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Ungulate use of an at-grade fauna passage and roadside animal detection system: A pilot study from Southern Sweden

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Wildlife-vehicle collisions (WVC) cost millions of euros each year in loss of life and damages. Wildlife crossing structures and fencing are commonly implemented mitigation strategies to reduce WVC and increase landscape connectivity for wildlife. Typically, crossing structures are over- or under-pass structures that allow animals to safely cross the road, while separating them from the road and traffic. An alternative strategy could be an at-grade fauna passage coupled with a Roadside Animal Detection System (RADS). At-grade fauna passages are designated locations where a gap in fencing allows animals to cross over the road, while RADS alert drivers of animals at the upcoming passage, so that they can adjust their driving behaviour accordingly and avoid collisions. In this pilot study, we investigated the use of one at-grade fauna passage by roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) in southern Sweden, and compared changes in the number of WVCs before, during and after the construction of the passage. We collected a total of 326 wildlife crossings from 722 individuals over 1 year of monitoring (24 January 2020–24 January 2021). We found that crossing events tended to be dominated by the time animals spent in the roadside verge from which they approached the at-grade fauna passage, particularly for roe deer that spent a lot of time browsing in the roadside verge during dusk. We also found that animals spent longer in the passage if vehicles were present. In our 1 year of surveys, we only recorded three accidents, and when comparing the annual collision statistics before, during, and after construction of the at-grade fauna passage, we demonstrated an overall reduction in collisions by 66%. While our pilot only evaluates a single site, it does provide promising preliminary results that suggest that at-grade fauna passages can help in efforts to reduce collisions, while maintaining connectivity over medium-sized roads for large ungulates.

KEYWORDS

at-grade fauna passage, animal behavior, road ecology, traffic, AADT, RADS

1 Introduction

Wildlife vehicle collisions (WVCs) are one of the most prominent, and detrimental impacts of roads on wildlife (Bruinderink and Hazebroek, 1996; van der Ree et al., 2011; Seiler and Bhardwaj, 2020). Wildlife crossing structures (i.e., over- and under-passes) and fencing are commonly implemented mitigation strategies to reduce WVCs while providing safe crossing opportunities for wildlife (Jaeger and Fahrig, 2004; Smith et al., 2015; van der Ree et al., 2015). Due to costs and technical restrictions, installation of fencing and crossing structures tends to be prioritized where they would benefit traffic-safety the most, i.e., along high traffic, high speed, primary roads (Huijser and McGowen, 2003; van der Ree et al., 2015). This often leaves secondary roads unmitigated, despite the fact that WVCs occur most frequently on roads with mid-range traffic volume and posted speed limits (Seiler, 2005). Thus, it is necessary to develop and implement mitigation strategies that reduce the impacts of roads on wildlife but are less costly than traditional crossing, particularly for implementation on secondary road networks.

At-grade fauna passages, paired with roadside animal detection systems (RADS), may be an alternative solution to traditional fauna passages (Huijser et al., 2015; Gagnon et al., 2019). At-grade fauna passages with RADS consist of three components: 1) The passage, which is an opening along a fenced roadway. The fencing is used to guide animals to the passage, and across the road at a specific, designated location while reducing access of the individuals to the rest of the road (up to the fencing limits); 2) A detection system, which detects animals as they approach the fence opening; and 3) An alerting system, which alerts drivers of the presence of animals, usually through variable traffic signs. While static signs become less effective over time (Bond and Jones, 2013), variable and temporary sign have been shown to decrease WVC occurrences by at least 50% along non-fenced roads (Sullivan et al., 2004; Huijser et al., 2009). When paired with an at-grade fauna passage, signs can reduce WVCs by up to 80% (Kistler, 1998; Romer et al., 2003). The main difference between at-grade fauna passages and traditional crossing structures is that at-grade fauna passages do not physically separate where animal cross from the flow of traffic. Thus, the success of at-grade fauna passage depends on how the focal species approach and cross the road.

Recently, it has become increasingly popular to investigate the response of wildlife to roads and oncoming vehicles (e.g., Jacobson et al., 2016; Jasińska et al., 2019; Bhardwaj et al., 2022; Breiger et al., 2022; Lunn et al., 2022). While a lot of literature supports the connection between WVCs and road characteristics (e.g., Clevenger et al., 2003; Jaarsma et al., 2007; Barrientos et al., 2009; Chyn et al., 2021), or driver behaviour (e.g., Litvaitis and Tash, 2008; Collinson et al., 2019), the way wildlife respond to traffic and cross roads has been identified as another key

component of WVCs (Lima et al., 2015; Jacobson et al., 2016; Breiger et al., 2022). Wildlife that do not detect or avoid vehicles (i.e., 'nonresponders') and those that pause or slow down when a vehicle is approaching ('pausers'), tend to spend the most time on roads, and thus have the greatest potential to be involved in WVCs (Jacobson et al., 2016). Investigating how much time the animals spend in at-grade fauna passages, either in the roadside verge or on the road, can help improve the design of the structure and warning system, and provide insights into how effective they may be to reducing WVCs.

Ungulates are the most commonly studied taxa in regards to WVCs (Bhardwaj et al., in press). This is largely due to the fact that ungulate-vehicle collisions often entail high risks to human safety, and the damages are often reported to police and insurance companies, thus the data is abundantly available (Conover et al., 1995; Langbein et al., 2011; Hill et al., 2021; Bhardwaj et al., in press). Approximate 60% of the total number of police reported traffic accidents in Sweden involved ungulates (Seiler and Folkesson, 2006). Between 2012 and 2019, roe deer (*Capreolus capreolus*) was the most common species involved in WVCs, with an average of 40 940 (sd = 5689) police reported accidents per year, followed by moose (*Alces alces*) with in average 5 640 (sd = 407) WVC/year and wild boar (*Sus scrofa*) with 5 150 (sd = 1534) WVC/year (Nationella viltolycksrådet, 2022). Red deer (*Cervus elaphus*) are less abundant throughout Sweden, however, they are still involved in an average 374 (sd = 66) WVC/year, particularly in the southern parts of Sweden (Nationella viltolycksrådet, 2022). At-grade fauna passages paired with RADS have successfully reduced the rate of ungulate-vehicle collisions in North America (Gordon et al., 2004; Huijser et al., 2003; 2015; Gagnon et al., 2019), however they are not as widely implemented in Sweden, and their effectiveness, particularly along secondary roads, remains to be investigated.

In this study, we evaluated the crossing behaviour of roe deer, red deer, and wild boar at one at-grade fauna passage paired with RADS. Using video footage, we explored how groups of each species approached and crossed the road. Since we were interested in the interplay between how wildlife cross roads, or respond to traffic, and the risk of potential collision, we explored: the success of a group to cross the road, the time it took for them to cross, and the average number of WVC before, during and after construction of the at-grade fauna passage. We predicted that: 1) Species that travel in larger groups would have lower crossing success, as they would take longer to cross and groups may get separated; 2) The presence of vehicles would reduce crossing success, and increase the time animals spent in the at-grade fauna passage; 3) Daily and seasonal use of the at-grade fauna passage would correspond to the ecology of these species, in that they would be used most during dawn and dusk, and through spring and summer and autumn when these species are most active; and 4) WVCs would be lower after the at-grade fauna passage was constructed. The results of this pilot can be

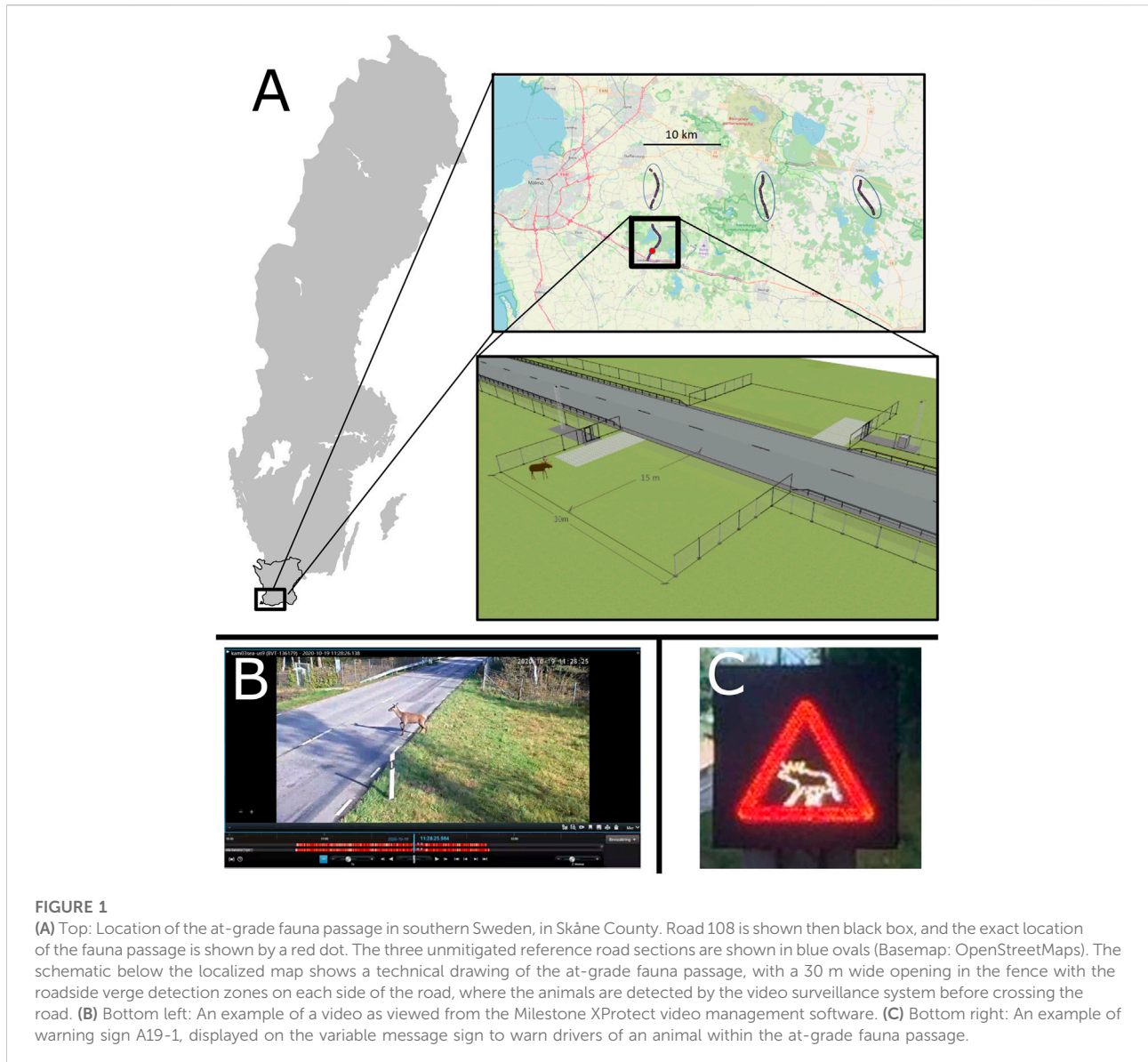


FIGURE 1

(A) Top: Location of the at-grade fauna passage in southern Sweden, in Skåne County. Road 108 is shown then black box, and the exact location of the fauna passage is shown by a red dot. The three unmitigated reference road sections are shown in blue ovals (Basemap: OpenStreetMaps). The schematic below the localized map shows a technical drawing of the at-grade fauna passage, with a 30 m wide opening in the fence with the roadside verge detection zones on each side of the road, where the animals are detected by the video surveillance system before crossing the road. (B) Bottom left: An example of a video as viewed from the Milestone XProtect video management software. (C) Bottom right: An example of warning sign A19-1, displayed on the variable message sign to warn drivers of an animal within the at-grade fauna passage.

used to evaluate whether wild ungulates use at-grade fauna passages and to lay the foundation for a larger study at multiple sites.

2 Materials and methods

2.1 Study site

We conducted this study at one at-grade fauna passage along Road 108 in Skåne County, south-east of Malmö in southern Sweden (Figure 1). This region is predominated by agricultural fields, scattered forests, and large urban/suburban developments. The region supports large densities of ungulates, namely roe deer,

red deer, wild boar, and fallow deer (*Dama dama*). The density of roads, in combination with the scattered patches of natural habitat have resulted in numerous incidents of WVCs, and this region is among the densest for WVCs in Sweden (Nordström, 2014).

Road 108 is 7.5 m wide, runs in a north-south direction and has one lane for traffic in each direction. The posted speed limit is 80 km/h, and the annual average daily traffic volume (AADT) is 6000 vehicles/day, of which approximately 600 vehicles/day are transport trucks (Nordström, 2014). In 2019, a 5.2 km section of Road 108 was upgraded, which included introducing various strategies to reduce the occurrence of WVCs along this segment of the road. These strategies included wildlife fencing, jump-outs and cattle guards at private roads that intersect Road 108, in

addition to the at-grade fauna passage and RADS structure which is the focus of this study. Prior to the upgrade, there was a poorly-maintained private fence on one-side of the road, and, on average, 30 WVC/year involving wild ungulates (Nordström, 2014). Now, Road 108 is fenced on both sides along the entire length of the 5.2 km upgrade, except for at the at-grade fauna passage, where there is a 30 m wide opening in the fence (Figure 1). At the opening, fencing extends 15 m perpendicularly from the road into the roadside verge, to create two well-defined approaching areas where animals are detected as they enter the fauna passage (further referred to as the “roadside verge”). On Road 108, approximately 100–130 m before the at-grade fauna passage, there is a 1 × 1 m variable message sign, mounted on a 2 m high pole, directed towards oncoming traffic to warn drivers of wildlife within the at-grade fauna passage (Figure 1).

The at-grade fauna passage and RADS is monitored and activated using the Swedish Transport Administration’s technical platform (Trafikverket, 2021), which includes thermal imaging cameras, control systems and external communication for function control. Three heat cameras (Axis, Q1941-E), two radars (Axis, D2050-VE) and two Infrared-sensitive Pan-Tilt-Zoom (PTZ) cameras with external Infrared-lamps (Axis, Q6155-E PTZ R2) are mounted on two 5 m high masts, which survey the road and both roadside verges on each side of the at-grade fauna passage. One mast is located in the north-western corner of the at-grade fauna passage, and consists of one heat camera, one radar, and one PTZ camera with an Infrared-lamp. The second mast is in the south-eastern corner of the at-grade fauna passage, and has two heat cameras, one radar and one PTZ camera with an Infrared-lamp. Video footage from the at-grade fauna passage is stored on a technical platform that uses Milestone with XProtect video management software (Milestone Systems A/S; <https://www.milestonesys.com/video-technology/platform/xprotect/>) (Figure 1). The pilot site cost approximately 300 000 Euro and 6 months to plan and build.

The cameras are continuously recording the site. The heat and radar cameras detect wildlife on the roadside verges, and the PTZ camera can rotate, zoom in and follow animal movements across the whole at-grade fauna passage, from one roadside verge across the road and into the second roadside verge. At each animal detection, the variable message signs are automatically activated, and a conventional “warning of moose” graphic sign (A19-1, Transportstyrelsen, 2007) is displayed and remains active until 60 s after the last animal is detected at the at-grade fauna passage (Figure 1). The software stores video sequences of animals that use the at-grade fauna passage.

2.2 Data collection and analysis

We analysed every animal detection captured between 24 January 2020 and 24 January 2021. The camera angles and

technical setup allowed us to follow each individual as it approached, crossed and exited the at-grade fauna passage. Since the videos were continuous, with no time restrictions, we could observe wildlife for the full duration that they were within the detection area of the cameras. We defined videos as “events” that could have included one or more individuals of conspecifics within the at-grade fauna passage. Events finished once all of the detected individuals were no longer within the at-grade fauna passage.

For each event, we summarized the behaviour of individuals/groups into crossing success and time spent in the passage in total, in the roadside verge or on the road. We assumed that if individuals were detected in the roadside verge (i.e., within the detection area of the milestone system), they had the intention to cross. Thus, if individuals only spent time in the roadside verge and did not cross, this was recorded as an unsuccessful crossing. A crossing was only considered successful if all individuals of the group crossed the road (i.e., without turning back, or being involved in a collision).

In events with more than one individual detected (i.e., a group), we summarized the behaviour of the group rather than treating each individual independently. Thus, the duration of time spent in the passage or crossing the road spans from the time the first individual is detected until the last individual completes the behaviour (e.g., from the time that the first individual steps on the road until the last individual steps off the road). The at-grade fauna passage was used by many species, for example, fox (*Vulpes vulpes*), and fallow deer. However, our analysis focuses on the most frequently observed species: roe deer, red deer, and wild boar. Finally, we also documented how many vehicles passed the at-grade fauna passage during each event.

Crossing activity and the risk of WVC could change depending on the time of day, and the season. We recorded the time of day that the events occurred in, and categorized this into dawn (morning twilight to sunrise), day (sunrise to sunset), dusk (sunset to evening twilight) and night (evening twilight to morning twilight). The hours of the day and duration of each time period changed throughout the year with changes in sunrise and sunset time. To account for changes in animal behaviour throughout the year, we also recorded four meteorological seasons: autumn (September–November), winter (December–February), spring (March–May) and summer (June–August).

We explored crossing success as a binomial regression, in relation to the presence of a vehicle during the event, the group size, and the time of day. To explore the time ungulates spent at the at-grade fauna passage we explored three separate measurements of time, recorded in seconds: total time of an event, the time the individual/group spent on the roadside verge, and the time the individual/group spent on the roads. For each time measure, we used gamma regressions (with a log link) to explore the influence of vehicle presence, crossing success, group size, time of day and season on the time spent. In each model, the

TABLE 1 Summary of number of events and group sizes for each species.

	Total number of events	Minimum group size	Average group size	Maximum group size
Roe Deer	91	1	1.2	2
Red Deer	99	1	1.9	5
Wild Boar	136	1	3.2	10

reference time of day was dawn, and the reference season was autumn. We explored these relationships separately for roe deer, red deer and wild boar. All analyses were performed using R (v.3.5.3, R Core Team, 2019), using the 'glm' function, in the 'stats' package.

To determine if mitigation along the focal segment of Road 108 reduced the number of WVC, we undertook posthoc analyses, comparing the number of WVC at the focal road section, to three unfenced roads within the same road network (Figure 1). The three reference sections were similar to our focal road segment: 5.2 km in length, had similar traffic volume and posted speed limits. We explored WVC data from 1 January 2015 to 30 December 2021, covering 1307 days before, 424 days during, and 822 days after the focal road segment was upgraded and the at-grade fauna passage was constructed. At the focal road segment, we collected WVC data for the entire 5.2 km upgraded extent, as well as 300 m to the north of the fence-end. The 100 m furthest from the fence-end had a lower posted speed limit of 60 km/h as the road approached a roundabout. In the southern part, Road 108 intersected Highway 65 (Figure 1), and so the fencing was connected to the existing highway fencing.

Since roe deer, red deer and wild boar populations in this region are long-established, stable and controlled through hunting, we assumed that populations densities and spatial extent are relatively similar across this time period, and thus an equal opportunity for collisions exists (with the exception of natural fluctuations). Further, since this is a long human-populated and developed part of Sweden, we assumed that the landscape surrounding the roads did not change significantly enough to change the likelihood of wildlife to occur around the roads, over the duration that we recorded WVCs.

3 Results

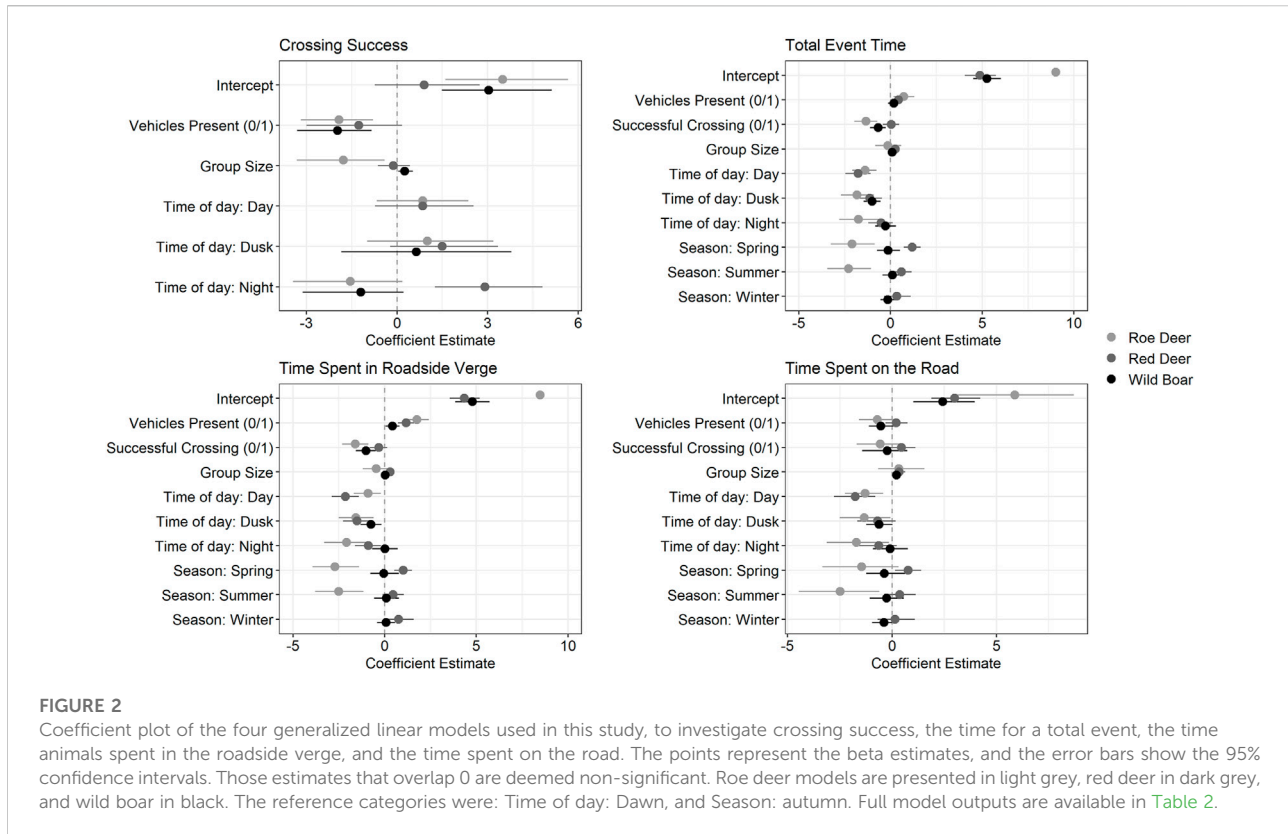
Through the Milestone System at the at-grade fauna passage, we collected a total of 332 events with 737 individual animals over the one-year sampling period. We analysed 326 of these events, of which 91 included roe deer ($n_{\text{individuals}} = 186$), 99 included red deer ($n_{\text{individuals}} = 105$) and 136 included wild boar ($n_{\text{individuals}} = 431$). A total of 608 individual animals crossed through the at-grade fauna passage in 248 of the 326 events (Table 1). Roe deer were only active at the at-grade fauna passage from April to November.

Red deer activity was highest from April to December, and wild boar were active throughout the year, but less so from January to May. On average, roe deer tend to spend the most time in the at-grade fauna passage (7 min, range: 0–55 min) and wild boar tended to spend the least amount of time (2.5 min, range 0–62 min). Red deer spent 5 min on average (range: 0–33 min).

Generally, all individuals in a group responded the same way; either the whole group crossed or the whole group were repelled. In 62% of roe deer events (56/91), 77% of red deer events (76/99), and 84% of wild boar events (114/136), the whole group crossed the road. In only one roe deer event, five red deer events and three wild boar events did the groups get split up. In two of the three events where the whole group of wild boars did not cross, the individual that did not cross were involved in an accident. In the remaining events (34 roe deer events, 18 red deer events and 19 wild boar events), no members of the group crossed the road.

3.1 Crossing success and time spent at the at-grade fauna passage

Roe deer events included either one or two individuals (Table 1). Roe deer crossing success was lower in events with two individuals than in events with one individual. However, group size did not have any influence on the time roe deer spent at the at-grade fauna passage, in the roadside verge or on the road (Figure 2; Table 2). Roe deer events tended to be longest during dawn, compared to other times of the day (dawn: 555 ± 699 s [34, 2113] (mean \pm SD [range]); day: 164 ± 477 s [14, 3255]; dusk: 162 ± 262 s [19, 908]; night: 1244 ± 1224 s [18, 3322]); Figure 2 and Table 2). The time roe deer spent at the at-grade fauna passage tended to be dominated by time spent in the roadside verge, and the longer roe deer spent at the at-grade fauna passage, the less likely they were to cross the road (roadside verge: 347 ± 769 s [0, 3322]; road: 18 ± 58 s [0, 482]; Figures 2, 3 and Table 2). Roe deer spent most of the time at the at-grade fauna passage during autumn, compared to spring and summer (autumn: 1837 ± 1041 s [225, 3322]; spring: 193 ± 563 s [14, 3255]; summer: 249 ± 458 s [14, 2113]). Roe deer were not present at the fauna passage during winter; Figure 2 and Table 2). Again, this mainly reflects the time roe deer spent in the roadside verge. However, this is also true, while more uncertain, of the time roe



deer spend on the road (Figures 2, 3; Table 2). When vehicles were present, roe deer spent more time in the roadside verge but had lower crossing success, regardless of time of day (Figures 2, 3; Table 2).

Red deer had higher crossing success at night, compared to other times of the day, (Figure 2; Table 2). Like roe deer, red deer events were dominated by time spent in the roadside verge, particularly during dawn (roadside verge (average throughout day): 173 ± 272 s [12, 1453]; road (average throughout day): 43 ± 67 s [0, 492]; dawn (total event time): 607 ± 605 s [37, 1966]; day (total): 110 ± 112 s [20, 404]; dusk (total): 272 ± 244 s [17, 978]; night (total): 311 ± 357 s [22, 1439]; Figures 2, 3 and Table 2). During night and dawn, red deer spent less time on the road than during the day, which is also reflected in the measure of total time spent in the at-grade fauna passage (Figure 2; Table 2). Red deer events were longer during spring compared to other times of the year (autumn: 151 ± 162 s [22, 831]; spring: 449 ± 493 s [20, 1966]; summer: 225 ± 228 s [17, 712]; winter: 306 ± 361 s [68, 1198] Figure 2 and Table 2). While group size did not influence the crossing success of red deer, as groups got bigger, events got longer (Figure 2; Table 2). The time red deer took to cross the at-grade fauna passage did not differ significantly between successful and unsuccessful crossings. However, the presence of vehicles did increase the time red deer spent in the roadside

verge and in the at-grade fauna passage overall (Figures 2, 3; Table 2).

While wild boar spent, on average, less time at the at-grade fauna passage than roe deer and red deer, their behaviour was often similar. Wild boar spent the majority of the total event time in the roadside verge, and at events where they spent more time in the roadside verge, they were less successful at crossing the road (roadside verge: 76 ± 94 s [6, 588]; road: 14 ± 27 s [0, 259]; Figures 2, 3 and Table 2). Vehicle presence was also negatively associated with wild boar crossing success, but positively associated with the time they spent in the roadside verge (Figures 2, 3; Table 2). Crossing success, and total time spent at the at-grade fauna passage increased with increasing group size (Figure 2; Table 2). There were only nine events of wild boar during the day, so we incorporated these events into dawn if they were before 12:00 ($n = 7$) and dusk if there were after 12:00 ($n = 2$). Wild boar crossing success did not differ throughout the day. However, events during dusk were shorter than events during night and dawn (dawn: 162 ± 177 s [32, 810]; dusk: 65 ± 42 s [15, 226]; night: 105 ± 106 s [15, 588]; Figures 2, 3 and Table 2). Finally, there was no difference in the amount of time wild boar spent at the at-grade fauna passage throughout the year (autumn: 135 ± 115 s [15, 588]; spring: 112 ± 136 s [29, 445]; summer: 120 ± 138 s [20, 810]; winter: 100 ± 93 s [17, 481]; Figure 2 and Table 2).

