

Factors affecting wildlife–vehicle collision on the expressway in a suburban area in northern Poland

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Abstract. Wildlife–vehicle collisions (WVC) pose a serious socio-economic and traffic safety issue. We investigated factors affecting the location and number of WVC on the expressway “Tri-City Bypass” in a suburban area in N Poland. We analysed WVC with large-sized (LSM; ungulates; 54% of roadkills) and small-sized mammals (SSM; mainly carnivores; 46% of roadkills) and both groups combined (AM). We identified WVC hotspots and analysed factors affecting their spatial distribution with Poisson regression based on four sets of landscape and road-related features (area, patchiness, presence and other features). The most frequent mammal victims of WVCs were wild boar *Sus scrofa* (31%), roe deer *Capreolus capreolus* (21%) and European badger *Meles meles* (13%), among LSM, and red fox *Vulpes vulpes* (27%) among SSM. In general, our results indicated that most WVCs occurred in areas with a higher number of forest patches and a higher total length of forest edge (AM, LSM), in curvy sections of the road (LSM). The number of WVCs was lower in locations covered by urbanized areas and grassland (LSM), in the sections with fences, exits and overpasses (LSM, AM). The road sections where there is a higher risk of severe collisions (involving large species) are situated in areas where the Tri-City Bypass bisects a highly forested area, which serve as movement corridors for LSM between fragmented forest complexes. We conclude that the number of WVCs can be reduced by preventing animals from accessing the road and ensuring a safe road crossing. This could be achieved by extending fencing and retrofitting some existing underpasses.

Key words: wildlife–vehicle collisions, mammals, Tri-City Bypass, fencing, suburban area.

Introduction

The current increase of traffic volumes and development of road networks pose a serious socio-economic and traffic safety issue due to the increasing risk of wildlife–vehicle collisions (WVC) (Hughes et al. 1996). Such accidents can cause fatalities and contribute to a significant loss in wildlife population numbers (Malo et al. 2004, Saeki & Macdonald 2004). Roads and transport infrastructures induce habitat modifications and landscape fragmentation resulting in a barrier effect reducing movement, and isolating animals from resources and potential mates (Richardson et al. 1997, Forman & Alexander 1998, Gerlach & Musolf 2000). The reduction of WVCs has become a primary consideration in road design and management (Zuberogoitia et al. 2014). Determination of the WVC distribution patterns along roads is crucial to the detection of the most problematic group of animals and collision hotspots, and useful for decision making with regard to the placement and design of preventive measures by transportation professionals (Gunson et al. 2011). Research on various vertebrate species has demonstrated that they do not occur randomly but are clustered spatially and temporally (reviewed in Gunson et al. 2011). Traffic volume and speed are generally considered to be important factors affecting the number of WVCs (Bashore et al. 1985, Hubbard et al. 2000, Seiler 2005). Landscape- and road-related structures have also been recognized as important factors (Hubbard et al. 2000, Clevenger et al. 2003, Malo et al. 2004; Gunson et al. 2011 and references therein), because wildlife tends to be linked to specific habitats and adjacent land use types. WVCs commonly occur when roads bisect favourable land cover and/or foraging or breeding habitats for specific species or groups of species (Gunson et al. 2011). Thus, landscape, habitat and road spatial patterns are expected to play an important role in determining road-kill locations and

rates (Forman & Alexander 1998).

Studies of WVCs in suburban and peri-urban areas are particularly important as the current development of cities is characterized by the movement of inhabitants from urban locations to more suburban and rural areas, which results in an increased traffic volume on the main roads around the cities (Insurance Institute for Highway Safety 1993), and affects wildlife by increasing collision rates and/or creating a strong barrier effect. In the suburban and peri-urban environment, wildlife is often restricted to non-urbanized areas. Protected areas, such as parks and nature reserves serve as wildlife refugia in suburban zones, however, the impact of roads can be prevalent even in these environments (Lopez 2004, Ramp et al. 2006).

The aim of this study was to investigate landscape and road-related factors affecting the number of WVCs on the expressway Tri-City Bypass in northern Poland. This road is located in a suburban area surrounded by forest complexes. We also aimed to identify the sections of the road where the risk of WVC is higher (involving many individuals and/or larger species), and where mitigation measures should be thus adopted to reduce the problem. Based on the findings of previous similar studies, we expected that the number of collisions would be higher in areas with good habitat connectivity, e.g. in the highly forested sections of the road (Coulon et al. 2008), while it would be lower in urbanized areas avoided by many animal species (Gunson et al. 2011). We also expected that the frequency of WVCs would be lower in sections of the road with fencing and underpasses, as proper fencing in conjunction with passages can help prevent animal access to roads and facilitate the movement of animals towards crossing structures (Glista et al. 2009). However, considering the effect of fencing ends (e.g. Clevenger et al. 2001, Cserkészi et al. 2013), we have also counted upon elevated roadkill numbers close to fence ends.

Materials and methods

Study Area

The study was performed along a 38 km section of the S6 expressway, called the Tri-City Bypass (in Polish Obwodnica Trójmiasta) between Gdynia and Pruszcz Gdański (Fig. 1 and 2). This road functions as a bypass around three cities in northern Poland: Gdańsk, Sopot and Gdynia, which form a conurbation known as the Tri-City (in Polish Trójmiasto), with 747,800 inhabitants in 2014.

