2.916		+	-0.0034456		5	-67.08	144.5	1.98	0.137
11	2.442		+		+	5	-67.09	144.5	1.99	0.136
8	2.645	+	+	-0.0031352		7	-65.76	146.2	3.65	0.06

Table 8 and figure 7 show that roe deer were significantly more likely to flee when positioned inside corridor (n = 68 out of 73) compared to when positioned outside corridor. The probability of flight for individuals positioned less than 25 meters from corridor were approximately 75% (n = 71 out of 91). There were no individuals of roe deer that fled when positioned more than 25 meters from corridor (n = 0 out of 14).

Table 8: Parameter estimates from the most parsimonious model for probability of flight in roe deer.

	Estimate	Std. Error	z-value	p-value
Intercept (inside corridor)	2.474	0.623	3.97	<0.001
Outside corridor <25	-1.204	0.497	-2.424	0.015
Outside corridor >>25	-5.373	1.094	-4.91	<0.001
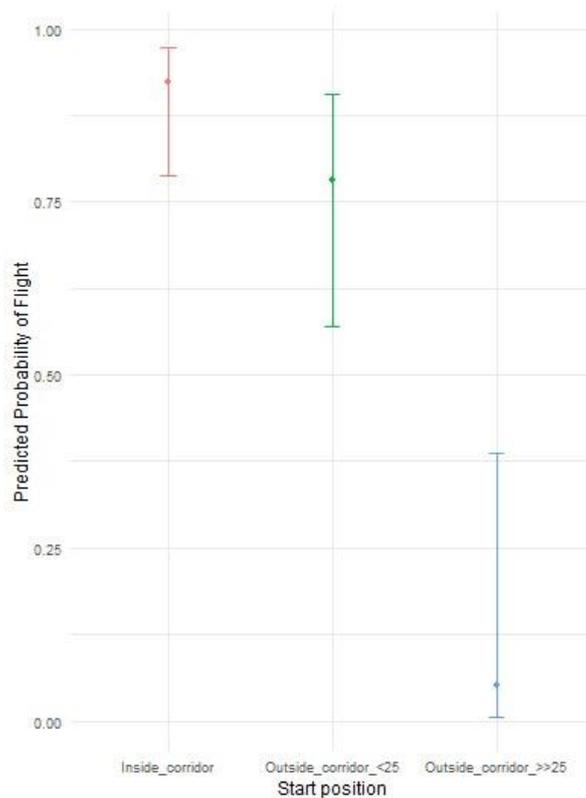
Figure 7: Predicted probability of flight in roe deer with 95% confidence intervals, based on the explanatory variable; 'start position'.

3.1.4 Moose

In the analysis examining the probability of flight in moose, model 7 was considered as the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. Model 7 included the variables 'start position' and 'train speed' (table 9).

Table 9: AIC model selection table for moose, where the best fitting models are ranked from top.

	(Intercept)	Day_period	Start_pos	Train_speed	Warning	df	logLik	AICc	delta	weight
7	5.558		+	-0.01924		4	-43.7	95.68	0	0.426
8	5.534	+	+	-0.02022		6	-42	96.74	1.06	0.25
15	5.489		+	-0.01951	+	5	-43.4	97.21	1.53	0.198
16	5.536	+	+	-0.02100	+	7	-41.6	98.12	2.44	0.126

Table 10 and figure 8 show that moose were significantly more likely to flee from an oncoming train when positioned inside corridor (n = 42 out of 44) compared to when positioned more than 25 meters from corridor (n = 4 out of 20). Similar they were significantly more likely to flee when positioned less than 25 meters from corridor (n = 51 out of 62) in comparison when positioned more than 25 meters from corridor. Unlike the other species, train speed had a significant effect on probability of flight in moose. With an increasing train speed, the individuals were significant less likely to flee.

Table 10: Parameter estimates from the most parsimonious model for probability of flight in moose.

	Estimate	Std. Error	z-value	p-value
Intercept(near track)	5.558	1.328	4.184	<0.001
Outside corridor <25	-1.422	0.815	-1.745	0.081
Outside corridor >>25	-4.841	0.977	-4.956	<0.001
Train speed	-0.019	0.008	-2.525	0.0116
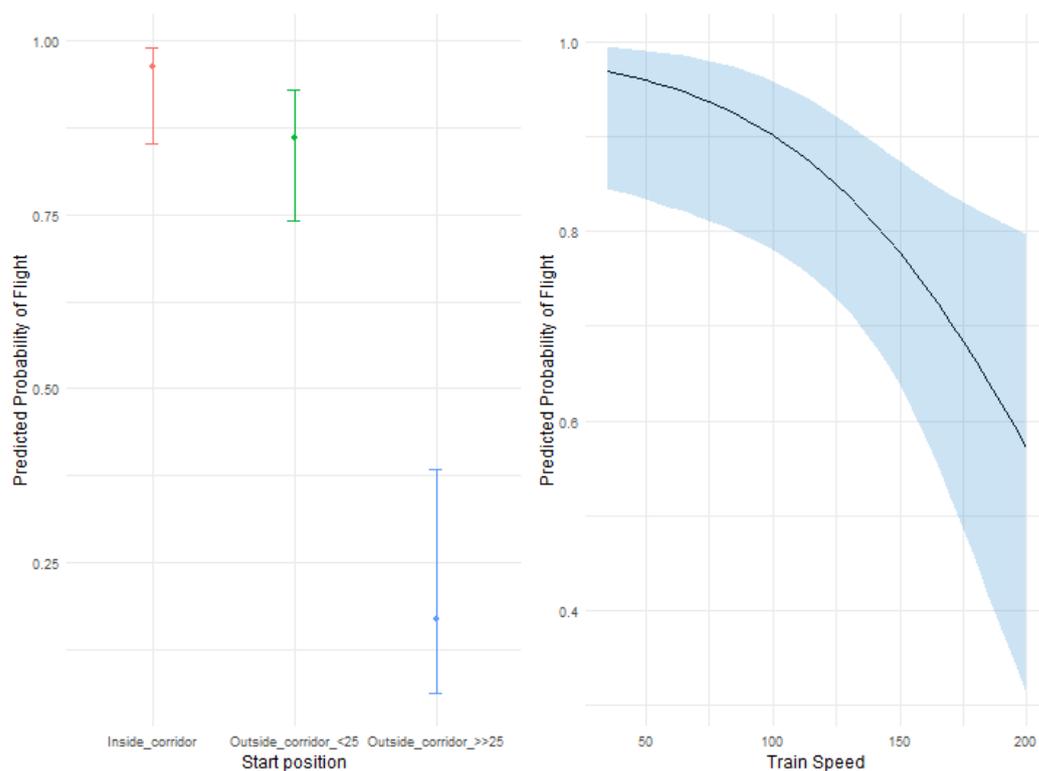
Figure 8: Predicted probability of flight in moose with 95% confidence intervals, based on the explanatory variables; 'start position' and 'train speed'.

3.2 Flight direction – probability of flight across track compared to away from track

3.2.1 Wild ungulates in total

In the analysis examining the probability of flight across track compared to away from track in wild ungulates, model 12 was considered as the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. Model 12 included the variables 'herd size, 'start position' and 'railside vegetation' (table 11).

Table 11: AIC model selection table for the total of observed ungulates, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	Herd_size	Railside_veg	Snow	Start_pos	Train_speed	df	logLik	AICc	delta	weight
28	0.214	+	+		+	-0.017976	12	-125.9	276.6	0.00	0.364
32	0.542	+	+	+	+	-0.019135	13	-125.6	278.0	1.41	0.180
12	-1.773	+	+		+		11	-127.9	278.4	1.76	0.151
26	1.517	+			+	-0.017798	10	-129.4	279.4	2.79	0.090
16	-1.545	+	+	+	+		12	-127.4	279.6	2.99	0.082

Table 12 and figure 9 show that probability of flight across the track was significantly lower for ungulates positioned outside corridor (n = 11 out of 264) compared to ungulates positioned on (n = 14 out of 50) and near the track (n = 31 out of 101). Individuals in medium sized groups of 6-15 animals were significantly less likely to flee across the track (n = 4 out of 94). Similar individuals in a group of 15-30 animals also had a low average probability of flight across the track (n = 2 out of 42) compared to away from the track. On the other hand, individuals in smaller groups (1-5 animals) and very large groups (>30 animals) had a higher likelihood of flight across the track (1-5 individuals: n = 45 out of 224, >30 individuals: n = 5 out of 55). The likelihood of flight across the track was significantly higher when there were low shrub (n = 11 out of 66) and trees (n = 36 out of 157) along the rail embankment compared to a clearcut rail embankment (n = 9 out of 192).

Table 12: Parameter estimates from the most parsimonious model for flight direction in total of observed ungulates.

	Estimate	Std. Error	z-value	p-value
Intercept(near track, clear vegetation, herd size: 1-5)	-1.851	0.649	-2.852	<0.001
On track	-0.227	-0.395	-0.576	0.565
Outside corridor	-2.138	0.429	-4.983	<0.001
Low shrub	1.732	0.721	2.402	0.016
Trees	1.353	0.652	2.074	0.038
Herd size: 15-30	-0.371	0.902	-0.412	0.681
Herd size: 6-15	-1.127	0.570	1.977	0.048
Herd size: >30	1.136	0.800	1.420	0.156
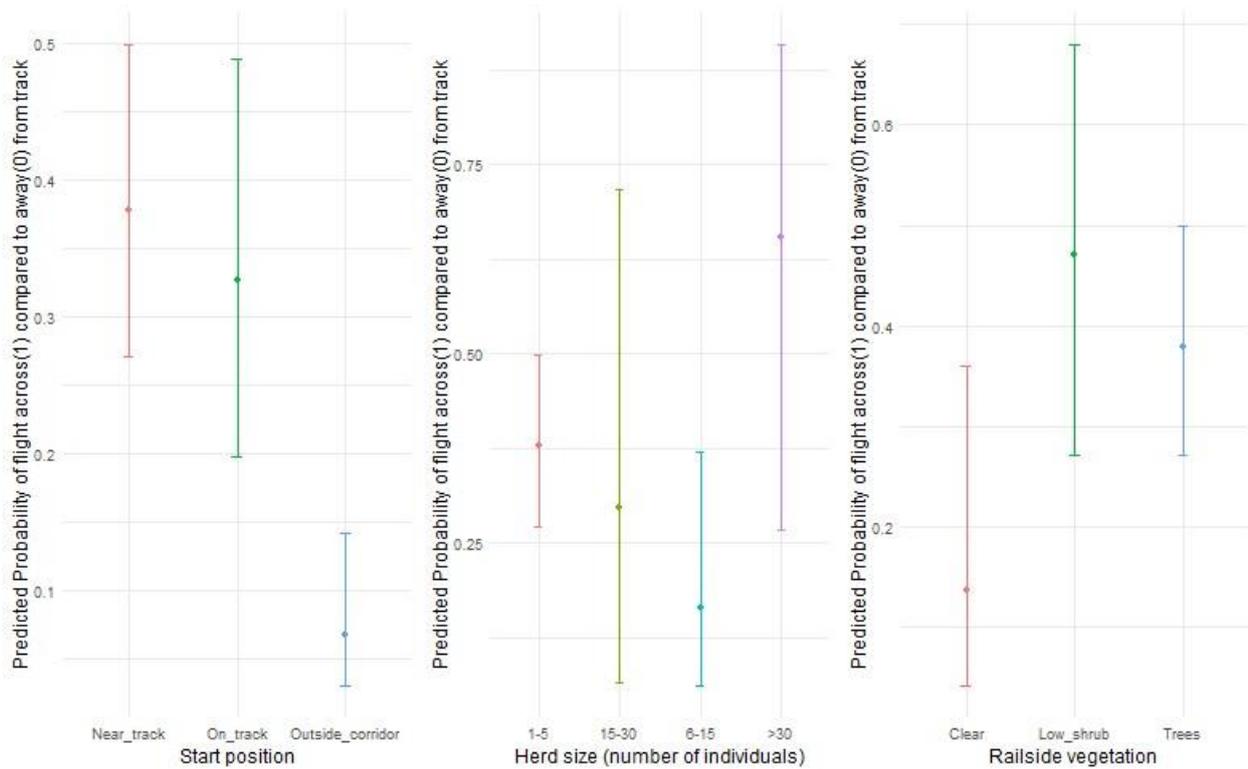
Figure 9: Predicted probability of flight across compared to away from track on the total of observed ungulates with 95% confidence intervals, based on the explanatory variables; 'start position', 'herd size' and 'railside vegetation'.

