

Note

Temporal Pattern of Wildlife-Train Collisions in Poland

DAGNY KRAUZE-GRYZ,¹ Department of Forest Zoology and Wildlife Management, Forest Faculty, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

MICHAŁ ŹMIHORSKI, Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland; and Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE 750 07 Uppsala, Sweden

KAROLINA JASIŃSKA, Department of Forest Zoology and Wildlife Management, Forest Faculty, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

ŁUKASZ KWAŚNY, Department of Forest Management Planning, Geomatics and Forest Economics, Forest Faculty, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

JOANNA WERKA, Department of Forest Zoology and Wildlife Management, Forest Faculty, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

ABSTRACT The development and modernization of railway infrastructures in many countries has increased the frequency of wildlife-train collisions. Our objective was to describe the temporal pattern of train accidents related to wild ungulates (i.e., roe deer [*Capreolus capreolus*], red deer [*Cervus elaphus*], moose [*Alces alces*], and wild boar [*Sus scrofa*]) to determine when the risk of collision is highest. We gathered data on train collisions with wild ungulates throughout Poland between 2012 and 2015 from Polish Railways Polskie Koleje Państwowe SA. We used generalized additive mixed models to investigate whether the number of collisions changed over time. The number of wildlife-train collisions varied depending on time of year. Most collisions occurred in autumn when animals form winter herds and migrate to and stay in winter refugia. The fewest collisions occurred in summer during breeding season. For all species except red deer, the number of collisions was significantly lower during weekends compared to weekdays. The distribution of collisions with regard to time of day was significantly different from simulated uniform random distribution, with peaks before dawn and after dusk, which reflect activity peaks of ungulates. During the day, the probability of collision was lower, with only single events observed between 0800 and 1600. We observed another collision-free period after midnight until 0400, probably because train traffic was minimal during this period. Most train collisions with ungulates took place in relatively narrow time windows in terms of time of year and time of day (i.e., 50% of the recorded cases took place in ~17% of the total time observed). Consequently, mitigation measures of lowering speed limits can be applied during times when the risk of collision is highest. © 2017 The Wildlife Society.

KEY WORDS *Alces alces*, *Capreolus capreolus*, *Cervus elaphus*, season, *Sus scrofa*, time of a day, ungulates, wildlife-train collisions.

The development and modernization of railway infrastructures in many countries has increased the frequency of wildlife-train collisions (Jaren et al. 1991, Modafferi 1991, Joshi et al. 2009, Wasilewski et al. 2009, Jasińska et al. 2014). Railway and road infrastructures cause habitat fragmentation by cutting through individual territories and migration corridors (Cain et al. 2003, Di Giulio et al. 2009, Ito et al. 2013). As a result, animals may be forced to cross railways to reach feeding grounds, mate, or disperse (Belant 1995, Bolger et al. 2008, Joshi et al. 2009). Wildlife-train collisions result in animal deaths, passenger safety, damage to freight, and train delays (Child and Stuart 1987, Andersen et al.

1991, Child et al. 1991). The frequency of collisions may be affected by factors associated with the biology and behavior of animals and population parameters (e.g., population density). Moreover, the variation of collisions usually shows spatiotemporal patterns that are influenced by topography surrounding railways (Joshi et al. 2009, Becker et al. 2011, Kušta et al. 2011, Schwender 2013, Jasińska et al. 2014), the intensity of rail traffic, train velocity (Seiler 2003), and weather conditions (Andersen et al. 1991, Gundersen et al. 1998). The effects of season and time of day on the frequency of railway collisions may also be important (Onoyama et al. 1998, Wells et al. 1999, Ando 2003). However, in comparison to roads, these seasonal and temporal effects are relatively poorly studied for railways (Steiner et al. 2014).

The temporal distribution of collisions on roads has been described with respect to various groups of mammals, including small- and medium-sized predators (Grilo et al.

Received: 8 July 2016; Accepted: 7 June 2017

¹E-mail: dagny.krauze@wl.sggw.pl

2009), large predators (Colino-Rabanal et al. 2011), and ungulates (Gundersen and Andreassen 1998, Eloff and van Niekerk 2008, Diaz-Varela et al. 2011, Lagos et al. 2012, Steiner et al. 2014). However, studies on the temporal distribution of collisions on railways are rare (Steiner et al. 2014) and pertain mainly to moose (*Alces alces*; Andersen et al. 1991, Child et al. 1991, Modafferi 1991, Gundersen et al. 1998) or sika deer (*Cervus nippon*; Onoyama et al. 1998, Ando 2003). Nevertheless, the distribution of wildlife mortality on railways can be substantially different from that recorded on roads (Child et al. 1991, Steiner et al. 2014), and there are no studies on the dynamics of ungulate mortality on railways at the country scale. In regard to the safety of railway traffic, collisions with large wild mammals are the most important to study; in Europe, these are mainly collisions with moose, red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*; Andersen et al. 1991, Gundersen et al. 1998, Kušta et al. 2011, Schwender 2013, Jasińska et al. 2014). One may expect a high probability of collisions with these animals in areas where population density is highest (Gundersen et al. 1998) and when animals show great mobility or form large groups (Gundersen et al. 1998, Bertwistle 2001, Lagos et al. 2012). Human disturbances may be an additional anthropogenic factor that increases the frequency of collisions (Lagos et al. 2012, Steiner et al. 2014).