The Tri-City Bypass is located in the moraine hills at the edge of the Kashubian Lake District. It passes a highly forested area (protected within the Tri-City Landscape Park), especially in the northern sections, and suburban districts of Gdańsk and Gdynia (Fig. 1 and 2). Forest covers 58% of the area within the 2 km buffer along 19 km of northern sections vs 18% area along the remaining southern sections. Forests in this buffer consist of deciduous (87%), mixed (8%) and coniferous (5%) forest stands. Among these, 74% of all forests consist of beech forests dominated by the European Beech *Fagus sylvatica*. The Tri-City Bypass features two lanes in each direction and in some places a third lane is available during curved and uphill sections. The Tri-City Bypass was planned and constructed in the 1970s. At that time, traffic was relatively light [Average Annual Daily Traffic in 1985 was 2,400–4,600 vehicles per day (GPR 1985)]. Thus, the hazards related to collision with wild animals were almost negligible, no fences, over- or under-passes and other mitigation structures dedicated to wildlife were considered. However, some underpasses dedicated to forestry with dirt roads (Fig. 1) are regularly used by mammals (Ryś 2011). Mitigation measures to prevent road-kills have been partially taken into account in some sections of the Tri-City Bypass since 2008, following increased traffic [Average Annual Daily Traffic from 2,400–4,600 vehicles per day in 1985 (GPR 1985), 7,300–14,700 in 1995 (GPR 1995), 9,239–26,261 in 2000 (GPR 2000), 25,945–26,235 in 2005 (GPR 2005) to 26,824–53,736 in 2010 (GPR 2010)]. In 2008–2010, some sections of the road (mainly highly forested) were fenced to reduce the number of WVCs (Fig. 1 and 2). The fence is made of wire and is characterized by a lower mesh size (width 0.3 m x height 0.05 m) in the lower part of the fence (up to 0.8 m) and a larger size above (Fig. 2) to prevent both large-sized and smaller-sized mammals from crossing. The official speed limit was 110 km/h (in 2010) and is currently 120 km/h (from 2011). The main game mammal species in forests adjoining the Tri-City Bypass are: roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, red deer *Cervus elaphus* and red fox *Vulpes vulpes* (data of Regional Forestry Directorate in Gdańsk). The area along the expressway is a hunting zone, with a regular hunting season for the majority of ungulates starting at the beginning of October and ending in winter.

Sources of data

In this study, we primarily used the official roadkill database of the General Directorate for National Roads and Motorways, Gdańsk Division (GDNRM). The database contains the following data about the respective roadkill: collision date, species, exact place on the highway (in the form of kilometers+meters), side of the road (from Gdynia to Pruszcz Gdański: right side, from Pruszcz Gdański to Gdynia: left side). Road maintenance inspectors of GDNRM check the road daily (excluding holidays) in morning hours and record the location of WVC sites with an accuracy of 100 m using road section signs. The species of the dead animal is noted, and the carcass is removed. In this study, only identified species/taxa were included. We combined data on mustelids other than the European badger *Meles meles* into a *Mustelidae* category. The roadkill database also contains collision records reported to GDNRM by the police. We considered the GDNRM data from the period between March 2010 and December 2013. Additionally, we included data from our own controls performed by one of the authors (MR) 8–10 times monthly at various times of day during the period from March 2010 to April 2011, employing the method used by the road maintenance inspectors of GDNRM.

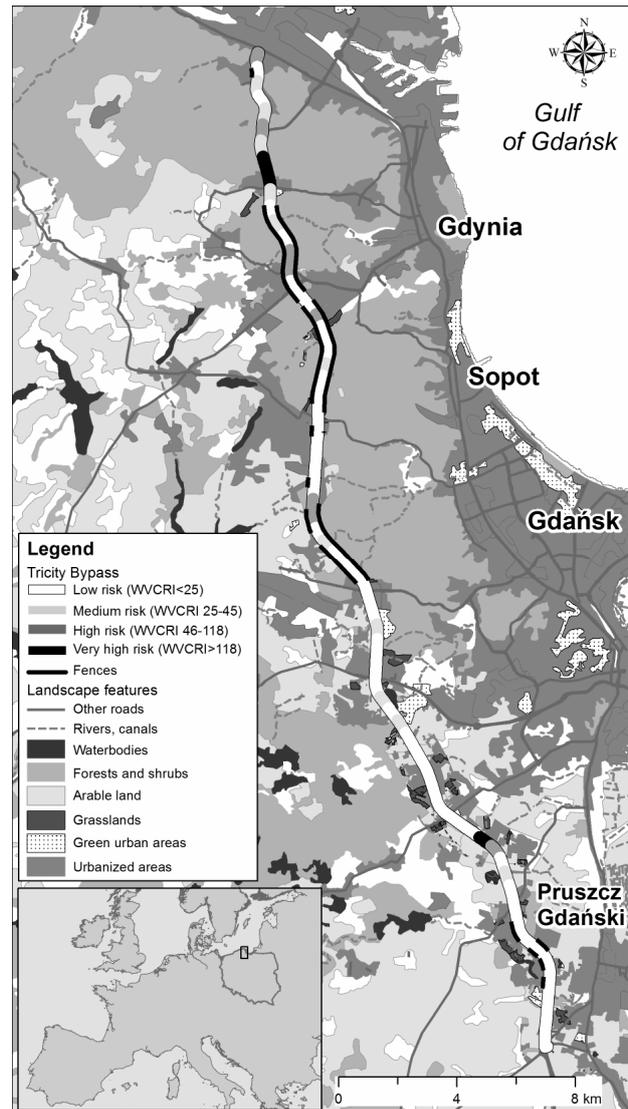


Figure 1. Study area with location of the Tri-City Bypass and wildlife-vehicle collision classification for particular 500 m sections of the road. WVCRI – wildlife-vehicle collision risk index.