TABLE 2 Model outputs for roe deer, red deer and wild boar. Crossing success was estimated using a binomial regression, in relation to the presence of a vehicle during the event, the group size, and the time of day. A crossing was only considered successful if all individuals of the group crossed the road (i.e., without turning back, or being involved in a collision). Total time of an event, the time the individual/group spent on the roadside verge, and the time the individual/group spent on the roads were estimated using gamma regressions (with a log link) to explore the influence of vehicle presence, crossing success, group size, time of day and season on the time spent. In each model, the reference time of day was dawn, and the reference season was autumn. Roe deer, red deer and wild boar were modelled separately.

Coefficients	Estimate	Standard error	<i>p</i> -value
Crossing success			
Roe Deer			
Intercept (No vehicles, Dawn)	3.50	1.02	<0.001
Vehicles Present (0/1)	-1.92	0.60	0.001
Group Size	-1.78	0.73	0.015
Time of day: Day	0.85	0.76	0.266
Time of day: Dusk	1.00	1.05	0.338
Time of day: Night	-1.55	0.91	0.090
Red deer			
Intercept (No vehicles, Dawn)	0.90	0.86	0.299
Vehicles Present (0/1)	-1.27	0.79	0.109
Group Size	-0.12	0.27	0.653
Time of day: Day	0.85	0.82	0.298
Time of day: Dusk	1.49	0.90	0.097
Time of day: Night	2.91	0.89	0.001
Wild Boar			
Intercept (No vehicles, Dawn)	3.04	0.90	<0.001
Vehicles Present (0/1)	-1.97	0.62	0.001
Group Size	0.26	0.12	0.032
Time of day: Dusk	0.64	1.30	0.622
Time of day: Night	-1.20	0.81	0.139
Total Event Time			
Roe Deer			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	9.01	0.86	<0.001
Vehicles Present (0/1)	0.73	0.27	0.008
Successful Crossing (0/1)	-1.35	0.31	<0.001
Group Size	-0.15	0.36	0.676
Time of day: Day	-1.39	0.34	<0.001
Time of day: Dusk	-1.82	0.45	<0.001
Time of day: Night	-1.75	0.54	0.002
Season: spring	-2.09	0.56	<0.001
Season: summer	-2.29	0.57	<0.001
Red Deer			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	4.87	0.40	<0.001
Vehicles Present (0/1)	0.43	0.22	0.055
Successful Crossing (0/1)	0.03	0.23	0.880
Group Size	0.26	0.09	0.006
Time of day: Day	-1.76	0.34	<0.001
Time of day: Dusk	-1.13	0.35	0.002
Time of day: Night	-0.51	0.33	0.119
Season: spring	1.19	0.23	<0.001
Season: summer	0.59	0.28	0.039
Season: winter	0.34	0.34	0.329
Wild Boar			

(Continued on following page)

TABLE 2 (Continued) Model outputs for roe deer, red deer and wild boar. Crossing success was estimated using a binomial regression, in relation to the presence of a vehicle during the event, the group size, and the time of day. A crossing was only considered successful if all individuals of the group crossed the road (i.e., without turning back, or being involved in a collision). Total time of an event, the time the individual/group spent on the roadside verge, and the time the individual/group spent on the roads were estimated using gamma regressions (with a log link) to explore the influence of vehicle presence, crossing success, group size, time of day and season on the time spent. In each model, the reference time of day was dawn, and the reference season was autumn. Roe deer, red deer and wild boar were modelled separately.

Coefficients	Estimate	Standard error	p-value
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	5.26	0.37	<0.001
Vehicles Present (0/1)	0.18	0.15	0.235
Successful Crossing (0/1)	-0.67	0.21	0.002
Group Size	0.08	0.03	0.004
Time of day: Dusk	-1.01	0.24	<0.001
Time of day: Night	-0.28	0.28	0.317
Season: spring	-0.14	0.31	0.648
Season: summer	0.11	0.26	0.678
Season: winter	-0.15	0.20	0.463
Time Spent in Roadside Verge			
Roe Deer			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	8.48	0.92	<0.001
Vehicles Present (0/1)	1.76	0.29	<0.001
Successful Crossing (0/1)	-1.60	0.32	<0.001
Group Size	-0.46	0.38	0.220
Time of day: Day	-0.90	0.36	0.016
Time of day: Dusk	-1.56	0.48	0.002
Time of day: Night	-2.08	0.58	0.001
Season: spring	-2.71	0.59	<0.001
Season: summer	-2.51	0.60	<0.001
Red Deer			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	4.34	0.40	<0.001
Vehicles Present (0/1)	1.17	0.22	<0.001
Successful Crossing (0/1)	-0.32	0.25	0.205
Group Size	0.30	0.10	0.002
Time of day: Day	-2.13	0.37	<0.001
Time of day: Dusk	-1.51	0.37	<0.001
Time of day: Night	-0.88	0.35	0.014
Season: spring	1.01	0.24	<0.001
Season: summer	0.47	0.30	0.122
Season: winter	0.75	0.37	0.042
Wild Boar			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	4.79	0.46	<0.001
Vehicles Present (0/1)	0.43	0.19	0.027
Successful Crossing (0/1)	-1.01	0.26	<0.001
Group Size	0.03	0.04	0.452
Time of day: Dusk	-0.75	0.29	0.012
Time of day: Night	0.01	0.34	0.981
Season: spring	-0.05	0.38	0.890
Season: summer	0.09	0.32	0.772
Season: winter	0.07	0.24	0.770
Time Spent on the Road			
Roe Deer			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	5.88	1.41	<0.001
Vehicles Present (0/1)	-0.70	0.47	0.144

(Continued on following page)

TABLE 2 (Continued) Model outputs for roe deer, red deer and wild boar. Crossing success was estimated using a binomial regression, in relation to the presence of a vehicle during the event, the group size, and the time of day. A crossing was only considered successful if all individuals of the group crossed the road (i.e., without turning back, or being involved in a collision). Total time of an event, the time the individual/group spent on the roadside verge, and the time the individual/group spent on the roads were estimated using gamma regressions (with a log link) to explore the influence of vehicle presence, crossing success, group size, time of day and season on the time spent. In each model, the reference time of day was dawn, and the reference season was autumn. Roe deer, red deer and wild boar were modelled separately.

Coefficients	Estimate	Standard error	p-value
Successful Crossing (0/1)	-0.56	0.50	0.271
Group Size	0.33	0.56	0.563
Time of day: Day	-1.29	0.45	0.006
Time of day: Dusk	-1.32	0.59	0.028
Time of day: Night	-1.71	0.71	0.019
Season: spring	-1.46	0.88	0.102
Season: summer	-2.49	0.92	0.009
Red Deer			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	3.00	0.54	<0.001
Vehicles Present (0/1)	0.20	0.27	0.462
Successful Crossing (0/1)	0.45	0.36	0.219
Group Size	0.34	0.12	0.005
Time of day: Day	-1.76	0.49	0.001
Time of day: Dusk	-0.70	0.47	0.143
Time of day: Night	-0.63	0.45	0.169
Season: spring	0.78	0.31	0.014
Season: summer	0.36	0.38	0.339
Season: winter	0.14	0.44	0.746
Wild Boar			
Intercept (No Vehicle, Unsuccessful Crossing, Dawn, autumn)	2.44	0.70	0.001
Vehicles Present (0/1)	-0.53	0.29	0.069
Successful Crossing (0/1)	-0.23	0.52	0.659
Group Size	0.22	0.04	<0.001
Time of day: Dusk	-0.61	0.32	0.055
Time of day: Night	-0.09	0.39	0.828
Season: spring	-0.37	0.42	0.381
Season: summer	-0.26	0.38	0.498
Season: winter	-0.38	0.29	0.194

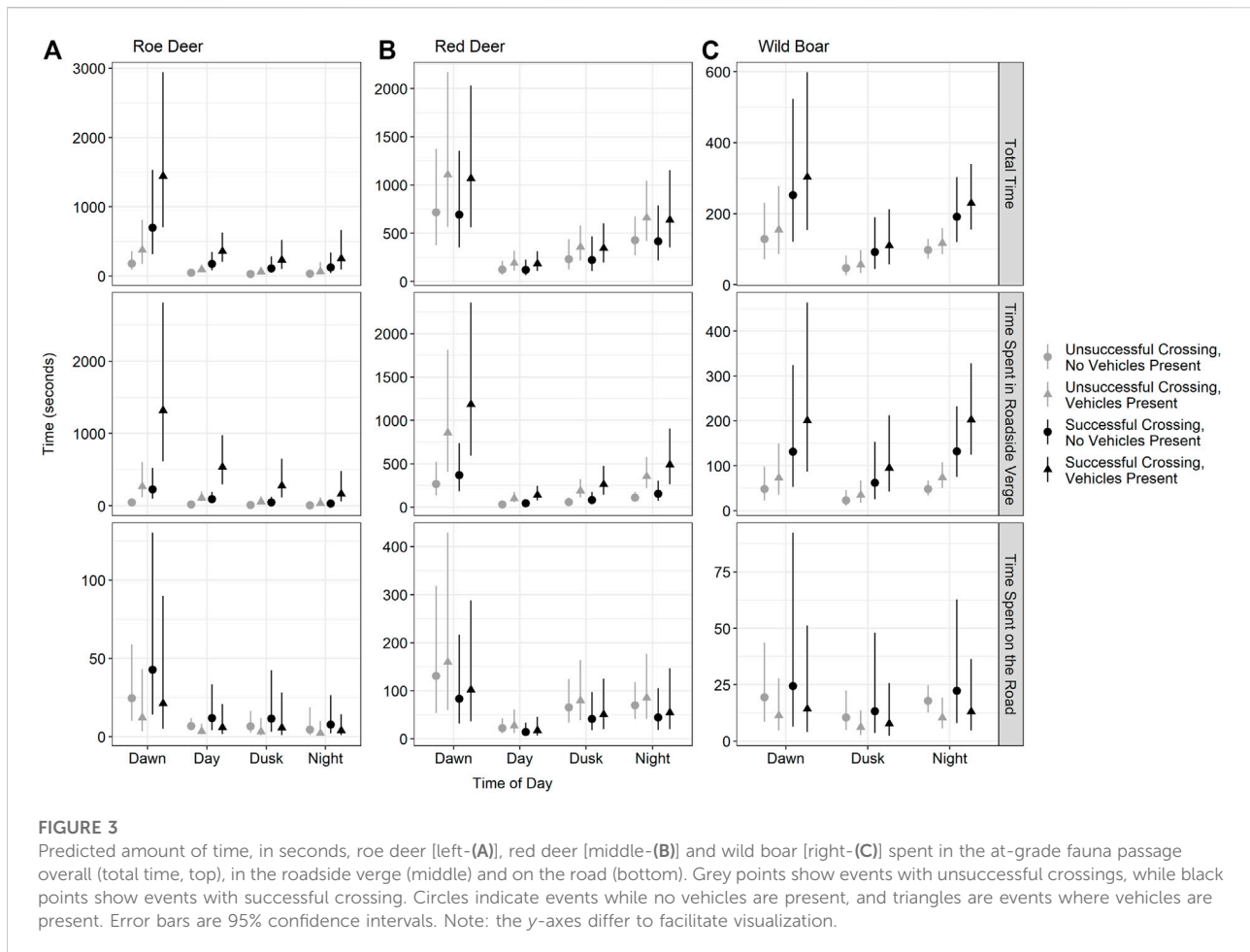
3.2 Wildlife-vehicle collisions

Along the section of Road 108 where the at-grade fauna passage was constructed, there was a 66% decrease in WVCs, compared to before mitigation (from 0.078 WVC/day to 0.027 WVC/day; Figures 1, 2, 3, 4 and Table 3). Comparatively, there was relative increase in WVCs at three unmitigated but otherwise similar road segments (reference 1: 0.047 WVC/day to 0.052 WVC/day; reference 2: 0.130 WVC/day to 0.141 WVC/day; reference 3: 0.142 WVC/day to 0.139 WVC/day; Figure 4 and Table 3). During the year of data collection for this study, we captured three WVC at the at-grade fauna passage. All of the accidents involved wild boar, resulting in an individual accident rate of 0.5% of the crossing animals ($N_{\text{crossing wild boar}} = 608$ from 248 events).

4 Discussion

4.1 Ungulate use of at-grade fauna passage with RADS

In this study, we used 1 year of high-quality, detailed video footage to investigate the use of an at-grade fauna passage by roe deer, red deer and wild boar in southern Sweden. Generally, groups of all three species responded the same way—either the whole group crossed or the whole group remained on one side of the road. We expected group size to have a strong impact on how long events at the at-grade fauna passage lasted, with the expectation that larger groups would take longer to cross the road. However, we did not see any clear influence of group size on



the time to cross. Rather, contrary to our expectations, in larger groups, wild boar were more likely to cross the road than in smaller groups. Roe deer tended to have lower crossing success with increased group size, but since the maximum number of individuals recorded was two, this may just be an artefact of the sampling method. Further, the roadside verge appeared to be an attractive browsing resource for roe deer, and individuals spent a lot of time there without attempting to cross the road.

Since there were very few events where the whole group did not cross the road, we suggest that the “decision” to cross was made before individuals entered the field of view of the detection system. This is also evident by the fact that when groups crossed, they spent little time on the road. We also found that roe deer, red deer and wild boar spent longer in the roadside verge when a vehicle was present than when there were no vehicles present, which also resulted in longer events overall. However, vehicle presence did not affect the amount of time that roe deer, red deer or wild boar spent on the road. The relationship between total time spent in at the at-grade fauna passage and the number of vehicles is circular—when individuals spend up to an hour in the roadside verge, they have a greater chance of a car passing them

during that time. Thus, it is not possible to disentangle if they spent more time in the roadside verge because of vehicles or if the vehicle count simply increases as time goes on. To derive these answers, it may be important to investigate the landscape-level effect that roads have on wildlife, and the decision-making processes, and behaviour of individuals as they approach or cross the road (Neumann et al., 2012; Meisingset et al., 2013; Kämmerle et al., 2017). Furthermore, understanding the composition of the landscape around the road may provide insights into how valuable the roadside verge is as a resource, and if that would motivate individuals to spend more time near a road without the intent to cross. Finally, investigation of the way wildlife approach a road could also provide insights to the larger question of landscape-connectivity. In the current set up of our data collection, we are only able to observe the response of wildlife that are already within 15 m of the road, however if the road is having a filtering effect on wildlife, and few individuals are approaching the road, that impact may occur further away from the road. Thus, observing the behaviour of wildlife further away from the road, as they approach the road, would provide further insights into the behavioural response of wildlife to roads.

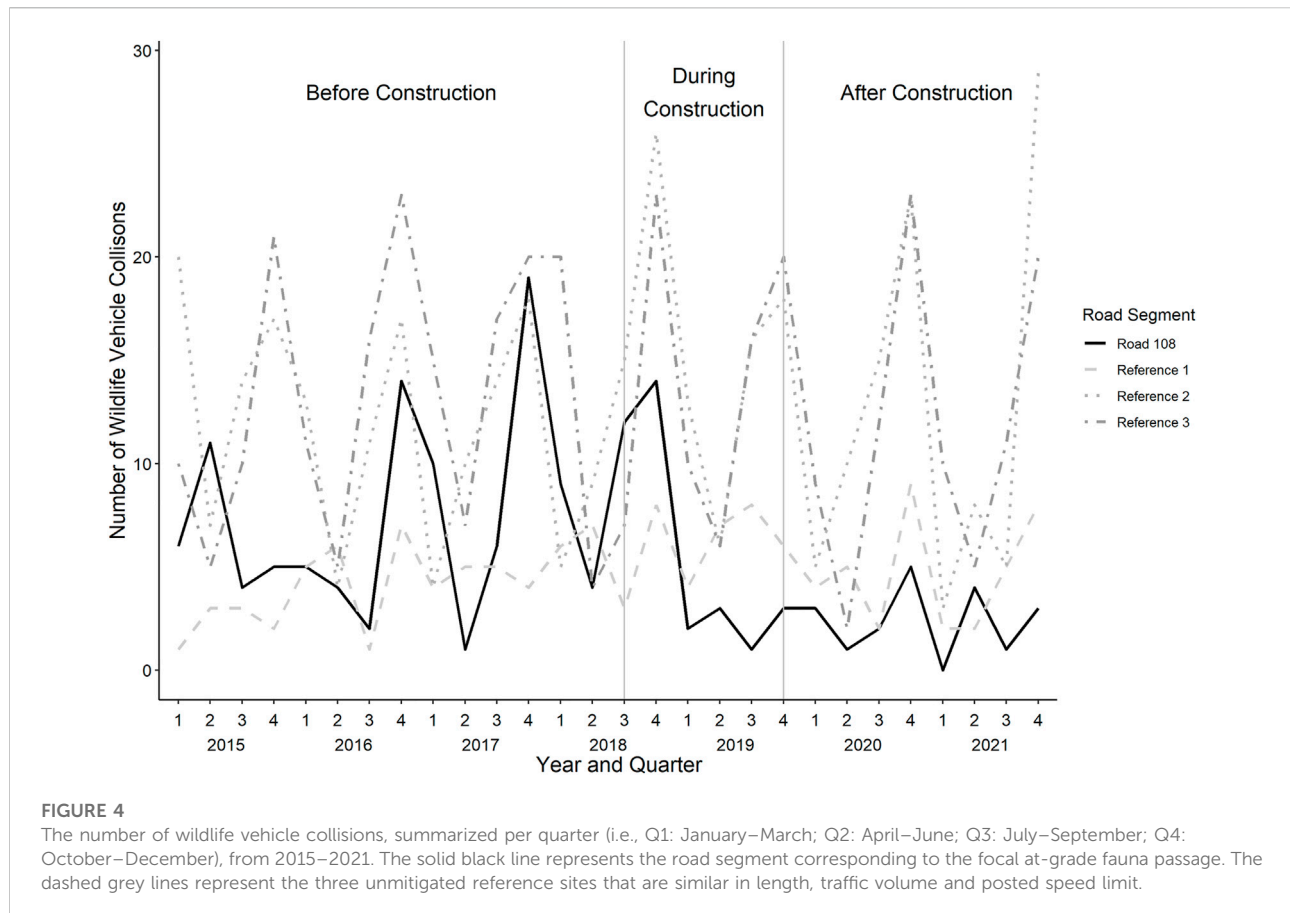


TABLE 3 Average number of WVC per annual quarter (i.e., Q1: January–March; Q2: April–June; Q3: July–September; Q4: October–December), before, during and after the construction of the focal at-grade fauna passage. WVC are summarized for the focal road segment, Road 108, as well as three unmitigated reference road segments that are similar in size, traffic volume and posted speed limit.

	Before construction	During construction	After construction
Road 108	7.1	5.8	2.4
References 1	4.2	6	4.6
References 2	11.6	15.7	12.3
References 3	13.1	13.7	11.5

We recorded more crossing events over dusk and night compared to during the day, and this may be because of a combination of species activity patterns, and reduced traffic volume/vehicle presence (Ensing et al., 2014; Ikeda et al., 2016; Gagnon et al., 2019; Knufinke et al., 2019; Mysłajek et al., 2020; Elfström, 2021; Mayer et al., 2021). Roe deer spent less time at the at-grade fauna passage during spring and summer compared to autumn. In the autumn, other foliage and food resources may be limited, and so roe deer may be spending more time browsing in the roadside verge. Red deer, on the other hand, tended to spend more time during the spring and summer than during the autumn. These results

corroborate previous findings, that show activity level and frequency of animal road visits also often varies by season, with most activity during summer and autumn (Mata et al., 2009; Grace et al., 2017; Knufinke et al., 2019; Mysłajek et al., 2020; Mayer et al., 2021). One potential reason for this increase can be mating displays. For example, ungulates often have an increased road crossing activity during the rutting period (Neumann and Ericsson, 2018; Mayer et al., 2021). Alternatively, increased human disturbance, e.g., during the hunting season typically in autumn, can also result in increased animal movement and displacement, and thus more road crossing behaviour (Mayer et al., 2021). Wild boar showed

little variability in use of the at-grade fauna passage throughout the year, and this is also similar to the findings from other studies (Elfström, 2021; Brieger et al., 2022).

4.2 Collisions

The focal road segment was one of the densest for WVCs in southern Sweden, prior to the installation of fencing in 2019 (Nordström, 2014). Through the road mitigations, including jump-outs and cattle guards in addition to fencing and the at-grade fauna passage, overall WVCs have reduced by 66% along this road. This is in line with other studies that demonstrate that fencing in addition to safe crossing opportunities can reduce WVCs from between 50%–66% (Clevenger et al., 2001; Olsson, 2007; Sullivan et al., 2004; Strein et al., 2008; Huijser et al., 2009). While it was not the direct aim of the present study, future studies should compare the effectiveness of at-grade fauna passages to under- and overpass crossing structures, in order to determine how well they perform by comparison. These studies should also expand the focus away from ungulates and identify if at-grade crossings are used by other wildlife. If they are similarly effective, and feasible (according to traffic safety, road class, speed, and AADT), the reduced costs may warrant installation of at-grade fauna passage frequently within the road network. These investigations would contribute significantly to guidelines as to when at-grade fauna passages are appropriate strategies to mitigate the impacts of roads on wildlife.

In the present study, we did not demonstrate any “fence-end effects”, such as an increased frequency of WVCs at the end of the mitigated road section (Huijser et al., 2016). At the individual level, three out of 608 (0.5%) crossing animals were involved in a WVC at the at-grade fauna passage. Previous studies have reported a quite high variation of WVCs within the at-grade fauna passage, for example, 0.26% (Strein, 2010), 0.4% (Elfström, 2022) or 5.2% (Kastdalen, 1996) of crossing animals involved in WVC. But with an individual rate of 0.5% per year, the accumulated risk during the 4 years this at-grade fauna passage was operational would amount to a 2% risk of a WVC. Thus, while this study is limited in replication, we feel confident to suggest that at-grade fauna passage may be useful to reducing WVCs. Future studies should expand this work and incorporate more sites in order to develop more definitive answers.

The impact of traffic on ungulates depends highly on the speed and traffic volume on the road, and the landscapes through which the roads cross. Roads with an AADT ranging from 500 to 10 000 have been shown to deter animals during peak traffic hours (Alexander et al., 2005; Coe et al., 2015; Riginos et al., 2018; Gagnon et al., 2019; Kušta et al., 2017). Proximity to riparian habitat, on the other hand, can make high AADT-levels tolerable for ungulates (Gagnon et al., 2007). Roads with these aforementioned AADT could possibly be crossed by animals

during the night when traffic volume is low (Gagnon et al., 2019; Kušta et al., 2017). The time between vehicles is also an important factor in the success of crossing. For example, mule deer (*Odocoileus hemionus*) were less likely to cross if the time between vehicles was shorter than 30. Only when there was 60 s or more between vehicles could mule deer cross the road safely (Riginos et al., 2018). Followers within a group of animals may accept a shorter distance between vehicles than leading animals or single individuals (Riginos et al., 2018). This may be problematic due to an increased risk of accidents. Given the influence traffic flow and speed have on the ability of ungulates to cross roads, these factors may also influence how often ungulates use an at-grade fauna passage. Thus, it is important to know what species are the target users of the at-grade fauna passage, and for future studies to investigate the effectiveness of at-grade fauna passage on roads with different traffic volumes and speeds.

4.3 Technical design considerations

One of the main limitations with at-grade fauna passage is that, by design, they provide access for animals to the roadway. If this is not carefully controlled, it is possible that wildlife will walk along the road and get trapped between the fencing, effectively rendering the fauna passage useless. In 12 of the 326 events we recorded over the year (3.7% of total events), animals walked around the fence terminus in the at-grade fauna passage, adjacent to the roadway, thus entering the fenced corridor. On all of those occasions these animals returned to the at-grade fauna passage without incident. This behaviour was primarily observed in roe deer (9 out of 12 events), that were browsing in the roadside verge, and then continued to do so in the road edge. It is important to consider vegetation in the design of the at-grade fauna passages to avoid such problems. Adding cattle guards to the edges of the crossing area may help to reduce ungulate access to the roadway, but may not necessarily work for all wildlife. Further, reducing the amount of roadside vegetation entirely may reduce browsing opportunities, thus reducing the amount of time individuals spend near the road. However, such actions should be considered on a site-by-site basis, since it can also come at a cost for other fauna, and may simply reduce how attractive the at-grade fauna passage is to wildlife to begin with. Further investigation into different vegetation and guarding schemes would help to improve the design of at-grade fauna passages.

In this study, we observed animal response to vehicles but could not observe driver reactions to wildlife or the warning signs. Detailed information of vehicle speed and time between vehicles related to the activation of RADS are missing in our database. In approximately 70% of the occasions when animals were within the at-grade fauna passage (in the road verges or on the road), there was at least one vehicle passing along the road through the fauna passage. Thus, it is imperative that drivers react to the warning sign and slowdown in order to limit the risk of WVC and allow animals pass successfully. Cars travelling at

slower speeds are more likely to avoid WVC, particularly if drivers reduce their speed to 73 km/h or lower (Gunther et al., 1998; Muurinen and Ristola, 1999; Gordon et al., 2004; Sharafsaleh et al., 2012; Grace et al., 2017; Druta and Alden, 2019; Gagnon et al., 2019; Riginos et al., 2019). However, the difficulty is understanding and controlling driving behaviour (Collinson et al., 2019; Riginos et al., 2022). While drivers tend to slow down more during the night than during the day (Murrinen and Ristola, 1998; Sharafsaleh et al., 2012), some studies have shown habituation effects of drivers to signs (e.g., Sullivan et al., 2004), while others demonstrate high reactivity throughout their entire study period (e.g., Sharafsaleh et al., 2012). To what extent a reduction of speed has on traffic safety and wildlife protection near an at-grade fauna passage remains to be determined. In addition to activation of a moose warning sign, we recommend that signs also suggest a slower speed. Furthermore, we suggest at-grade fauna passage should be coupled with speed cameras to help enforce speed reductions. Future studies should address this issue and incorporate it in the study design (see: Grace et al., 2017; Huijser et al., 2009), with traffic counters and vehicle speed monitors on the road before, within and after the at-grade fauna passage.

4.4 Recommendations and conclusion

In this study, we demonstrate the effectiveness of one at-grade fauna passage with RADS to provide safe crossing opportunities for wildlife, while, together with other measures, reducing the risk of WVCs. Typically, mitigation of WVCs are viewed from a traffic-safety perspective, rather than the wildlife perspective. As such, roads with medium to low AADT tend not to be fenced or otherwise mitigated. However, it is also apparent that WVCs are more frequent along medium and small roads. Different strategies will serve different purposes, and at-grade fauna passages can be included as another tool in the toolbox to reduce WVCs and improve landscape connectivity. On the landscape level, connectivity may be better benefited from several small crossing opportunities along the road network, rather than few, large, concentrated opportunities (Helldin 2022). Over- and underpasses will likely serve their purposes, and benefit those species that avoid roads and traffic, by providing a crossing opportunity that is separated from the flow of traffic. In areas where over- and underpasses are not possible to construct, at-grade fauna passages may provide a cost-efficient solution to improving the permeability of road networks for wildlife. The feasibility of this suggestion warrants investigation, the ultimate goal of reducing WVCs and maintain landscape connectivity for wildlife will likely be achieved through a combination of different mitigation measures. While our pilot only evaluates a single site, it does provide promising preliminary results that suggest that at-grade fauna passages can help in efforts to reduce collisions, while maintaining connectivity over medium-sized roads for large ungulates.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

MB: Statistical analysis–lead, writing–lead, editing–lead. FE: Data collection–equal contribution, statistical analysis–equal contribution, editing–equal contribution. IH: Data collection–equal contribution, statistical analysis–equal contribution, editing–equal contribution. AS: Conceptualization and design–contribution; Editing–contribution. EH: Data collection–equal contribution, statistical analysis–equal contribution, editing–equal contribution. ME: Conceptualization and design–contribution; Data collection–equal contribution, editing–equal contribution; writing–contribution. MO: Conceptualization and design–lead; Data collection–lead, writing–contribution, editing–equal contribution.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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