Journal of Environmental Management 313 (2022) 114992

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Ungulates and trains – Factors influencing flight responses and detectability

Manisha Bhardwaj[a,b,*], Mattias Olsson[c], Emma Håkansson[c], Pär Söderström[d], Andreas Seiler[a]

[a] Swedish University of Agricultural Sciences, Department of Ecology, Grimsö Wildlife Research Station, 730 91, Riddarhyttan, Sweden
[b] University of Freiburg, Faculty of Environment and Natural Resources, Chair of Wildlife Ecology and Management, Tennenbacherstr. 4, Freiburg, D-79106, Germany
[c] EnviroPlanning AB, Lilla Bommen 5c, 411 04, Gothenburg, Sweden
[d] SJ AB, Rolling Stock Division, 105 50, Stockholm, Sweden

ARTICLE INFO

Keywords:
Animal behaviour
Linear infrastructure
Railway ecology
Road ecology
Detection
Flight

ABSTRACT

Wildlife-train collisions can have deleterious effects on local wildlife populations and come with high socio-economic costs, such as damages, delays, and psychological distress. In this study, we explored two major components of wildlife-train collisions: the response of wildlife to oncoming trains and the detection of wildlife by drivers. Using dashboard cameras, we explored the flight response of roe deer (*Capreolus capreolus*) and moose (*Alces alces*) to oncoming trains and explored which factors, such as lighting and physical obstructions, affect their detection by drivers. In a majority of cases, roe deer and moose fled from an oncoming train, at an average flight initiation distance (FID) of 78 m and 79 m respectively. Warning horns had unexpected influences on flight behaviour. While roe deer initiated flight, on average, 44 m further away from the train when warned, they usually fled towards the tracks, in the direction of danger. FID of moose, however, was unaffected by the use of a warning horn. As train speed increased, moose had a lower FID, but roe deer FID did not change. Finally, detection of wildlife was obstructed by the presence of vegetation and uneven terrain in the rail-side verge, which could increase the risk of collisions. Our results indicate the need for early detection and warning of wildlife to reduce the risk of collisions. We propose that detection systems should include thermal cameras to allow detection behind vegetation and in the dark, and warning systems should use cues early to warn of oncoming trains and allow wildlife to escape the railway corridor safely.

Credit author statement

AS and MO conceived the ideas and secured funding, and designed methodology; AS and PS collected the data; EH led video analysis and MB assisted; MB led statistical analysis; AS, EH, and MO contributed to interpretations of the results; MB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

1. Introduction

Currently, more than 1 million kilometres of railway support the transport of goods, services and people across the globe (CIA, 2014). The rising popularity and investments in railways may lead to a predicted 30% increase in the global railway network by 2050 (Dulac, 2013). Despite the advantages of climate-friendly, economic and rapid transport, trains and railways can pose severe ecological impacts on wildlife. One of the most prominent impacts include wildlife-train collisions (Borda-de-Água et al., 2017; Barrientos et al. 2019), which lead to animal mortality as well as costs in repairs, disruptions to traffic flows and train schedules, and psychological distress to drivers, passengers and onlookers (Child and Stuart, 1987; Seiler et al. 2014; Rolandsen, 2015). Given the expected expansion of railway networks across the globe, the need to investigate and mitigate wildlife-train collisions is growing.

Reports of wildlife-train collisions are plentiful around the globe. In Canada, bear-train collisions are the leading cause of mortality in the vulnerable grizzly bear (*Ursus arctos*) population in Banff National Park (Bertch and Gibeau, 2009; St Clair et al. 2019). Between 2004 and 2013, 25% of Asian elephant (*Elephas maximus*) deaths recorded in northern West Bengal, India were due to elephant-train collisions (Roy & Sukumar 2017). In Europe, collisions with large ungulates, such as moose (*Alces alces*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) are a major concern in countries such as Poland, Norway, Czechia and Sweden, amongst others (Gundersen and

* Corresponding author. University of Freiburg, Faculty of Environment and Natural Resources, Chair of Wildlife Ecology and Management, Tennenbacherstr. 4, Freiburg, D-79106, Germany.
E-mail address: manisha.bhardwaj@live.ca (M. Bhardwaj).

https://doi.org/10.1016/j.jenvman.2022.114992
Received 20 September 2021; Received in revised form 21 March 2022; Accepted 27 March 2022
Available online 12 April 2022

Andreassen, 1998; Seiler et al. 2011; Krauze-Gryz et al. 2017; Jasińska et al. 2019; Nezval and Bíl, 2020). In each case, the conclusions are similar: wildlife-train collisions are a known problem with a deleterious effect on local populations and a high cost to railway companies; however, current mitigation strategies are not always sufficient to reduce collisions.

Much of what is known about mitigating the impacts of railways on wildlife is adopted from the road ecology literature (Dorsey et al., 2015; Borda-de-Água et al., 2017; Barrientos et al. 2019). Although roads and railways share many similarities – they are both linear transportation infrastructure, with large mortality and landscape-fragmentation effects on wildlife – railways also present challenges that are unique from roads (Borda-de-Água et al., 2017; Popp and Boyle, 2017; Barrientos et al. 2019). Train traffic volume is generally lower than car traffic volume, presenting long intervals of time when railways are non-threatening for wildlife. Trains tend to travel faster and quieter than cars, thus can be harder to detect by wildlife. Train drivers have little opportunity to stop trains and cannot deviate from tracks to avoid collisions. Finally, railways tend to be narrow in width and surrounded by natural landscapes, in which wildlife can range freely without encountering humans or human-related threats (Borda-de-Água et al., 2017; Popp and Boyle, 2017; Barrientos et al. 2019). The combination of these characteristics can contribute to an increased risk of collisions on railways.