Data analyses

To investigate factors affecting frequency of WVCs, we used a generalised linear model with Poisson linear regression with the number of collisions as an analysed variable and a set of landscape and road-related predictors (Table 1). We collected all the data in buffers around 76 sections of 500 m each (according to 1 km division of the Tri-City Bypass) of the road.

Due to the relatively small sample size, we analysed roadkills of all mammal species combined (hereafter AM) and in two separate groups according to body size criterion (see details below):

1) Large-sized mammals (hereafter LSM; $n = 95$ individuals) including ungulates: mainly wild boar (58%), roe deer (38%), and additionally red deer (2%), elk *Alces alces* (1%), and fallow deer *Dama dama* (1%);

2) Small-sized mammals (hereafter SSM; $n = 80$ ind.), mainly carnivores, including red fox (59%), European badger (28%) and mustelids, mainly *Martes* sp. (6%), European otter *Lutra lutra* (3%), raccoon dog *Nyctereutes procyonoides* (1%) and also two species representing two other groups, i.e. European hare *Lepus europaeus* (3%), and Eurasian red squirrel *Sciurus vulgaris* (1%).

Considering the relatively small sample size and rule of thumb (10 events needed per candidate predictor; e.g. Harrell 2001), we cal-



Figure 2. General view of the fenced section of the Tri-City Bypass (top) and of one of the underpasses with visible fence in sides (bottom left), fence with visible differentiated, height-dependent mesh size (bottom right). All photos DJ.

culated separate models with a maximum of six predictors. We constructed these models based on the following sets of predictors:

1) area covered by the following habitats: forests (all types combined), grassland, green urban zone, urban areas, shrubs, water bodies in buffers around 500 m sections of the road; we extracted those habitat features from Corine Land Cover model CLC 2006 (<http://www.eea.europa.eu/>, EEA Copenhagen, 2012) and Geoport (http://mapy.geoportal.gov.pl).

2) habitat patchiness, i.e. number of patches of particular habitat types: forests (all types combined), urban areas, non-irrigated areas, grassland, green urban zone, water bodies based in buffers around 500 m sections of the road;

3) presence/absence of man-made structures along the road: fences, exits (exits may serve as collision hotspots, especially in the fenced sections; Cserkés et al. 2013), underpasses (some of them were used by mammals; Ryś 2011) and overpasses (viaducts with roads, generally unsuitable as wildlife crossings);

4) other features – total length of forest edge, water body edges and rivers/streams, and also road curvature (proportion of horizontal to actual distance between the start and end of a given section of the road, affected by the number and angle (degree) of curves; lower values indicate curvy sections of the road).

We measured the predictors in the buffer zones of the 500 m sections. We selected two buffer sizes (400 and 800 m) to measure factors related to WVCs (Table 1). As habitats like forests or grasslands influence animal occurrence and movement at a larger spatial scale, we used an 800 m buffer zone to measure these features (e.g. Finder et al. 1999, Hubbard et al. 2000, Found & Boyce 2011). In the case of water bodies and river features, we used a smaller buffer zone of 400 m, as the home ranges of aquatic mammals like the European otter are about 1/10 the size of a forest-associated species, such as the wild boar or red deer (Singer et al. 1981, Néill et al. 2009).

Prior to analyses, we used Pearson product-moment correlation to check whether any of the variables were highly correlated, i.e., $|r| > 0.7$. We found that area covered by non-irrigated land showed strong negative correlation with forest ($r = -0.79$). Also, the number of shrub patches was strongly correlated with water body patchiness

Table 1. Landscape-, road-related variables measured for the studied sections of the Tri-City Bypass. Variable abbreviation in parenthesis. n – number of sections with occurrence of the particular predictor.

Variables in 76 buffer zones around the 500 m sections	Buffer zone	n
Habitat area - Area covered [m ²] by...		
Forest (For)	800 m	74
Grassland (Gras)	800 m	62
Green urban zone (GreUrb)	800 m	43
Urban areas (Urb)	800 m	76
Shrubs (Shru)	800 m	26
Water bodies (WatBod)	400 m	38
Habitat patchiness - number of patches of...		
Forest (For_pa)	800 m	74
Urban areas (Urb_pa)	800 m	76
Non-irrigated areas (NonIrri_pa)	800 m	71
Grassland (Gras_pa)	800 m	62
Green urban zone (GreUrb_pa)	800 m	43
Water bodies (WatBod_pa)	400 m	38
Presence/absence (1/0) of...		
Fence (Fen)	-	39
Exit (Ex)	-	30
Underpasses (Underp)	-	47
Overpasses (Overp)	-	47
Other features		
Forest edge total length [m] (ForEdge)	800 m	74
Water bodies edge total length [m] (WatBodEdge)	400 m	58
Rivers/streams total length [m] (RivLe)	400 m	21
Curvature [horizontal distance/actual distance] (Curv)	-	34*

* - number of curvy sections (values < 1)

($r = 0.79$). To avoid collinearity, we removed non-irrigated areas and shrub patchiness from analyses in habitat area and patchiness sets, respectively.

To select the best models describing number of WVCs, we used Akaike information criterion (AIC), delta AIC ($\Delta AIC = AIC_i - AIC_{\min}$) and AIC weights. We considered the models with the lowest ΔAIC values and highest AIC weights as the best ones (Burnham & Anderson 2002). We considered only the models with $\Delta AIC \leq 1$. We checked the significance of candidate models using Wald statistics at the alpha level 0.05.