Although various methods for protecting animals along railways have been tested (Babińska-Werka et al. 2015), empirical evidence on the spatial and temporal variations in the frequency of collisions in Poland is largely absent. The recent development and modernization of railways in Poland was followed by the appearance of fast trains, which when coupled with the high number of ungulates in Poland (Polish Hunting Association, www.czempin.pzlow.pl, accessed 12 Jun 2017) substantially increased the risk of collisions. We investigated the temporal variation of train collisions with the 4 most common ungulate species in Poland: roe deer, red deer, moose, and wild boar. Our objective was to describe the temporal pattern of train accidents related to these 4 ungulates. More specifically, using data on over 3,600 accidents that occurred throughout Poland and data on train traffic intensity from 2012 to 2015, we analyzed how the risk of collisions changed throughout the year, week, and time of day. We predicted that collision frequency would be highest during periods of high animal mobility, which can be influenced by behavior (e.g., higher during dispersal of young) and disturbances caused by people (e.g., hunting).

STUDY AREA

We conducted studies in Poland, east-central Europe ($14^{\circ}07' E$ – $24^{\circ}09' E$ and $49^{\circ}00' N$ – $54^{\circ}50' N$). Poland is mainly a lowland country with a mean elevation of 173 m but has uplands and mountains situated in the south. The country area is $312,680 \text{ km}^2$, 99.7% of which is terrestrial. Agricultural lands constitute 60% of the area, and the forest cover is 30.5% of the area. The climate in Poland is moderate with a transitional character between oceanic and continental climates. Annual mean temperature ranged from 7 – 8°C ,

with July being the warmest month of the year, and January the coldest month of the year. The length of the growing season lasted, on average, approximately 200 days. Annual precipitation was approximately 500 mm. The number of days with snow cover varied from 35 to 90 days, depending on the region, and the mean number of days with snow cover $>5 \text{ cm}$ throughout Poland was 35.5 days per year.

The railway infrastructure in Poland included 20,705 km of railways or $6.4 \text{ km of railways}/100 \text{ km}^2$ of the country area, and the total annual distance traveled by all the trains during a year exceeded $200,000,000 \text{ trains} \times \text{kilometer}$, which was over 500,000 km traveled by all trains each day. All 4 species of ungulates were game species in Poland; the moose, however, was subject to year-long protection. Hunting seasons differed depending on the species, sex, and age of game. Roe deer hunting was open from 11 May until 15 January, male red deer hunting was open from 21 August until 28 February, boar-hunting was yearlong but females were protected from 16 January until 14 August. Drive hunting was allowed only between 1 October and 31 January. In spring 2015, the estimated populations of the ungulate species before reproduction were 12,300 moose, 178,000 red deer, 806,000 roe deer, and 257,000 wild boar (www.czempin.pzlow.pl, accessed 12 Jun 2017).

METHODS

We gathered data on train collisions with wild mammal species in Poland from the Bureau of Environmental Protection, Polish Railways Polskie Koleje Państwowe SA. Specifically, the data were from the System of Exploitation Registering (SEPE), where live-time information is gathered by train dispatchers and on-duty officers. We collected date and hour of collision, animal species, number of train line, length of the railway, location where the collision occurred, and type of train (passenger or freight). We used data between 2012 and 2015 in the analyses. We recorded 4,037 collisions with mostly ungulates but also with other medium-sized mammals and large birds. We used only collisions with roe deer, red deer, moose, and wild boar (3,644 cases in total) because collisions with large ungulates pose a serious threat to the safety of railway traffic. Because information on the number of individuals killed on railways was incomplete and the data were collected for only a part of the study period, we considered each collision as a single case regardless of the number of individuals present during the collision.

We coded each recorded collision for day of year (ordinal day ranging from 1 to 366), time of week (weekdays vs. weekend), and season (spring = Mar–May, summer = Jun–Aug, autumn = Sep–Nov, winter = Dec–Feb). In addition, we noted the time of day (i.e., hr and min) of each collision based on reports from the SEPE system. Based on these attributes, we calculated the number of collisions/day (1,461 days: $365 \text{ days} \times 3 \text{ yr} + 366 \text{ days} \times 1 \text{ yr}$) and the distribution of collisions over a 24-hour period during a day. We based our estimations of dawn and dusk for any given day of the year on the predicted times for Łódź, Poland. For each ungulate species in our study, we distinguished their main life

cycles: rut, reproduction, dispersal, feeding newborns (Grilo et al. 2009), periods of higher demand for food (e.g., during pregnancy, antler development), and periods of higher mobility of animals (e.g., migration to winter or summer refugia), and herd formation (Table 1).

