Factors influencing wolf roadkills in Northwest Spain

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Factors influencing wolf *Canis lupus* roadkills in Northwest Spain

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Abstract Roadkill is one of the most prominent causes of wildlife mortality. Much research effort has focussed on collisions with ungulates because of traffic safety. However, studies about large carnivore roadkills are scarce despite vehicles being a main cause of mortality. The absence of studies can be explained in part because of difficulties in obtaining sufficient sample sizes. We collected data from locations of 82 wolf roadkill sites in the Castilla y León Region, northwest Spain. We evaluated different models to characterise collision localities using logistic regressions with corrections for rare events. The best models included traffic and human disturbance parameters. Landscape variables did not improve predictive power. Fencing was a decisive key predictor; roadkill was proportionally higher along fenced highways than on similar major roads that lacked fences. Wolf–vehicle collisions were more common in agricultural areas, although wolf densities were lower in these zones. Both the higher density of important roads and a greater proportion of roaming wolves on the plateau may explain this pattern.

Keywords Animal–vehicle collisions · Carnivores · Fencing · Logistic modelling · Roads · Wolf

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Introduction

Wildlife–vehicle collisions have increased in many parts of the world in recent decades with associated property damage, injury and fatalities (Conover et al. 1995). In Europe, accidents involving large mammals include wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and elk *Alces alces* (Groot-Bruinderink and Hazebroek 1996). Although some populations may be at risk, road mortality is not a global threat to these species. The objective of mitigation is typically enhanced traffic safety rather than conservation. Important research efforts have focussed on identifying factors that explain the spatio-temporal distribution of roadkills, especially ungulates (Puglisi et al. 1974; Bashore et al. 1985; Finder et al. 1999; Hubbard et al. 2000; Joyce and Mahoney 2001; Nielsen et al. 2003; Malo et al. 2004; Mysterud 2004; Seiler 2004, 2005), but also large carnivores (Kolowski and Nielsen 2008) and smaller mammals (Inbar and Mayer 1999; Clevenger et al. 2003; Ramp et al. 2005; Bissonette and Rosa 2009; Grilo et al. 2009).

Nonetheless, roads can be one of the main mortality factors for large carnivores and have serious negative impacts on carnivore populations. Large carnivores have several characteristics that make them more vulnerable to road impacts: small population sizes, large home ranges with long daily movements and often behaviour that results in conflicts with human interests (Noss et al. 1996; Crooks 2002). For the Iberian lynx *Lynx pardinus*, roadkills accounted for 37.1% of the deaths (33 of 89) in the Parque Nacional de Doñana, Spain, between 1982 and 2004 (Ferreras et al. 1992; Ministerio de Medio Ambiente 2004). In Florida, half of cougar *Felis concolor* deaths are caused by vehicles (Harris and Gallagher 1989; Maehr 1991).

The impact that roads have had on large carnivores is not limited to road mortality; habitat fragmentation and barrier effects may be the largest long-term threats to their population viability (McLellan and Shackleton 1988; Mace et al. 1996; Tigas et al. 2002; Kaczensky et al. 2003). Crossing structures are intended to improving connectivity by joining landscapes. The improvements made by underpasses and overpasses for use by large carnivores have been confirmed in several studies (Foster and Humphrey 1995; Rodríguez et al. 1996, 1997; Gloyne and Clevenger 2001; Grilo et al. 2008).

We investigated the possibility of modelling the spatial distribution of road-killed wolves *Canis lupus* that have large home ranges and long daily movements and use several kinds of habitat. Wolf–roads interactions have been studied previously. Wolves prefer landscapes without roads and avoid establishing territories in areas with a road density higher than 0.6 km/km^2 (Thiel 1985; Mech 1989; Mladenoff et al. 1995). Highways and major roads impede long-distance movements (Thurber et al. 1994; Paquet and Callaghan 1996), but transverse structures across linear infrastructures can reduce the barrier effect (Clevenger and Waltho 2000). Other authors have reported that highways are not a significant obstacle (Kohn et al. 1999) or, at least, fragmentation caused by a linear natural element, such as the River Duero, is greater than that caused by a four-lane highway (Blanco et al. 2005).