To indicate the sections of the Tri-City Bypass at the highest risk of severe collision (with the largest mammals involved), we calculated wildlife-vehicle collision risk index (WVCRI) for each 500 m section of the road. We measured the severity of collision based on the size of the species of animal involved assuming that the body mass of the animal is directly proportional to the seriousness of the accident (Cserkés et al. 2013). Collisions with large-sized mammal species are often hazardous, involving serious damage, including human casualties (e.g. Conover 2002).

We considered the body mass of the red fox as the reference unit. Thus, we scored the body mass of the otter as 1 unit, roe deer 3 units, wild boar 22 units, red deer 29 and elk 48 units (Table 2). To assess the risk of severe collisions, we calculated WVCRI according to the formula: $WVCRI = \sum[n_i \times m_i]$, where (n_i) is the number of animals killed and (m_i) is their body mass index (Cserkés et al. 2013). We distinguished four categories of WVCRI: >118 - Very high risk; 46–118 - High risk; 25–45 - Medium risk; and <25 - Low risk (Fig. 1). To investigate factors affecting collision severity, we used a general linear model with WVCRI as an analysed variable and a set of landscape and road-related predictors (the same as in the analyses of WVCs number).

To test whether WVCs are evenly distributed throughout the seasons and days of week, we used the chi square test. We considered the period of March–May as spring, June–August as summer, September–November as autumn and December–February as win-

Table 2. Mammalian victims of wildlife-vehicle collision recorded in the Tri-City Bypass in 2010–2013 ordered by body mass unit.

Species	No. reported individuals	Mean body mass [kg]*	Body mass / red fox mass	Body mass unit
Small-sized mammals				
Eurasian red squirrel <i>Sciurus vulgaris</i>	1	0.3	0.05	0.1
Unidentified mustelids <i>Mustelidae</i>	5	0.6	0.10	0.1
European hare <i>Lepus europaeus</i>	2	4	0.69	1
Red fox <i>Vulpes vulpes</i>	47	6	1	1
European otter <i>Lutra lutra</i>	2	6	1	1
Raccoon dog <i>Nyctereutes procyonoides</i>	1	7	1	1
European badger <i>Meles meles</i>	22	14	2	2
Large-sized mammals				
Roe deer <i>Capreolus capreolus</i>	36	17	3	3
Fallow deer <i>Dama dama</i>	1	60	10	10
Wild boar <i>Sus scrofa</i>	55	131	22	22
Red deer <i>Cervus elaphus</i>	2	176	29	29
Elk <i>Alces alces</i>	1	289	48	48

* - according to data for Poland (Pucek 1984)

ter.

Considering elevated fatality rates reported close to the end of fencing (e.g. Clevenger et al. 2001, Cserkés et al. 2013), we used Pearson correlation to test whether the distance to the nearest fence end affected the number of collisions. We measured the distance to the nearest end of a fence for all unfenced sections of the road. We excluded completely fenced sections from the analyses.

Statistical analyses were performed with the R software (R Development Team 2014), using the MuMIn (Bartoń 2013) and aod (Lesnoff & Lancelot 2012) packages.

Results

In total, 175 roadkills were reported to be found on the Tri-City Bypass (in that 54% with LSM and 46% with SSM) between March 2010 and December 2013. The most frequent mammal victims of WVCs were wild boar (31%), red fox (27%), roe deer (21%) and European badger (13%).

Seasonal distribution of collisions

The seasonal distribution of fatalities was uneven, for AM (χ^2 test, $\chi^2_3 = 41.1$, $p < 0.0001$), SSM ($\chi^2_3 = 21.3$, $p < 0.0001$) and LSM ($\chi^2_3 = 23.4$, $p < 0.0001$). The highest number of WVCs with AM was recorded in autumn (37%) and spring (33%). In the case of SSM, it was recorded in autumn (42%). In the case of LSM, the highest number of collisions was recorded in spring (38%) and summer (33%). The lowest number of WVCs was recorded in winter (5% for LSM and 6% for SSM and AM) (Table 3).

The weekly distribution of fatalities was uneven, for AM (χ^2 test of goodness of fit, $\chi^2_6 = 30.0$, $p < 0.0001$), SSM ($\chi^2_6 = 15.2$, $p = 0.02$) and LSM ($\chi^2_6 = 21.5$, $p = 0.001$). The highest number of WVCs with AM was recorded on Monday (26% for AM, 28% for SSM and 25% for LSM) (Table 3). The proportion of fatalities on weekdays and weekends differed significantly from the expected proportion (i.e. 71% vs 29% considering the number of weekdays and weekend days, respectively) for AM (χ^2 test of goodness of fit with Yates' correction, $\chi^2_1 = 4.38$, $p = 0.036$) and LSM (χ^2 test with Yates' correction, $\chi^2_1 = 3.97$, $p = 0.046$) with a higher proportion of animal casualties on weekdays (79% in AM and 81% in LSM vs expected 71%) and lower at weekends (21% in AM and

Table 3. Temporal distribution [%] of wildlife-vehicle collisions in the Tri-City Bypass in 2010–2013 for particular road-killed species. SSM – small-sized mammals, LSM – large-sized mammals, AM – all mammals combined

Categories / Seasons	Spring	Summer	Autumn	Winter	N
SSM	27.5	23.7	42.5	6.2	80
LSM	37.9	24.2	32.6	5.3	95
AM	33.1	24.0	37.1	5.7	175

Categories / Days of week	Mon	Tue	Wen	Thu	Fri	Sat	Sun	N
SSM	27.5	12.5	11.3	8.8	16.3	16.3	7.5	80
LSM	25.3	18.9	12.6	6.3	17.9	4.2	14.7	95
AM	26.3	16.0	12.0	7.4	17.1	9.7	11.4	175

Categories / Types of days of week	Weekdays	Weekends	N
SSM	76.3	23.8	175
LSM	81.1	18.9	80
AM	78.9	21.1	95

19% in LSM vs expected 29%). The proportion of roadkills of SSM on weekdays and weekends did not differ significantly from expectations (χ^2 test with Yates' correction, $\chi^2_1 = 0.69$, $p = 0.41$).

Collisions models

Among the habitat area set, the area covered by urban zone was the best predictor of WVC number both for AM and SSM (Table 4). The number of collisions decreased with the increasing area of urban zones around the road (Table 5). For LSM, the best model included urban zone area and grassland areas (Table 4). The number of collisions decreased with increasing area of grasslands and tended to decrease also with increasing area of urban zone (Table 5).

The number of forest and grassland patches and of water bodies were the best predictors of WVCs number in the patchiness set for AM and LSM (Table 4). The number of collisions increased with the increasing number of forest patches and water bodies and decreased with the increasing number of grassland patches (Table 5). In the case of SSM, the best model included only the number of water body patches (Table 4). However, this model was not significant ($p = 0.26$) (Table 4).

Table 4. Highest-ranking Poisson regression fatality models $\Delta AIC \leq 1$ estimating WVCs number. Int- intercept. Codes for predictors in Table 1.

Models	df	Wald statistic p	AICc	Delta AIC	AIC weight
Area - All mammals					
Int - Urb	2	<0.001	307.8	0.00	0.209
Int - GreUrb - Urb	3	<0.001	307.9	0.08	0.201
Int - Gras - Urb	3	<0.001	308.2	0.42	0.170
Int - GreUrb - Gras - Urb	4	<0.001	308.5	0.67	0.150
Area - Small-sized mammals					
Int - Urb	2	0.006	205.1	0.00	1.000
Area - Large-sized mammals					
Int - Gras - Urb	3	<0.001	240.5	0.00	0.431
Int - Gras - GreUrb - Urb	4	<0.001	241.3	0.82	0.287
Int + For - Gras	3	<0.001	241.3	0.85	0.282
Patchiness - All mammals					
Int + For_pa - Gras_pa + WatBod_pa	4	<0.001	318.9	0.00	1.000
Patchiness, Small-sized mammals					
- Int + WatBod_pa	2	0.26	212.2	0.00	0.378
- Int	1	0.65	212.3	0.07	0.365
- Int + Gras_pa	2	0.42	213.0	0.77	0.257
Patchiness - Large-sized mammals					
Int + For_pa - Gras_pa + WatBod_pa	4	<0.001	239.5	0.00	0.313
Int + For_pa - Gras_pa - NonIrr_pa + WatBod_pa	5	<0.001	239.9	0.41	0.255
Int - Gras_pa - NonIrr_pa + WatBod_pa	4	<0.001	240.0	0.53	0.240
Int + For_pa - Gras_pa - GreUrb_pa + WatBod_pa	5	<0.001	240.5	0.98	0.192
Other features - All mammals					
Int + ForEdg	2	<0.001	318.8	0.00	0.589
Int + ForEdg - RivLeng	3	<0.001	319.5	0.72	0.411
Other features - Small-sized mammals					
Int - Curv + WatBodEdg	3	0.13	211.5	0.00	0.216
Int - Curv	2	0.19	211.7	0.15	0.201
Int	1	0.65	212.3	0.78	0.147
Int + ForEdg + WatBodEdg	3	0.18	212.3	0.78	0.147
Int - Curv + ForEdg + WatBodEdg	4	0.12	212.3	0.79	0.146
Int - RivLeng	2	0.34	212.4	0.82	0.144
Other features - Large-sized mammals					
- Int + Curv + ForEdg	3	<0.001	242.9	0.00	1.000
Presence - All mammals					
Int - Ex - Fen - Overp	4	<0.001	312.9	0.00	1.000
Presence - Small-sized mammals					
-Int - Ex + Underp	3	0.076	210.0	0.00	0.294
-Int + Fen + Underp	3	0.074	210.2	0.18	0.268
Int - Ex	2	0.120	210.4	0.41	0.240
-Int - Ex + Fen + Underp	4	0.074	210.8	0.79	0.198
Presence - Large-sized mammals					
Int - Ex - Fen - Overp	4	<0.001	234.3	0.00	1.000

In the set of other features, forest edge length was the best predictor of WVCs number for AM. In the case of SSM, all models were not significant ($p > 0.12$). For LSM, curvature and forest edge length were the best predictors (Table 4). The number of WVCs with AM and LSM increased with the increasing total length of forest edge (Table 5). We recorded an increasing number of collisions in curvy sections of the road for LSM.

In the last analysed set, presence of exits, fences, and over-passes were recognized as the best predictors of WVCs number for AM and LSM (Table 4). The number of WVCs was lower in the fenced sections of the road, in the sections with exits and overpasses (Table 5). In the case of SSM, all models were not significant ($p > 0.07$).

There was no significant relationship between the number of WVCs and distance to the nearest end of fence (Pearson correlation, AM: $r = 0.06$, $p = 0.64$, $n = 57$; LSM: $r = -0.02$, $p = 0.91$, $n = 57$; SSM: $r = 0.19$, $p = 0.16$, $n = 57$).

Wildlife-vehicle collision risk index

Sections of the Tri-City Bypass with very high risk of severe collisions, especially those in the northern part, are situated in areas where the Tri-City Bypass divides a dense forest (Fig. 2). In the southern part of the road, a section with a very high risk of collision with LSM is situated in an area characterised by a mixture of dense forest and open areas (mainly green urban areas) connected to smaller forest patches.

We found that among the habitat area set, the area covered by forest was the best predictor of collision severity (expressed by WVCRI) (Table 6). The risk of collisions increased with the increasing area of forests around the road (Table 7). The number of forest patches was the best predictor of collision severity in the patchiness set (Table 6). The WVCRI increased with the increasing number of forest patches (Table 7). In the set of other features, forest edge length and road curvature were the best predictors of colli-

Table 5. Parameter estimates for the best WVC models. Only significant models (Wald test, $p > 0.05$) are presented. Int - intercept. Codes for predictors in Table 1.

Features	Model	Estimate	SD	Z	<i>p</i>
Area - All mammals	Intercept	1.4108	0.1580	8.931	< 0.001
	Urb	-0.0064	0.0017	-3.848	< 0.001
Area - Small-sized mammals	Intercept	0.7150	0.2210	3.109	0.002
	Urb	-0.0074	0.0025	-3.014	0.003
Area - Large-sized mammals	Intercept	0.8915	0.22256	4.006	< 0.001
	Gras	-0.02931	0.011415	-2.568	-0.010
	Urb	-0.0043	0.00224	-1.935	0.053
Patchiness - All mammals	Intercept	0.6220	0.2203	2.823	0.005
	For_pa	0.1134	0.0617	1.838	0.066
	Gras_pa	-0.1414	0.0623	-2.270	0.023
	WatBod_pa	0.0669	0.0309	2.165	0.030
Patchiness - Large-sized mammals	Intercept	0.03945	0.30171	0.131	0.896
	For_pa	0.1740	0.08146	2.136	0.033
	Gras_pa	-0.2804	0.0924	-3.035	0.002
	WatBod_pa	0.0899	0.0459	1.957	0.050
Other features - All mammals	Intercept	<0.001	<0.001	3.956	< 0.001
	ForEdg	<0.001	<0.001	1.997	0.046
Other features - Large-sized mammals	Intercept	<-0.001	<0.001	-2.353	0.019
	Curv	<0.001	<0.001	2.302	0.021
	For_edg	<0.001	<0.001	2.765	0.006
Presence - All mammals	Intercept	1.4031	0.1689	8.306	< 0.001
	Fen	-0.3916	0.1716	-1.282	0.022
	Ex	-0.5029	0.1756	-2.863	0.004
	Overp	0.3860	0.1590	-2.428	0.015
Presence - Large-sized mammals	Intercept	1.2036	0.2180	5.521	< 0.001
	Fen	-0.9230	0.2466	-3.743	< 0.001
	Ex	-0.6214	0.2371	-2.621	0.009
	Overp	-0.7266	0.2168	-3.352	< 0.001

Table 6. Highest-ranking general linear models $\Delta AIC \leq 1$ estimating wildlife-vehicle collision risk index (WVCRI). Int - intercept. Codes for predictors in Table 1.

Models	df	Wald statistic <i>p</i>	AICc	Delta AIC	AIC weight
Area					
Int + For	3	<0.001	319.9	0.00	0.621
Int - Urb	3	<0.001	320.8	0.99	0.379
Patchiness					
Int + For_pa	3	<0.001	319.2	0.00	0.616
Int + For_pa - Grass_pa	4	<0.001	320.1	0.95	0.384
Other features					
- Int + Curv + ForEdg	4	<0.001	319.8	0.00	0.608
Int + ForEdg	3	<0.001	320.7	0.88	0.392
Presence					
Int - Ex - Overp	4	<0.001	320.3	0.00	0.501
Int - Overp	3	<0.001	320.3	0.01	0.499

Table 7. Parameter estimates for the best WVCRI models. Codes for predictors in Table 1.

Features	Model	Estimate	SD	Z	<i>p</i>
Area	Intercept	0.8040	0.3326	2.417	0.018
	For	0.0052	0.0025	2.063	0.043
Patchiness	Intercept	0.3501	0.4867	0.719	0.474
	For_pa	0.3825	0.1718	2.226	0.029
Other features	Intercept	<0.001	<0.001	-1.619	0.110
	For_edg	<0.001	<0.001	2.272	0.026
	Curv	<0.001	<0.001	1.746	0.085
Presence	Intercept	2.0990	0.3889	5.397	<0.001
	Ex	-0.6671	0.4518	-1.477	0.144
	Overp	-0.8398	0.4546	-1.847	0.069

sion severity (Table 6). The WVCRI increased with the increasing total length of forest edge ($p = 0.03$) and tended to

be lower in the curvy sections of the road ($p = 0.08$) (Table 7). In the present set, we recognized the presence of exits and overpasses as the best predictors of collision severity (Table 6). The WVCRI was lower in the sections with exits and overpasses. However, the first predictor was insignificant ($p = 0.14$) and the second marginally significant ($p = 0.07$) (Table 7).

Discussion

The most frequent mammal victims of WVCs on the Tri-City Bypass were wild boar (31%), red fox (27%), and roe deer (21%). These species are often reported as the most numerous victims of WVCs in other European countries [Lithuania - roe deer 50% and wild boar 23% (Ignatavicius et al. 2011),

Spain - wild boar 47% and roe deer 32% (Sáenz-de-Santa-María & Tellería 2015)]. Ungulate species are often the main victim of WVCs due to their common and abundant occurrence in many areas. They are considered to be the most problematic species in traffic security in Europe (Groot-Bruinderink & Hazebroek 1996, Langbein et al. 2011), as being involved in the highest number of collisions, they are responsible for the most damage (Sáenz-de-Santa-María & Tellería 2015). These ungulates, despite being closely associated with forest patches, frequently forage in open areas [wild boars in grass fields and agricultural lands (Fonseca 2008, Colino-Rabanal et al. 2012), roe deer in meadows, hedges, and cultivated fields (Torres et al. 2011), which forces them to cross the roads and increases the probability of being killed. The red fox was the most numerous victim among the carnivore guild in roads in southern Portugal (Grilo et al. 2009). The species composition of road-killed mammals on the Tri-City Bypass corresponds closely to the most numerous game species occurring in the area, i.e. wild boar, roe deer and red fox (data of the Regional Forestry Inspectorate in Gdańsk).