Fencing combined with crossing structures is a common strategy to reduce wildlife-vehicle collisions, however, railway networks are rarely completely fenced due to cost and technical restrictions, and wildlife inevitably come onto the tracks. Furthermore, complete fencing would exacerbate a barrier-to-movement effect that is often otherwise small at railways (Huijser et al., 2009; Barrientos et al., 2019). Thus, alternative methods of collision-prevention must be developed. In order to do so effectively, it is important to identify the mechanisms that lead to collisions. While many studies evaluate the spatiotemporal patterns of collisions occurrence (Gundersen and Andreassen, 1998; Krauze-Gryz et al. 2017; Jasińska et al. 2019; Nezval and Bíl, 2020; St Clair et al. 2020), few studies investigate the behaviours that lead to collisions, such as the response of wildlife to oncoming trains and the detection of wildlife by drivers (Lima et al. 2015; Santos et al., 2017; Barrientos et al. 2019; for exceptions, see: Backs et al. 2017; Jasińska et al. 2019; St Clair et al. 2020). To address this gap in knowledge, in the present study, we use dashboard cameras to study how animals respond to an approaching train, and the factors that limit their detectability by a train driver. Dashboard cameras record from the point-of-view of the driver and capture the entire encounter between animal and train (e.g. Rea et al., 2010; Olson et al. 2014; de la Morena et al. 2017; Hetman et al. 2019), providing a vantage point which is not often available. We investigated how the location of an individual animal in relation to the train, train speed, and the use of a warning horn could influence flight behaviour and successful avoidance of a collision. We predicted that when the train was first detected at a far distance, travelling slowly, and had used the warning horn, individuals would flee away from danger. We were also interested in how the detection of animals by the driver changed in relation to the animal's distance from the train, the time of day, or visual obstructions by landscape or railway features. We predicted that animals would be detected later at night, and if obstructions such as rail curvature, vegetation and terrain were present, compared to when the tracks were straight and rail side verges were cleared. Using this information, we aim to inform train operators and railway companies on how they can manage railways to reduce the risk of collisions with wildlife.

2. Methods

2.1. Video data collection

We conducted this study in Sweden. Each year, there are approximately 5000 collisions between wildlife and trains across the Swedish railway network; the majority of incidents involving roe deer and moose (Seiler et al. 2011, 2014; Trafikverket, 2020). The railways surveyed in this study were sampled from throughout the Swedish passenger rail network. In this network, trains travel up to 250 km/h, and rail-side verges are maintained to keep vegetation low (within 4 m of the tracks) and cleared of trees (within 20 m of electrified tracks; Trafikverket, 2017).

Between 2015 and 2019, we elicited the help of 24 train drivers to record when they detected animals on or near the railway track while driving trains (each driver contributed with an average of 29 videos, ranging from videos 1–154 per driver, collected over an average of 15 days, ranging from 1 to 84 days per driver). Train drivers mounted DOD LS460W dash cameras (http://www.dod-tech.com) onto the windshield in the drivers' cabin pointing out towards the tracks (Fig. 1). These cameras record video continuously, rewriting unsaved footage. When the train drivers detected wildlife near or at the railway, they triggered the camera to save the current video-sequence. Recorded sequences spanned between 10 s and 5 minutes, depending on the settings each driver used for the cameras, however we only used the immediate footage leading up to the encounter between train and animal (maximum 20 s) in our analyses. At the end of each day, the train drivers uploaded their saved videos to an online server and filled out an online form with metadata and comments. Camera operations and reporting criteria were described in a manual developed by the train company for their employees for this project (SJ, 2015). A risk analysis was conducted before drivers used the cameras, with regards to the impact on the driver's operational traffic safety perspective and personal data security. Video sequences containing identifiable humans were removed during the analysis and scenes with known compromising content were erased before upload.

2.2. Video analysis and behavioural data collection

We analysed each encounter between trains and animals and extracted data according to the two aspects we were interested in exploring: the animals' response to the oncoming train and their detectability by the driver. When multiple individuals were featured in the video, each individual's behaviour was analysed separately.

2.2.1. Response variables

We explored three different aspects of the flight response: 1) the occurrence of flight, 2) direction of flight, and 3) flight initiation distance (FID). For each video, we recorded if the individuals fled from the train. If individuals fled, we qualified the direction that they fled into two categories –away from the tracks (i.e. out of danger) or towards/along the tracks. We obtained FID from the videos by calculating the animal's distance from the train when they first began to flee. We used the regularly-placed power line poles (60 m; measurement accuracy ± 15 m) as distance references.

To quantify 'detection distance', we used the distance from the trains at which the animals were first detected. To calculate detection distance from the videos, we assumed that when the animal is first visible to the video analyser would also be when it was first visible to the driver. Once this moment was identified, we calculated the distance between the train and the animal, using the regularly-placed power line poles as references.

2.2.2. Explanatory variables

Starting position – To explore the influence of where the individual was first visible, we categorized their starting position as: a) on the track, b) within the railway corridor (i.e. between the rail-side verges but not on the tracks) and c) outside the railway corridor (i.e. >10 m from the railway tracks; Fig. 1). The rail-side verges usually ended with a clearing, or the beginning of vegetation/terrain features that we used to denote the border between "within" and "outside" railway corridor.

Time of day – We extracted time of day from the videos and used the apparent ambient light conditions to categorize videos into day, dawn/

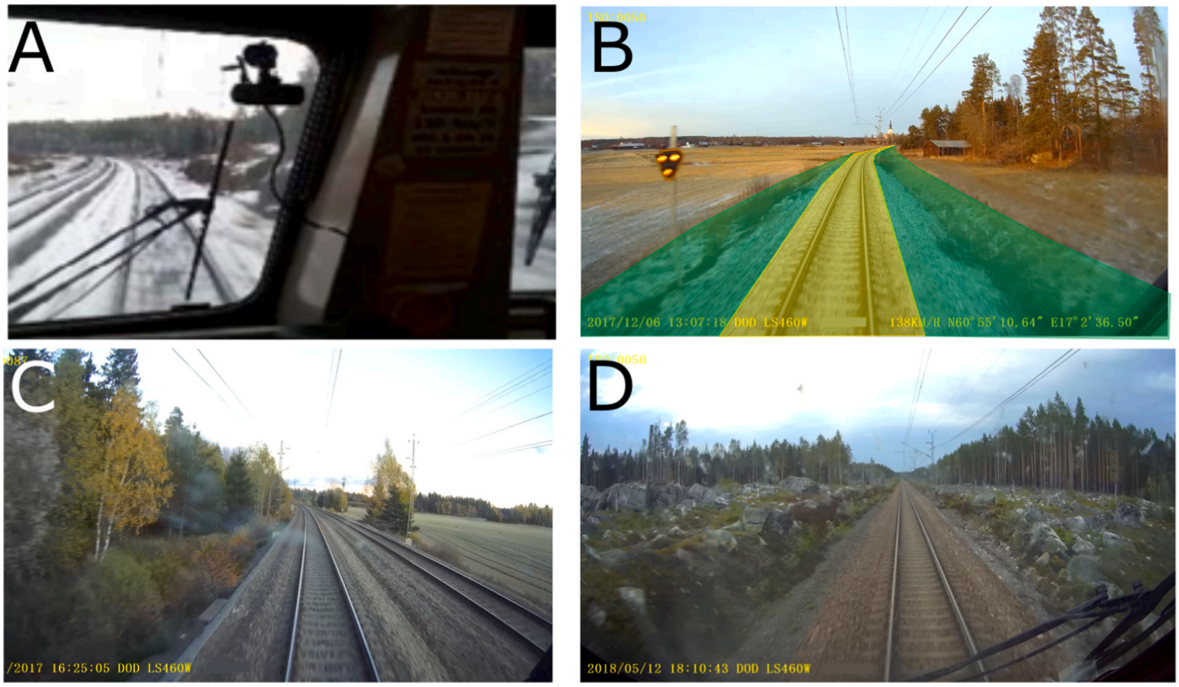

Fig. 1. **A**: An example of the dashboard camera set up from inside the train cabin, from SJ (2015). **B:** Visual depiction of the starting position of the animal - on tracks (yellow), within railway corridor (green) or outside railway corridor (uncoloured). **C:** Example of a railway that has vegetation that could obscure an animal from view. **D:** Example of a railway that has terrain that could obscure an animal from view.

dusk and night. Ambient light is relatively similar during dawn and dusk, and thus would have relatively similar impact on visibility (both for the driver of the animal, and the animal of the train), therefore, we pooled these data into one category.

Type of obstruction – We recorded when animals were obstructed from view due to: the curvature of the railway (i.e., the individual was visible after the train went around a bend), vegetation (i.e., the individual was behind shrubs and trees) and terrain (i.e., the individual was hidden by rocks, or unlevel ground; Fig. 1).

Speed of train – Train speed data was obtained from the videos. Where speed was not available (due to e.g., setting failures or issues with the GPS system), we estimated the speed of the train by measuring the time it took for the train to pass 20 power line poles (~60 m apart). We compared calculated speeds to the speeds obtained from video data and found calculated speeds were accurate within 5 km/h. In 3 videos ($n_{roe\ deer} = 6$), it was not possible to calculate the train speed due to lack of visibility, so those cases were removed from any analysis with train speed.

Use of a warning horn – We recorded whether or not drivers used the warning horn when they observed the animals.

2.3. Data analysis

2.3.1. Flight behaviour

To understand flight behaviour, we explored the likelihood of flight, direction of flight, and flight initiation distance (FID). The likelihood of flight was modelled as a logistic regression, using flight as the binary response variable (yes = 1, no = 0), and the individual's starting position, the time of day, the speed of the train and use of warning horn as explanatory variables. To explore the direction an individual fled, we used logistic regression to determine if the individual's starting position and the train speed influenced if they fled away from (1) or towards (0) the tracks. FID was modelled as a linear regression, using the starting position, time of the day, and train speed as explanatory variables. Individuals that were already in flight when first observed were not included in the FID analysis, as their FID could not be measured. We also excluded individuals first observed outside the railway corridor in the analyses of FID because calculating their distance from the train from the video footage was not reliable. Videos at night were also removed from the analysis of FID as they were too dark to determine when the individual first initiated flight. Thus, in the analyses of FID, we focused only on events during the day, dawn or dusk, with individuals on the tracks or within the railway corridor that commenced flight after being detected. In all analyses, 'on tracks' is the reference category for starting position, and 'day time' is the reference category for time of day.

2.3.2. Detection distance

We evaluated the distance at which the animal was first detected based on: 1) whether the animal was already in flight when they were first observed; 2) the time of day; 3) the starting position; and 4) type of obstruction. Similar to FID, we did not include individuals first observed outside the railway corridor because calculating their distance from the train using the video footage was not reliable. Therefore, in these analyses, we focused only on those individuals on the tracks and within the railway corridor. To explore the difference in detection distance if the individuals were in flight or not at first observation, we used a logistic regression with in flight (1) or not (0) as a binary variable. To explore if time of day influenced the distance at which animals are first detected, we used a linear regression to estimate detection distance during day, night, and dawn/dusk. Finally, we used linear regressions to estimate how detection distance is influenced by starting position and type of obstructions. Given the low visibility of night-time videos, we were unable to accurately say if animals were obstructed by any physical feature and thus those videos were removed from the third analysis.

Each of these relationships was explored separately for roe deer and moose. All analyses were performed using R (v.3.5.3, R Core Team, 2019). Linear regression models were fit using the 'lm' function and logistic regression models were fit using the 'glm' function, in the 'stats' package.

3. Results

We analysed a total of 394 videos, which featured 501 roe deer individuals (n_{videos} = 297) and 128 moose individuals (n_{videos} = 98; 1 video featured both moose and roe deer). In 58% of the videos featuring roe deer, there was only one individual visible (n_{videos} = 174). In 23% of the videos, there were two individuals (n_{videos} = 69), and in 14% of the videos there were three individuals (n_{videos} = 43). At maximum, there were six roe deer visible in the same video (n_{videos} = 3). 83% of the moose videos (n_{videos} = 81) featured a single individual. The next largest group size was two, representing 13% of videos featuring moose (n_{video} = 13). In one video, there were 10 moose visible, standing outside of the railway corridor on an adjacent field.

3.1. Flight behaviour

3.1.1. Likelihood to flee

A majority of roe deer and moose fled from an oncoming train (roe deer: 74%, moose: 67%). Roe deer were most likely to flee an oncoming train when they were on the tracks (Table 1). Roe deer outside the railway corridor were significantly less likely to flee and those within the railway corridor had the same likelihood to flee as those on the tracks (outside railway corridor 44% fled; within railway corridor 93% fled; on tracks 95% fled). Neither time of day nor use of warning horn significantly influenced the likelihood of roe deer to flee from an oncoming train (time of day p = 0.297, warning horn p = 0.119). Increased train speed tended to reduce the likelihood of roe deer to flee, however this relationship was not significant (p = 0.051). The likelihood for moose to flee was not influenced by their starting position, time of day, train speed or the use of warning horns (Table 1).

Table 1
Model output for the likelihood that roe deer or moose would flee from an oncoming train, the direction they flee and their Flight Initiation Distance (FID).

Coefficient	Estimate	Standard Error	P Value
Likelihood to Flee			
Roe Deer			
Intercept (On tracks, during day, no warning horn)	4.20	0.71	<0.001
Within Railway Corridor	−0.56	0.55	0.303
Outside Railway Corridor	−3.40	0.51	<0.001
Night	−0.21	0.52	0.689
Dawn/Dusk	−0.27	0.32	0.297
Train Speed	−0.01	0.00	0.051
Use of Warning horn	−0.43	0.28	0.119
Moose			
Intercept (On tracks, during day, no warning horn)	2.13	1.09	0.050
Within Railway Corridor	0.51	0.83	0.537
Outside Railway Corridor	−0.94	0.81	0.244
Night	−0.76	0.71	0.282
Dawn/Dusk	−0.59	0.44	0.177
Train Speed	−0.01	0.00	0.252
Use of Warning horn	0.72	0.63	0.251
Likelihood to Flee Away from an Oncoming Train			
Roe Deer			
Intercept (On tracks, no warning horn)	−1.51	0.50	0.002
Within Railway Corridor	0.57	0.30	0.058
Outside Railway Corridor	2.73	0.38	<0.001
Train Speed	0.00	0.00	0.148
Use of Warning horn	−0.80	0.30	0.007
Moose			
Intercept (On tracks, no warning horn)	−0.29	1.06	0.783
Within Railway Corridor	0.17	0.81	0.833
Outside Railway Corridor	1.59	0.82	0.053
Train Speed	0.00	0.01	0.883
Use of Warning horn	−0.46	0.58	0.424
Flight Initiation Distance (FID)			
Roe Deer			
Intercept (On tracks, day, no warning horn)	70.83	34.08	0.042
Within Railway Corridor	10.19	19.20	0.597
Dawn/Dusk	8.28	15.91	0.604
Train Speed	−0.16	0.20	0.426
Use of Warning horn	43.74	18.36	0.020
Moose			
Intercept (Day, no warning horn)	149.96	33.21	<0.001
Dawn/Dusk	44.17	33.86	0.142
Train Speed	−0.63	0.30	0.022
Use of Warning horn	0.66	28.95	0.980

3.1.2. Flight direction

To evaluate flight direction, we only included those individuals who fled from an oncoming train in the analysis ($n_{roe\ deer}$ = 374, n_{moose} = 86). Roe deer that were outside the railway corridor were more likely to flee away from the tracks rather than towards the tracks (82%; Table 1). When on the tracks, roe deer were significantly more likely to flee towards/along the tracks than away (77%; Table 1). The likelihood of roe deer to flee away from the tracks did not differ significantly if the individuals were within the railway corridor (36%), or on the tracks (24%; Table 1). When drivers used the warning horn, roe deer were significantly more likely to flee toward/along the tracks (70%) than away from the track (30%; Table 1). Train speed did not influence the direction roe deer fled (p = 0.148). The direction of flight in moose was not influenced by their starting position, the speed of the train or the use of the warning horn (Table 1).

3.1.3. Flight initiation distance

In 198 videos ($n_{roe\ deer}$ = 242 from 162 videos; n_{moose} = 42 from 33 videos), the animals were already in flight when first detected; thus a FID could not be calculated and these individuals were not used in analysis of FID. Furthermore, events at night or when the individuals were outside the railway corridor were excluded from this analysis since FID could not be calculated reliably in these conditions. Therefore, in this analysis we used the FID of 72 roe deer and 27 moose. Of these events, there was only one occurrence of moose on the tracks when first detected, so starting position was not included in the model for moose.

On average, roe deer initiated flight 78 m from the train, and moose initiated flight 79 m from the train. Roe deer initiated flight 44 m further away from the train when a warning horn was used (p = 0.020), however starting position, time of day and train speed did not have a significant influence on roe deer FID (Table 1, Fig. 2). Moose had a significantly lower FID as train speed increased (p = 0.022), but starting position, time of day and use of warning horn did not influence moose FID (Table 1).

3.1.4. Collisions

There were 18 videos which included a collision between the train and the animal ($n_{roe\ deer}$ = 11, n_{moose} = 7; escapes: $n_{roe\ deer}$ = 496, n_{moose} = 121). In six of these videos ($n_{roe\ deer}$ = 3, n_{moose} = 3) the animal did not initiate flight at all, while in five videos (from which FID could be calculated), FID was 23 m and 40 m for roe deer and moose, respectively. Most collisions occurred when individuals were first detected within the railway corridor ($n_{roe\ deer}$ = 8, n_{moose} = 4), compared to on the tracks ($n_{roe\ deer}$ = 3, n_{moose} = 3). Collisions occurred more at night ($n_{roe\ deer}$ = 5, n_{moose} = 3), followed by dawn/dusk ($n_{roe\ deer}$ = 5, n_{moose} = 2), and day ($n_{roe\ deer}$ = 1, n_{moose} = 2). A majority of collisions occurred when no warning horn was used ($n_{roe\ deer}$ = 9, n_{moose} = 5). There were no obvious differences among the number of collisions when individuals were obstructed by a curve in the track ($n_{roe\ deer}$ = 1, n_{moose} = 1), or vegetation ($n_{roe\ deer}$ = 1, n_{moose} = 0). There were no collisions when individuals were obstructed by terrain.

3.2. Detection distance

In 14 videos ($n_{roe\ deer}$ = 12 from 9 videos; n_{moose} = 5 from 5 videos), the focal individual was already in view at the start of the recording. It was not possible to calculate the distance at which those individuals

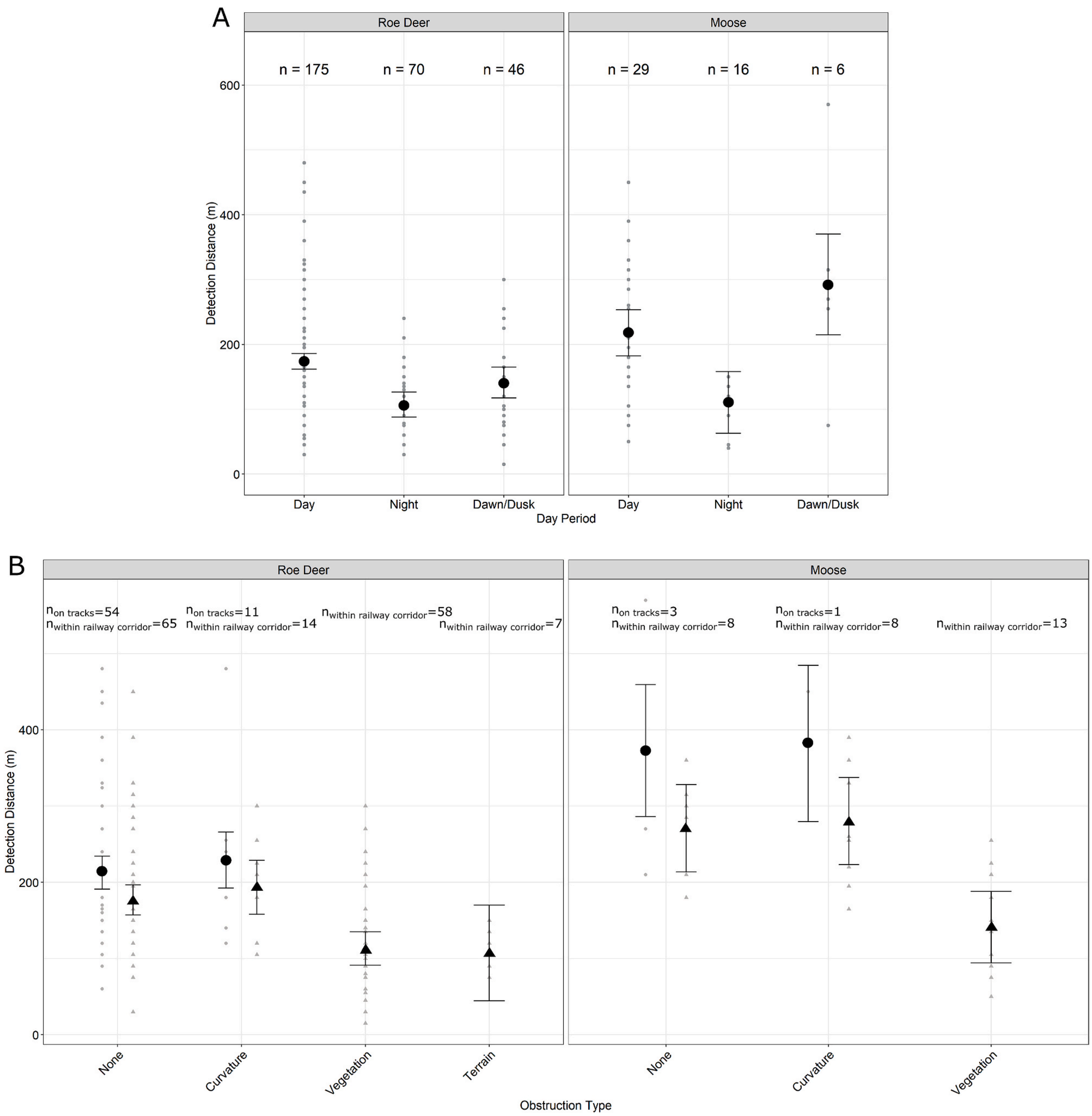

Fig. 2. Model outputs for roe deer (left) and moose (right). Black points and error bars reflect the model estimated mean detection distances and 95% confidence intervals, and the grey points reflect the true data. **A:** Detection distance for each day period. **B:** Detection distance depending on the different obstructions that could reduce the visibility of an individual on the tracks (circles) or within the railway corridor (triangles). Note: Vegetation and terrain were not relevant to those individuals on the tracks, and there were no videos where moose were obstructed by terrain.

were first detected, thus they were removed from these analyses. Additionally, as with the analysis for FID, we removed events when the individuals were outside the railway corridor since detection distance could not be calculated reliably. Thus, in these analyses we include data from 291 roe deer and 51 moose.

Roe deer that were in flight when first detected were detected on average 146 m away from the train, which is significantly closer than those that were first detected not in flight (171 m, $p = 0.018$). Moose, however, were detected equally as far, whether or not they were in flight when first detected ($p = 0.450$).

For both roe deer and moose, low light conditions at night significantly reduced detection distances (average: 106 m and 111 m, respectively) compared to day (roe deer: 174 m, $p < 0.001$; moose: 232 m, $p = 0.001$; Fig. 2). Roe deer were also detected significantly closer to the train during dawn/dusk compared to day (average 141 m, $p = 0.017$), but the effect of dawn/dusk on the detection of moose was not significant, maybe due to small sample size ($p = 0.086$).

Roe deer that were first observed on the tracks were detected, on average, 215 m from the train, which is significantly further than when they were in the railway corridor (average: 149 m, $p < 0.01$). Curvature in the track had no influence on the distance at which roe deer were detected ($p = 0.375$), however vegetation and terrain both significantly decreased roe deer detection distance (average: 113 m, $p < 0.001$, and 107 m, $p = 0.038$, respectively; Fig. 2). Similarly, moose were detected at a greater distance when on the track (average: 375 m) than when in the corridor (average: 149 m, $p = 0.007$). When the view was clear, moose were detected on average 299 m from the train, but when vegetation obstructed the view, detection distance reduced significantly to an average 141 m ($p = 0.001$; Fig. 2). Curvature of the railway did not influence the detection distance for moose ($p = 0.804$). In these analyses, we removed videos at night, since the darkness makes it hard to reliably detect starting position and obstructions ($n_{roe\ deer} = 221$, $n_{moose} = 35$).

4. Discussion

In Sweden, train drivers encounter large fauna on the tracks multiple times a week, and experience approximately 4.5 accidents involving roe deer and moose per year (Olsson et al. 2011). The results we present in this study coincide with train driver experiences: ungulates tend to escape by running on the tracks in front of the train; and accident risks are higher where vegetation near the railroad limits visibility (Olsson et al. 2011).

Ungulates tended to flee an oncoming train rather than remaining on the spot, especially when they were first detected on the tracks or within the railway corridor. Outside the railway corridor, the proportion of animals fleeing reduced significantly, suggesting proximity to the train can influence how animals react to the train. Where FID could be calculated (i.e. individuals were not already in flight when first observed), roe deer fled approximately 78 m from the train, and moose fled 79 m from the train. Earlier warning of a train, by use of a warning horn, increased roe deer FID by 44 m, on average.

Our results suggest roe deer and moose rely on acoustic triggers or vibrations to detect oncoming trains, based on four pieces of evidence: 1) neither light conditions (i.e. the time of day), nor visual obstructions (i.e. vegetation, terrain or railway curvature) seemed to influence the likelihood of an individual to flee or their FID; 2) in 49% of cases individuals initiated flight prior to visual detection from the train; 3) roe deer have a greater FID when warned using a warning horn; and 4) the majority of collisions occurred when no horn is used. These results suggest that earlier warning of the train may be best through acoustic or vibratory methods, which corroborates existing findings (Backs et al. 2017; Backs et al. 2020).

Detecting wildlife sooner would facilitate warning wildlife earlier. Detection of animals from the train was strongly obstructed by poor light conditions and vegetation or terrain cover in the rail corridor. Poor lighting conditions can be addressed through stronger headlights or through use of thermal cameras that can detect wildlife in dark conditions. Rail-side verges must also be maintained and regularly cleared in order to provide increased visibility of wildlife. Clearing trees alone may not be sufficient to reduce accident risks (Eriksson, 2014), however, when coupled with clearing shrubs and other attractive vegetation, the occurrence of ungulates in the railway corridor may be reduced, by decreasing the amount of browsing resources available (Jaren et al. 1991). Diversionary tactics like supplemental feeding may also draw wildlife away from railways and give them additional foraging options outside the rail-side vegetation, thus reducing the amount of time individuals spend in railway corridors (Andreassen et al. 2005). Environmental conditions, such as snow, may make it tough for wildlife to escape onto rail-side verges, pushing them to flee along the tracks (Rea et al., 2010). Thus, verges should also be maintained, in order to allow an opportunity for wildlife to escape the tracks.

Earlier detection of trains may be particularly important as trains continue to become faster and more efficient. In Sweden, trains have a maximum travelling speed of 250 km/h, which means the average FID of 79 m is covered within 1.14 s. High-speed passenger trains travel up to 350 km/h (Nunno, 2018), which would cover the FID in 0.8 s. The standard warning horn of the train increased roe deer FID by 44 m, resulting in an average FID of 122 m (Table 1), providing valuable time to allow for collisions to be avoided (Backs et al. 2020). The problematic aspect, however, is the direction of flight. Individuals fled towards/along the tracks in most cases, often continuing in their direction of travel, especially when a horn is used. Where access to the tracks cannot be completely restricted (e.g., by fencing), accident prevention measures should seek to detect wildlife sooner, and to warn wildlife early enough to allow animals to initiate flight and to cross the tracks into the opposite rail-side verge or beyond. Early detection and warning systems using deep-learning techniques have been trialled to reduce elephant-train collisions and could be an option with other large wildlife (Gupta et al. 2021).

Our results met some but not all of our predictions. We expected individuals outside of the railway corridor to show little reaction to the train, which they did. However, time of day and obstructions appeared to have little impact on flight behaviour. As expected, train speed had a negative impact on flight, in that the likelihood to flee, and FID, was lower as train speed increased. The most surprising result was that roe deer fled into the line of danger when warned using a horn, rather than fleeing away. Low-light conditions, vegetation and terrain reduced the detectability of roe deer and moose as we had expected.

While dashboard cameras provided us an opportunity to observe wildlife-train encounters, they are not without their limitations. In poor weather or lighting conditions, video quality was compromised and the video data was difficult to analyse. Improving camera quality or using thermal imaging may resolve this limitation. Another potential limitation is that the distance of animals outside the railway corridor is difficult to calculate from the video. In our study, this was not problematic, as it is unlikely that individuals outside of the railway corridor will be involved in a collision, and so their FID and detection distance was not a priority for our purposes. However, if future studies will need a reliable measure of far distances, the researchers should consider how that can be calculated from videos, for example, using software that are designed to do so. LIDAR technologies may also improve detection of animals at a distance, and the calculation of the distance at which they are detected. Finally, gathering this data is heavily reliant on a strong collaboration and trust with the railway company and drivers. However, in our experience, taking the time to develop this relationship has been extremely valuable and fruitful and we would recommend researchers see this as an opportunity rather than a limitation.

In this study, we analysed the complexity of wildlife-train collisions from a novel perspective, from the train drivers' field of view, and provide new insights to how wildlife respond to trains and are detected by train drivers. We suggest that earlier detection and warning systems can provide a solution to wildlife-train collisions (e.g., Gupta et al. 2021). Acoustic cues improve detection of the train by wildlife and thus increasing the flight initiation distance (Babińska-Werka et al., 2015; Seiler and Olsson, 2017; Shimura et al., 2018; Backs et al. 2020), and may be more successful than visual cues (Benten et al. 2019). When implemented early enough, this may allow wildlife enough time to leave the railway corridor, even if they follow their path of travel and cross the railway tracks. Detection of wildlife by drivers could be improved through implementing thermal cameras, LIDAR technology and longer-ranging headlights to provide increased vision during low-visibility conditions. Additionally, clearing railway verges to reduce rail-side obstructions would improve detection. Future research and technology development into these areas can help to reduce wildlife-train collisions, to protect wildlife and save millions of euros spent on repairs and loss of life each year.

Declaration of competing interest

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

Acknowledgements

We are most grateful to the 24 train drivers and to Anders Forsberg who helped us by collecting video data for this study. We are also grateful to Linda Höglund and Pernilla Abrahamsson for their support in data collection and video analysis. We thank the Swedish passenger train operator, SJ, the Swedish Transport Administration (particularly Anders Sjölund), and Marie-Claire Cronstedts foundation for providing support. Thank you to Molly Grace and Cassandra Moore for proof-reading the final version. Finally, we thank the three reviewers for providing valuable feedback and helping to improve our manuscript. Funding: this work was supported by the Swedish Transport Administration and Marie-Claire Cronstedts foundation.

References

Andreassen, H.P., Gundersen, H., Storaas, T., Hudson, 2005. The effect of scent-marking, forest clearing, and supplemental feeding on moose–train collisions. J. Wildl. Manag. 69, 1125–1132.

Babińska-Werka, J., Krauze-Gryz, D., Wasilewski, M., Jasińska, K., 2015. Effectiveness of an acoustic wildlife warning device using natural calls to reduce the risk of train collisions with animals. Transport. Res. Transport Environ. 38, 6–14.

Backs, J.A.J., Nychka, J.A., St Clair, C.C., 2017. Warning systems triggered by trains could reduce collisions with wildlife. Ecol. Eng. 106, 563–569.

Backs, J.A.J., Nychka, J.A., St Clair, C.C., 2020. Warning Systems Triggered by Trains Increase Flight-Initiation Times of Wildlife, vol. 87. Transportation Research Part D: Transport and Environment.

Barrientos, R., Ascensão, F., Beja, P., Pereira, H.M., Borda-de-Água, L., 2019. Railway ecology vs. road ecology: similarities and differences. Eur. J. Wildl. Res. 65.

Benten, A., Balkenhol, N., Vor, T., Ammer, C., 2019. Wildlife warning reflectors do not alter the behavior of ungulates to reduce the risk of wildlife-vehicle collisions. Eur. J. Wildl. Res. 65, 12.

Bertch, B., Gibeau, M., 2009. Grizzly Bear Monitoring in and Around the Mountain National Parks: Mortalities and Bear/human Encounters 1990–2008. Summary report to Parks Canada, Banff, Alberta, Canada.

Railway Ecology. In: Borda-de-Água, L., Barrientos, R., Beja, P., Pereira, H.M. (Eds.), 2017. Springer Nature.

Child, K.N., Stuart, K.M., 1987. Vehicle and Train Collision Fatalities of Moose: Some Management and Socio-Economic Considerations. Swedish Wildlife Research *(Sweden)*.

Cia, C., 2014. CIA World Factbook. United States Central Intelligence Agency (CIA), Washington, DC.

de la Morena, E.L.G., Malo, J.E., Hervas, I., Mata, C., Gonzalez, S., Morales, R., Herranz, J., 2017. On-board video recording unravels bird behavior and mortality produced by high-speed trains. Front. Ecol. Evol. 5, 9.

Dorsey, B., Olsson, M., Rew, L.J., 2015. Ecological effects of railways on wildlife. In: van der Ree, R., Grilo, C., Smith, D. (Eds.), Handbook of road ecology (219-227). John Wiley & Sons, West Sussex.

Dulac, J., 2013. Global Land Transport Infrastructure Requirements, vol. 20. International Energy Agency, Paris, p. 2014.

Eriksson, C., 2014. Does Tree Removal along Railroads in Sweden Influence the Risk of Train Accidents with Moose and Roe Deer? Masters. Swedish University of Agricultral Sciences.

Gundersen, H., Andreassen, H.P., 1998. The risk of moose (*Alces alces*) collision: a predictive logistic model for moose-train accidents. Wildl. Biol. 4, 103–110.

Gupta, S., Mohan, N., Nayak, P., Nagaraju, K.C., Karanam, M., 2021. Deep vision-based surveillance system to prevent train–elephant collisions. Soft Comput. (8/2002) https://doi.org/10.21203/rs.3.rs-192950/v1.

Hetman, M., Kubicka, A.M., Sparks, T.H., Tryjanowski, P., 2019. Road kills of non-human primates: a global view using a different type of data. Mamm Rev. 49, 276–283.

Huijser, M.P., Duffield, J.W., Clevenger, A.P., Ament, R.J., McGowen, P.T., 2009. Cost–benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: a decision support tool. Ecol. Soc. 14, 15.

Jaren, V., Andersen, R., Ulleberg, M., Pedersen, P.H., Wiseth, B., 1991. Moose-train collsison: the effects of vegation removal with a cost-benefit analysis. Alces 27, 93–99.

Jasińska, K.D., Żmihorski, M., Krauze-Gryz, D., Kotowska, D., Werka, J., Piotrowska, D., Pärt, T., Cadotte, M., 2019. Linking habitat composition, local population densities and traffic characteristics to spatial patterns of ungulate-train collisions. J. Appl. Ecol. 56, 2630–2640.

Krauze-Gryz, D., Żmihorski, M., Jasińska, K., Kwaśny, Ł., Werka, J., 2017. Temporal pattern of wildlife-train collisions in Poland. J. Wildl. Manag. 81, 1513–1519.

Lima, S.L., Blackwell, B.F., DeVault, T.L., Fernandez-Juricic, E., 2015. Animal reactions to oncoming vehicles: a conceptual review. Biol. Rev. 90, 60–76.

Nezval, V., Bíl, M., 2020. Spatial analysis of wildlife-train collisions on the Czech rail network. Appl. Geogr. 125, 102304.

Nunno, R., 2018. In: Werner, C. (Ed.), Fact Sheet: High Speed Rail Development Worldwide. Environmental and Energy Study Institute, Washington, DC.

Olson, D.D., Bissonette, J.A., Cramer, P.C., Green, A.D., Davis, S.T., Jackson, P.J., Coster, D.C., 2014. Monitoring wildlife-vehicle collisions in the information age: how smartphones can improve data collection. PLoS One 9, e98613.

Olsson, M., Helldin, J.O., Seiler, A., Norrin, H., 2011. Wildlife – Train Accidents and Interactions – Results from a Locomotive Engineers Questionnaire. *ICOET*. Seattle, Washington.

Popp, J.N., Boyle, S.P., 2017. Railway ecology: underrepresented in science? Basic Appl. Ecol. 19, 84–93.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rea, R., Child, K., Aitken, D.A., 2010. Youtube TM insights in to moose-train interactions. Alces 46, 183–187.

Rolandsen, C.M., 2015. In: Animal-Train Accidents on the Railway in Norway 1991–2014 (In Norwegian with English Summary: Dyrepåkjørsler På Jernbanen I Norge 1991–2014). Norwegian Institute for Nature Research (NINA), Trondheim. Report 1145.

Roy, M., Sukumar, R., 2017. Railways and wildlife: a case study of train-elephant collisions in northern West Bengal, India. In: Borda-de-Água, L., Barrientos, R., Beja, P., Pereria, H.M. (Eds.), Railway Ecology. Springer, Cham, pp. 157–177.

Santos, S.M., Carvalho, F., Mira, A., 2017. Current knowledge on wildlife mortality in railways. In: Borda-de-Água, L., Barrientos, R., Beja, P., Pereria, H (Eds.), Railway Ecology. Springer, Cham, pp. 11–22.

Seiler, A., Olsson, M., 2017. In: Borda-de-Água, L., Barrientos, R., Beja, P., Pereira, H.M. (Eds.), Wildlife Deterrent Methods for Railways—An Experimental Study. *Railway Ecology*, pp. 277–291.

Seiler, A., Olsson, M., Helldin, J.O., Norin, H., 2011. Klövviltolyckor På Järnväg - Kunskapsläge, Problemanalys Och Åtgärdsförslag. Swedish Transport Administration, Borlänge. Report 2011:058.

Seiler, A., Söderström, P., Olsson, M., Sjölund, A., 2014. Costs and effects of deer-train collisions in Sweden. In: Seiler, A. (Ed.), IENE 2014 International Conference on Ecology and Transportation. Infra Eco Network Europe (IENE), Malmö, Sweden.

Shimura, M., Ushiogi, T., Ikehata, M., 2018. Development of an acoustic deterrent to prevent deer-train collisions. Quart. Rep. RTRI 59, 207–211.

SJ, 2015. In: CFP (Ed.), Filmning Av Djur Från Tåg. Sweden.

St Clair, C.C., Backs, J., Friesen, A., Gangadharan, A., Gilhooly, P., Murray, M., Pollock, S., 2019. Animal learning may contribute to both problems and solutions for wildlife-train collisions. Philos. Trans. R. Soc. Lond. B Biol. Sci. 374, 20180050.

St Clair, C.C., Whittington, J., Forshner, A., Gangadharan, A., Laskin, D.N., 2020. Railway mortality for several mammal species increases with train speed, proximity to water, and track curvature. Sci. Rep. 10, 20476.

Trafikverket, 2017. Hur Vi Genomför Trädsäkringen. Retrieved from. https://www.trafikverket.se/resa-och-trafik/underhall-av-vag-och-jarnvag/Sa-skoter-vi-jarnvagar/Tradsakra-jarnvagar/Hur-vi-genomfor-tradsakringen/.

Trafikverket, 2020. Ofelia. Retrieved from. https://www.trafikverket.se/tjanster/system-och-verktyg/forvaltning-och-underhall/Ofelia.