We used generalized additive mixed models (GAMMs) to determine whether the number of collisions changed over time during 2012–2015. We used the number of collisions per day over 4 years as response variables in the 4 GAMMs (1 for each species). Each model was based on 1,461 daily estimates. In each GAMM, we used the day of year (ranging from 1 to 366) as an explanatory variable fitted with cyclic penalized cubic regression splines whose ends match (i.e., assumed no. accidents is the same in day 1 and day 366; Wood 2006). To control the complexity of the fit, we set the upper limit for the effective degrees of freedom of the splines at 10. Splines used in GAMMs allow for the determination of nonlinear fit directly from the data, which is not the case when parametric nonlinear function is determined *a priori*, and allowed us to model non-linear relationships between the day of year and number of collisions. As a second explanatory variable, we used the time of week (with 2 levels, weekend vs. weekdays), which we used as a fixed categorical variable. Originally, we also tested the day of week (i.e., fixed categorical variable with 7 levels) but chose to use 2 levels instead for simplicity (i.e., there was a similar proportion of variance explained with fewer degrees of freedom). To account for possible variation in train traffic over time, we used the log-transformed number of kilometers traveled by all trains in a given month as an offset because we were not able to gather data on train traffic for each day. We addressed the between-year variation by including year as a random effect in the models. We performed GAMMs with a Poisson error distribution and log link using the mgcv package (Wood 2006) in R (R Core Team 2016).

We also analyzed the distribution of collisions during the day by comparing the observed distribution of the time of collisions against 1,000 random vectors of uniform distributions of the same length (independently for each species) to formally test whether the observed peaks of activity significantly deviated from random expectations. For all 1,000 permutations, we counted how many times the observed distribution was above or below the random distribution for each 30-minute interval. We assumed results outside the 25–975 range (i.e., 5% of permutations) indicated a significant (i.e., $P < 0.05$) deviation from random expectations. We plotted all 3,644 collisions along time of day and day of year axes to show non-random distribution of the collisions over the 2 time scales. Finally, we outlined 50% kernel density estimation (using the bivariate normal kernel) of plotted day of year and time of day (i.e., extracted contour of minimum area in which half of all the data points are located; Calenge 2006) to show that collisions are aggregated in time. All the simulations were conducted in R.

RESULTS

We recorded 3,644 train collisions of wild ungulates: 362 in 2012, 750 in 2013, 1,074 in 2014, and 1,458 in 2015. The most frequent ungulates in collisions were roe deer (52%), then wild boar (29%), red deer (14%), and moose (5%). The highest number of recorded collisions in 1 day throughout Poland was 9. In addition, there were 5 days with 7 collisions recorded, 8 with 6, 17 with 5, 42 with 4, and 78 with 3 collisions in 1 day throughout the country.

The monthly distribution of train collisions with ungulates varied over the year (Fig. 1, Table 2). Most cases were recorded during autumn and winter; 68% of all collisions occurred between October and March. The fewest animals (7% cases) died on railways in June and July. The temporal pattern of collisions was similar for all species: the highest

Table 1. Life cycles of the 4 ungulate species (roe deer, red deer, moose, wild boar) involved in wildlife-train collisions, Poland, 2012–2015.

Species	Class	Description	Period
Roe deer	1	In winter herds	15 Nov–Feb
	2	Disintegration of winter herds, occupying territories by males	Mar–Apr
	3	Pregnant females give birth, dispersion	May–15 Jun
	4	Parental care of newborn young	15 Jun–15 Jul
	5	Rut	15 Jul–15 Aug
	6	Breeding, males leaving territories	15 Aug–15 Oct
	7	Forming winter herds	15 Oct–15 Nov
Red deer	1	In winter herds, concentration in forests	Nov–Jan
	2	Males shedding antlers, disintegration of winter groups	Feb–Mar
	3	Feeding (growing antlers, pregnancy)	Apr–15 May
	4	Pregnant females give birth, dispersion of the previous year's young	15 May–Jun
	5	Parental care of newborn young, feeding before rut	Jul–Aug
	6	Forming larger herds, rut	Sep–Oct
Moose	1	Concentration in forest refugia	Nov–Feb
	2	Spread into summer refugia	Mar–15 May
	3	Pregnant females give birth, dispersion of previous year's young	15 May–Jun
	4	Parental care of newborn young, feeding before rut	Jul–Aug
	5	Rut	Sep–15 Oct
Wild boar	6	Migration to forest refugia	15–30 Oct
	1	Winter herds, concentration in forests	Jan–15 Feb
	2	Disintegration of herds, pregnant females give birth, and dispersion of previous year's young	15 Feb–15 May
	3	Parental care of newborn young, feeding on fields, and migration among crops	15 May–Oct
	4	Migration to forest areas, forming herds and rut	Nov–Dec