Temporal distribution of collisions

Temporal variations in road-kill are related to differences in species behaviour and activity, e.g., foraging and resting, mating, and dispersal of juveniles (Saeki & Macdonald 2004). The highest number of collisions was recorded in the case of the SSM in autumn (41%) and summer (22%), and in the case of LSM in spring (38%) and autumn (35%). In many studies, bimodal distribution in seasonal roadkill mammal frequency (i.e. in spring and autumn) has been reported (e.g. Pintur et al. 2012, Rodríguez-Morales et al. 2013, Kitowski et al. 2014). Spring and autumn are considered to be the seasons with the highest risk of WVCs because of the seasonal movements of mammals. The highest number of collisions in mammals occurring in spring may be largely explained by breeding activity, including the roe deer parturition. At this time the fawns born in preceding years abandon their family group and wander erratically in search of new areas to settle in (Rodríguez-Morales et al. 2013). An increase in WVCs in autumn, especially in the case of LSMs may be explained by the rut period with territorial fights and movements within the home range in search for females for mating (Rodríguez-Morales et al. 2013). In autumn, the higher number of WVCs with ungulates is likely to be caused by the start of the hunting season. Hunting activity causes an increase in daily movement and changes in the home range of ungulates (e.g. Sforzi & Lovari 2000, Etter et al. 2002, Morelle et al. 2015). The higher number of collisions with the wild boar in NW Spain in autumn has been explained in terms of the combined effect of hunting and longer nights (it is usually active at night and twilight, thus, the probability of collision is higher when nights are longer) (Lagos et al. 2012).

Weekly variation in road-kill frequency often reflects the weekly dynamic of traffic. In our study, the highest number of WVCs was recorded on Monday, when the traffic is less intense, especially cargo traffic (GPR 2010) including large trucks, semi-trailer trucks etc. A similar pattern has been reported for collisions with roe deer in S Poland (Kitowski et al. 2014). A reverse pattern, with a higher number of collisions at weekends has been reported for traffic accidents

with ungulates in NW Spain (Lagos et al. 2012) and Italy (Putzu et al. 2014). Those contradictory results may be caused by different local traffic dynamics and/or customs (e.g. traditional collective hunting for the wild boar in Spain takes part on Sundays; Lagos et al. 2012).

Landscape variables affecting the number of collisions

As we expected, the number of WVCs in our study was lower (AM, SSM) or tended to be lower (LSM) in the section where the predominant land-cover was urban area. The studied LSM, i.e. forest-associated ungulates, may have avoided urban areas due to the high risk of human disturbance and due to the possibility of road crossing in nearby areas with good habitat connectivity, i.e. highly forested sections of the road. Other studies have also indicated that urban areas surrounding roads decreased the number of collisions with ungulates, red fox and European badger (Bashore et al. 1985, Nielsen et al. 2003, Malo et al. 2004, Seiler 2005, Grilo et al. 2009). Studies on ungulates have indicated that the number of collisions is higher in open areas and green patches (Hubbard et al. 2000, Seiler 2005). In contrast, in our study, the number of WVCs was lower in sections of the road with larger open areas covered by grassland and characterized by a higher number of grassland patches. This contradictory finding may be explained by the fact that in our study LSM probably avoided road crossing in open habitats, preferring nearby highly forested areas.

As we predicted, the number of WVCs increased or tended to increase with the increasing number of forest patches and water bodies. A higher number of those habitat patches along the road indicates a higher probability of existing migration corridors serving as corridor between their fragmented patches. Those natural corridors are cut by the road, which generates a high risk of WVCs. The number of collisions increased with increasing forest edge length in the case of AM and LSM. Also in other studies, various variables describing forest habitat surrounding roads (e.g. proximity to forest edge, number of woody patches with interior areas greater than 50 m from edge, density and size of forest) increased the number of collisions with ungulates (Finder et al. 1999, Hubbard et al. 2000, Malo et al. 2004, Seiler 2005).

In our study, road curvature has been recognized as an important predictor of the number of WVCs for LSM with more collisions in the curvy sections. WVCs typically occur when visibility is obstructed either by road curvature or sight line distance (Gunson et al. 2011). On curvy road sections, both vehicle drivers and animals have little time to realize each other's proximity, resulting in a shorter response time to avoid collision. Thus, increasing visibility along roads should decrease collisions.

As we predicted, the number of collisions was lower (AM, LSM) in fenced sections of the road. Thus, in contrast to other studies where fencing does not reduce the number of WVCs [due to poor fencing, i.e. with openings, inadequately buried into the ground or damaged (Zuberogitia et al. 2014), not buried into the ground or interruption of fence continuity at exits (Cserkés et al. 2013)], the fence along the Tri-City Bypass has proven to be a generally effective barrier for LSM. The presence of fencing was not a significant factor in the best model describing the number of WVCs with SSM. Probably, the mesh size in the lower part of the fence and

larger size above does not prevent efficiently SSM from road crossing.