We are unaware of specific research about spatio-temporal distributions of wolf roadkill, although wolf mortality on roads is widely documented. There are several studies from the Mediterranean region documenting road mortality in wolves. In Italy, 52.0% (76 roadkills) between 1991 and 2001 (Lovari et al. 2007) and in Croatia, 24.2% (15 roadkills) between 1996 and 2001 (Huber et al. 2002) of the wolf mortality recorded were due to collisions with vehicles. Elsewhere, in Scandinavia, 26% of deaths (n=84) were roadkill (Olsen 2003). In North America, on US Highway 53 in Wisconsin, one of 59 radio-tracked wolves and two non-telemetered wolves were killed on a road network during a 6-year study (Kohn et al. 1999). In Banff National Park, Canada, 16 wolf roadkills were recorded during an 18-year period (Clevenger et al. 2001).

The aim of this research is to describe which variables best characterise wolf–vehicle collisions in order to reduce the number of roadkills and improve mitigation planning decisions (Bissonette and Adair 2008). These parameters can be relative to traffic, landscape features or the degree of human presence.

Materials and methods

Study area and wolf populations

We conducted this study in the Castilla y León Region, which is situated in the Northwest Iberian Peninsula and including the North Plateau and the peripheral mountainous area around it. Its total area is 94,223 km^2, but wolf populations are not present in the whole region. Human population density is low, 26.57 inhabitants/km^2, and concentrated in towns and cities; there are also, however, many small villages throughout the region. There are two main landscapes within the study region. The plateau, now a grain-producing farmland landscape, is situated in the centre of the region, with a flat topography associated with the sediments of the River Duero and its tributaries. Surrounding the plateau, there is a range of mountains that can exceed 2000 m in height. Cattle grazing and forestry uses are the most common land-uses in the peripheral mountains (Fig. 1). Castilla y León road type characteristics are described in Table 1.

Wolf populations have increased in both Europe and North America, re-colonising agricultural regions where they were formerly extirpated (Mech 1995; Boitani 2003). Wolves now occupy the northwestern quadrant of the Iberian Peninsula and have a current population estimated at 2,000 individuals (Blanco et al. 2007). In the Castilla y León Region, the most recent census is 149 packs (107 confirmed and 42 probable). Wolves occupy a part of 75,200 km^2, mainly to the north of the River Duero, although some have managed to cross the river and some packs are established to the south of this river. Populations have experienced a continuous expansion that indicates saturation of areas previously occupied and re-colonisation of former parts of their distribution that are now transformed into agricultural lands. Both spatial distribution and population size have increased slowly, but continuously. Maximum densities are found in the northwest (32 packs estimated in 8,000 km^2) and the north (30 packs in 7,000 km^2). The lowest density is located to the south of the River Duero, with only around 15 packs in 19,700 km^2 (Llaneza and Blanco 2005).

Data collection

We collected a total number of 82 reports about road-killed wolves in the period 2001–2007. The data were derived from reports submitted by traffic safety authorities. We have also collected data from the Section of Natural Spaces and Protected Species of the Junta de Castilla y León (Regional Government). These data include information about the road and the kilometre point where the collision took place and the date and time of the event. Only 77 of the 82 collision sites were well defined. In 9.09% of the data, the level of accuracy had an error of 500 m, and in the other 90.90%, the level of accuracy was 50 m (if the hectometre was included in the record). This level of accuracy avoids the problem cited by Gunson et al. (2009). Nonetheless, higher errors could be introduced by the collision localities in fenced highways because, once they have managed to enter the fenced highway zone, wolves could move and be road-killed on