3.2.2 Fallow deer

In the analysis on fallow deer examining the probability of flight across track compared to away from track, model 4 was considered as the most parsimonious model with a ∆AIC of less than 2 and lower degrees of freedom. Model 4 included the variable 'herd size' and 'railside vegetation' (table 13).

Table 13: AIC model selection table for fallow deer, where the best fitting models are ranked from top.

	(Intercept)	*Herd_size*	*Railside_veg*	*Snow*	*Start_pos*	*Train_speed*	*df*	*logLik*	*AICc*	*delta*	*weight*
8	-5.032	+	+	+			7	-58.18	130.8	0.00	0.166
4	-5.537	+	+				6	-59.47	131.3	0.47	0.131
20	-3.947	+	+			-0.0209074	7	-58.56	131.6	0.76	0.113
24	-3.752	+	+	+		-0.0173543	8	-57.54	131.7	0.88	0.107
16	-4.174	+	+	+	+		9	-56.79	132.4	1.53	0.077
15	-2.274		+	+	+		6	-60.25	132.9	2.03	0.060

Table 14 and figure 10 show that fallow deer exhibited a low probability of flight across the track in general. Individuals occurring in large groups of more than 30 individuals had a significant higher likelihood of flight across the track (n = 5 out of 55) compared to individuals occurring in smaller groups of 1-5 (n = 9 out of 64) and 6-15 individuals (n = 4 out of 79). Furthermore, there was a lot of variation in the results of individuals occurring in

groups of 15-30 individuals (n = 2 out of 42) and >30 individuals. Probability of flight across the track were significantly higher when there were trees along the rail embankment (n = 13 out of 78) compared to a clearcut rail embankment (n = 6 out of 146). There was a lot of variation with vegetation of low shrub with an average low probability of flight across the track (n = 1 out of 16).

Table 14: Parameter estimates from the most parsimonious model for flight direction in fallow deer.

	Estimate	Std. Error	z-value	p-value
Intercept (herd size: 1-5, clear vegetation)	-5.537	1.548	-3.576	<0,001
Herd size: 15-30	1.732	1.337	1.295	0.195
Herd size: 6-15	-0.578	0.645	-0.896	0.370
Herd size: >30	3.235	1.618	1.999	0.046
Low shrub	3.013	1.844	1.634	0.102
Trees	4.066	1.510	2.692	0.007
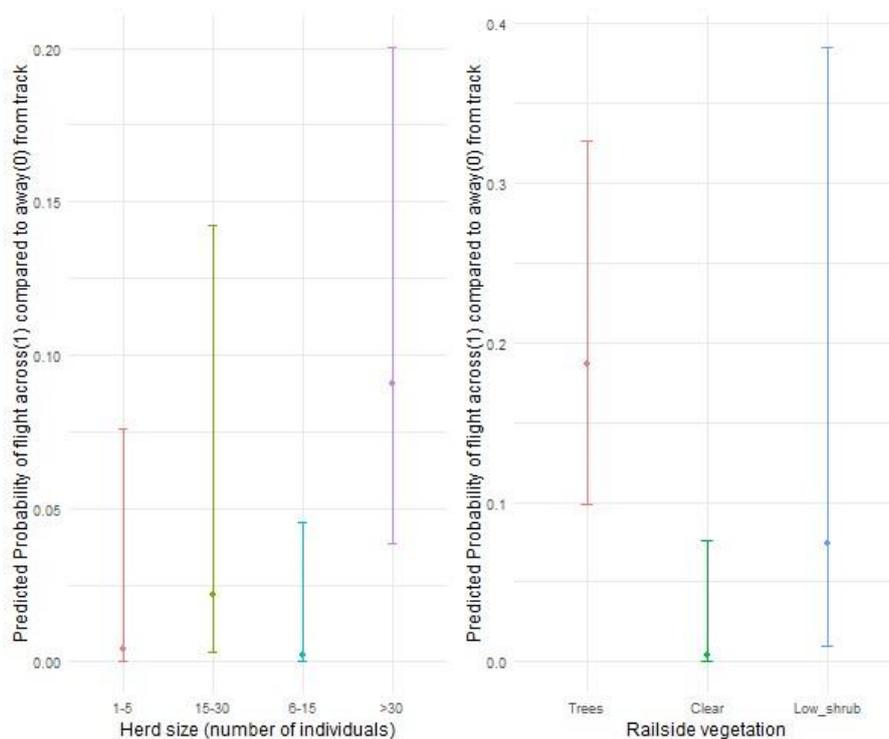
Figure 10: Predicted probability of flight across compared to away from track on fallow deer with 95% confidence intervals, based on the explanatory variables; 'herd size', and 'railside vegetation'.

3.2.3 Roe deer

In the analysis on roe deer examining the probability of flight across track compared to away from track, model 5 was considered as the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. Model 5 included the variable 'start position' (table 15).

Table 15: AIC model selection table for roe deer, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	Railside_veg	Snow	Start_pos	Train_speed	df	logLik	AICc	delta	weight
5	0.080			+		6	-32.81	78.75	0.00	0.461
13	1.692			+	-0.01774764	7	-32.33	80.20	1.45	0.223
7	-0.122		+	+		7	-32.36	80.25	1.50	0.218
15	1.442		+	+	-0.01710451	8	-31.92	81.84	3.10	0.098

Probability of flight across the track was significantly lower for individuals positioned outside corridor (n = 2 out of 41) compared to when individuals were positioned near (n = 13 out of 25) the track. Probability of flight across the track was also lower for individuals positioned on the track (n = 3 out of 15) compared to near the track (table 16, figure 11).

Table 16: Parameter estimates from the most parsimonious model for flight direction in roe deer.

	Estimate	Std. Error	z-value	p-value
Intercept(near track)	0.080	0.400	0.200	0.842
On track	-1.466	0.760	-1.931	0.054
Outside corridor	-3.050	0.828	-3.683	<0.001
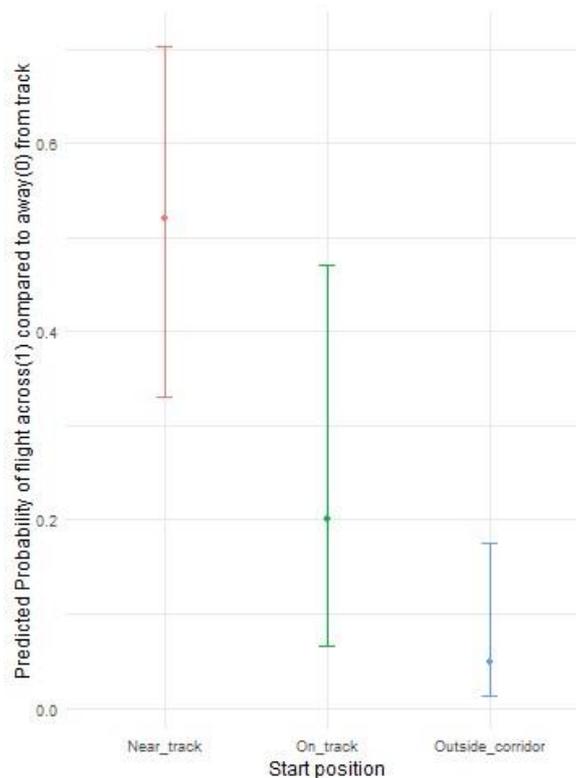
Figure 11: Predicted probability of flight across compared to away from track on roe deer with 95% confidence intervals, based on the explanatory variables; 'start position', and 'railside vegetation'.

3.2.4 Moose

In the analysis on moose examining the probability of flight across track compared to away from track, I combined the factor variables 'near track' and 'on track' and excluded the variable 'snow' in order to facilitate the interpretation of the results. In the model selection, model 4 was considered as the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. Model 4 included the variables 'start position' and 'railside vegetation' (table 17).

Table 17: AIC model selection table for moose, where the best fitting models are ranked from top.

	(Intercept)	*Railside_veg*	*Start_pos*	*Train_speed*	*df*	*logLik*	*AICc*	*delta*	*weight*
8	-15.56	+	+	-0.0395038	5	-11.47	34.36	0.00	0.613
4	-18.29	+	+		4	-13.34	35.62	1.26	0.327
7	2.24		+	-0.0204811	3	-16.84	40.22	5.86	0.033
3	<0.001		+		2	-18.18	40.62	6.26	0.027

Table 18 and figure 12 show that the probability of flight across the track were significantly lower for individuals positioned outside corridor (n = 1 out of 28) compared to when positioned inside corridor (n = 10 out of 20). Individuals positioned inside corridor had an approximately 50% probability of flight across the track. With a clearcut rail embankment, there were no individuals crossing the track (n = 0 out of 13). With vegetation of trees and low shrub along the rail embankment, the probability of flight across track were high in general (trees: n = 7 out of 17, low shrub: 4 out of 18).

Table 18: Parameter estimates from the most parsimonious model for flight direction in moose.

	Estimate	Std. Error	z-value	p-value
Intercept(inside corridor, clear vegetation)	-18.288	2483.601	-0.007	0.994
Low shrub	18.649	2483.601	0.008	0.994
Trees	19.225	2483.601	0.008	0.994
Outside corridor	-3.572	1.168	-3.059	0.002
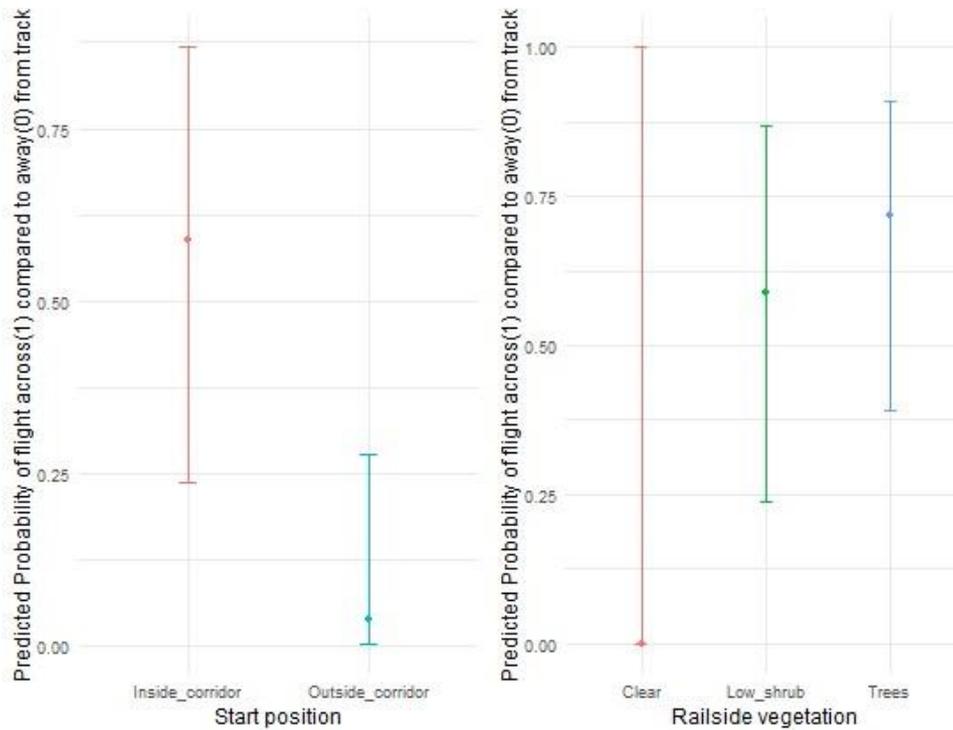
Figure 12: Predicted probability of flight across compared to away from track on roe deer with 95% confidence intervals, based on the explanatory variables; 'start position', and 'railside vegetation'.