The number of collisions (AM, LSM) was lower in the road sections with exits and overpasses. Those areas contained additional lanes and had higher traffic volumes. Almost all overpasses along the Tri-City Bypass are viaducts dedicated to local roads with heavy traffic. Noise from vehicle traffic can cause stress in animals and potentially restrict habitat use and movement. A study into wide-ranging large carnivores and their prey species in Banff National Park (Canada) revealed that noise was a significant factor negatively affecting animal passage along the highway crossing structures (Clevenger & Waltho 2005).

We expected that the presence of underpasses would reduce collision numbers, especially in the fenced sections of the road. Many studies have also reported that animals tend to use conventional bridges and tunnels (not wildlife-dedicated) to cross roads, thereby decreasing the frequency of road crossing deaths (i.e. Clevenger & Waltho 2000, Seiler 2004). Surprisingly, in our study none of the significant models contained underpass presence. As the dimensions of structures are crucial for their use by vertebrates (Glista et al. 2009), our results may suggest that the parameters of at least some underpasses were not suitable for LSM. Inadequate width and height may have discouraged mammals from using those constructions to cross the road safely (Glista et al. 2009). All current underpasses were designed in the 1970s, and their function as animal underpasses was not a design concern. Also, lack of fence continuity on one of the sides of the underpass may decrease the chance of it being used by mammals. One of our collision hotspots, situated in a highly forested northern part of the Tri-City Bypass, was characterized by the presence of an underpass with a lack of fencing north off this structure. Some studies report regular use of underpasses by smaller mammals, e.g. the red fox (Grilo et al. 2008). Moreover, photos taken by a camera trap and tracks from one monitored culvert under the Tri-City Bypass indicated regular use by the European badger, red fox and mustelids (Ryś 2011). The lack of a significant effect of underpasses on the frequency of WVCs with SSM in our study is in concordance with suggestions that smaller passages are better for SSM (Glista et al. 2009) and a low number of culverts with size fitting SSM would be recommended along the Tri-City Bypass.

In our study, the risk of collisions with LSMs (WVCRI) increased with increasing forest area, length of forest edge, and number of forest patches in buffers around the road. All sections of the Tri-City Bypass with the highest risk of collision with large mammals are situated in corridors connecting forest complexes, two large patches in the north, and one large patch connecting to a smaller one in the south (Fig. 2). Well-connected habitat patches are especially prone to WVCs (Grilo et al. 2011). Landscape connectivity influences population flow at a broad spatial scale which has been reported e.g. for the roe deer (Coulon et al. 2004). Thus, landscape elements favourable to movement diminish the barrier effects of roads for the roe deer, which may result in an elevated number of roe deer-vehicle collisions (Coulon et al. 2008). Also in smaller mammals, e.g. the beech marten *Martes foina*, the incidence of roadkills was significantly higher in road segments traversing continuously forested

habitat (Grilo et al. 2011).

Management implications

Mitigation measures should be implemented locally in the areas with a high risk of collisions in order to decrease the fatality rate of mammals. For example, signs indicating the road sections with high WVCRI could be provided. Given that the number of WVCs for AM and LSM was significantly lower in the fenced sections of the road, extension of current fencing is recommended in order to prevent animals from accessing the road and promote guidance to existing underpasses. For many larger mammals, fencing is necessary because of their avoidance of passages, e.g. many ungulates avoid underpasses unless there is no other way to cross a road (Ward 1982). Considering the aforementioned reluctance to use underpasses and reported collision hotspots at fence endings (e.g. Cserkés et al. 2013), as well as the lack of complete fencing around some underpasses under the studied expressway, it is recommended to fence the whole Tri-City Pass. Indeed, in previous years, GDNRM extended fencing and currently it covers all highly forested sections of the studied expressway. Modifications of existing underpasses, as well as the installation of new crossings for wildlife would be needed, especially in forested areas with good habitat connectivity serving as migration corridors. Field studies revealed that different dimensions and design of fauna crossing structures appear to favour different taxa (e.g. Clevenger & Waltho 2000, 2005, McDonald & St. Clair 2004), with larger species much more likely to use larger structures. To maximize connectivity across roads for multiple LSM, road construction schemes should include various crossing structures with mixed size classes (Clevenger & Waltho 2005). In practice, the expensive installation of new crossings along the Tri-City Bypass will only be possible after the addition of the planned third lane. However, minor modernization of some existing structures should be possible. For example, the incorporation of dry ledges/shelves along drainage culverts frequently inundated with water can facilitate the passage of terrestrial small to medium-sized vertebrates (Glista et al. 2009). As continuity of natural vegetation can encourage animals (especially small to mid-sized mammals) to use crossing structures (Glista et al. 2009), some habitat modifications at entrances (e.g. cease mowing vegetation close to the underpass entrance enabling succession) could be applied to some existing underpasses along the Tri-City Bypass.

Conclusions

Our study is the first reporting factors affecting WVCs frequency and recognizing collision hotspots in a suburban area of the Tri-City Bypass as it passes a highly forested area. We are aware that our study has some limitations. It accounts for only a small portion of the actual number of road kills, since most small animal collisions go unnoticed by GDNRM and police reports. We did not include other potentially important factors, e.g. local animal density. Despite these shortcomings, the data presented here provides a credible picture of the spatial distribution of WVCs in the Tri-City Bypass and factors affecting their occurrence. The results of our study may be of partial relevance considering the current rapid development of the highway and express-

way network in Poland and Central Europe. Road managers need reliable data to identify WVC hotspots in order to implement mitigation measures during the road exploration stage.

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