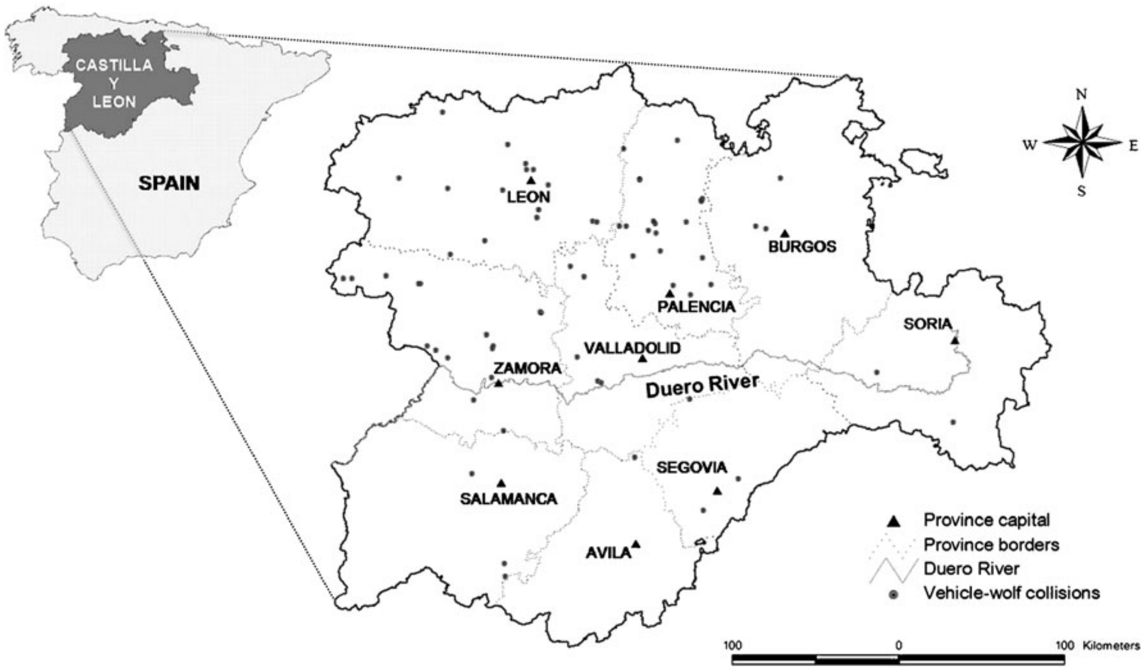

Fig. 1 Location of the study area. *White points* indicate wolf roadkill localities in the Castilla y León road network from 2001 to 2007. Data were obtained from reports by traffic safety and environmental authorities

the road far away from the access point. The number of road-killed wolves is likely to be higher (Slater 2002). We have not been able to estimate the unreported collision percentage, but it could be significant. The wolf is an emblematic species, and it is probable that some drivers involved in a vehicle–wolf collision, frightened of being fined, may decide not to report the collision to traffic safety authorities.

Table 2 shows the 17 variables included in wolf–vehicle collision modelling. Traffic volume and velocity were extracted from the 2005 Map of Traffic Volume and Speed recorded by the Department of Development of the Junta de Castilla y León or by the Ministry of Development depending on the authority responsible. Sinuosity was calculated from digital road maps using a 2-km segment with the roadkill location as the centre of the segment.

Land uses were obtained from the National Forestry Map made from aerial photography by the Spanish Ministry of the Environment at a scale of 1:50,000. This land-use classification defines 33 land uses. We have only taken into account those which have greater ecological and quantitative importance (Table 2). Other geographical elements were extracted from topographic digital maps at a scale of 1:50,000. Slope was derived from a digital elevation model (resolution of 25 m) produced by the Spanish National

Table 1 Main characteristics of the different types of roads within Castilla y León road network