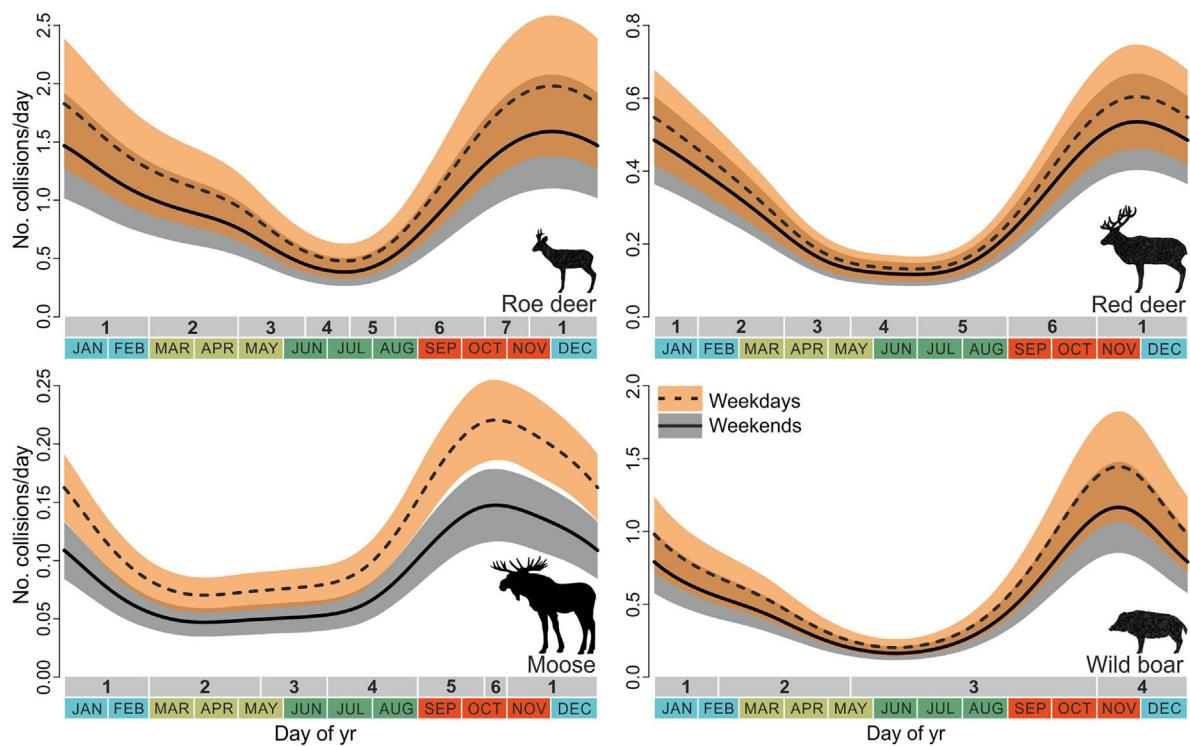


Figure 1. Average number of wildlife-train collisions of roe deer, red deer, moose, and wild boar per day (curves, accompanied by SE marked with transparent polygons) in Poland, 2012–2015, as predicted by generalized additive mixed models (GAMMs). Numbers at the bottom of each subplot refer to life cycle of the species (Table 1).

numbers of collisions were recorded in autumn and winter (all species), whereas the lowest were in summer (roe deer, red deer, and wild boar) or spring (moose; Fig. 1). Most collisions with roe deer occurred in November and December when animals formed and stayed in large winter herds. The fewest collisions occurred between June and August (i.e., during the breeding season; Fig. 1, Table 1). The pattern of red deer mortality by train collisions was similar with the

peak in November and December when red deer formed winter herds and concentrated in winter forest refugia. The fewest collisions occurred when females gave birth and calves stayed with their mothers (i.e., between May and Aug; Fig. 1). The pattern was slightly different for moose; they were most often struck on railways between September and December, with a peak in October (16% of cases), when moose migrate to forest refugia, but the lowest probability of collision was recorded in March (Fig. 1, Table 2). The highest mortality for wild boar occurred between October and December (>16% of cases in each month), which was associated with rutting, forming winter herds, and migrating to forest areas. The fewest collisions for wild boar occurred between May and July (2–3% of cases), when wild boar take care of newborn young and feed on agricultural lands (Fig. 2, Table 1).

For all species except red deer, the number of collisions was significantly lower during weekends compared to weekdays (Fig. 1, Table 2). The distribution of collisions over time of day, which was significantly different from uniform random distribution, showed 2 peaks: morning and evening. A similar pattern was recorded for all 4 species (permutation test, $P < 0.001$ in all cases). The probability of train collisions with ungulates was much lower during the day, with only single events observed between 0800 and 1600 (Fig. 2). The duration of this collision-free period in the middle of the day was substantially shorter in winter and longer in summer, following changes in the duration of daylight over the year. We observed another collision-free period between midnight and 0400 (Fig. 2). Half of all the collisions were reported in

Table 2. Generalized additive mixed models analyzing the effects of type of day (weekdays vs. weekend) and day of year (1–366) fitted with spline (s) on the number of wildlife-train collisions of 4 ungulate species (roe deer, red deer, moose, wild boar) in Poland, 2012–2015. We present the estimated number of degrees of freedom of splines (edf) and explanatory power of each model (R^2_{adj}).