3.3 What influences FID?

3.3.1 Wild ungulates in total

In the analysis of wild ungulates examining factors influencing FID, model 4 was identified as the most effective explanatory model with a ΔAIC of less than 2. The model was characterised by the inclusion of the variables 'day period' and 'start position' (table 19).

Table 19: AIC model selection table for the total of observed ungulates, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	Day_period	Start_pos	Train_speed	df	logLik	AICc	delta	weight
4	111.11	+	+		5	-837.25	1684.90	0.00	0.750
8	94.91	+	+	0.146955	6	-837.53	1687.62	2.72	0.192
3	113.55		+		4	-841.11	1690.48	5.59	0.046
7	96.83		+	0.151531	5	-841.38	1693.16	8.26	0.012

The average FID for ungulates collectively was 107m (n = 157). Table 20 and figure 13 show that predicted FID was significantly higher for individuals positioned on the track (n = 50) compared to near the track (n = 107). Day period did not show any significant effect on FID, but predicted FID was higher during dusk/dawn (n = 58) compared to daytime (n = 99).

Table 20: Parameter estimates from the most parsimonious model for predicted FID in total of observed ungulates.

	Estimate	Std. Error	t-value	p-value
Intercept(near track, daytime)	111.11	20.136	5.518	<0.001
On track	31.13	8.860	3.513	<0.001
Dusk/dawn	10.76	8.505	1.266	0.208
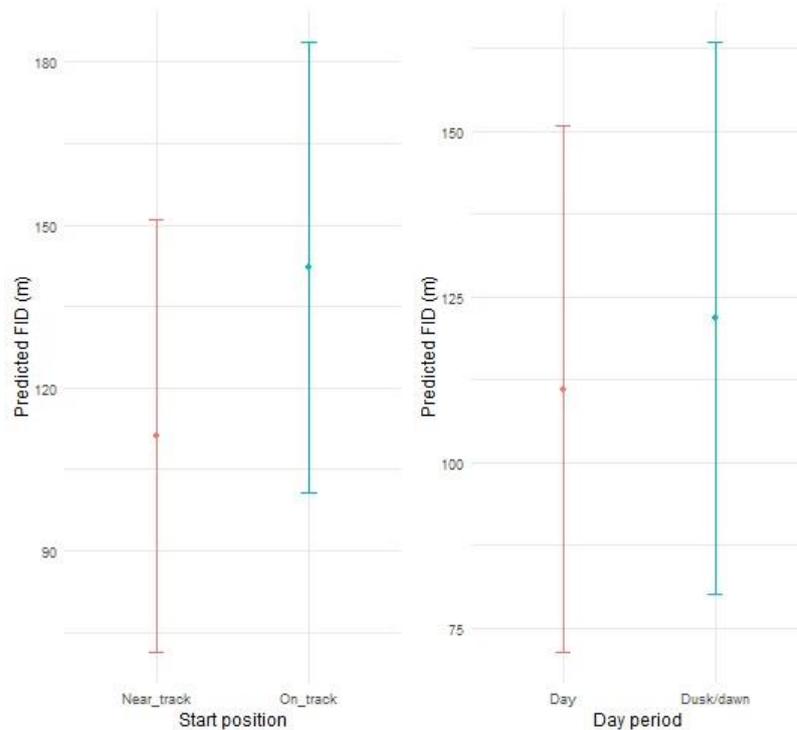
Figure 13: Predicted FID in total of observed ungulates with 95% confidence intervals, based on the explanatory variables; 'start position', and 'day period'.

3.3.2 Fallow deer

In the analysis examining factors influencing FID in fallow deer, model 4 was the most parsimonious model with a ΔAIC of less than 2 and lower degrees of freedom. The model was characterised by the inclusion of the variables 'day period' and 'start position' (table 21).

Table 21: AIC model selection table for fallow deer, where the best fitting models are ranked from top.

	(Intercept)	Day_period	Start_pos	Train_speed	df	logLik	AICc	delta	weight
8	13.29	+	+	0.9385022	5	-360.09	731.13	0.00	0.497
4	88.95	+	+		4	-362.24	733.11	1.98	0.185
3	97.13		+		3	-363.89	734.14	3.01	0.110
7	45.77		+	0.6588343	4	-362.82	734.26	3.13	0.104
6	5.25	+		1.0899963	4	-362.83	734.28	3.15	0.103

The average FID for fallow deer was 106m (n = 69). Table 22 and figure 14 show that predicted FID was significantly higher for fallow deer positioned on the track (n = 5)

compared to near track (n = 54). Individuals were also significantly more likely to have a high FID during dusk/dawn (n = 31) compared to daytime (n = 38).

Table 22: Parameter estimates from the most parsimonious model for predicted FID in fallow deer.

	Estimate	Std. Error	t-value	p-value
Intercept(near track, daytime)	88.95	7.87	11.302	<0.001
On track	36.40	14.14	2.575	0.012
Dusk/dawn	21.05	11.72	1.796	0.077
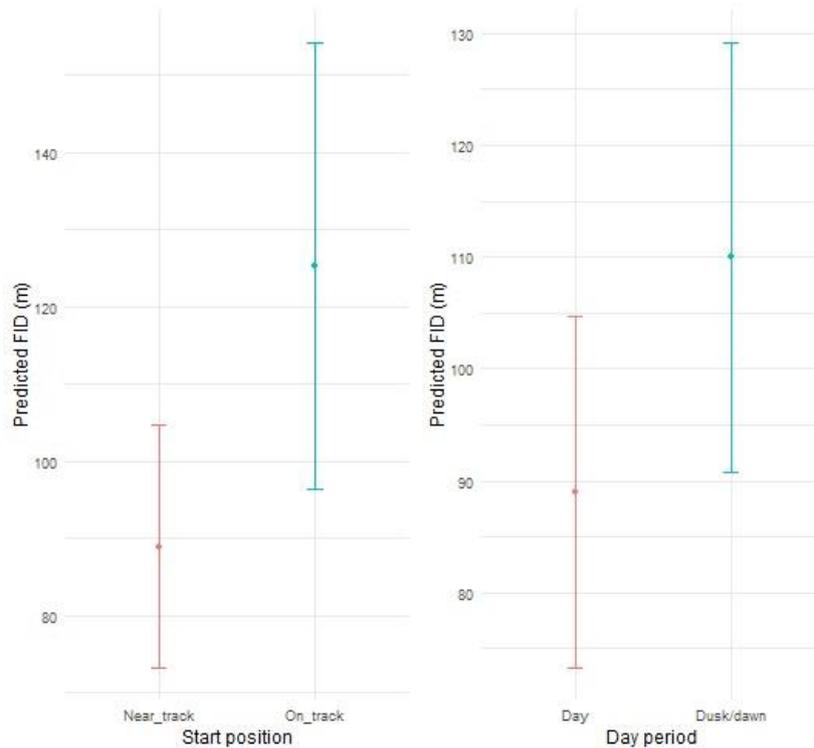
Figure 14: Predicted FID in fallow deer with 95% confidence intervals, based on the explanatory variables; 'start position', and 'day period'.

3.3.3 Roe deer

In the analysis of factors influencing FID in roe deer, model 4 and was considered the most parsimonious model with a ΔAIC less than 2 and lower degrees of freedom. This model included the variables 'day period' and 'start position' (table 23).

Table 23: AIC model selection table for roe deer, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	Day_period	Start_pos	Train_speed	df	logLik	AICc	delta	weight
4	92.11	+	+		5	-189.88	391.64	0.00	0.492
8	22.67	+	+	0.812992	6	-188.65	392.02	0.38	0.407
6	20.29	+		0.875013	5	-192.51	396.90	5.26	0.035
2	96.28	+			4	-193.85	396.92	5.28	0.035
3	88.67		+		4	-193.99	397.18	5.54	0.031

The average FID for roe deer was 93m (n = 38). Table 24 and figure 15 show that neither start position nor day period had a significant effect on FID. Nevertheless, roe deer had a higher predicted FID when positioned on the track (n = 14) compared to near track (n = 24). There was a lower average predicted FID during dusk/dawn (n = 10) compared to daytime (n = 28).

Table 24: Parameter estimates from the most parsimonious model for predicted FID in roe deer.

	Estimate	Std. Error	t-value	p-value
Intercept(near track, daytime)	92.109	11.006	8.369	<0.001
On track	11.682	16.538	0.706	0.485
Dusk/dawn	-13.763	18.117	-0.760	0.453
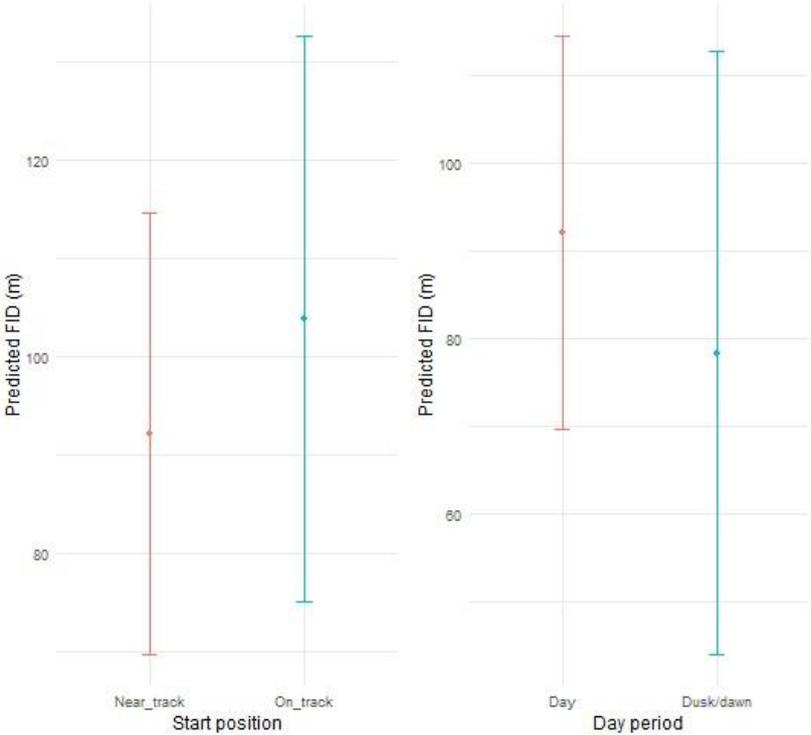
Figure 15: Predicted FID in roe deer with 95% confidence intervals, based on the explanatory variables; 'start position', and 'day period'.

3.3.4 Moose

In the analysis of factors influencing FID in moose, only 'train speed' was considered as a valid explanatory variable due to lack of variation in data in 'start position' and 'day period'. Train speed did affect FID in moose, but there was only a trend. Table 25 and figure 16 show that FID decreased with increasing speed of train. The average FID for moose was 140m (n = 20).

Table 25: Parameter estimates from the most parsimonious model for predicted FID in moose.

	Estimate	Std. Error	t-value	p-value
Intercept	233.544	60.904	3.835	<0.001
Train speed	-0.811	0.497	-1.631	0.120
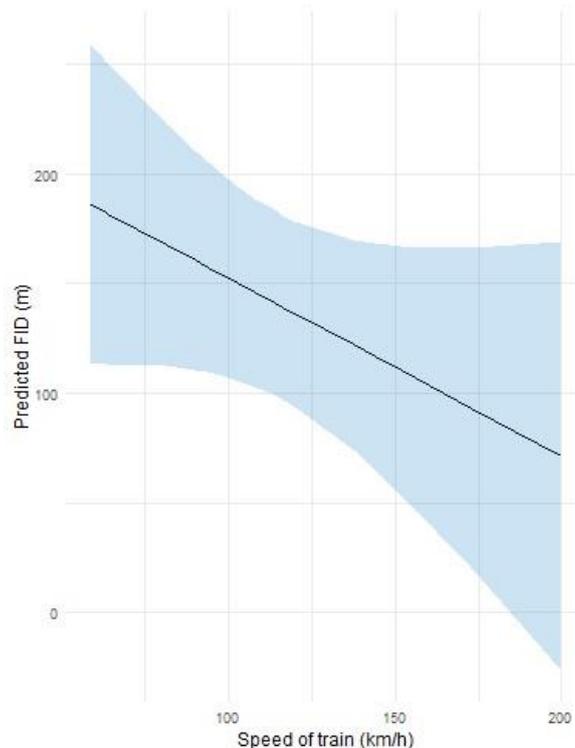
Figure 16: Predicted FID in moose with 95% confidence intervals, based on the explanatory variable; 'train speed'

3.4 Impact of obstruction on the likelihood of ungulate flight at video onset

3.4.1 Wild ungulates in total

In the analysis, I tested the likelihood that ungulates collectively were already running at the onset of the video as a function of different types of obstructions. Model 54 was the most parsimonious model with a ΔAIC under 2 and lower degrees of freedom. Model 54 included the variables 'curvature', 'detection distance', 'railside vegetation' and 'terrain' (table 26).

Table 26: AIC model selection table for the total of observed ungulates, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	Curvature	Day_period	Detection_distance	Railside_veg	Terrain	df	logLik	AICc	delta	weight
56	0.267	+	+	-0.005455	+	+	9	-473.6	965.5	0.00	0.424
54	0.451	+		-0.005530	+	+	7	-475.9	965.9	0.39	0.349
38	0.831	+		-0.006115		+	5	-479.0	968.0	2.55	0.119
40	0.698	+	+	-0.006096		+	7	-477.0	968.2	2.73	0.109

Table 27 and figure 17 show that predicted probability of flight from start of the video was significant higher when the railway was curved (n = 116 out of 298) compared to when it was straight (n = 127 out of 599). Individuals also had a higher probability of flight from start of the video with vegetation along the rail embankment (trees: n = 114 out of 318, low shrub: n = 51 out of 151), where trees along the rail embankment emerged as a significant factor variable compared to a clear-cut rail embankment (n = 78 out of 428). Terrain as obstruction caused a significant higher probability of flight from start (n = 29 out of 64). The probability of flight from start decreased with increased detection distance.

Table 27: Parameter estimates from the most parsimonious model for probability of flight from start in total of observed ungulates.

	Estimate	Std. Error	z-value	p-value
Intercept (curvature: bend, clear vegetation, terrain: no)	0.452	0.367	1.232	0.218
Curvature: straight	-0.421	0.173	-2.441	0.015
Low shrub	0.230	0.243	0.947	0.343
Trees	0.464	0.187	2.482	0.013
Terrain: yes	0.737	0.283	2.607	0.009
Detection distance	-0.006	0.001	-5.290	<0.001
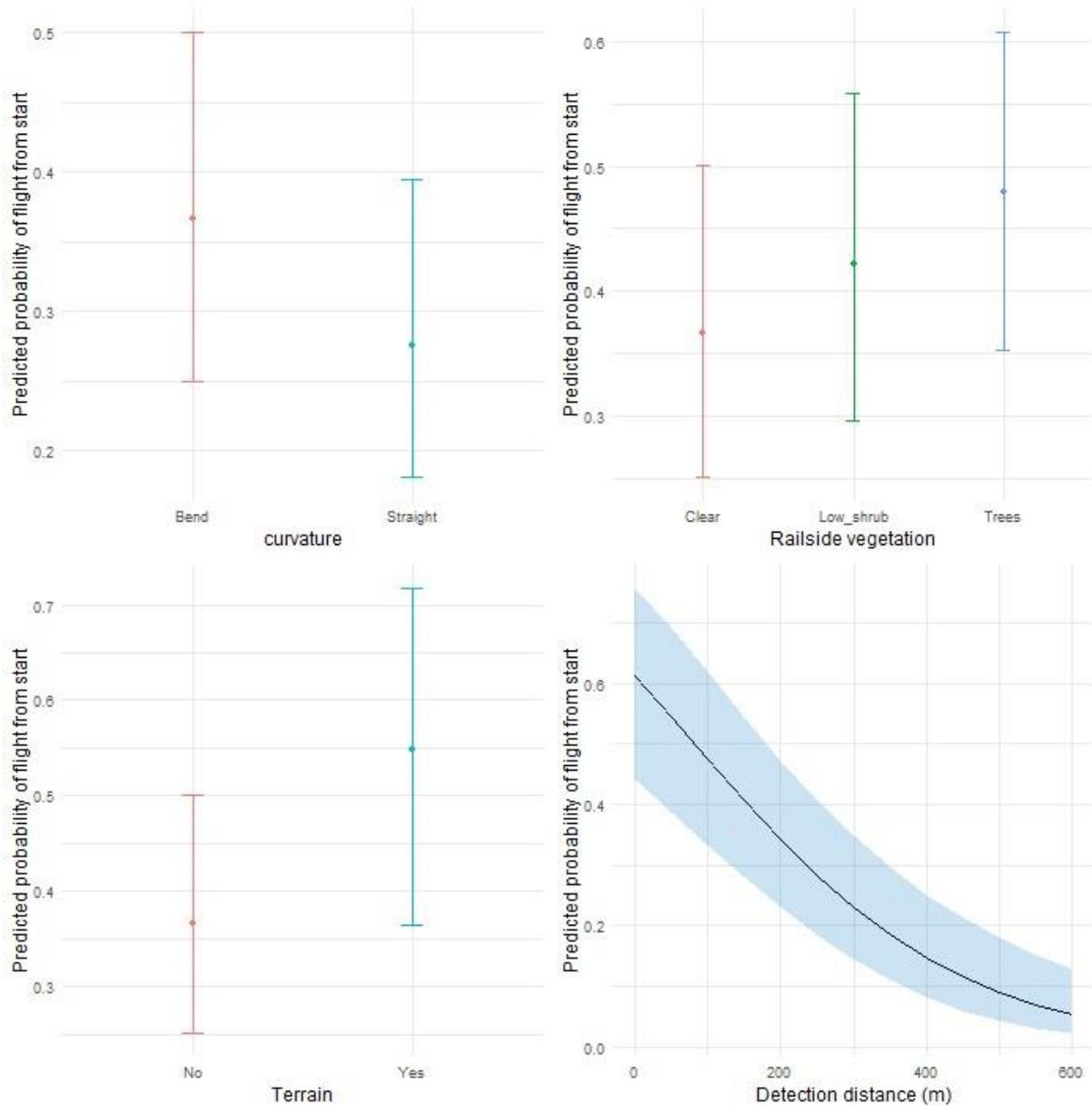
Figure 17: Predicted probability of flight from start of the video in total of observed ungulates with 95% confidence intervals, based on the explanatory variables; 'curvature', 'railside vegetation', 'terrain' and 'detection distance'.

3.4.2 Fallow deer

In the analysis, I tested the likelihood that fallow deer were already running at the onset of the video as a function of different types of obstructions. Model 31 was the most parsimonious model with a ΔAIC under 2 and lower degrees of freedom. Model 31 included the variables 'day period', 'detection distance', 'railside vegetation' and 'terrain' (table 28).

Table 28: AIC model selection table for fallow deer, where the best fitting models are ranked from top.

	(Intercept)	Curvature	Day_period	Detect_dist	Railside_veg	Terrain	df	logLik	AICc	delta	weight
31	-1.213		+	-0.0044721	+	+	7	-203.0	420.29	0.00	0.580
32	-1.127	+	+	-0.004309	+	+	8	-202.9	422.07	1.78	0.238
15	-1.125		+	-0.0046450	+		6	-205.2	422.61	2.32	0.182

Table 29 and figure 18 show that there was a significant higher probability of flight from start during dusk/dawn (n = 44 out of 150) compared to daytime (n = 57 out of 356). Average predicted probability of flight from start was also higher during night-time (n = 3 out of 11) than during daytime, but there was a lot of variation in the prediction. When the rail embankment was covered by trees, there was also a significant higher probability of flight from start (n = 52 out of 180) compared to when the rail embankment had been clearcut (n = 46 out of 300) or was covered by low shrub (n = 6 out of 37). Visibility obstructed by terrain also caused a significant higher probability of flight from start (n = 13 out of 31). The probability of flight from start decreased with increased detection distance.

Table 29: Parameter estimates from the most parsimonious model for probability of flight from start in fallow deer.

	Estimate	Std. Error	z-value	p-value
Intercept (daytime, clear vegetation, terrain: no)	-1.213	0.358	-3.385	<0.001
Dusk/dawn	0.726	0.260	2.793	0.005
Night	0.233	1.090	0.214	0.831
Low_shrub	-1.900	1.051	-1.808	0.071
Trees	0.546	0.272	2.007	0.045
Terrain: yes	0.978	0.455	2.149	0.032
Detection distance	-0.004	0.002	-2.779	0.005
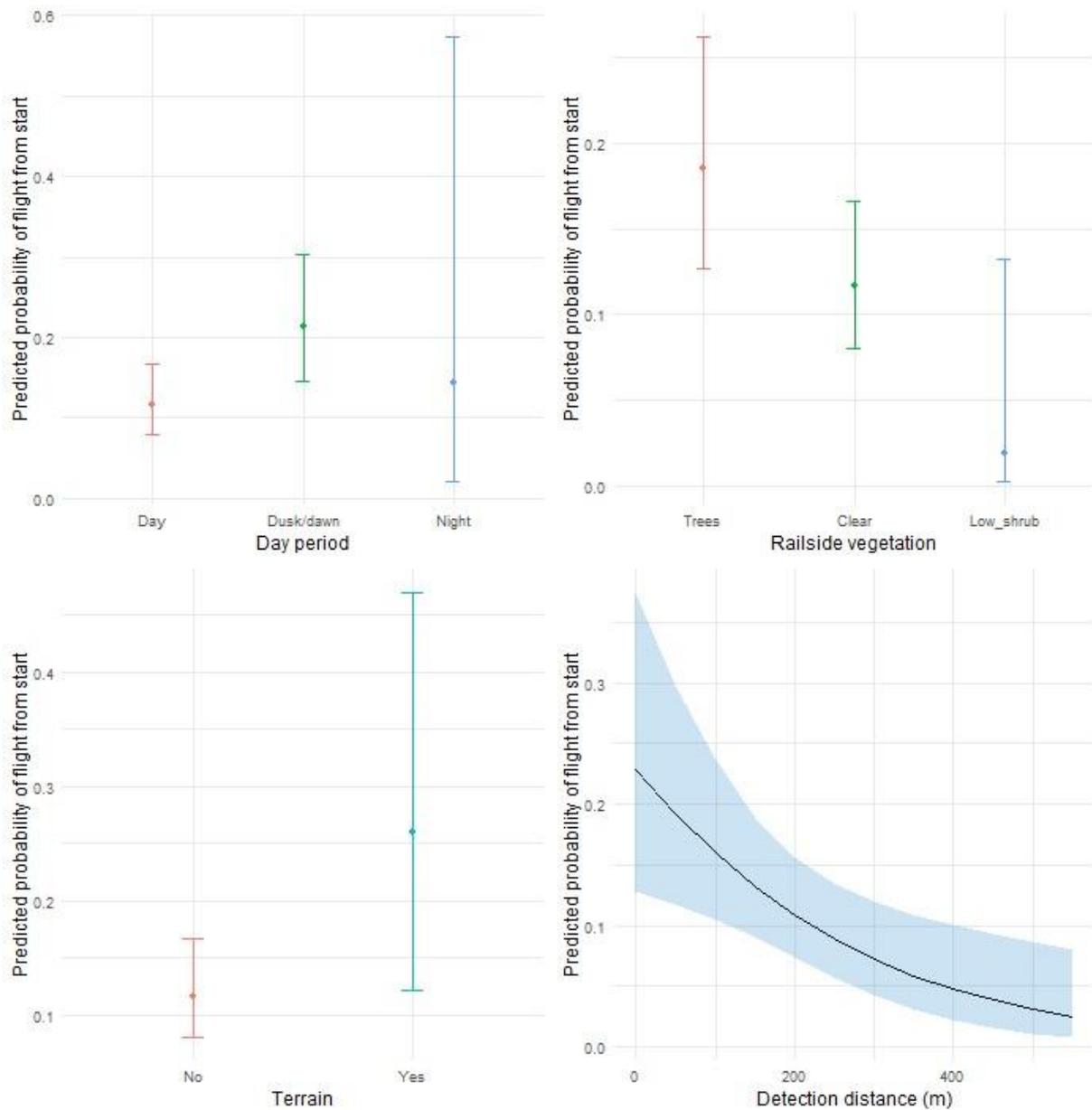
Figure 18: Predicted probability of flight from start of the video in fallow deer with 95% confidence intervals, based on the explanatory variables; 'curvature', 'railside vegetation', 'terrain' and 'detection distance'.

3.4.3 Roe deer

In the analysis, I tested the likelihood that roe deer were already running at the onset of the video as a function of different types of obstructions. Model 22 was the best fitting model with a ΔAIC under 2, including the variables 'curvature', 'terrain' and 'detection distance' (table 30).

	(Intercept)	Curvature	Day_period	Detection_distance	Railside_veg	Terrain	df	logLik	AICc	delta	weight
22	1.186	+		-0.0085159		+	5	-77.9	166.23	0.00	0.587
24	1.167	+	+	-0.0084543		+	6	-77.9	168.38	2.14	0.201
6	1.407	+		-0.0090466			4	-80.8	169.84	3.61	0.097
30	1.143	+		-0.0084149	+	+	7	-77.9	170.57	4.34	0.067

Table 31 and figure 19 show that 'curvature', 'terrain' and 'detection distance' were all significant variables affecting probability of roe deer's flight from start of the video. When individuals were positioned on a straight railway line, probability of flight from start were significantly lower (n = 31 out of 131) compared to when positioned on a curved railway line (n = 39 out of 84). Probability of flight from start were significantly higher when visibility was obstructed by terrain (n = 10 out of 18). With an increasing detection distance, probability of flight from start decreased.

Table 31: Parameter estimates from the most parsimonious model for probability of flight from start in roe deer.

	Estimate	Std. Error	z-value	p-value
Intercept (curvature: bend, terrain: no)	1.186	0.502	2.362	0.018
Curvature: straight	-1.219	0.394	-3.095	0.002
Terrain: yes	1.925	0.886	2.171	0.030
Detection distance	-0.009	0.003	-3.105	0.002
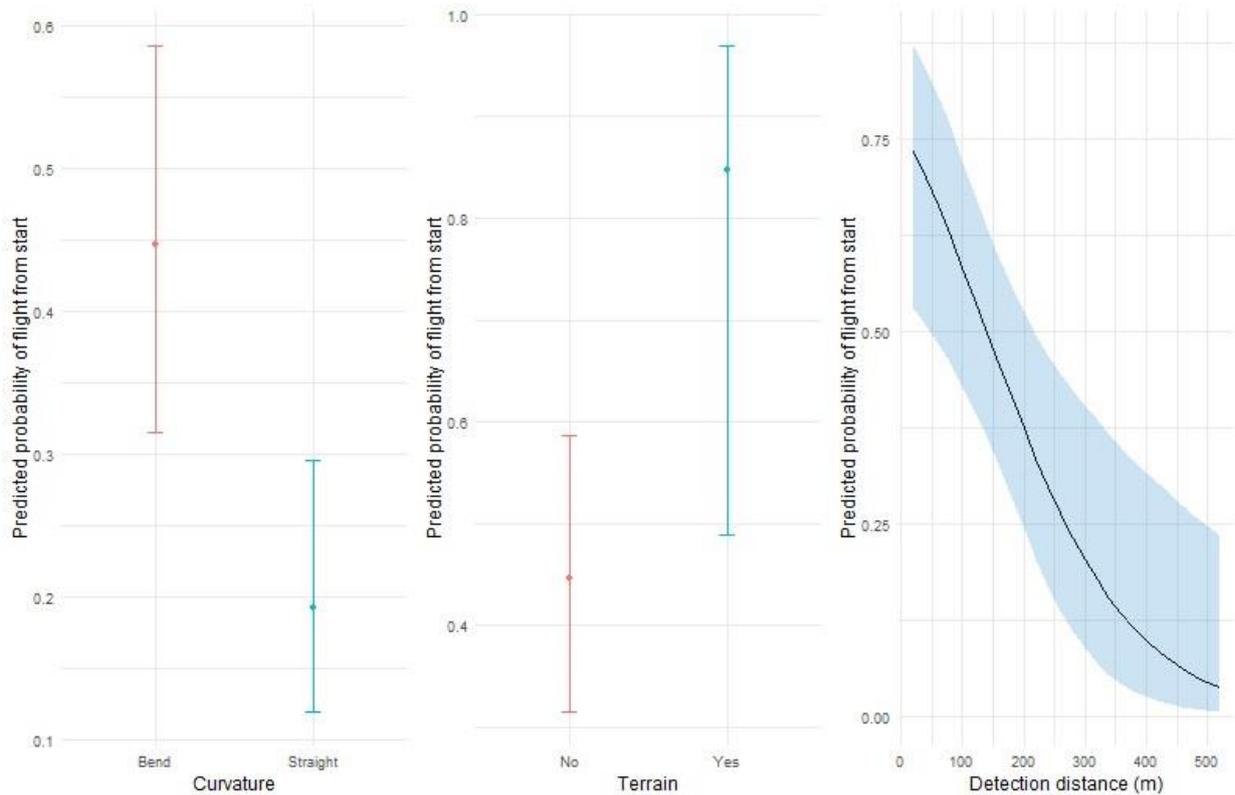
Figure 19: Predicted probability of flight from start of the video in roe deer with 95% confidence intervals, based on the explanatory variables; 'curvature', 'terrain' and 'detection distance'.

3.4.4 Moose

In the analysis, I tested the likelihood that moose were already running at the onset of the video as a function of different types of obstructions. Model 5 were considered as the most parsimonious model with a ΔAIC under 2 and lower degrees of freedom. Model 5 included the variable 'detection distance' (table 32).

Table 32: AIC model selection table for moose, where the best fitting models are ranked from top.

	(Intercept)	*Curvature*	*Day_period*	*Detection_distance*	*Railside_veg*	*Terrain*	*df*	*logLik*	*AICc*	*delta*	*weight*
6	0.985	+		-0.0045884			3	-70.92	148.1	0.00	0.392
8	0.704	+	+	-0.0035057			5	-69.58	149.7	1.64	0.173
5	0.713			-0.0052550			2	-72.87	149.8	1.79	0.161
7	0.463		+	-0.0037584			4	-70.89	150.1	2.07	0.139

Table 33 and figure 20 show that individuals of moose had a significant lower probability of flight from start with an increasing detection distance.

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Table 33: Parameter estimates from the most parsimonious model for probability of flight from start in moose.

	Estimate	Std. Error	z-value	p-value
Intercept	0.713	0.406	1.755	0.079
Detection distance	-0.005	0.002	-3.197	0.001
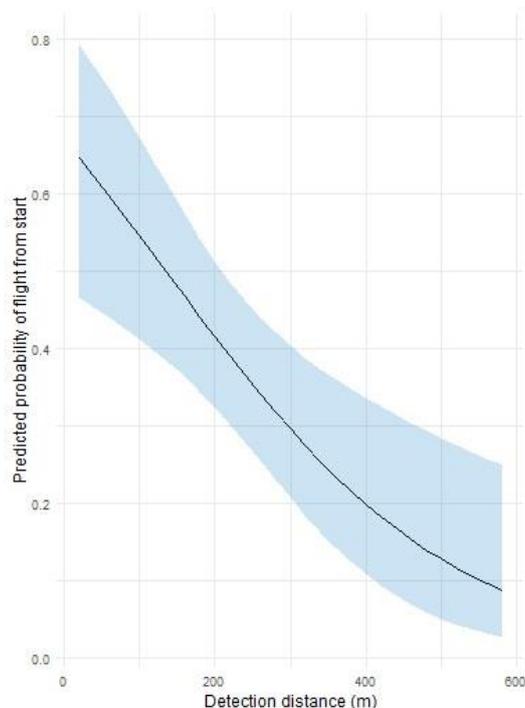
Figure 20: Predicted probability of flight from start of the video in moose with 95% confidence intervals, based on the explanatory variable; 'detection distance'.

3.5 Factors influencing detection distance

3.5.1 Wild ungulates in total

In the analysis of factors influencing detection distance in wild ungulates, model 16 was the best explanatory model with a ΔAIC less than 2, including the variables 'curvature', 'day period', 'railside vegetation' and 'start position' (table 34).

Table 34: AIC model selection table for the total of observed ungulates, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	*Curvature*	*Day_period*	*Railside_veg*	*Start_pos*	*df*	*logLik*	*AICc*	*delta*	*weight*
16	285.7	+	+	+	+	8	-1220.5	2457.7	0.00	0.877
15	284.5		+	+	+	7	-1223.9	2462.4	4.69	0.084
14	280.9	+		+	+	7	-1224.7	2464.0	6.24	0.039

Table 35 and figure 21 show that predicted detection distance was significantly lower with a rail embankment covered by trees (n = 146) or low shrub (n = 27) compared to a clearcut rail

embankment (n = 40). Predicted detection distance was significant higher for individuals positioned on the track (n = 58) compared to near the track (n = 155). Neither the curvature of the railway (straight track: n = 124, bended track: n = 89) nor day period (dusk/dawn: n = 65, daytime: n = 148) affected detection distance significantly.

Table 35: Parameter estimates from the most parsimonious model for predicted detection distance in total of observed ungulates.

	Estimate	Std. Error	t-value	p-value
Intercept (near track, clear vegetation, curvature: bend, daytime)	285.733	31.748	9.000	<0.001
On track	63.731	12.770	4.991	<0.001
Low shrub	-99.300	22.372	-4.439	<0.001
Trees	-81.321	14.751	-5.513	<0.001
Curvature: straight	-2.727	11.938	-0.228	0.820
Dusk/dawn	-15.235	12.210	-1.248	0.214
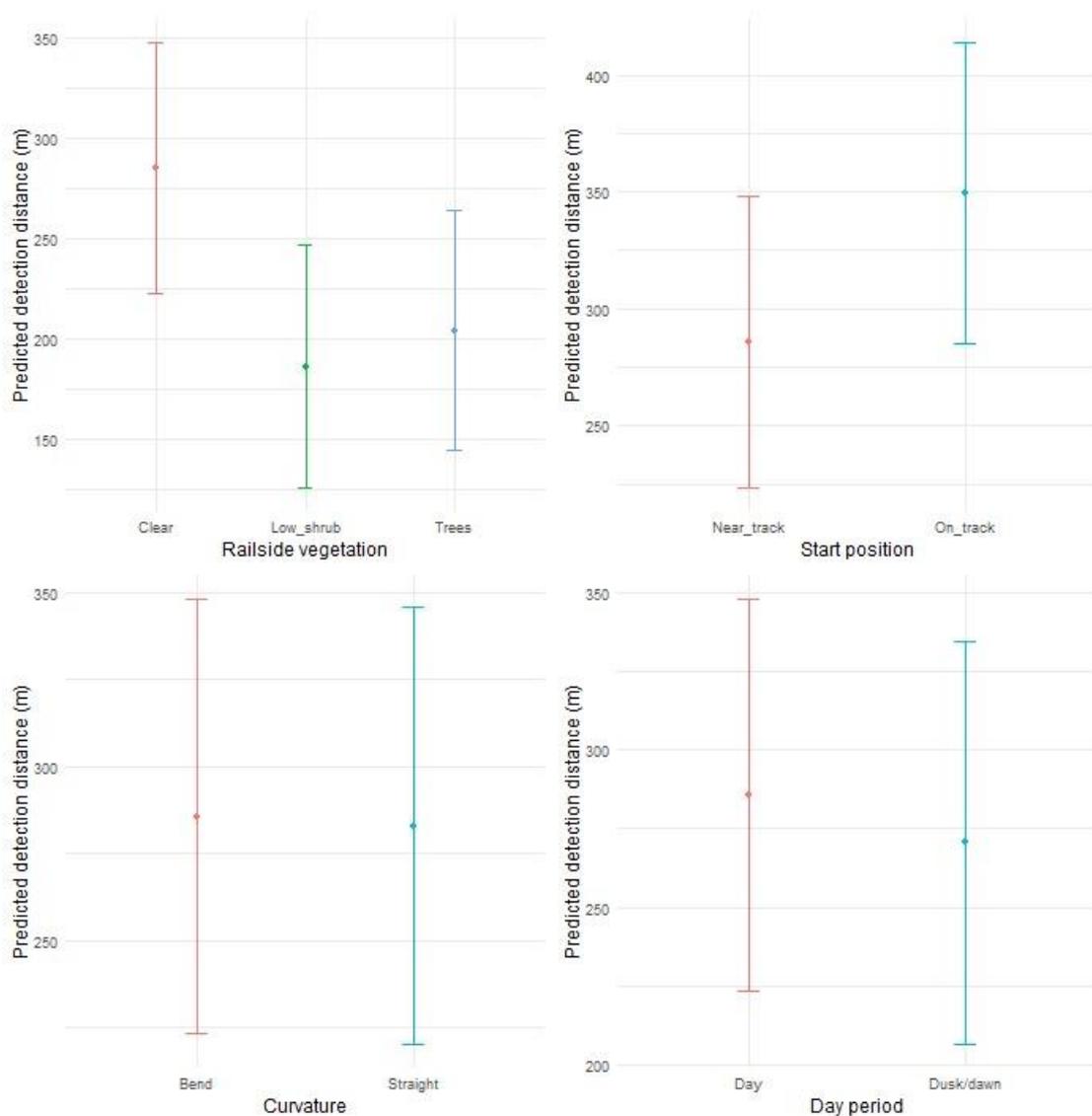
Figure 21: Predicted detection distance in total of observed ungulates with 95% confidence intervals, based on the explanatory variables; 'railside vegetation', 'start position', 'curvature' and 'day period'.

3.5.2 Fallow deer

In the analysis of factors influencing detection distance in fallow deer, model 13 was the most parsimonious model with a ΔAIC less than 2 and lower degrees of freedom, including the variables 'railside vegetation' and 'start position' (table 36).

Table 36: AIC model selection table for fallow deer, where the best fitting models are ranked from top.

	(Intercept)	Curvature	Day_period	Railside_veg	Start_pos	df	logLik	AICc	delta	weight
13	244.20			+	+	4	-541.6	1091.6	0.00	0.415
15	258.35		+	+	+	5	-540.7	1092.1	0.45	0.331
14	248.47	+		+	+	5	-541.5	1093.8	2.12	0.144
16	261.87	+	+	+	+	6	-540.7	1094.3	2.65	0.110

Table 37 and figure 22 show that both 'railside vegetation' and 'start position' had significant effect on detection distance for fallow deer. Observed vegetation at the rail embankment was either trees or clearcut. Predicted detection distance was significantly lower when rail embankment was covered by trees (n = 67), compared to when it had been clearcut (n = 25). Predicted detection distance was significantly higher for individuals that were positioned on the track (n = 18) compared to individuals positioned near the track (n = 74).

Table 37: Parameter estimates from the most parsimonious model for predicted detection distance in fallow deer.

	Estimate	Std. Error	t-value	p-value
Intercept (near track, clear vegetation)	244.203	20.264	12.051	<0.001
Trees	-103.129	21.884	-4.712	<0.001
On track	62.799	24.541	2.559	0.012
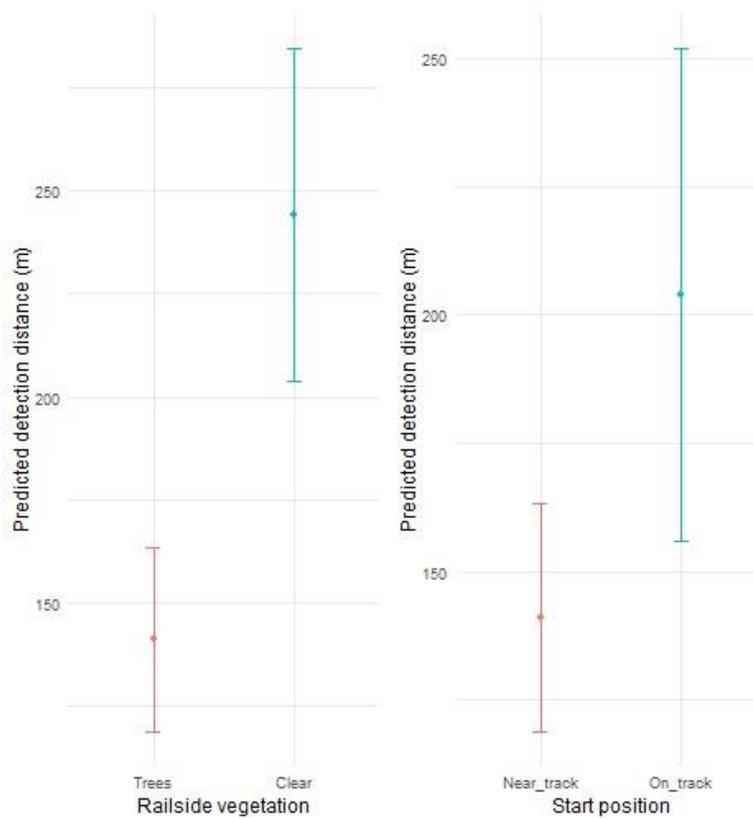
Figure 22: Predicted detection distance in fallow deer with 95% confidence intervals, based on the explanatory variables; 'railside vegetation' and 'start position'.

3.5.3 Roe deer

In the analysis of factors influencing detection distance in roe deer, model 8 was considered as the best explanatory model with ΔAIC less than 2. Model 8 included the variables 'curvature', 'railside vegetation' and 'start position' (table 38).

Table 38: AIC model selection table for roe deer, including 'railway' as random factor, where the best fitting models are ranked from top.

	(Intercept)	*Curvature*	*Railside_veg*	*Start_pos*	*df*	*logLik*	*AICc*	*delta*	*weight*
8	173.05	+	+	+	7	-243.3	503.5	0.00	0.944
7	178.01		+	+	6	-247.6	509.3	5.76	0.053
4	208.88	+	+		6	-250.5	515.2	11.66	0.003

Table 39 and figure 23 show that individuals of roe deer positioned on the track (n = 18) had a significant higher predicted detection distance than individuals positioned near the track (n = 28). There was a lot of variation in detection distance based on railside vegetation and curvature of the railway. Neither vegetation of trees (n = 25) or low shrub (n = 12) along the rail embankment had any effect on detection distance compared to a clearcut rail embankment

(n = 9). There was also no difference in predicted detection based on the curvature of the railway (bended: n = 19, straight: n = 27).

Table 39: Parameter estimates from the most parsimonious model for predicted detection distance in roe deer.

	Estimate	Std. Error	t-value	p-value
Intercept (near track, clear vegetation, curvature: bend)	173.055	61.114	2.832	0.007
On track	61.869	24.047	2.573	0.014
Low shrub	-7.501	33.879	-0.221	0.826
Trees	15.905	31.043	0.512	0.611
Curvature: straight	7.041	28.047	0.251	0.803
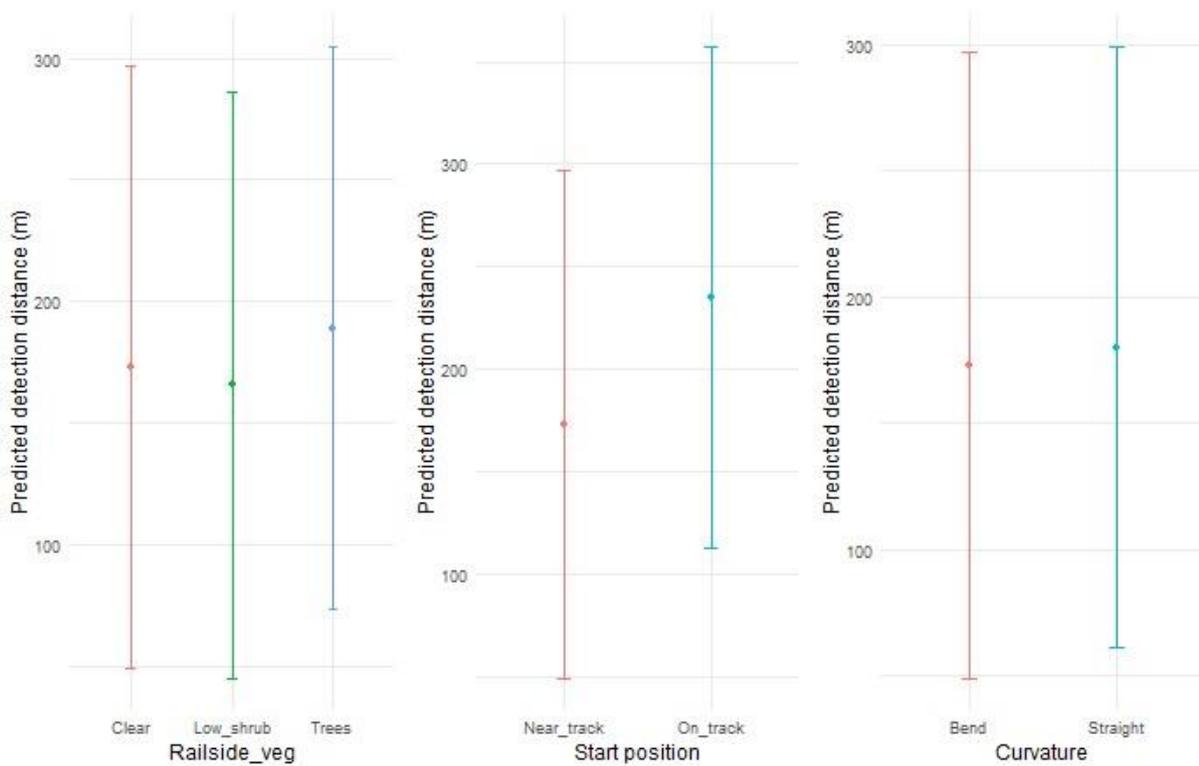
Figure 23: Predicted detection distance in roe deer with 95% confidence intervals, based on the explanatory variables; 'railside vegetation', 'start position', 'curvature' and 'day period'.