Type of road	Function	Number of lanes	Traffic volume and speed	Fencing
Motorways	Connect the main cities throughout the country	4 or more	High	Always fenced; conventional road fences of 1.8 m in height, made of galvanised steel with a mesh size of 10–15 cm and a distance of about 4 m between posts
National roads	Connect important populated areas at a national scale	2	High–medium	Rarely fenced
Regional roads	Connect important populated areas at a regional scale	2	Medium	Rarely fenced
Secondary roads	Connect villages and other less frequented places	2	Low	Rarely fenced

Table 2 Traffic, landscape and human presence variables measured for both roadkill localities and random distributed control sites

	Variables	Units	Type
TM	Traffic density (density)	Hundreds of vehicles per day	Continuous
	Traffic speed (speed)	Kilometres per hour	Continuous
	Road length/linear distance (sinuosity)	Dimensionless	Continuous
	1.8-m height fences along roads (fences)	Presence/absence	Discrete
LM	Slope	%	Continuous
	Proportion of forest (forest)	%	Continuous
	Proportion of reforested area (reforest)	%	Continuous
	Proportion of shrubs (shrubs)	%	Continuous
	Proportion of unirrigated crops (unirrigat)	%	Continuous
	Proportion of irrigated crops (irrigated)	%	Continuous
	Distance to river or stream (water)	Hundreds of metres	Continuous
	Shannon landscape diversity index (SDI)	Dimensionless	Continuous
	Ecotone density (ED)	Dimensionless	Continuous
AM	Distance to populated area (popularea)	Hundreds of metres	Continuous
	Distance to municipal border (municbord)	Hundreds of metres	Continuous
	Distance to railway (railway)	Hundreds of metres	Discrete
	Distance to canal (canal)	Hundreds of metres	Discrete

Variables were grouped in three types of models: traffic parameters' model (TM), landscape parameters' models (LM) and anthropogenic influence parameters model (AM). Landscape variables were considered on three spatial scales using buffers of 1,000, 2,500 and 5,000 m

Geographic Institute from contour lines and elevation points contained in the National Topographic Map at a scale of 1:25,000. Software used in geographical information system analyses was ArcGis 9.0. (ESRI Corp).

Statistical analysis

Logistic regression for rare events

We modelled the characteristics of wolf roadkill sites using a logistic regression. This kind of regression describes the relationship between a dichotomous variable (Y) and a group of independent variables (x_1, x_2,..., x_n). Explanatory variables can be continuous or discrete and do not have to follow normal distribution. The function can be written as

$$P(Y=1)=\widehat{p}=\frac{1}{1+e^{-(\alpha+\beta_1x_1+\beta_2x_2+\ldots+\beta_nx_n)}}$$

We compared the observed distribution to a random distribution. Because the sample sizes of large carnivore roadkills in studies, such as ours, are often small, the random point distribution will be low too, and we could introduce a bias in spite of random assumption. A solution could be to compare roadkill distribution with a larger number of generated random points. Thus, we can treat wolf roadkills as a rare event in a finite sample. For rare events, the positive event number is much lower than negative events. However, logistic regression robustness requires that positive/negative observations are not unbalanced. Unbalanced data can introduce severe bias in probability prediction (Cramer 1999; King and Zeng 2001). King and Zeng (2001) have developed a method for these cases that incorporates three corrections for logistic regression.

Firstly, we do not compare wolf roadkill distribution with a matched number of random points, but rather we selected a 0-s sample five times more numerous, which is more representative and less influenced by randomness.

If sample generation responds to a case-control design, a second correction is required. This so-called prior correction is intended to avoid bias in logistic coefficients because of dependent variable selection (King and Zeng 2000, 2001). Intercept β_0 is corrected using the following equation:

$$\beta_0=\widehat{\beta}_0-\ln\left[\left(\frac{1-\tau}{\tau}\right)\left(\frac{\overline{y}}{1-\overline{y}}\right)\right] \quad (1)$$

where τ is the actual fraction of 1 s in the population, and y the observed fraction of 1 s in the sample data.

However, we can underestimate the probability when we substitute the corrected coefficient in Eq. 1 because of uncertainty in the estimation of $\hat{\beta}$. For this reason, a third correction is required, incorporating the sum of a factor C_i to $\widetilde{p}_i$. Corrected probabilities are

$$P(Y_i=1)=\widetilde{p}_i+C_i$$

Factor C_i for each element can be obtained using the equation:

$$C_i=(0.5-\widetilde{p}_i)\widetilde{p}_i(1-\widetilde{p})XV(\beta)X'$$

where $V(\beta)$ is the variance–covariance matrix, X is a $1\times(n+1)$ vector of values for each independent variable and X' is the transposed matrix of X.

Initially, in order to identify which of the selected putative predictor variables differed between roadkill and random point distributions, we developed a univariate means comparison using an unpaired sample *t* test. Univariate logistic regressions were used for categorical variables. Variables with significant differences between both distributions ($\alpha>0.1$) were included in later models. We generated stepwise logistic models with rare event corrections using the zelig analysis package available in the statistical software *R* (Imai et al. 2007, 2008). Before this analysis, we calculated bivariate correlations to detect undesired multi-co-linearity effects. We removed one of the variables when the correlation was higher than 0.7, selecting the variable with a lower *t* statistic in the univariate test for elimination.

We generated several models with the different variable types that could explain the spatial distribution of wolf–vehicle collisions (Table 3): traffic and road characteristics (traffic model (TM)), surrounding landscape (landscape model (LM)) or degree of disturbance by human elements (anthropogenic model (AM)). Each model was first tested separately, and later, all possible combinations between them were tried. We analysed the landscape model using three spatial scales (radii of 1,000, 2,500 and 5,000 m around a point) to identify the optimum spatial scale for analysis. Significance level to enter models was 0.05.

The most parsimonious model was obtained using the Akaike information criterion (AIC; Akaike 1973), which is a good method to select which variables should be included or excluded in models. This criterion considers both fit and complexity and allows simultaneous comparison among several models (Burnham and Anderson 2002). The predictive value of the models was evaluated using a receiver operating characteristic (ROC) curve. Area under the ROC curve (AUC) varies from 0.5 to 1, where higher values indicate better predictive utility of the model (Fielding and Bell 1997; Pearce and Ferrier 2000). Predictive models require a validation of results; with this objective, the sample was divided into two groups: 80% of the data was used in model creation, and the other 20% was used in model validation. We have validated our models applying them to a sample of 95 data points not used previously in the calibration stage.

Other statistical analysis

As the fence was only located on motorways, we found necessary to draw out the confounding effects of traffic volume and fence presence. With this purpose, the number of wolf roadkill per kilometre grouped by road type was analyzed with a repeated-measures analysis of covariance (ANCOVA). A repeated-measures time factor (year) and a between-subjects road fence presence factor were included in the analysis. Since the number of wolf roadkills per kilometre may be affected by traffic volume, this variable was included as a covariate. The Greenhouse–Geisser degrees of freedom adjustment procedure was applied to the repeated-measures time factor to correct for violations of sphericity that often occur with repeated-measures analyses. Moreover, to investigate temporal variations in wolf roadkills, annual and daily wolf–vehicle collision patterns were analysed using the Kruskal–Wallis test.

Results

Univariate tests

We found significant differences between roadkill localities and the random sites, especially in traffic parameters, but also with variables related to the degree of human presence. Landscape parameter differences were less clear (Table 4). Observed collision sites vary from random points because they tended to be located on fenced roads, with low sinuosity, higher traffic intensity and higher speeds, further away from anthropogenic elements and closer to adminis-

Table 3 Models tested to identify the predictors of roadkill sites

		Abbreviation
Model		
Traffic parameters' model		TM
Landscape parameters' model (radius 1,000 m)		LM1000
Landscape parameters' model (radius 2,500 m)		LM2500
Landscape parameters' model (radius 5,000 m)		LM5000
Anthropogenic influence parameters' model		AM
Combined models		
TM+LM1000	TM+LM1000	TM+LM1000+AM
TM+LM2500	TM+LM2500	TM+LM2500+AM
TM+LM5000	TM+LM5000	TM+LM5000+AM
TM+AM		

We generated five simple models. Each model contains traffic variables, surrounding landscape elements or variables indicating the degree of human presence. We evaluated landscape models on three spatial scales with buffers of 1,000, 2,500 and 5,000 m around the collision site. In addition, we evaluated some models that include multiple thematic variables

Table 4 Results of univariate comparisons of variables shown in Table 1 comparing 62 roadkill localities with 320 random sites in the road network

	t value	*df*	*p*	γ^2
Density	5.062	75	<0.001	
Speed	9.672	380	<0.001	
Sinuosity	−5.130	210	<0.001	
Slope	−0.768	380	0.443	
Forest1000	−0.382	380	0.703	
Reforest1000	−0.397	380	0.692	
Shrub1000	−0.644	380	0.520	
Unirrigat1000	2.055	380	0.041	
Irrigated1000	1.650	74	0.093	
SDI1000	−1.514	380	0.131	
ED1000	−1.714	380	0.087	
Forest2500	−0.376	380	0.707	
Reforest2500	0.003	380	0.998	
Shrub2500	−0.600	380	0.549	
Unirrigat2500	1.458	93	0.148	
Irrigated2500	1.634	72	0.107	
SDI2500	−0.142	380	0.887	
ED2500	0.119	380	0.906	
Forest5000	−1.746	99	0.084	
Reforest5000	0.350	380	0.726	
Shrub5000	−0.743	380	0.458	
Unirrigated5000	2.021	380	0.044	
Irrigated5000	1.984	74	0.051	
SDI5000	−0.542	380	0.588	
ED5000	−1.770	380	0.078	
Municbord	−2.976	99	0.004	
Water	1.508	380	0.132	
Popularea	2.222	119	0.028	
Fences		1	<0.001	32.013
Railway		1	0.404	0.697
Canal		1	0.516	0.422

trative borders. With the landscape variables, we found significant differences only for those obtained with radii of 1,000 and 5,000 m. There were no differences between roadkill points and random sites for a radius of 2,500 m. At both scale extents, 1,000 and 5,000, wolf roadkill localities were more common in homogeneous landscapes with low ecotone density and both non-irrigated and irrigated crop predominance.

Logistic regression with rare event correction

Table 5 presents the results for logistic regression models with the rare event correction included. We only developed four of the five simple models considered at the beginning, because no significant differences were found for variables included in the landscape parameters' model with a radius of 2,500 m (LM2500). The Wald Chi test only found significant variables for the traffic parameters' model (TM) and the anthropogenic influence parameters' model (AM). For the landscape parameters' model with a radius of 1,000 m (LM1000) and the landscape parameters' model with a radius of 5,000 m (LM5000), no variable had a significance level below 0.05. TM includes speed, sinuosity and fence presence. AM only includes distance to municipal limits.

Table 5 shows the comparison among models by means of AIC. Between all simple models, TM had the lowest AIC value (289.2). For the other three simple models, the results are slightly higher. A small decrease in AIC values among regression models without significant variables indicates a limited predictive capacity for all models. TM+AM has an AIC value of 284.3, which means that TM improved by the addition of AM variables. However, the small decrease indicates that AM contribution to model predictive power is not very substantial.

The area under the ROC curve (AUC) for calibration data differs among models (Table 5), being moderate for those that include traffic parameters and low for the others (lower than 0.634). TM+AM+LM5000 works slightly better (0.847) than TM+AM (0.843) and TM (0.841). These small differences can also be observed in the ROC curve shown in Fig. 2. Nevertheless, TM+AM+LM5000 shows a higher AIC value than the TM+AM. