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Effect of conventional bridges on deer-vehicle accidents

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Abstract

This study evaluated whether the density and design of conventional bridges affected the frequency of reported deer-vehicle collisions along a given road or railroad section. I used official accident data from roads for 2008-2010 and from railways for 2001-2010, data on bridges and infrastructure together with digital topographic information, and estimates of regional abundances of moose (*Alces alces*) and roe deer (*Capreolus capreolus*) to develop generalized linear models of the parameters influencing the occurrence of deer-vehicle collisions. Among the obtained models, the most parsimonious were distinguished using the Akaike's Information Criterion. Single regressions revealed that the density of bridges was negatively related to the occurrence of accidents along railways but not on roads. Traffic volume on both the barrier infrastructure and inside the passage, as well as other bridge characteristics such as use, width, integrity type and shape had some but not consistent effect on the occurrence of wildlife-vehicle collisions. However, as expected, multiple regression analyses revealed that environmental variables were the main factors influencing the occurrence of accidents on railways and roads, with forest cover, the density of buildings, of infrastructure and other linear features such as watercourses as the most relevant parameters. I conclude that even conventional bridges, especially if widened and placed appropriately, can contribute to the safe crossing of barrier infrastructure by animals, reducing the occurrence of deer-vehicle collisions.

Key words: Conventional bridges, Deer-vehicle collisions, Fauna adaptations, Moose, Roe deer, Traffic mortality, Wildlife passages.

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Introduction

Transport infrastructure is essential for our society and its welfare, but can be harmful to wildlife. Roads and railways dissect ecosystems, interrupt habitat connectivity, fragment free-living populations destroying natural resources, and compromise wildlife and human safety (Bruinderink & Hazebroek 1996, Coffin 2007, Bissonette & Adair 2008, Beckmann et al. 2010). Factors such as the physical dimensions of infrastructure, traffic intensity, speed and noise, influence the barrier effect of infrastructure and the risk for animal-vehicle collisions (Seiler 2004, Ascensão & Mira 2005, Coffin 2007, Seiler et al. 2011).

Traffic volumes steadily rose during the past decennium, so did the number of accidents involving animals (Seiler 2004, Seiler et al. 2011, National Council on Wildlife Accidents (NCWA) unpubl. data). Official statistics of wildlife-vehicle collisions are dominated by ungulates (Seiler 2003, Jędrzejewski et al. 2009, Swedish Road Administration 2010). In particular moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are the most frequent wildlife victims on Swedish roads and railways (Sjölund et al. 2005, von Celsing 2008, Seiler et al. 2011, NCWA unpubl. data). Wildlife-vehicle collisions cause human injuries and fatalities, vehicles damages, and entail other economic costs involving extra maintenance of the infrastructure, dealing with injured or dead animals, medical assistance, traffic delays, and loss of hunting opportunities (Andersen et al. 1991, Bruinderink & Hazebroek 1996, Seiler 2003, Langbein et al. 2011).

To prevent wildlife-vehicle collisions, exclusion fencing is one of the most commonly used measures, mainly on roads and railways with higher traffic volume and speed, where collisions with wildlife entail a greater risk for human injuries (Huijser et al. 2008, Olsson & Widén 2008, Elvik et al. 2009, Jędrzejewski et al. 2009). In Sweden, great part of highways and some national roads are fenced (Olsson & Widén 2008, NCWA unpubl. data), while on railways fencing against deer is used only rarely and along some northern sections (von Celsing 2008, Seiler et al. 2011). However, fencing increases the barrier effect of roads and railways (Seiler et al. 2003, Huijser et al. 2008, Olsson et al. 2008, Helldin et al. 2010). To maintain habitat connectivity for local animal populations while preserving the safety of humans and wildlife, additional mitigation actions may become necessary (Iuell et al. 2003, Elvik et al. 2009, Jędrzejewski et al. 2009, Beckmann et al. 2010).

Crossing structures, either specifically designed for or adapted to wildlife, are used to provide a safe passage for animals across roads and railways (Clevenger et al. 2001, Iuell et al. 2003, Glista et al. 2009, Beckmann et al. 2010). There are different types of crossing structures, which can bear multiple uses or serve explicit ecological purposes: i) overpasses, such as a constructed bridge or a tunnel, and ii) underpasses, either as a larger viaduct (long bridge over e.g. a valley), or as a smaller portic bridge, or culvert (Iuell et al. 2003, Sjölund et al. 2005, Jędrzejewski et al. 2009, Beckmann et al. 2010). Culverts are generally cheap and small structures (hence not adequate for larger animals), often used for wet areas or watercourses. Underpasses can be good promoters of animal crossings since they comport natural terrain features, but can be expensive due to construction costs (Jackson 2000, Iuell et al. 2003, Glista et al. 2009). Some species, particularly ungulates, are sensitive to underpasses dimensions and shape, and tend to avoid it unless there is no other alternative way to cross the infrastructure (Seiler et al. 2003, Glista et al. 2009, Seiler & Olsson 2009). Overpasses are less confining and maintain natural conditions of light, rainfall and temperature, but can be expensive constructions and do not provide natural surfaces (Iuell et al. 2003, Glista et al. 2009, Langbein et al. 2011).

Several aspects seem to influence the use of a crossing structure by wildlife. Besides its dimensions and configuration, in particular its openness (Glista et al. 2009, Seiler & Olsson 2009), also its relative location (distance to nearest suitable habitat, distance to other crossing structures, distance to human disturbance areas), the traffic intensity both at the barrier route or within the passage, and how animals are lead to the structure (fencing, vegetation, visibility) can enhance the attractiveness of crossing structures to animals (Jackson 2000, Glista et al. 2009, Seiler & Olsson 2009). Previous studies show clear pattern in which aspects are more important on enhancing the objective of crossing structures to promote the safe crossing of the infrastructure and thus reduce the risk of occurrence of wildlife-vehicle collisions. Depending on the scale of analysis (Bissonette & Adair 2008), landscape parameters may have strong influence on the number of wildlife accidents registered, but the density of crossing structures and the design characteristics of those available structures may also have some effect. In some cases, hotspots of accidents lead to the decision of constructing fewer but larger especially designed wildlife bridges that solve the problem locally (Iuell et al. 2003, Bissonette & Adair 2008, van Langevelde et al. 2009). In other cases relevance is given to the location of the bridges and its relation with adjacent habitats, suggesting that in areas with higher risk of occurrence of accidents should exist multiple, even if smaller, passages (Olsson et al. 2008, Corlatti et al. 2009, Clevenger & Huijser 2011, Langbein et al. 2011). Therefore, some authors defend that conventional bridges, if adequately placed and object of minor adaptations to increase their attractiveness for wildlife, can contribute to a minimum connectivity between both sides of the infrastructure, serving as safe passage for animals and thus having beneficial effects on traffic safety, as fewer animals may get exposed to traffic (Rodriguez et al. 1996, Clevenger et al. 2001, Sjölund et al. 2005, Seiler & Olsson 2009).

The aim of this study is thus to evaluate:

- if the **density** of conventional bridges in a road or railway section has any effect on the number of accidents occurring in that section;
- if the **design characteristics** of a given bridge affect the number of accidents occurring in its surroundings.

The decision on whether a bridge is adequately designed or several bridges are distributed properly in a certain area, depends on the species in focus (Iuell et al. 2003, Bissonette & Adair 2008, Seiler & Olsson 2009, Helldin et al. 2010). This study focuses on moose and roe deer, which, besides their frequent involvement in wildlife-vehicle collisions, are spread almost all over Sweden (Helldin et al. 2010).

Materials and methods

Selected infrastructure

I focused my study on the following transport corridors (Figure 1):

- Highways E4, E6, E18, E20, E22, and the most southern part of E45, are roads in long parts fenced against wildlife, and most road crossings are not at-grade, i.e. smaller roads or railways pass over or under these highways.
- Railway lines (in Swedish: stråk) 1, 3, 5, 16, 17, 73, 75, 83, most part of lines 2 and 84, and a small part of lines 9, 14 and 15, were also among the most trafficked infrastructure in Sweden. In contrast to the highways, most railway lines are not fenced.

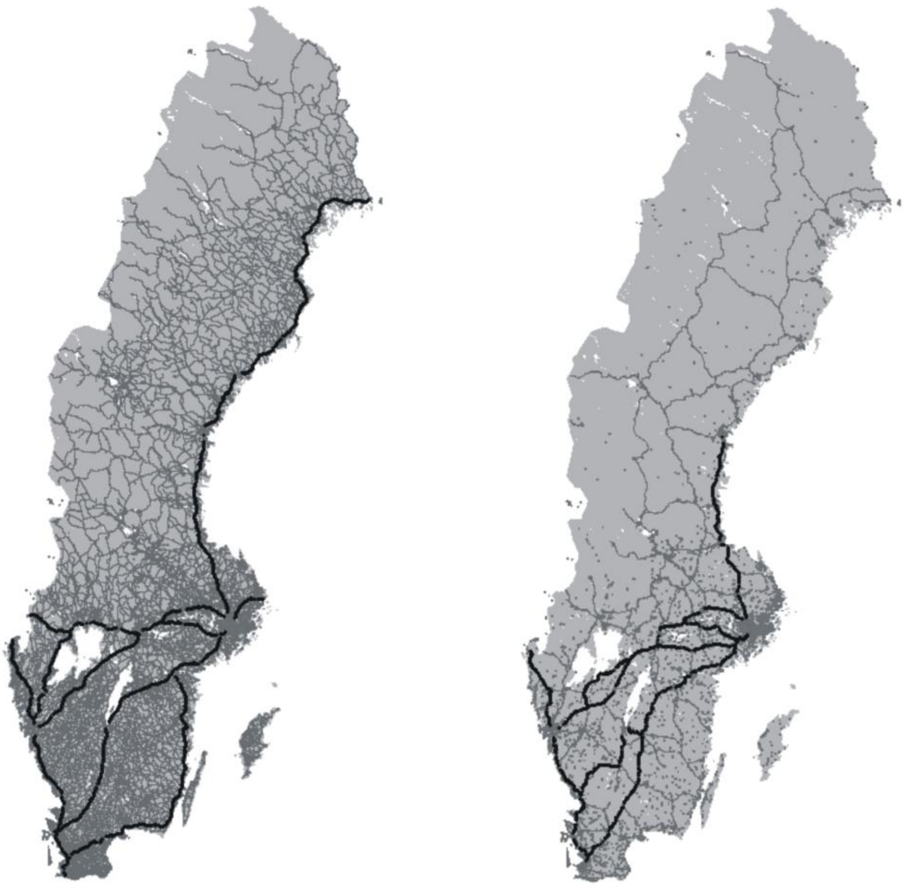

Figure 1. Selected (black) roads (left) and railways (right) studied in this project (Data source: Swedish Transport Administration).

From the chosen roads and railways, segments closer than 500 m to an urban area (as defined on topographical maps) were excluded.

Data on roads and railways were provided by the Swedish Transport Administration (STA).

In order to quantify the density of accidents and bridges along the selected infrastructure, I created road and railway sections based on the line-segment structure in the digital maps, according to common road or railway line number, and traffic volume. I obtained 468 road sections with average length of 8.180 km, and 173 railway sections with average length of 12.405 km.

Wildlife-vehicle collisions

The Swedish National Police Board (in Swedish: Rikspolisstyrelsen) provided data of wildlife-vehicle collisions on roads (HOBBIT database) registered between 2008-01-01 and 2011-06-30. The original data, which included 128861 accidents registered with moose and roe deer on all Swedish roads during the above period, required considerable cleaning and spatial adjustment. From it, I obtained 3682 accidents occurred during 2008-2010 on the roads chosen for this study, including 618 with moose and 3064 with roe deer (Table 1).

Table 1. Number of road accidents, per year, considered for this study, involving moose and roe deer, occurred between 2008-01-01 and 2010-12-31 (NCWA unpubl. data).

Year	Moose	Roe deer
2008	198	907
2009	185	997
2010	235	1160

Data on wildlife-vehicle collisions on railways covers the period 2001-2010 and was provided by Andreas Seiler (Seiler et al. 2011). It is based on incident reports made by train drivers and registered at the STA (OFELIA database). In contrast to the police reports from roads, this data is not spatially explicit but provides merely the frequency of observed collisions along a given track (accidents per km). To obtain a comparable picture on railways as on roads, with absolute numbers of accidents, I multiplied the total length of the lines chosen for this study by the frequency of accidents per year, and obtained a total of 4188 railway accidents, 1656 involving moose and 2532 with roe deer (Table 2).

Table 2. Number of train collisions with moose and roe deer registered on the study railways between 2001-01-01 and 2010-12-31 (Seiler et al. 2011, STA unpubl. data).

Year	Moose	Roe deer
2001	144	188
2002	151	227
2003	134	227
2004	137	252
2005	100	226
2006	147	256
2007	134	215
2008	173	263
2009	224	309
2010	312	369

Bridges

Data about bridges was obtained mostly from BaTMan (*Bro och Tunnel Management (http://batman.vv.se*), the bridge database of the STA. *Bridges* denote here all grate-separated crossing constructions larger than 2 m in width (i.e. bridges, tunnels and culverts). I used ground and aerial photos, as well as technical drawings, to register physical characteristics of the bridges. Some details had to be confirmed through field visits. In total, 1798 structures on roads and 680 on railways were described by the following parameters:

- National identification number, Knr;
- Number of the road/rail line the bridge crosses;
- Year of construction (or at least, when the last construction changes occurred);
- Main use of the passage: pedestrian or bicycle path, railway, road, watercourse, or terrestrial habitat (“field”);
- Type: overpass or underpass;
- Shape of the passage opening: arc, square, or irregular-ground (“trapezoid”);
- Passage dimensions (as viewed from the animals’ perspective): width, height (on underpasses only), length, openness index (passage entrance area / length);
- Passage integrity type: single or double passage (for underpasses);
- Presence of water, independently of the main use;
- Effective width of passage, i.e. width usable by terrestrial animals excluding water/wet parts and areas with a transversal slope greater than 1:2;
- Vegetation cover at the entrance of the passage: no vegetation (“n”), some vegetation but “hiding” only partially the passage structure (“p”), or vegetation covering walls of passage (“y”); vegetation can provide shelter for the animal when inspecting the passage (Iuell et al. 2003);
- Traffic volume within the passage, if a public road or railway track passing through it;
- Road, rail and traffic characteristics of the infrastructure barrier (occurrence of exclusion fencing, central barriers, traffic volume), obtained from the roads and railways databases (Data source: STA).

Only 3.1% of the road bridges studied were built in 2008-2010 (period of road accidents data used in this study), and also 3.1% of the railway bridges were built 2001-2010 (period of railway accidents data used in this study), and these newer bridges are located all over the infrastructure chosen for this study and not concentrated in certain specific locations. Therefore, I decided, for the further analysis, not to make any distinct analysis per year, and thus to consider all bridges together and relate them with the average number of yearly accidents registered.

Other GIS data

I used hunting statistics on roe deer and moose, from 2006-2007 (Kindberg et al. 2008), as a proxy for the relative abundance of these species near the selected infrastructure sections and bridges. Three levels of abundance were established (Table 3).

Table 3. Levels of abundance of moose and roe deer, based on hunting statistics (animals killed per 1000 ha) from 2006-2007 (Kindberg et al. 2008).

Level	Moose	Roe deer
low	0.6 - 1.4	< 5
medium	1.5 - 2.4	5 - 10
high	2.5 - 3.9	> 10

Around each road and railway section, and around each bridge, I quantified environmental parameters within a distance of 1 km and 4 km. The geographical data (land cover, topography, watercourses, private roads, etc.) used for this calculations were provided by the Swedish Land Survey. The distances of 1 and 4 km were chosen based on the square root of the average home range size which is used as a measure of movement distance (Bowman et al. 2002, Bissonette & Adair 2008, Huijser et al. 2008), so 1 km applies for roe deer's typical range of movements and 4 km for moose (Cederlund & Sand 1994, Cederlund & Liberg 1995, Kjellander et al. 2004, Jędrzejewski et al. 2009).

The environmental parameters quantified included: the area of different land uses (forest, open land — includes agriculture fields —, urban area, water area); the length of public and private roads, paths, railways, and watercourses; the number of crossings between watercourses and the road or railway section on focus; the number of buildings. The distances to each land use and to the nearest building were also calculated for bridges. These parameters are described in the Tables 4 and 5.

Table 4. Parameters measured for road and railway sections. Environmental variables were quantified within a distance of 4 km (for moose) and 1 km (for roe deer) from the respective infrastructure section, i.e. the section's buffer zone; for further description see text.

Variable	Description
AccidMKm / AccidRKm	Average number of accidents involving moose / roe deer, per km, per year, during the period 2001-2010 (for railways) or 2008-2010 (for roads)
ADT	Average daily traffic (vehicles/day on roads, or trains/day on railways)
BridgesKm	Number of bridges per km
BridgesMKm	Number of bridges adequate for moose, per km
BridgesRKm	Number of bridges adequate for roe deer, per km
BuildBuff	Number of buildings inside the section's buffer zone (buildings/km^2)
FenceKm	Proportion of the road section where there is exclusion fencing
ForestBuff	Proportion of the section's buffer zone occupied by forest
MedBarrKm	Proportion of the road section where there is median barrier
MooseAbu / RoedeerAbu	Level of abundance of moose / roe deer at the location of the section ("low"/"medium"/"high")
OpenBuff	Proportion of the section's buffer zone occupied by open land
PathsBuff	Total length of paths (bicycle, walk) inside the section's buffer zone (km/km^2)
PrivRdsBuf	Total length of private roads inside the section's buffer zone (km/km^2)
PublRdsBuf	Total length of public roads inside the section's buffer zone (km/km^2)
RailwayBuf	Total length of railways inside the section's buffer zone (km/km^2)
UrbanBuff	Proportion of the section's buffer zone occupied by urban area
WatCourBuf	Total length of watercourses inside the section's buffer zone (km/km^2)
WaterBuff	Proportion of the section's buffer zone occupied by water area
WaterCross	Number of water crossings along the section (watercrossings/km)

Table 5. Parameters measured for road and railway bridges. Environmental variables were quantified within a distance of 4 km (for moose) and 1 km (for roe deer) from the respective bridge, i.e. the bridge's buffer zone; for further description see text.

Variable	Description
AccidMBuff / AccidRBuff	Average number of accidents involving moose / roe deer, in the bridge's buffer zone, per year during the period 2008-2010 (for roads)
AccMKmBuff / AccidRKmBuff	Average number of accidents involving moose / roe deer, per km of bridge's buffer zone, per year during the period 2001-2010 (for railways)
ADTins	Average daily traffic within the bridge (vehicles/day, or trains/day)
ADTout	Average daily traffic at the main road/railway (vehicles/day, or trains/day)
BridgesBuf	Number of bridges inside the bridge's buffer zone
BridgMBuff / BridgRBuff	Number of bridges adequate for moose / roe deer, inside the bridge's buffer zone
BuildBuff	Number of buildings inside the bridge's buffer zone
DistBridge	Distance to the nearest bridge (km)
DistBridgM / DistBridgR	Distance to the nearest bridge adequate for moose / roe deer (km)
DistBuild	Distance to the nearest building (km)
DistForest	Distance to the nearest forest (km)
DistOpen	Distance to the nearest open land (km)
DistUrban	Distance to the nearest urban area (km)
DistWater	Distance to the nearest water area (km)
Fence	Existence of exclusion fencing at the location of the bridge ("y"/"n"); on roads
ForestBuff	Area of the bridge's buffer zone occupied by forest (km^2)
Height	Height of the bridge (m); for underpasses
Length	Length of the bridge (m)
MedianBarr	Existence of median barrier at the location of the bridge ("y"/"n"); on roads
MooseAbu / RoedeerAbu	Level of abundance of moose / roe deer at the location of the bridge ("low"/"medium"/"high")
OpenBuff	Area of the bridge's buffer zone occupied by open land (km^2)
OpnsIndx	Openness index of the bridge (entrance area / length)
PathsBuff	Total length of paths (bicycle, walk) inside the bridge's buffer zone (km)
PrivRdsBuf	Total length of private roads inside the section's buffer zone (km)
PublRdsBuf	Total length of public roads inside the bridge's buffer zone (km)
RailwayBuf	Total length of railways inside the bridge's buffer zone (km)
Shape	General shape of the bridge transversal section ("a"/"s"/"t"); for underpasses
IntegrType	Bridge integrity type ("s"/"d"); for underpasses
UrbanBuff	Area of the bridge's buffer zone occupied by urban area (km^2)
UsableWd	Proportion of the width of the bridge assumed to be usable by moose or roe deer
Use	Main use of the bridge ("field"/"path"/"railway"/"road"/" water")
VegetEntra	Existence of vegetation at the entrance of the bridge ("n"/"p"/"y")
Water	Existence of water within the bridge ("y"/"n"); for underpasses
WaterBuff	Area of the bridge's buffer zone occupied by water area (km^2)
WatCourBuf	Total length of watercourses inside the bridge's buffer zone (km)
WatCrosBuf	Number of water crossings inside the bridge's buffer zone
Width	Total width of the bridge (m)

To classify a bridge as adequate for the use by moose and roe deer, the parameters "width", "height", "length" and "openness index" are taken into account (Seiler & Olsson 2009) on underpasses. On overpasses only "width" is usually referred in the literature (Iuell et al. 2003, Jędrzejewski et al. 2009) as relevant parameter, so here I used the same minimum values as on underpasses (Table 6).

Table 6. Minimum width, height and openness index, and maximum length, for an overpass or underpass to be considered adequate for use by moose and roe deer (Seiler & Olsson 2009).

Parameter	Overpass		Underpass	
	Moose	Roe deer	Moose	Roe deer
Width (m)	11.0	7.0	11.0	7.0
Height (m)	NA	NA	4.5	4.5
Length (m)	---	---	22.0	23.0
Openness index	NA	NA	2.3	1.4

Statistics

All the data presented above was organized in 12 databases, 6 for each species: railway sections, road sections, railway overpasses and underpasses, and road overpasses and underpasses. I used the software StatSoft® STATISTICA 10, to detect outliers and discrepant data and eliminated it from the further analysis. The final databases used for model construction and following analyses contained the sample sizes indicated in Table 7.

Table 7. Number of sections, overpasses and underpasses considered for the analysis of the effect of all independent variables on the frequency of accidents with moose and roe deer registered on railways and roads.

	Sections		Overpasses		Underpasses	
	Railways	Roads	Railways	Roads	Railways	Roads
Moose	149	396	158	259	294	864
Roe deer	148	393	151	262	284	809

I used cross-correlations between all variables, in order to detect those that were highly correlated ($r \geq 0.70$; Pestana & Velosa 2002), and thus should not be included together in the same model to avoid multicollinearity. I used the Akaike's Information Criterion (AIC) to identify those variable subsets that produced the most parsimonious model (Crawley 2005). Among all models with $\Delta AIC < 2$ from the smallest AIC value, I chose the model with smallest number of variables, and that best matched the focus of the study, including variables related to bridges density or design (which I call "relevant variables") that are shown to have significant effect on the dependent variable, the frequency of registered accidents.

In the following, I only discuss the selected favourite models. All remaining candidate models are given in the Appendix.

I performed the favourite model (for each of the 12 databases mentioned above), under the option Generalized Linear Models (GLZ), where the frequency of accidents is the dependent variable, and both categorical and continuous independent variables are included.

As a complementary analysis, I used single regression analyses and one-way ANOVAs between the frequency of registered accidents and the continuous or categorical variables, to reveal significant individual effects which might not be evident in the multiple GLZ approach.

Results

Sections analyses

Bridge density significantly reduced the frequency of moose (N = 149) and roe deer (N = 148) accidents registered on railways ($p < 0.0001$, $F > 21.304$, $R^2_{Adj} > 0.121$). Limiting the density of bridges to only those with species-adequate design, it did not produce better results ($p < 0.0001$, $F > 15.176$, $R^2_{Adj} > 0.088$). On roads, bridge density was similarly effective in moose ($p < 0.001$, $F = 6.894$, $N = 396$, $R^2_{Adj} = 0.0147$), but not in roe deer ($p = 0.235$).

The frequency of moose-train accidents decreased with the density of public roads, and increased with the density of forest and watercourses. The frequency of roe deer accidents decreased with the density of railways, and was lower in areas with low roe deer abundance, while it was higher where watercourses were frequent and roe deer abundant (Table 8). The single regression analysis showed that railway sections in areas with lower moose abundance had lower frequency of accidents involving this species ($p = 0.0008$, $F = 7.434$, $N_{param} = 2$, $N = 149$, $SS = 0.120$). The frequency of moose-train collisions also decreased with the density of railways ($p = 0.0090$, $F = 7.008$, $N = 149$, $R^2_{Adj} = 0.0390$), while the frequency of accidents with roe deer also decreased with the density of public roads ($p = 0.0254$, $F = 5.097$, $N = 148$, $R^2_{Adj} = 0.0271$). The density of water crossings also had significant effect on the frequency of moose-train collisions ($p = 0.0117$, $F = 6.525$, $N = 149$, $R^2_{Adj} = 0.0360$), but not in roe deer ($p = 0.8303$), (Table 8).

Table 8. Generalized Linear Models of the frequency of collisions with moose and roe deer on railway sections. Significant results are shown in bold.