3.5.4 Moose

In the analysis of factors influencing detection distance in moose, model 13 was considered as the best explanatory model with a ΔAIC less than 2, including the variables 'railside vegetation' and 'start position' (table 40).

	(Intercept)	Curvature	Day_period	Railside_veg	Start_pos	Terrain	df	logLik	AICc	delta	weight
13	304.41			+	+		5	-192.4	397.1	0.00	0.558
14	296.58	+		+	+		6	-192.1	399.5	2.49	0.161
5	324.81			+			4	-195.2	399.8	2.73	0.142
9	216.55				+		3	-196.5	399.8	2.77	0.140

Table 41 and figure 24 show that predicted detection distance significantly increased when individuals of moose was positioned on the track (n = 5) compared to near the track (n = 27). With a rail embankment covered by trees (n = 15), predicted detection distance was also significantly lower than with low shrubs (n = 11) at the rail embankment or with a clearcut embankment (n = 6).

Table 41: Parameter estimates from the most parsimonious model for predicted detection distance in moose.

	Estimate	Std. Error	z-value	p-value
Intercept (near track, clear vegetation)	304.406	44.007	6.917	<0.001
On track	122.452	53.138	2.304	0.029
Low shrub	-55.529	53.884	-1.031	0.312
Trees	-137.703	51.281	-2.685	0.012
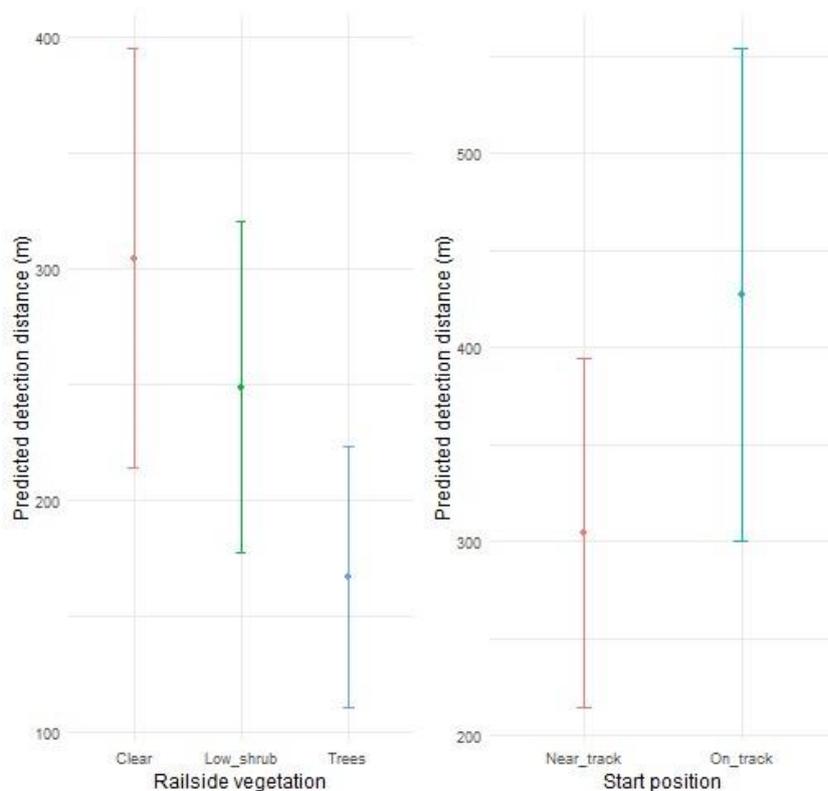
Figure 24: Predicted detection distance in moose with 95% confidence intervals, based on the explanatory variables; 'railside vegetation' and 'start position'.

4. Discussion

4.1 Factors influencing the probability of flight

The probability of flight tended to decrease with greater distance from the railway for all species. The same results have been observed in a previous study by Bhardwaj et al. (2022). Individuals positioned more than 25 meters from the railway corridor had a very low probability of flight, suggesting that ungulates do not perceive trains as a genuine threat from longer distances. If an animal decides to flee, it does so economically if the costs staying exceed the benefits of fleeing (Stankowich, 2008). A theory could be that the ungulates choose to remain stationary instead of expending energy on fleeing because they did not find themselves in a life-threatening situation.

By comparing the species, the results indicate that roe deer and moose still have a relatively high likelihood of flight (77% and 82% respectively) when positioned within 25 meters of the corridor, compared to fallow deer, which have approximately a 50% likelihood of flight at the same position. This can be explained by the fact that fallow deer often occur in larger groups. Studies suggest that animals often exhibit decreased vigilance with an increase in group size (Hunter & Skinner, 1998; Quenette, 1990; Roberts, 1996). This is due to more animals in a herd having more eyes to detect danger, in addition to the dilution effect, which implies that an individual has a greater likelihood of avoiding predation if it is part of a larger group (Roberts, 1996). The results also indicate that herd size matters for flight behaviour, especially in fallow deer which stands for almost every observation of groups of more than 6 individuals. The probability of flight was higher in small groups than larger groups, until the group size reached more than 30 individuals. The reason for the high probability of flight in large herds in this study could be that the individuals that were analysed were standing closer to the railway, often clustered in smaller groups, and usually fled towards the rest of the herd when the train approached. This supports the theory of the dilution effect (Roberts, 1996) and might be why the probability of flight is significantly higher for individuals in large herds. Previous studies shows that synchronisation of movement was poor in larger groups of fallow deer than smaller ones (Focardi & Pecchioli, 2005), which supports why smaller groups of 1-5 individuals flee more often than medium sized groups of 6-30 individuals.

The fact that the ungulates fled more frequently when the train driver used the typhoon warning also corresponded with the findings of Bhardwaj et al. (2022). Though in the separate analysis on the different species, the use of the typhoon warning was not significant. Previous studies have found that typhoon signals are not an effective measure against wildlife

collisions, partly because the warning led to ungulates fleeing towards the track instead of away from the track (Bhardwaj et al., 2022; Rolandsen et al., 2017). It is also worth noting that train drivers often use the typhoon when animals are positioned in proximity to, running towards, or not moving away from the tracks. In this study, which only considered ungulates that were not struck, it was natural to find a high likelihood of fleeing due to the use of the typhoon warning.

Furthermore, there was an increased likelihood of ungulates fleeing at dusk/dawn compared to lighter hours of the day (daytime). Previous studies have found that ungulates tend to spend more time being vigilant during dusk/dawn (Matson et al., 2005; Wolff & Horn, 2003), in addition to a greater likelihood of collisions due to increased activity (Krauze-Gryz et al., 2017; Seiler & Olsson, 2017). This is also evident in the separate analysis on fallow deer where individuals fled significantly more often during dusk/dawn. According to De Marinis et al. (2022), fallow deer are more active and forage to a greater extent at dusk/dawn, and also tend to gather in larger groups during this time of day. This can be linked to the results indicating that individuals of fallow deer, in proximity to the railway track, tend to flee more often in large herds.

Train speed only had a significant effect on the probability of flight in moose. The results indicated that moose are not as vigilant to trains when it moves at high speed. Previous studies have also found a positive correlation between increasing train speed and increased risks of collision on moose (Gundersen & Andreassen, 1998), other ungulates (Cserkész & Farkas, 2015; Dorsey, 2011; Dorsey et al., 2017; Jasińska et al., 2019) and other species (St. Clair et al., 2020; Visintin et al., 2018). The results support the theory of Bhardwaj et al. (2022) that the ungulates do not have enough time to react when a train approaches at a high speed. At the same time, all registered cases of train speeds exceeding 150km/h occurred on electrified railway lines. Electric trains are in general quieter than diesel trains, and a study conducted in Italy found that there was no significant difference in variation of noise levels by change of 20-30 km/h for electrified railway lines when traveling below 80 km/h, in contrast to diesel trains that had a significant variation in noise level (Pronello, 2003). Reduced noise variations and quieter trains on electrified railways may also contribute to animals being less vigilant to approaching trains at higher speeds.

4.2 Factors influencing flight direction

There was an overall higher probability of flight for all species away from the track rather than across the track. For the train driver, it is desirable that the animals choose to flee away from the track rather than across or along the track, to prevent a possible collision. The fact that the results only represent the flight direction of surviving ungulates likely influenced the outcome as well. 'Start position' emerged as a significant variable in the analysis for ungulates collectively and in the separate analysis for roe deer and moose, with lower probability of flight across the track with decreasing distance from the railway tracks. The probability of flight across the track, when positioned inside the railway corridor was overall higher for roe deer and moose, with an approximate probability of 50% for roe deer positioned near the track, and approximately 60% for moose positioned inside corridor.

In the overall analysis on ungulates, the results show that the probability of flight across track was significantly lower in a group of 6-15 individuals compared to 1-5 individuals. In the analysis on fallow deer, the probability of flight across the track was significantly higher for individuals in a group of more than 30 individuals. The reason for the large variation in the results of groups with more than 15 individuals, was because of a low amount of data material, and therefore it is not possible to draw any conclusions based on these results.

The probability of flight across the track increased significantly when there was vegetation along the rail embankment for ungulates collectively and for the separate analysis on fallow deer. A study by Jasińska et al. (2019) found that the risk of ungulate-train collisions was positively correlated with the amount of forest along the railway. Rolandsen et al. (2005) and Helldin et al. (2011) also found that the proportion of moose collisions was high in forested areas. At the same time, these same studies indicate that roe deer collisions were high in open agricultural areas, since this is an important grazing habitat for roe deer (Helldin et al., 2011; Rolandsen et al., 2005). This may explain why 'railside vegetation' does not emerge as a significant variable in my results for roe deer. In the separate analysis on moose, 'railside vegetation' did not emerge as a significant variable because moose fled away from track in all cases where the rail embankment had been cleared from vegetation. Due to a low number of observations, there is also a lot of variation in all the factors explaining flight behaviour in moose.

Neither snow nor train speed significantly affected the direction of flight in any of the analyses. The reason why snow did not have the expected impact may be that it primarily affects flight along the track rather than flight across the track. Since I am examining the

behaviour of surviving animals, very few are observed running along the track, as they would most likely have been struck. Additionally, a significant portion of the data was recorded in areas further south in Sweden. Here, snow depth was not very high during data collection (10-30 cm at maximum) (SMHI, s.a.), allowing animals to move more freely in the terrain. Andersen et al. (1991) found a significant increase in proportion of moose killed in collisions with trains when the snow depth exceeded 100cm, compared to snow depths between 0-35cm. Other studies have also reported a positive correlation between snow depths and increase in moose-train collisions in Norway (Gundersen & Andreassen, 1998; Gundersen et al., 1998), and moose- and elk-train collisions in Canada (Hamr et al., 2019).

4.3 Factors influencing FID

There was some variation in average Flight Initiation Distance (FID) among the species. Generally, roe deer and fallow deer exhibited similar average FID values (93m and 106m, respectively), while moose exhibited a higher average FID of 140m. This difference was likely influenced by a low number of moose observations (n = 20). At the same time, Bhardwaj et al. (2022) reported that both moose and roe deer had an average FID of under 80, despite less than 30 observations of moose. Contrary to my research, Bhardwaj et al. (2022) included instances of ungulate-train collisions, which might account for lower FID values.

When positioned on the track, FID was higher than when animals were positioned near the track for ungulates both collectively and for fallow deer and roe deer analysed separately. This is probably because the animals can perceive the train from a further distance, in addition to considering the train as a genuine threat when positioned on the track. Roe deer's starting position did not significantly affect their FID, and there are several observations of individuals with an FID of only a few meters even though they were positioned on the track. The average expected FID is around 150 meters for individuals positioned on the track and just over 100 meters for individuals positioned near the track for ungulates analysed collectively. Train speed was not a significant factor affecting FID in any of the analyses, indicating that individuals have only a few seconds to move if the train is approaching at high speed. In the separate analysis on moose, we even see a tendency to lower FID with increasing speed of train, kept in mind that the results regarding moose are based on a low number of observations.

Neither did any of the analyses indicate that light conditions (day period) significantly affected FID. Fallow deer tended to increase their FID during dusk/dawn while roe deer had a higher average predicted FID during daytime. Their difference is most likely because of a low

amount of data during dusk dawn in the analysis for roe deer. A theory to explain that light condition did not appear to have any significant influence on FID, could be that it is not the visual impression that triggers the flight, but rather an acoustic one.

Since FID depends on detection distance, obstructed visibility of the train might be a reason why individuals in some cases have a very short FID. Bonnot et al. (2017) found that roe deer adjust their flight initiation distance to the local risk-resource trade-off and were less tolerant to an approaching threat when they were far from refuge. Stankowich and Blumstein (2005) also suggested that animals' FID is highly influenced by distance to refuge, physical condition and experiential factors. The study's findings suggest that FID increases under certain conditions, such as when the distance to the nearest refuge is long, when the animal is in good condition, and when predator density is low. However, assessing the animal's condition based on video recordings from trains can be challenging. Further research is needed to examine the relationship between the animal's proximity to refuges (dense vegetation) and the frequency of train traffic in relation to FID towards approaching trains.

4.4 Factors influencing flight before detection by train driver

In all analyses done collectively and separately for the three species, detection distance significantly influenced the likelihood of flight from the start of the video. The shorter the distance between the ungulate and the train when the ungulate first becomes visible to the train driver, the greater the likelihood that the ungulate is already in flight when first visible on the video.

Conversely, we observe that ungulates have a lower likelihood of flight from start when they have a clear view of the situation, and the opportunity to detect the train from a greater distance. Curvature of the corridor, with vegetation or variation in topography, can impede detection of an oncoming train (Hamr et al., 2019; Jasińska et al., 2019; St. Clair et al., 2020). This aligns with my results. Terrain obstruction emerges as a significant factor in all analyses except for the analysis done separately on moose. Terrain acts as an obstruction that impedes detection for both the train driver and the ungulates. In the analysis of ungulates collectively and the separate analysis on roe deer, a straight track contributed to a lower likelihood of flight from start, probably because the straight track promotes a longer detection distance of the train. In addition, vegetation along the rail embankment was a significant factor for ungulates collectively and for fallow deer, that promoted a higher likelihood of flight from start. Low shrub did not emerge as a significant variable, presumably because the vegetation isn't dense enough to impede visibility for the animal. In contrast to daytime, fallow deer had

a significant higher probability of flight from start during poor light conditions (dusk/dawn). A low number of observations during night-time causes a lot of variation in this analysis.

Until the train becomes visible to the animal, other factors such as sound of the train and ground vibrations alert the animals (Lucas et al., 2017), which can explain why the ungulates flee upon detection by the train driver. At the same time, terrain within curved railways and dense vegetation may reduce the audibility of the animals to approaching trains (Wiener & Keast, 1959; Yip et al., 2017). If the animal detects the train only moments before the train becomes visible, this could explain why the probability of flight at start is high when detection distance decrease.

Based on these findings it seems like the ungulates are more likely to already be in flight upon the train driver's detection when they notice the train at a close distance and lack control of the situation.

4.5 Factors influencing detection distance

Detection distance was significantly influenced by obstructions such as vegetation along the rail embankment and the animal's position within the corridor for all ungulates. These findings were consistent across all species, except for the analysis of roe deer, where 'railside vegetation' did not emerge as a significant factor. When the animal is positioned directly on track, it is easier to detect compared to when it is merely near the track. Often, vegetation near the railway corridor or slopes within the railway corridor obstruct clear visibility of animals that are not positioned directly on the track, resulting in shorter detection distances. Detection distance also decreases when trees or low vegetation obstruct visibility of ungulates. Studies from Norway have shown that vegetation clearing along the railroad has reduced the number of ungulate-train collisions (Andreassen et al., 2005; Jaren et al., 1991).

Neither reduced lighting conditions (dusk/dawn) nor curvature significantly influenced detection distance in any of the species. This may be due to a significant portion of the video material being captured on clear days without precipitation, making the detection of animals on or near the track challenging only at night-time. Additionally, 'night' was excluded from the analysis of detection distance due to the considerable difficulty in discerning any objects in the dark footage. This is partly related to video quality, but detection distance naturally becomes much shorter during night-time. Detection distance concerning the curvature of the railway track might depend more on factors such as vegetation cover and terrain along the railway line than the curvature itself. On the other hand, previous studies have found that

curvature indeed is associated with increased collision risk because of reduced detection distance both on railways (Jasińska et al., 2019) and roads (Gunson et al., 2011).

4.6 A problem with habituation or lack of safety measures?

Animals are often thought to perceive passing trains as a threat and real danger due to their sporadic occurrence and the high likelihood of fatal consequences in the event of a collision. However, the results indicate that ungulates frequently remain near the tracks when trains approach and often take considerable time before initiating flight away from the tracks. One may question whether ungulates have become habituated to trains regularly passing by. Train drivers also use the typhoon warning multiple times a day when approaching level crossings to warn other drivers and pedestrians (Bane Nor, 2024), potentially leading to animals habituating to this sound when they are regularly exposed to it. Several studies suggest that habituation to human infrastructure in large mammals is evident within a few years (Haskell & Ballard, 2008; Joacobson et al., 2016; Marino & Johnson, 2012; Martin, 2011; Pomeroy et al., 2023). Pomeroy et al. (2023) also indicate that large mammals are more likely to remain near roads when cars pass by instead of fleeing. To prevent habituation in animals, they must perceive trains as a real threat. It is uncertain whether the sounds from the approaching train are perceived as threatening enough and may not be comparable to sounds from predators.

Another question is how skilled the ungulates are at detecting trains. We humans have specific safety measures and regulations mandated by law (Jernbaneloven, 1993; Sikringsforskriften, 2022) to prevent potential accidents, in addition to effective marked crossings with lights and signs that we have been taught to interpret as warnings (Ahmed et al., 2024; El-Koursi & Bruyelle, 2016). Despite this, people continue to lose their lives in train-related incidents due to overlooking approaching trains, subways, or similar hazards. Since ungulates will not receive any warning before the train approaches, it is possible that in many cases, the animals may not be able to react in time until the train has passed, as seen in the results for moose, which often did not flee at all when the train approached at high speed. The implementation of new technology and the electrification of railway lines will contribute to quieter train operations. This has the potential to result in increased instances of wildlife-train collisions (Backs et al., 2022).

4.7 Further research.

Further research is recommended on methods to increase the Flight Initiation Distance (FID) in ungulates. We see a reduced likelihood of flight and FID in moose with increasing train speed, in addition to an increase in probability of flight for ungulates collectively by the use of the typhoon-warning. To be able to reduce ungulate-train collisions, it may be necessary to implement acoustic warning signals that could be activated before detection of the animals, alongside with a reduction in train speed. Acoustic warning signals can be audible over long distances, even through dense vegetation and varying terrain, if the sound is loud enough. This could facilitate earlier detection of the train from the perspective of animals. We also want an early detection of the animals from the train drivers' perspective, especially during dusk/dawn when the ungulates are more active. Based on AI and modern technology, automatic detection systems should be developed to be able to identify wildlife near or on the track from a far distance and alert the train drivers. Night-time vision systems based on IR technology could therefore be advantageous.

Currently, speakers are being installed at Nordlandsbanen railway in Norway, to emit natural sounds like human voices and mimicked predator calls, upon activation of the alarm trigger by the train driver, to see if this contributes to increased flight likelihood and FID among the ungulates.

4.8 Refinements to the approach.

When I began this master's program, my supervisors and I decided to focus only on animals that successfully evaded trains to avoid dealing with footage of collisions, because watching ungulate-train collisions can be quite dramatic and emotionally distressing over time. Even though I collected a considerable amount of data, I would probably have gathered more information on ungulates running along or crossing the railway tracks if I had included collision events.

On the original DASS units installed on the Gjøvikbanen railway, sound recording started after the trigger button was pressed. As a result, I could not hear the sound of the typhoon warning if it was used before pressing the trigger button. I may therefore have more videos with warning signals than what's recorded. Therefore, I suggest upgrading DASS units to enable continuous audio recording.

The train drivers who provided most of the video material for this study were highly experienced, and most of the video footage was operated by the same driver. To reduce

collisions, train drivers avoid using typhoon signals if they assume there is a risk of animals running towards the tracks instead of away from tracks. In simpler terms, they usually use the typhoon warning when they think not doing so might lead to a higher chance of a collision.

Moreover, to ensure comprehensive data collection during night-time, it is necessary to install thermal cameras capable of detecting animals during nocturnal hours.

5. Conclusion

This study aimed to examine ungulates' flight behaviour towards approaching trains and their detectability. The results show that collectively, ungulates are less likely to flee with increasing distance from the track and during dusk/dawn. The use of the typhoon warning also led to a higher probability of flight for ungulates collectively but had no significant effect on each species individually. Fallow deer were more likely to flee in smaller groups, especially when positioned near the track, separated from a larger herd. Conversely, moose showed a reduced likelihood of flight with an increasing train speed. When positioned near the track and with vegetation cover along the railway corridor, ungulates collectively displayed a higher likelihood of flight across the track. Additionally, the ungulates' FID increased when they were positioned directly on the track in comparison to near the track. All species also demonstrated a higher likelihood of initiating flight before being detected by the train driver with decreasing detection distance. Factors such as dense vegetation, terrain variations, railway curvature, and poor lighting conditions further contributed to the increased likelihood of flight at the start of the video, especially observed in roe deer and fallow deer. Detection distance from the train drivers' perspective decreased notably in areas with vegetation cover along the rail embankment, and increased when ungulates were positioned directly on the track. Implementation of early warning systems, alongside reduction in train speed, is necessary to increase the ungulates' FID. To increase detection distance of animals, the installation of night-time systems that can alert the train driver about animals near the track is advantageous.

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