Predictor	Estimate	SE	t or F	P
Roe deer ($R^2_{\text{adj}} = 13.4\%$)				
Intercept	-9.68	0.30	32.1	<0.001
Weekend	-0.22	0.05	4.1	<0.001
s(day of year)	edf = 5.90		39.2	<0.001
Red deer ($R^2_{\text{adj}} = 7.5\%$)				
Intercept	-11.00	0.23	48.4	<0.001
Weekend	-0.12	0.10	1.2	0.229
s(day of year)	edf = 4.42		15.2	<0.001
Moose ($R^2_{\text{adj}} = 2.5\%$)				
Intercept	-11.91	0.12	101.5	<0.001
Weekend	-0.40	0.19	2.1	0.032
s(day of year)	edf = 3.36		4.1	<0.001
Wild boar ($R^2_{\text{adj}} = 17.3\%$)				
Intercept	-10.35	0.26	40.0	<0.001
Weekend	-0.21	0.07	3.0	0.003
s(day of year)	edf = 5.47		40.2	<0.001

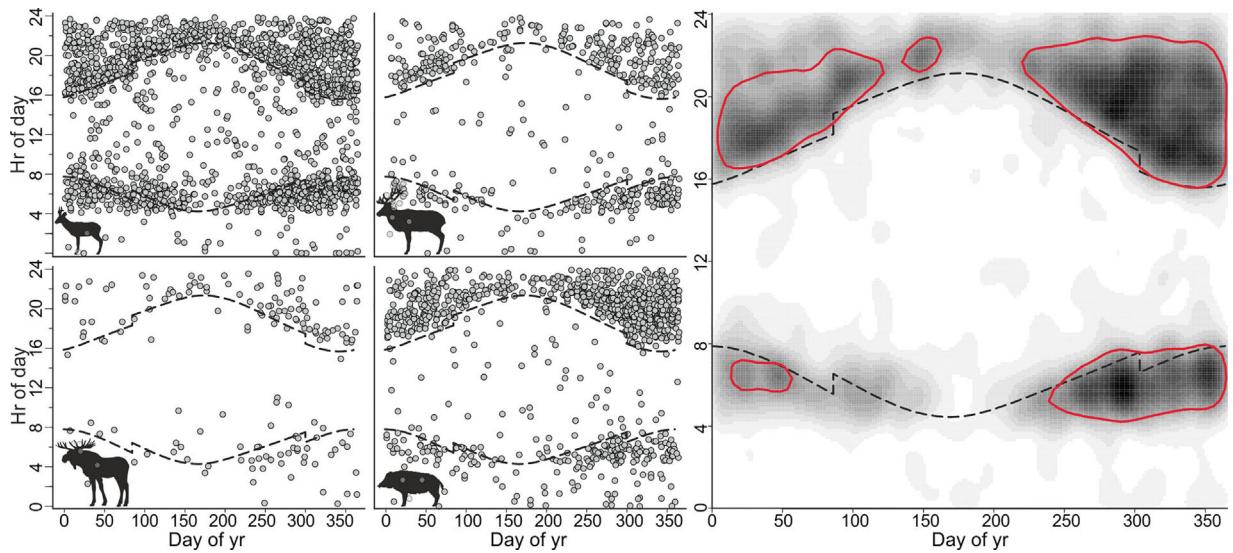


Figure 2. Distribution of the observed wildlife-train collisions over days of year and time of day for 4 species (roe deer, red deer, moose, wild boar; 4 left-hand subplots) and visualized with kernel density estimation for all the species pooled (right-hand subplot) in Poland, 2012–2015. Sunset and sunrise are shown with dashed curves at each subplot, solid line on the right-hand subplot outlines 50% of all the data points.

17% of the 2-dimensional time space (Fig. 2, right-hand subplot).

DISCUSSION

The distribution of wildlife mortality on roads and railways depends on animal behavior, which reflects annual fluctuations of weather and habitat conditions. It may be additionally affected by disturbances caused by predators, hunting, and tourists. The intensity of traffic is therefore unlikely to be the only factor that affects the pattern of mortality on commuter routes (Bertwistle 2001, Neumann et al. 2012, Steiner et al. 2014, Kušta et al. 2017). In our study, wildlife-train collisions varied with periods of high- and low-risk of collision depending on the time of year and time of day. This variability can be explained by seasonal variations in the number of animals and in changes in their behavior and activity associated with biological cycles (Steiner et al. 2014). However, train traffic intensity also contributed to the patterns of collisions. The collision-free period between midnight and 0400 corresponds to very low train traffic.

Many studies describe seasonal patterns in the mortality of ungulates on commuter routes, although they differ among species and regions (Steiner et al. 2014). In our study, the highest probability of collision for every species was autumn (mainly Oct–Nov). The pattern we observed could have at least 3 causes. First, all 4 ungulate species attain their highest population densities and form large winter herds in autumn. The higher abundance of animals may increase the risk of train collisions (Gundersen et al. 1998). The higher probability of collisions may also be due to altered animal behavior during the formation of winter herds (Steiner et al. 2014). For example, some individuals might be separated from the herd and become victims of collisions when trying to join their group (Eloff and van Niekerk 2008). In addition, it takes a longer time for large herds to cross commuter routes

than individuals or smaller groups (Baofa et al. 2006). However, Ando (2003) did not report a simple relationship between the size of sika deer herds crossing railways and the frequency of collisions, and the highest number of collisions occurred when sika deer populations were at their greatest densities in winter refugia.

Second, the high frequency of collisions during autumn and winter may be associated with higher mobility of animals during this period. Increased mobility may be from large-scale migration from summer areas to winter refugia and everyday movements between foraging and resting sites. Seasonal migration of animals to winter refugia is one of the factors reported to significantly increase the risk of collision on roads and railways in Canada (Bertwistle 2001), and increased mortality of roe deer on roads in winter has been explained by individuals searching for food (Steiner et al. 2014). According to our results and Steiner et al. (2014), red deer are killed on commuter routes mainly during the second half of the year (peak mortality is most often in Oct), which is associated with a greater mobility during rutting and the period afterwards. In studies on moose mortality on commuter routes, the time of rutting is indicated as a period of increased mortality (Steiner et al. 2014). In southern Sweden, animals died on roads mainly in September and October (Steiner et al. 2014). The distribution of moose mortality on roads, however, differs from that on railways (Child et al. 1991, Steiner et al. 2014). In Canada, 2 peaks of mortality were recorded on roads: the first one in December–January and a second smaller one in summer (Jun–Aug). However, >50% of collisions on railways took place in January and February, whereas the number of collisions in summer was low (Child et al. 1991). According to Steiner et al. (2014), in Sweden, moose mortality on railways is limited to 1 peak between December and March and depends on the amount of snow cover (Child 1983, Andersen et al. 1991, Gundersen et al. 1998). Seasonal

migrations of animals are associated with intensive snowfall. During a winter with high levels of snow cover, moose use railways as migration routes, and surrounding areas of high snow cover may make it difficult to escape approaching trains (Child 1983, Andersen et al. 1991, Gundersen et al. 1998). As with other ungulate species, wild boar died on Polish railways mainly in autumn. Our findings correspond with studies of wild boar in Spain where peak mortality on railways occurred between autumn and winter (Diaz-Varela et al. 2011, Lagos et al. 2012, Rodríguez-Morales et al. 2013). These incidents may be explained by higher mobility of animals during rutting (Diaz-Varela et al. 2011, Rodríguez-Morales et al. 2013) when animals form larger herds.

Thirdly, the number of collisions may be additionally boosted by local disturbances such as tourism and hunting. Several studies reported that hunting may increase the probability of collisions on roads (Lagos et al. 2012, Steiner et al. 2014) by inciting random movements in startled game (Diaz-Varela et al. 2011, Rodríguez-Morales et al. 2013). In Spain, hunting, even outside of the rutting season, affected the frequency of collisions with roe deer. Additionally, more than half of all collisions with wild boar occurred during the hunting season (Lagos et al. 2012). Similarly, in our study, most of the incidents took place during the hunting season so we cannot exclude the possibility that hunting activity contributed to the overall collision rate. However, the effect of hunting is confounded with remaining seasonal effects (e.g., weather conditions, increased herd size). Thus, this issue needs to be addressed in separate studies. We assume that drive hunting may be a factor that affects the frequency of ungulate collisions with trains. If so, one can expect a higher frequency of collisions on days when drive hunts are organized. In Poland, collective hunts are typically organized on Saturdays and Sundays between 1 October and 31 January. Hunting increased collisions of ungulates on roads in Spain (Lagos et al. 2012), but Rodríguez-Morales et al. (2013) reported no such dependence. Nevertheless, in our study, the number of collisions on weekdays was higher than on weekends throughout the year.

The period of reproduction and dispersal of young significantly affects the probability of collision with ungulates (Rodríguez-Morales et al. 2013, Steiner et al. 2014) and other animals (e.g., predators; Grilo et al. 2009, Colino-Rabanal et al. 2011). Most studies on roe deer reported peak mortality recorded in spring and summer (Diaz-Varela et al. 2011, Lagos et al. 2012, Rodríguez-Morales et al. 2013, Steiner et al. 2014) and was associated with reproduction and dispersal of yearlings (Rodríguez-Morales et al. 2013, Steiner et al. 2014). In addition, some studies explain higher mortality in July as being caused by rutting (Lagos et al. 2012, Rodríguez-Morales et al. 2013, Steiner et al. 2014), greater mobility of animals (Eloff and van Niekerk 2008, Rodríguez-Morales et al. 2013), and greater intensity of traffic on roads during holidays (Rodríguez-Morales et al. 2013). We found the lowest probability of wildlife-train collisions for all species during July. This divergence in pattern is likely due to differences between traffic intensity during summer on roads, where the

number of vehicles increases greatly, and on railways, where such differences are less pronounced.

Dawn and dusk were associated with increased risk of collision, probably reflecting the increased activity of animals moving between resting and foraging areas. Accidents with moose on traffic routes occurred mainly between 0400 and 0700 and between 2000 and midnight. These times refer to a biphasic crepuscular activity pattern in moose and other cervids (Steiner et al. 2014). In Spain, most collisions with wild boar on roads occurred during the night (Diaz-Varela et al. 2011, Rodríguez-Morales et al. 2013), with the length of night affecting the probability of collision with wild boar (Lagos et al. 2012). This pattern is especially noticeable in autumn and winter. When dusk occurs relatively early in a period where traffic intensity on roads is still high, the probability of collisions is high for a few hours afterwards (Rodríguez-Morales et al. 2013). According to Kušta et al. (2017), collisions peak when ungulates have the highest level of activity, which is a more important factor in probability of collision than road traffic intensity. We found a distinct collision-free gap between midnight and 0400, which is most likely caused by substantially lower levels of train traffic (Babińska-Werka et al. 2015). We therefore conclude that the final temporal pattern of wildlife-train collisions is influenced by both animal activity and traffic intensity.

MANAGEMENT IMPLICATIONS

Our study shows that train traffic is an important source of ungulate mortality. Also, collisions with wildlife can prolong journey time and as a result reduce cost-effectiveness of railway companies, and can result in delays and damage to freight, creating monetary losses. The observed pattern of wildlife-train collisions in Poland is a combination of temporal variation in train traffic and changes in the behavior and density of animals. Thus, in certain parts of the railway where collisions are most numerous, lowering speed limits could be implemented during periods of elevated collision risk. Future studies should focus on possible ways to warn drivers about animals presence on tracks (i.e., infrared cameras mounted on trains) to enable them to react by slowing down, stopping the train, or using acoustic signals that would deter animals from the railway track.

LITERATURE CITED

Andersen, R., B. Wiseth, P. H. Pedersen, and J. Jaren. 1991. Moose-train collisions: effects of environmental conditions. *Alces* 27:79–84.

Ando, C. 2003. The relationship between deer-train collisions and daily activity of the sika deer, *Cervus nippon*. *Mammal Study* 28:135–143.

Babińska-Werka, J., D. Krauze-Gryz, M. Wasilewski, and K. Jasieńska. 2015. Effectiveness of an acoustic wildlife warning device using natural calls to reduce the risk of train collisions with animals. *Transportation Research Part D* 38:6–14.

Baofa, Y., H. Huyin, L. Zhou, and W. WanHong. 2006. Influence of the Qinghai-Tibetan railway and highway on the activities of wild animals. *Acta Zoologica Sinica* 26:3917–3923.

Becker, S. A., R. M. Nielson, D. G. Brimeyer, and M. J. Kauffman. 2011. Spatial and temporal characteristics of moose highway crossings during winter in the Buffalo Fork Valley, Wyoming. *Alces* 47:69–81.

Belant, J. 1995. Moose collisions with vehicles and trains in Northwestern Minnesota. *Alces* 27:31–45.

Bertwistle, J. 2001. Description and analysis of vehicle and train collisions with wildlife in Jasper National Park, Alberta Canada, 1951–1999. Pages 433–434 in L. Irwin, P. Garrett, and K. P. McDermott, editors. Proceedings of the 2001 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, USA.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* 11:63–77.

Cain, A. T., V. R. Tuovila, D. G. Hewitt, and M. E. Tewes. 2003. Effects of a highway and mitigation projects on bobcats in Southern Texas. *Biological Conservation* 114:189–197.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

Child, K. N. 1983. Railways and moose in the central interior of British Columbia: a recurrent management problem. *Alces* 19:118–135.

Child, K. N., S. P. Barry, and D. A. Aitken. 1991. Moose mortality on highways and railways in British Columbia. *Alces* 27:41–49.

Child, K. N., and K. M. Stuart. 1987. Vehicle and train collision fatalities of moose: some management and socio-economic considerations. *Swedish Wildlife Research Supplement* 1:699–703.

Colino-Rabanal, V. J., M. Lizana, and S. J. Peris. 2011. Factors influencing wolf *Canis lupus* roadkills in Northwest Spain. *European Journal of Wildlife Research* 57:399–409.

Díaz-Varela, E. R., I. Vazquez-Gonzalez, and M. F. Marey-Pérez. 2011. Assessing methods of mitigating wildlife-vehicle collisions by accident characterization and spatial analysis. *Transportation Research, Part D* 16:281–287.

Di Giulio, M., R. Holderegger, and S. Tobias. 2009. Effects of habitat and landscape fragmentation on humans and biodiversity in densely populated landscapes. *Journal of Environmental Management* 90:2959–2968.

Eloff, R., and A. van Niekerk. 2008. Temporal patterns of animal-related traffic accidents in the Eastern Cape, South Africa. *South African Journal of Wildlife Research* 38:153–162.

Grilo, C., J. A. Bissonette, and M. Santos-Reis. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. *Biological Conservation* 142:301–313.

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

Gundersen, H., H. P. Andreassen, and T. Storaas. 1998. Spatial and temporal correlates to Norwegian moose-train collisions. *Alces* 34:385–394.

Ito, T. Y., B. Lhagvasuren, A. Tsunekawa, M. Shinoda, S. Takatsuki, B. Buuveibaatar, and B. Chimedderj. 2013. Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. *PLoS ONE* 8(2): e56995.

Jaren, V. R., R. Anderson, M. Ulleberg, P. Pederson, and B. Wiseth. 1991. Moose-train collisions: the effects of vegetation removal with a cost-benefit analysis. *Alces* 27:93–99.

Jasińska, K., J. Werka, D. Krauze-Gryz, and M. Wasilewski. 2014. Urządzenia akustyczne UOZ-1 sposobem na ograniczenie kolizji z udziałem zwierząt na liniach kolejowych. *Sylwan* 158:143–150. [In Polish.]

Joshi, R., R. Singh, B. D. Joshi, and R. S. Gangwar. 2009. Decline of the Asian elephants (*Elephas maximus*) from Hardwar Forest Range of the Rajaji National park, India: the first documented case of free-ranging wildlife species. *New York Science Journal* 2:1–12.

Kušta, T., M. Ježek, and Z. Keken. 2011. Mortality of large mammals on railway tracks. *Scientia Agriculturae Bohemica* 42:12–18.

Kušta, T., Z. Keken, M. Ježek, M. Holá, and P. Šmíd. 2017. The effect of traffic intensity and animal activity on probability of ungulate-vehicle collisions in the Czech Republic. *Safety Science* 91:105–113.

Lagos, L., J. Picos, and E. Valero. 2012. Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. *European Journal of Wildlife Research* 58:661–668.

Modafferi, R. D. 1991. Train moose-kill in Alaska: characteristics and relationship with snowpack depth and moose distribution in lower Sustina Valley. *Alces* 27:193–207.

Neumann, W., G. Ericsson, H. Dettki, N. Bunnefeld, N. S. Keuler, D. P. Helmers, and V. C. Radeloff. 2012. Difference in spatiotemporal patterns of wildlife road-crossing and wildlife-vehicle collisions. *Biological Conservation* 145:7–78.

Onoyama, K., N. Ohsumi, N. Mitsumochi, and T. Kishihara. 1998. Data analysis of deer-train collisions in eastern Hokkaido, Japan. Pages 746–751 in C. Hayashi, K. Yajima, H. H. Bock, N. Ohsumi, Y. Tanaka, and Y. Baba, editors. *Data science, classification, and related methods*. Springer, Tokyo, Japan.

R Core Team 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rodríguez-Morales, B., E. R. Díaz-Varela, and M. F. Marey-Pérez. 2013. Spatiotemporal analysis of vehicle collisions involving wild boar and red deer in NW Spain. *Accident Analysis and Prevention* 60:121–133.

Schwender, M. R. 2013. Mule deer and wildlife crossings in Utah, USA. Thesis, Utah State University, Logan, USA.

Seiler, A. 2003. The toll of the automobile: wildlife and road in Sweden. Dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Steiner, W., L. Friedrich, and K. Hackländer. 2014. A review on the temporal pattern of deer-vehicle accidents: impact of seasonal, diurnal and lunar effects in cervids. *Accident Analysis and Prevention* 66:168–181.

Wasilewski, M., J. Babińska-Werka, and P. Nasiadka. 2009. Możliwość wykorzystania sygnałów dźwiękowych do odstraszania zwierząt od torów kolejowych. *Studia i Materiały Centrum Edukacji Przyrodniczo-Leśnej* 2(21):97–104. [In Polish.]

Wells, P., J. G. Woods, G. Bridgewater, and H. Morrison. 1999. Wildlife mortalities on railways, monitoring methods and mitigation strategies. Pages 85–88 in G. L. Evink, P. Garrett, and D. Zeigler, editors. *Proceedings of the Third International Conference on Wildlife Ecology and Transportation*. Florida Department of Transportation, Tallahassee, Florida, USA.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Associate Editor: Melanie Bucci.