	Parameter	Eff.Level	Estimate	Std. Error	Wald Stat.	Low.CL95%	Upp.CL95%	p
Moose	Intercept	-----	0.113	0.0528	4.55	0.0091	0.216	0.0330
	ForestBuff	**-----**	**0.107**	**0.0484**	**4.93**	**0.0126**	**0.202**	**0.0264**
	PublRdsBuf	**-----**	**-0.0585**	**0.0206**	**8.10**	**-0.0989**	**-0.0182**	**0.0044**
	WatCourBuf	**-----**	**0.0580**	**0.0229**	**6.41**	**0.0131**	**0.103**	**0.0114**
	BridgesKm	**-----**	**-0.0500**	**0.0241**	**4.31**	**-0.0973**	**-0.0028**	**0.0378**
	Scale	-----	0.0751	0.0043	-----	0.0670	0.0841	-----
Roe deer	Intercept	-----	0.541	0.107	25.6	0.331	0.750	<0.0001
	BridgesKm	**-----**	**-0.146**	**0.0321**	**20.8**	**-0.209**	**-0.0834**	**<0.0001**
	RailwayBuf	**-----**	**-0.743**	**0.184**	**16.3**	**-1.10**	**-0.382**	**<0.0001**
	WatCourBuf	**-----**	**0.0767**	**0.0243**	**9.96**	**0.0291**	**0.124**	**0.0016**
	RoedeerAbu	**high**	**0.0428**	**0.0154**	**7.76**	**0.0127**	**0.0728**	**0.0053**
	RoedeerAbu	**low**	**-0.0846**	**0.0157**	**29.1**	**-0.115**	**-0.0539**	**<0.0001**
	Scale	-----	0.104	0.0061	-----	0.0930	0.117	-----

On road sections, the frequency of moose-vehicle accidents decreased with traffic volume and fencing (proportion of road fenced) (Table 9). Similar pattern was evident for roe deer: the frequency of roe deer accidents was lower in fenced sections and where roe deer abundance was lower, while it increased with the density of buildings. The single regression analyses showed that traffic volume was significantly related with an increase in the frequency of roe deer accidents ($p = 0.0005$, $F = 12.444$, $N = 393$, $R^2_{Adj} = 0.0284$). However, moose abundance had no significant effect on the frequency of road accidents with this species ($p = 0.0730$).

Table 9. Generalized Linear Models of the frequency of collisions with moose and roe deer on road sections. Significant results are shown in bold.

	Parameter	Eff.Level	Estimate	Std. Error	Wald Stat.	Low.CL95%	Upp.CL95%	p
Moose	Intercept	-----	0.109	0.0102	114	0.0890	0.129	<0.0001
	ADT	**-----**	**-0.000002**	**0.000001**	**7.72**	**-0.000003**	**-0.000001**	**0.0055**
	FenceKm	**-----**	**-0.0452**	**0.0113**	**16.1**	**-0.0673**	**-0.0232**	**<0.0001**
	Scale	-----	0.0939	0.0033	-----	0.0876	0.101	-----
Roe deer	Intercept	-----	0.354	0.0498	50.4	0.256	0.451	<0.0001
	FenceKm	**-----**	**-0.200**	**0.0512**	**15.3**	**-0.300**	**-0.0996**	**<0.0001**
	ADT	-----	0.000006	0.000004	3.25	-0.000001	0.00001	0.0712
	BuildBuff	**-----**	**0.653**	**0.297**	**4.83**	**0.0708**	**1.24**	**0.0279**
	RoedeerAbu	high	-0.0023	0.0385	0.0035	-0.0777	0.0731	0.9530
	RoedeerAbu	**low**	**-0.0817**	**0.0333**	**6.04**	**-0.147**	**-0.0165**	**0.0140**
	Scale	-----	0.414	0.0147	-----	0.386	0.444	-----

Passages analyses

Overpasses

The various design measures I tested produced a complex and not always consistent pattern. The main category of use of a passage was the only variable related to the structural characteristics of bridges that was significant related with accident frequencies. The number of road accidents with roe deer was higher near overpasses categorized as “path” than compare to overpasses build for public roads or railways ($p = 0.007$, $F = 5.061$, $N_{param} = 2$, $N = 262$, $SS = 14.979$). Variables related with distance to and density of alternative bridges, particularly species-adequate bridges, also obtained significant results for overpasses: the frequency of moose-train collisions near passages decreased with density ($p < 0.0001$, $F = 23.443$, $N = 158$, $R^2_{Adj} = 0.125$) and proximity ($p = 0.0002$, $F = 14.480$, $N = 158$, $R^2_{Adj} = 0.0790$) of moose-adequate bridges in their surroundings. A similar effect of proximity of railway bridges was found in roe deer ($p = 0.0053$, $F = 8.026$, $N = 151$, $R^2_{Adj} = 0.0447$). However, no effect was obtained for bridge density near road overpasses ($0.0645 < p < 0.5829$).

Multiple regression analyses also point at the effect of the density of species-adequate bridges, but showed also that environmental variables, such as the proportion of forest cover (in moose) or the density of public roads (in roe deer) near the passage affected the frequency of accidents on railways (Table 10). Single regressions analysis showed that the frequency of moose-train collisions also decreased with the density of public roads ($p < 0.0001$, $F = 28.836$, $N = 158$, $R^2_{Adj} = 0.151$), while the proportion of forest cover had no effect on the frequency of roe deer accidents ($p = 0.7001$).

The number of roe deer accidents near road overpasses increased with traffic volume both outside and inside the passage, as well as with the density public roads and the number of buildings in the vicinity (Table 11). Similarly, the frequency of moose accidents increased with the traffic volume inside the passage (but not outside), as well as with the density of paths, and the vicinity to water areas. Significantly fewer accidents occurred along fenced roads compared to unfenced roads (moose: $p = 0.0013$, $F = 10.566$, $N_{param} = 1$, $N = 259$, $SS = 1.655$; roe deer: $p < 0.0001$, $F = 37.586$, $N_{param} = 1$, $N = 262$, $SS = 50.298$).

Table 10. Generalized Linear Models of the frequency of collisions with moose and roe deer within a distance of 4 km and 1 km, respectively, from railway overpasses. Significant results are shown in bold.

	Parameter	Eff.Level	Estimate	Std. Error	Wald Stat.	Low.CL95%	Upp.CL95%	p
Moose	Intercept	-----	-0.0076	0.0167	0.208	-0.0403	0.0251	0.6481
	BridgMBuff	**-----**	**-0.0177**	**0.0040**	**19.7**	**-0.0256**	**-0.0099**	**<0.0001**
	ForestBuff	**-----**	**0.0043**	**0.0006**	**51.2**	**0.0031**	**0.0055**	**<0.0001**
	Scale	-----	0.0675	0.0038	-----	0.0604	0.0753	-----
Roe deer	Intercept	-----	0.191	0.0273	49.1	0.138	0.244	<0.0001
	DistBridgR	**-----**	**0.0040**	**0.0016**	**6.06**	**0.0008**	**0.0071**	**0.0139**
	PublRdsBuf	**-----**	**-0.0119**	**0.0035**	**12.0**	**-0.0187**	**-0.0052**	**0.0005**
	Scale	-----	0.0992	0.0057	-----	0.0886	0.111	-----

Table 11. Generalized Linear Models of the number of collisions with moose and roe deer within a distance of 4 km and 1 km, respectively, from road overpasses. Significant results are shown in bold.

	Parameter	Eff.Level	Estimate	Std. Error	Wald Stat.	Low.CL95%	Upp.CL95%	p
Moose	Intercept	-----	0.267	0.0595	20.2	0.151	0.384	<0.0001
	Width	-----	-0.0020	0.0019	1.09	-0.0056	0.0017	0.2957
	ADTins	**-----**	**0.00004**	**0.00001**	**8.22**	**0.00001**	**0.00006**	**0.0041**
	PathsBuff	**-----**	**0.0073**	**0.0031**	**5.42**	**0.0012**	**0.0135**	**0.0199**
	DistWater	**-----**	**-0.0720**	**0.0298**	**5.83**	**-0.130**	**-0.0136**	**0.0157**
	Scale	-----	0.386	0.0169	-----	0.354	0.420	-----
Roe deer	Intercept	-----	-0.0159	0.362	0.0019	-0.725	0.694	0.9650
	ADTins	**-----**	**0.0001**	**0.00005**	**10.9**	**0.00006**	**0.0002**	**0.0009**
	ADTout	**-----**	**0.00002**	**0.000009**	**5.38**	**0.000003**	**0.00004**	**0.0204**
	PublRdsBuf	**-----**	**0.0703**	**0.0314**	**5.00**	**0.0087**	**0.132**	**0.0253**
	BuildBuff	**-----**	**0.471**	**0.120**	**15.3**	**0.235**	**0.707**	**<0.0001**
	Use	road	-0.216	0.225	0.918	-0.657	0.226	0.3380
	Use	**path**	**0.696**	**0.295**	**5.55**	**0.117**	**1.27**	**0.0185**
	Fence	yes	-0.290	0.219	1.75	-0.721	0.140	0.1856
	Scale	-----	1.01	0.0442	-----	0.929	1.10	-----

Underpasses

Several variables related to design characteristics obtained significant results in underpasses, but also here, the pattern was not consistent over all databases and either of the variables explained a very small proportion of the observed variation in accident frequencies. The frequency of moose accidents registered near railway underpasses decreased with the width of the underpass ($p = 0.0023$, $F = 9.465$, $N = 294$, $R^2_{Adj} = 0.0281$), but no effect was obtained in roe deer or for road underpasses ($p > 0.1698$). Railway accidents with moose ($N = 294$) and roe deer ($N = 284$) were less frequent near underpasses of a greater height ($p < 0.0391$, $F > 4.295$, $R^2_{Adj} > 0.0115$). However, on roads, the opposite effect was found in moose ($p = 0.0132$, $F = 6.163$, $N = 864$, $R^2_{Adj} = 0.0059$), while no effect was obtained for roe deer. Consequently, accidents with moose were also less frequent near railway underpasses with higher openness index ($p = 0.0127$, $F = 6.287$, $N = 294$, $R^2_{Adj} = 0.0177$), but opposite result was obtained for road underpasses ($p = 0.0049$, $F = 7.944$, $N = 864$, $R^2_{Adj} = 0.0080$), while roe deer accidents were not affected by the openness index ($p > 0.6535$). The frequency of moose accidents was also lower near double-underpasses than near single-underpasses (railways: $p = 0.0235$, $F = 5.184$, $N_{param} = 1$, $N = 294$, $SS = 0.0432$; roads ($p < 0.0001$, $F = 30.669$, $N_{param} = 1$, $N = 864$, $SS = 8.528$), while no effect of the passage integrity type was found on roe deer accidents ($p > 0.1198$). Irregular-ground ("trapezoid"-shaped) passages were associated with fewer moose-train collisions compared to arc-shaped passages ($p = 0.0030$, $F = 5.923$, $N_{param} = 2$, $N = 294$, $SS = 0.0968$). But the shape of the passage opening did not affect the frequency of train-roe deer accidents and the frequency of accidents on roads ($p > 0.1554$). Near railway underpasses the frequency of accidents with roe deer increased when there was a watercourse within the passage ($p = 0.0122$, $F = 6.365$, $N_{param} = 1$, $N = 284$, $SS = 0.106$). Similar effect was found for moose accidents near road underpasses ($p = 0.0382$, $F = 4.309$, $N_{param} = 1$, $N = 864$, $SS = 1.235$), while no effect was obtained for moose collisions on railways and roe deer accidents on roads ($p > 0.4592$). The frequency of moose-train collisions ($N = 294$) decreased with the density of ($p < 0.0001$, $F = 21.659$, $R^2_{Adj} = 0.0659$) and the proximity to bridges adequate for moose ($p = 0.0005$, $F = 12.478$, $R^2_{Adj} = 0.0377$). No effect of bridge density was obtained for roe deer accidents or for road underpasses ($0.0680 < p < 0.9273$).

Moose accidents near railway underpasses were more frequent where the proportion of forest cover and density of watercourses was highest, while roe deer accidents were less frequent where the proportion of open areas was highest and roe deer were less abundant (Table 12). Similarly, single regression analysis also showed that moose accidents near railway underpasses ($N = 294$) were less frequent in areas with lower moose abundance ($p < 0.0001$, $F = 38.280$, $N_{param} = 2$, $SS = 0.515$).

Table 12. Generalized Linear Models of the frequency of collisions with moose and roe deer within a distance of 4 km and 1 km, respectively, from railway underpasses. Significant results are shown in bold.

	Parameter	Eff.Level	Estimate	Std. Error	Wald Stat.	Low.CL95%	Upp.CL95%	p
Moose	Intercept	-----	-0.0628	0.0204	9.51	-0.103	-0.0229	0.0020
	ForestBuff	**-----**	**0.0028**	**0.0005**	**26.5**	**0.0017**	**0.0039**	**<0.0001**
	WatCourBuf	**-----**	**0.0010**	**0.0003**	**12.9**	**0.0005**	**0.0016**	**0.0003**
	IntegrType	**double**	**-0.0338**	**0.0158**	**4.57**	**-0.0648**	**-0.0028**	**0.0325**
	MooseAbu	high	0.0285	0.0200	2.03	-0.0107	0.0677	0.154
	MooseAbu	low	0.0020	0.0268	0.0059	-0.0504	0.0545	0.939
	Scale	-----	0.0726	0.0030	-----	0.0670	0.0787	-----
Roe deer	Intercept	-----	0.197	0.0201	96.5	0.158	0.236	<0.0001
	OpenBuff	**-----**	**-0.0336**	**0.0086**	**15.3**	**-0.0505**	**-0.0168**	**<0.0001**
	Shape	trapezoid	-0.0116	0.0169	0.473	-0.0448	0.0215	0.4915
	Shape	arc	0.0141	0.0241	0.341	-0.0332	0.0613	0.5592
	Water	**yes**	**0.0386**	**0.0143**	**7.27**	**0.0105**	**0.0667**	**0.0070**
	RoedeerAbu	high	0.0365	0.0258	2.00	-0.0140	0.0870	0.1570
	RoedeerAbu	**low**	**-0.0571**	**0.0240**	**5.67**	**-0.104**	**-0.0101**	**0.0172**
	Scale	-----	0.118	0.0049	-----	0.109	0.128	-----

The number of moose-vehicle collisions decreased with the proportion of open areas and with fencing (Table 13). Road fencing had also significant effect on the reduction of the frequency of roe deer accidents, which increased with the density of buildings in the surrounding of the underpasses. The single regression analysis showed that moose accidents were more frequent in areas with higher density of paths ($p < 0.0001$, $F = 16.527$, $N = 864$, $R^2_{Adj} = 0.0177$). The number of roe deer accidents was not affected neither by the density of paths ($p = 0.1082$) nor the proportion of open areas ($p = 0.1818$).

Table 13. Generalized Linear Models of the number of collisions with moose and roe deer within a distance of 4 km and 1 km, respectively, from road underpasses. Significant results are shown in bold.

	Parameter	Eff.Level	Estimate	Std. Error	Wald Stat.	Low.CL95%	Upp.CL95%	p
Moose	Intercept	-----	0.461	0.0401	132	0.383	0.540	<0.0001
	OpenBuff	**-----**	**-0.0060**	**0.0018**	**10.7**	**-0.0096**	**-0.0024**	**0.0011**
	IntegrType	**double**	**-0.108**	**0.0192**	**31.4**	**-0.146**	**-0.0702**	**<0.0001**
	Fence	**yes**	**-0.0764**	**0.0191**	**15.9**	**-0.114**	**-0.0389**	**<0.0001**
	Scale	-----	0.514	0.0124	-----	0.491	0.539	-----
Roe deer	Intercept	-----	0.512	0.0367	194	0.440	0.584	<0.0001
	BuildBuff	**-----**	**0.341**	**0.0864**	**15.6**	**0.172**	**0.510**	**<0.0001**
	Fence	**yes**	**-0.0957**	**0.0358**	**7.16**	**-0.166**	**-0.0256**	**0.0075**
	Scale	-----	0.966	0.0240	-----	0.920	1.0140	-----

Discussion

I found that the density of conventional bridges along a given road or railway section in fact reduced the frequency of collisions with moose and roe deer. This is in congruence with other studies (Ascensão & Mira 2005, Olsson et al. 2008, Corlatti et al. 2009, Langbein et al. 2011) and suggests that the mere presence of a passage, even if not particularly adapted to wildlife, can contribute to mitigate ungulate-vehicle collisions.

This effect, however, was found more consistently on railways than on roads, and contrasts the report of Seiler et al. (2011), who showed that hotspots in deer-train collisions were distinguished from coldspots by a higher number of bridges. Seiler et al (2011) argued that inappropriate bridge dimensions but also the lack of fences could provoke animals to cross over the railway instead of using the safer passage. I conclude that bridge design characteristics (within the available ranges) seem to be of minor importance, but that fencing may be responsible for the observed difference between road and railway models. As described in other studies (Olsson & Widén 2008, Helldin et al. 2010), significantly fewer accidents with both moose and roe deer occurred on fenced sections than on unfenced roads. To differentiate the influence of fencing on the beneficial effect of bridge density, future studies should compare certain fenced and non-fenced sections of roads and railways, with and without bridges.

In moose, bridge density near passages did affect accident frequencies on railways, but not on roads. In roe deer, the effect was visible only near overpasses but not near underpasses. This may lend support to the findings of Olbrich (1984), who argued that roe deer avoided using overpasses, i.e. if they find other alternatives near an overpass to cross an infrastructure they choose this alternative or else they would rather try to cross the infrastructure despite the risk for accidents.

The frequency of accidents with roe deer near a road overpass increased when the overpass was mainly used for paths. Larger wildlife may sometimes use human paths or minor roads and it can hence be expected that also bridges for such paths may serve wildlife (Grilo et al. 2008, Corlatti et al. 2009) and in consequence decrease the risk for accidents in its surrounding. However, the overpasses mainly used for paths generally had, in this study, a small ratio of width to length, with average width of 4 m (between 2.5 and 6 m), and average length of 65 m (between 38 and 99 m). This is far below the recommendations for an appropriate use by ungulates, which suggest minimum width of 7 m for roe deer (particularly sensitive to overpasses; Olbrich 1984), and a length as short as possible (Bruinderink & Hazebroek 1996, Donaldson 2007, Langbein et al. 2011). However, I found no significant effect of width or length on overpasses, but I did not include the ratio of width to length in my analysis, similarly to the openness index on underpasses. Nevertheless, it is generally believed that increasing the width of a passage (increasing the ratio of width to length) and providing it with natural features (gravel or dirt pavement, vegetation), even maintaining its path, may increase its attractiveness for animals and thus be more efficient in reducing the risk of accidents with wildlife (Sjölund et al. 2005, Huijser et al. 2008, Clevenger & Huijser 2011, Langbein et al. 2011).

On railways, the width of a given underpass reduced the frequency of accidents, supporting previous studies where in some cases it is even the only bridge dimension obtaining significant results on the selection of underpasses by wildlife (Iuell et al. 2003, Mata et al. 2008, Seiler & Olsson 2009, Beckmann et al. 2010). However, I found an effect of width only in underpasses and in moose, suggesting that this species may be especially sensitive to underpasses dimensions (Seiler et al. 2003, Seiler & Olsson 2009, Clevenger & Huijser 2011). In addition, also the effect of underpasses integrity type on the frequency of moose accidents could be linked to openness, as suggested by Dodd et al. (2009). When crossing wider infrastructures, the distance an animal must travel through an underpass may become too large (Donaldson 2007, Dodd et al. 2009), and it is thus beneficial to divide the entire crossing length in two distinct parts, creating a double-underpass. The existence of natural light from the median opening between the sections of the underpass increases the virtual relative openness of the passage

(Iuell et al. 2003, Jędrzejewski et al. 2009, Clevenger & Huijser 2011), and Cramer & Bissonette (2006) also associated it with predation avoidance by many prey species. The result obtained for irregular-ground underpasses supports previous findings (Cramer & Bissonette 2006, Dodd et al. 2009), since this shape has a more "natural" appearance compared to regular underpasses, and ungulates seem to consider some squared structures characteristics as unnatural, avoiding it. However, the underpass opening shape had a significant effect on the frequency of accidents registered on railways only, while similar effects would be expected also on roads. Another relevant result I obtained for road underpasses was the positive correlation between the frequency of ungulate accidents near the passage and the existence of water crossing through the passage, in accordance with conclusions from other authors (Bruinderink & Hazebroek 1996, Hubbard et al. 2000, Iuell et al. 2003). Watercourses as linear features may direct movements and lead animals towards a traffic infrastructure, and at such a crossing point should a passage exist with appropriate conditions to be used by terrestrial wildlife (Land & Lotz 1996, Hubbard et al. 2000, Ascensão & Mira 2005, Seiler 2005). Underpasses that contain open water are believed to have a high potential, even economically, as they are more easily adapted for use by terrestrial animals (Bruinderink & Hazebroek 1996), either by leaving dry watercourse banks and providing riparian cover within the passage (Sjölund et al. 2005, Helldin et al. 2010, Clevenger & Huijser 2011), or by using more detailed techniques for regulating the watercourse bed (Huijser et al. 2008).

Environmental variables, however, were generally the dominant factors and hence most commonly included in the best Generalized Linear Models (Seiler 2004, Ascensão & Mira 2005, Coffin 2007, Seiler et al. 2011). Naturally, species abundance is an important factor influencing the risk for occurrence of accidents (Seiler 2003), but in my results the effect of that factor was found mostly on a larger scale, when analysing the frequency of accidents on railway and road sections. The measure of species abundance I used is based on hunting statistics and thus relates to a rather coarse and large scale (Kindberg et al. 2008). Therefore, no clear pattern should be expected at local scale (i.e. on passage analysis level), where habitat composition may give better indications on species abundance, and thus on the risk for wildlife-vehicle collisions on roads or railways crossing through that habitat (Rodriguez et al. 2006).

Most of the results obtained for habitat-related variables were as expected. The effect of forest cover I found on the frequency of accidents with moose supports previous studies (Malo et al. 2004, Seiler & Olsson 2009, McCollister & van Manen 2010), since moose have high preference for forest habitats (Putman 1988, MacDonald & Barrett 1993, Olovsson 2007). Fewer moose accidents seemed to occur in locations far from water areas, which was expected since this species also shows preference to forage in wet areas (Putman 1988, MacDonald & Barrett 1993). The reduction of the frequency of moose accidents I found near underpasses in locations with higher density of open areas supports previous knowledge about the ecology of moose, since this species in fact avoid such habitats (Putman 1988, MacDonald & Barrett 1993). On other hand, roe deer has high preference for feeding in edges between open areas and forest where they also can find protection (Putman 1988, MacDonald & Barrett 1993, Malo et al. 2004). Therefore, they may be less frequent in high proportion of open areas, which may explain the found effect of proportion of open areas on the reduction of the frequency of accidents with roe deer near railway underpasses. Roe deer-car accidents were more frequent in areas with higher density of buildings, and here buildings mean isolated constructions mostly associated with agricultural land, the preferred habitat for roe deer (Putman 1988, MacDonald & Barrett 1993, Malo et al. 2004).

As previously mentioned, linear features may direct movements and lead animals towards roads or railways (Bruinderink & Hazebroek 1996, Hubbard et al. 2000, Iuell et al. 2003, Seiler 2005). The points where these linear landscape features intersect traffic infrastructure are critical locations for the existence of safe passages for wildlife (Land & Lotz 1996, Hubbard et al. 2000, Ascensão & Mira 2005), otherwise animals may be forced to cross the barrier infrastructure not using any crossing structure (Putman 1997, McCollister & van Manen 2010) and thus increasing the risk for occurrence of accidents. The results I obtained for the effect of the density of watercourses, water crossings and paths on the frequency of ungulate accidents (mostly with moose but partly also with roe deer) support the previous statement. For the density of railways and public roads, however, I obtained different results, since these linear features are generally more trafficked, and high traffic intensities may have had a deterring effect on ungulates and thus reduced the likelihood that deer would approach the target road or railway (Eigenbrod et al. 2008, Seiler & Olsson 2009). Further analyses should hence include at-grate road crossings as an additional parameter.

The traffic load of the barrier or target road clearly influenced the effect of bridges on the frequency of accidents with deer. Moose accidents were less frequent where traffic volume was higher, suggesting the deterring effect of highly trafficked roads on moose, in accordance with the findings of Seiler (2003). Accidents with roe deer instead seemed to be more frequent on roads with higher traffic intensity, particularly near overpasses, which is supported by the findings of Olsson et al. (2008), who stated that roe deer do not seem to be especially attracted by overpasses over highly trafficked infrastructure. To overcome the avoidance and promote the use of overpasses by animals it is suggested the use of noise- or light-reducing materials and vegetation in and adjacent to the overpasses (Iuell et al. 2003, Glista et al. 2009). I also found that the number of collisions in the surrounding of road overpasses increased with vehicular traffic intensity through the passage, supporting the results of previous studies, which showed that traffic through crossing structures deterred animals and thus diminished their efficacy (Clevenger & Huijser 2011, Seiler & Olsson 2009).

To conclude, the density and design of conventional bridges have obvious effects on the frequency of deer-vehicle collisions, and should therefore be considered in mitigation plans of the transport sector. Still, the major factors determining the frequency of accidents are environmental variables, linked to species abundance and species movement. Planning effective mitigation measures must therefore build on controlling these environmental variables as well as providing optimal passage design and placement.

Conclusions

I conclude that density and design of conventional bridges indeed have an effect on the frequency of deer-vehicle collisions. Bridge density seems to be of higher importance and some studies suggest that a higher number of crossing structures, even if narrow and not specifically adapted for wildlife use, may overall be more effective than one single large ecoduct (Clevenger & Waltho 2005, Olsson et al. 2008, Corlatti et al. 2009, Langbein et al. 2011). For any given passage, design and structural characteristics are of importance, as is their position in the surrounding landscape and their use by humans. The decision on which parameters should receive special concern in mitigation planning must involve the level of disturbance (Rodriguez et al. 1996, Glista et al. 2009), species abundance, and, of course, practical limitations. Most often, passage width and shape will be the only parameters that can be easily adjusted, while location, use, height and length and other technical features may have rather limited adaptation possibilities (Yanes et al. 1995, Rodriguez et al. 1996). Watercourses and paths, which are probably the major routes ungulates take towards railway or road barriers, are landscape features that should be subject to particular attention, both on landscape and local scales.

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Appendix

All candidate models/variable subsets with ΔAIC < 2 from the smallest AIC value are shown. In each table the favourite model is in bold.

Table A1. Results from AIC model building, for accidents with moose on railway sections.

Model	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	BridgesMKm	ForestBuff	PublRdsBuf	WatCourBuf			4	-340.398	66.894	<0.0001
2	BridgesMKm	ForestBuff	OpenBuff	PublRdsBuf	WatCourBuf		5	-339.979	68.475	<0.0001
3	BridgesMKm	ForestBuff	PublRdsBuf	RailwayBuf	WatCourBuf		5	-339.640	68.136	<0.0001
4	BridgesKm	BridgesMKm	ForestBuff	PublRdsBuf	WatCourBuf		5	-339.284	67.780	<0.0001
5	BridgesKm	ForestBuff	PublRdsBuf	RailwayBuf	WatCourBuf		5	-339.269	67.765	<0.0001
6	BridgesMKm	ForestBuff	OpenBuff	PublRdsBuf			4	-339.168	65.664	<0.0001
7	BridgesKm	BridgesMKm	ForestBuff	PublRdsBuf	RailwayBuf	WatCourBuf	6	-338.900	69.396	<0.0001
8	BridgesMKm	ForestBuff	PublRdsBuf	BuildBuff	WatCourBuf		5	-338.873	67.369	<0.0001
9	BridgesKm	BridgesMKm	ForestBuff	OpenBuff	PublRdsBuf	WatCourBuf	6	-338.871	69.366	<0.0001
10	**BridgesKm**	**ForestBuff**	**PublRdsBuf**	**WatCourBuf**			**4**	**-338.812**	**65.308**	**<0.0001**
11	BridgesMKm	ForestBuff	RailwayBuf	WatCourBuf			4	-338.805	65.301	<0.0001
12	BridgesMKm	ForestBuff	OpenBuff	PublRdsBuf	RailwayBuf	WatCourBuf	6	-338.774	69.270	<0.0001
13	BridgesMKm	ForestBuff	PublRdsBuf	WaterCross	WatCourBuf		5	-338.543	67.039	<0.0001
14	BridgesKm	ForestBuff	OpenBuff	PublRdsBuf	WatCourBuf		5	-338.473	66.969	<0.0001
15	BridgesKm	BridgesMKm	ForestBuff	OpenBuff	PublRdsBuf		5	-338.411	66.907	<0.0001
16	BridgesMKm	ForestBuff	PublRdsBuf	PrivRdsBuf	WatCourBuf		5	-338.399	66.895	<0.0001

Table A2. Results from AIC model building, for accidents with roe deer on railway sections.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	**BridgesKm**	**RailwayBuf**	**WatCourBuf**	**RoedeerAbu**				**5**	**-237.414**	**61.505**	**<0.0001**
2	BridgesKm	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu			6	-237.220	63.311	<0.0001
3	BridgesKm	ForestBuff	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu		7	-236.937	65.029	<0.0001
4	BridgesKm	ForestBuff	OpenBuff	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu	8	-236.910	67.001	<0.0001
5	BridgesKm	ForestBuff	PublRdsBuf	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu	8	-236.703	66.795	<0.0001
6	BridgesKm	PublRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu			6	-236.623	62.714	<0.0001
7	BridgesKm	ForestBuff	OpenBuff	PublRdsBuf	PrivRdsBuf	RailwayBuf	WatCourBufRoedeerAbu	9	-236.507	68.598	<0.0001
8	BridgesKm	ForestBuff	RailwayBuf	WatCourBuf	RoedeerAbu			6	-236.369	62.460	<0.0001
9	BridgesKm	ForestBuff	PublRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu		7	-236.256	64.347	<0.0001
10	BridgesKm	PublRdsBuf	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu		7	-236.209	64.300	<0.0001
11	BridgesKm	OpenBuff	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu		7	-236.181	64.272	<0.0001
12	BridgesKm	ForestBuff	OpenBuff	RailwayBuf	WatCourBuf	RoedeerAbu		7	-236.058	64.149	<0.0001
13	BridgesKm	OpenBuff	RailwayBuf	WatCourBuf	RoedeerAbu			6	-235.881	61.972	<0.0001
14	BridgesKm	ForestBuff	OpenBuff	PublRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu	8	-235.790	65.882	<0.0001
15	BridgesKm	OpenBuff	PublRdsBuf	PrivRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu	8	-235.763	65.854	<0.0001
16	BridgesKm	OpenBuff	PublRdsBuf	RailwayBuf	WatCourBuf	RoedeerAbu		7	-235.585	63.676	<0.0001
17	ADT	BridgesKm	RailwayBuf	WatCourBuf	RoedeerAbu			6	-235.433	61.524	<0.0001
18	BridgesKm	BridgesRKm	RailwayBuf	WatCourBuf	RoedeerAbu			6	-235.414	61.505	<0.0001

Table A3. Results from AIC model building, for accidents with moose on road sections.

Model	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	**FenceKm**	**ADT**		**2**	**-743.581**	**26.948**	**<0.0001**
2	FenceKm	ADT	OpenBuff	3	-742.476	27.843	<0.0001
3	FenceKm	ADT	ForestBuff	3	-742.293	27.660	<0.0001
4	FenceKm	ADT	BridgesKm	3	-741.685	27.052	<0.0001
5	FenceKm	ADT	BridgesMKm	3	-741.582	26.949	<0.0001

Table A4. Results from AIC model building, for accidents with roe deer on road sections.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	FenceKm	ADT	BuildBuff	PrivRdsBuf	RoedeerAbu			6	433.910	54.327	<0.0001
2	FenceKm	ADT	BuildBuff	ForestBuff	PrivRdsBuf	RoedeerAbu		7	434.040	56.196	<0.0001
3	FenceKm	ADT	BuildBuff	OpenBuff	PrivRdsBuf	RoedeerAbu		7	434.434	55.802	<0.0001
4	FenceKm	BuildBuff	ForestBuff	PrivRdsBuf	RoedeerAbu			6	434.730	53.506	<0.0001
5	**FenceKm**	**ADT**	**BuildBuff**	**RoedeerAbu**				**5**	**435.041**	**51.196**	**<0.0001**
6	FenceKm	ADT	ForestBuff	PrivRdsBuf	RoedeerAbu			6	435.092	53.144	<0.0001
7	FenceKm	BuildBuff	OpenBuff	PrivRdsBuf	RoedeerAbu			6	435.389	52.848	<0.0001
8	FenceKm	ADT	OpenBuff	PrivRdsBuf	RoedeerAbu			6	435.757	52.480	<0.0001
9	FenceKm	ADT	BuildBuff	PrivRdsBuf	WatCourBuf	RoedeerAbu		7	435.831	54.406	<0.0001
10	FenceKm	ADT	BuildBuff	ForestBuff	OpenBuff	PrivRdsBuf	RoedeerAbu	8	435.876	56.361	<0.0001
11	FenceKm	ADT	BuildBuff	PublRdsBuf	PrivRdsBuf	RoedeerAbu		7	435.900	54.337	<0.0001
12	FenceKm	ADT	BridgesKm	BuildBuff	PrivRdsBuf	RoedeerAbu		7	435.905	54.331	<0.0001

Table A5. Results from AIC model building, for accidents with moose near railway overpasses.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	BridgMBuff	ForestBuff	Use					4	-399.527	72.444	<0.0001
2	BridgMBuff	ForestBuff	OpenBuff	Use				5	-399.335	74.252	<0.0001
3	DistBridgM	BridgMBuff	ForestBuff	OpenBuff	Use			6	-399.261	76.178	<0.0001
4	DistBridgM	BridgMBuff	ForestBuff	Use				5	-399.114	74.031	<0.0001
5	DistBridgM	BridgMBuff	ForestBuff	OpenBuff	MooseAbu	Use		9	-398.728	81.645	<0.0001
6	BridgMBuff	ForestBuff	MooseAbu	Use				7	-398.713	77.630	<0.0001
7	BridgMBuff	ForestBuff	OpenBuff	PublRdsBuf	MooseAbu	Use		9	-398.693	81.610	<0.0001
8	BridgMBuff	ForestBuff	OpenBuff	MooseAbu	Use			8	-398.616	79.533	<0.0001
9	DistBridgM	BridgMBuff	ForestBuff	MooseAbu	Use			8	-398.431	79.348	<0.0001
10	BridgMBuff	ForestBuff	PublRdsBuf	MooseAbu	Use			8	-398.393	79.310	<0.0001
11	BridgMBuff	ForestBuff	OpenBuff	PublRdsBuf	Use			6	-398.362	75.279	<0.0001
12	BridgMBuff	ForestBuff	PublRdsBuf	Use				5	-398.361	73.278	<0.0001
13	BridgMBuff	ForestBuff	WatCourBuf	Use				5	-398.221	73.137	<0.0001
14	DistBridgM	BridgMBuff	ForestBuff	WatCourBuf	Use			6	-398.106	75.023	<0.0001
15	DistBridgM	BridgMBuff	ForestBuff	OpenBuff	PublRdsBuf	MooseAbu	Use	10	-398.020	82.937	<0.0001
16	DistBridgM	BridgMBuff	ForestBuff	OpenBuff	PublRdsBuf	Use		7	-397.755	76.671	<0.0001
17	**BridgMBuff**	**ForestBuff**						**2**	**-397.554**	**66.471**	**<0.0001**
18	Width	BridgMBuff	ForestBuff	Use				5	-397.527	72.444	0.000000

Table A6. Results from AIC model building, for accidents with roe deer near railway overpasses.

Model	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	Width	DistBridgR	PublRdsBuf		3	-263.696	21.776	<0.0001
2	**DistBridgR**	**PublRdsBuf**			**2**	**-263.359**	**19.438**	**<0.0001**
3	Width	ADTout	DistBridgR	PublRdsBuf	4	-262.373	22.452	0.0002
4	Width	DistBridgR	PublRdsBuf	PathsBuff	4	-262.211	22.290	0.0002
5	DistBridgR	PublRdsBuf	PathsBuff		3	-262.030	20.109	0.0002
6	ADTout	DistBridgR	PublRdsBuf		3	-261.971	20.050	0.0002
7	Width	DistBridgR	BridgRBuff	PublRdsBuf	4	-261.808	21.887	0.0002
8	Width	DistBridgR	PublRdsBuf	Use	5	-261.719	23.798	0.0002

Table A7. Results from AIC model building, for accidents with moose near road overpasses.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	ADTins	PathsBuff	DistWater	Fence				4	250.699	23.005	0.0001
2	Width	ADTins	PathsBuff	DistWater	Fence			5	250.997	24.707	0.0002
3	ADTins	BridgMBuff	PathsBuff	DistWater	Fence			5	251.242	24.461	0.0002
4	ADTins	ForestBuff	PathsBuff	DistWater	Fence			5	251.362	24.341	0.0002
5	Width	ADTins	BridgMBuff	PathsBuff	DistWater	Fence		6	251.460	26.243	0.0002
6	Width	ADTins	ForestBuff	PathsBuff	DistWater	Fence		6	251.499	26.204	0.0002
7	ADTins	PathsBuff	DistWater					3	251.756	19.948	0.0002
8	ADTins	BridgMBuff	PathsBuff	DistWater				4	251.776	21.928	0.0002
9	PathsBuff	DistWater	Fence					3	252.095	19.608	0.0002
10	ADTins	BridgMBuff	ForestBuff	PathsBuff	DistWater	Fence		6	252.321	25.383	0.0003
11	Width	ADTins	ForestBuff	DistWater	Fence			5	252.362	23.341	0.0003
12	ADTins	ForestBuff	DistWater	Fence				4	252.381	21.322	0.0003
13	Width	ADTins	BridgMBuff	ForestBuff	PathsBuff	DistWater	Fence	7	252.412	27.292	0.0003
14	ADTins	ForestBuff	PathsBuff	DistWater				4	252.484	21.219	0.0003
15	BridgMBuff	PathsBuff	DistWater	Fence				4	252.517	21.186	0.0003
16	Width	ADTins	BridgMBuff	PathsBuff	DistWater			5	252.558	23.146	0.0003
17	Width	PathsBuff	DistWater	Fence				4	252.646	21.058	0.0003
18	ADTins	PathsBuff	DistWater	Use	Fence			6	252.652	25.052	0.0003
19	**Width**	**ADTins**	**PathsBuff**	**DistWater**				**4**	**252.665**	**21.039**	**0.0003**

Table A8. Results from AIC model building, for accidents with roe deer near road overpasses.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	**ADTins**	**ADTout**	**PublRdsBuf**	**BuildBuff**	**Use**	**Fence**			**7**	**767.877**	**101.347**	**<0.0001**
2	ADTins	ADTout	WatCrosBuf	PublRdsBuf	BuildBuff	Use	Fence		8	767.915	103.308	<0.0001
3	ADTins	ADTout	WatCourBuf	PublRdsBuf	BuildBuff	Use	Fence		8	768.788	102.435	<0.0001
4	ADTins	ADTout	WatCrosBuf	PublRdsBuf	OpenBuff	BuildBuff	Use	Fence	9	768.995	104.228	<0.0001
5	ADTins	ADTout	PublRdsBuf	OpenBuff	BuildBuff	Use	Fence		8	769.337	101.886	<0.0001
6	ADTins	ADTout	WatCourBuf	PublRdsBuf	OpenBuff	BuildBuff	Use	Fence	9	769.789	103.434	<0.0001
7	ADTins	ADTout	WatCrosBuf	WatCourBuf	PublRdsBuf	BuildBuff	Use	Fence	9	769.872	103.351	<0.0001

Table A9. Results from AIC model building, for accidents with moose near railway underpasses.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	ForestBuff	WatCourBuf	IntegrType	MooseAbu	Shape			9	-693.815	143.507	<0.0001
2	BridgMBuff	ForestBuff	WatCourBuf	IntegrType	MooseAbu			6	-693.799	137.490	<0.0001
3	**ForestBuff**	**WatCourBuf**	**IntegrType**	**MooseAbu**				**5**	**-693.774**	**135.466**	**<0.0001**
4	BridgMBuff	ForestBuff	WatCourBuf	IntegrType	MooseAbu	Shape		10	-693.184	144.876	<0.0001
5	BridgesBuf	BridgMBuff	ForestBuff	WatCourBuf	IntegrType	MooseAbu		7	-693.058	138.750	<0.0001
6	OpnsIndx	ForestBuff	WatCourBuf	IntegrType	MooseAbu	Shape		10	-692.310	144.002	<0.0001
7	BridgesBuf	BridgMBuff	ForestBuff	WatCourBuf	IntegrType	MooseAbu	Shape	11	-692.172	145.864	<0.0001
8	OpnsIndx	ForestBuff	WatCourBuf	IntegrType	MooseAbu			6	-692.145	135.836	<0.0001
9	OpnsIndx	BridgMBuff	ForestBuff	WatCourBuf	IntegrType	MooseAbu		7	-692.115	137.807	<0.0001
10	BridgesBuf	ForestBuff	WatCourBuf	IntegrType	MooseAbu	Shape		10	-691.816	143.508	<0.0001

Table A10. Results from AIC model building, for accidents with roe deer near railway underpasses.

Model	Variable	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	**OpenBuff**	**Water**	**RoedeerAbu**	**Shape**				**8**	**-385.394**	**51.757**	**<0.0001**
2	BridgRBuff	OpenBuff	Water	RoedeerAbu	Shape			9	-385.172	53.535	<0.0001
3	BridgRBuff	PrivRdsBuf	OpenBuff	Water	RoedeerAbu	Shape		10	-384.961	55.324	<0.0001
4	PrivRdsBuf	OpenBuff	Water	RoedeerAbu	Shape			9	-384.755	53.118	<0.0001
5	UsableWd	OpenBuff	Water	RoedeerAbu	Shape			9	-384.225	52.588	<0.0001
6	UsableWd	BridgRBuff	OpenBuff	Water	RoedeerAbu	Shape		10	-383.888	54.250	<0.0001
7	OpnsIndx	BridgRBuff	OpenBuff	Water	RoedeerAbu	Shape		10	-383.571	53.934	<0.0001
8	UsableWd	BridgRBuff	PrivRdsBuf	OpenBuff	Water	RoedeerAbu	Shape	11	-383.567	55.930	<0.0001
9	OpnsIndx	OpenBuff	Water	RoedeerAbu	Shape			9	-383.538	51.901	<0.0001
10	UsableWd	PrivRdsBuf	OpenBuff	Water	RoedeerAbu	Shape		10	-383.495	53.858	<0.0001
11	OpnsIndx	BridgRBuff	PrivRdsBuf	OpenBuff	Water	RoedeerAbu	Shape	11	-383.398	55.761	<0.0001

Table A11. Results from AIC model building, for accidents with moose near road underpasses.

Model	Variable	Variable	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	PathsBuff	OpenBuff	IntegrType	Fence			5	1311.205	75.082	<0.0001
2	PathsBuff	UsableWd	OpenBuff	IntegrType	Fence		6	1311.359	76.928	<0.0001
3	ForestBuff	PathsBuff	IntegrType	Fence			5	1311.897	74.391	<0.0001
4	ForestBuff	PathsBuff	UsableWd	IntegrType	Fence		6	1312.329	75.959	<0.0001
5	ForestBuff	PathsBuff	OpenBuff	IntegrType	Fence		6	1312.418	75.869	<0.0001
6	ForestBuff	PathsBuff	UsableWd	OpenBuff	IntegrType	Fence	7	1312.633	77.654	<0.0001
7	PathsBuff	OpenBuff	DistBridge	IntegrType	Fence		6	1313.068	75.219	<0.0001
8	**OpenBuff**	**IntegrType**	**Fence**				**4**	**1313.115**	**71.172**	**<0.0001**
9	PathsBuff	OpenBuff	ADTout	IntegrType	Fence		6	1313.204	75.083	<0.0001

Table A12. Results from AIC model building, for accidents with roe deer near road underpasses.

Model	Variable	Variable	Variable	Variable	DF	AIC	L.Ratio Chi^2	p
1	BuildBuff	DistBuild	Fence		3	2245.079	26.356	<0.0001
2	**BuildBuff**	**Fence**			**2**	**2245.530**	**23.906**	**<0.0001**
3	BuildBuff	DistBuild	IntegrType	Fence	4	2246.879	26.556	<0.0001
4	BuildBuff	OpnsIndx	DistBuild	Fence	4	2246.898	26.537	<0.0001
5	BuildBuff	DistBuild	OpenBuff	Fence	4	2246.973	26.462	<0.0001
6	BuildBuff	OpenBuff	Fence		3	2247.049	24.387	<0.0001
7	BuildBuff	DistBuild	ForestBuff	Fence	4	2247.061	26.374	<0.0001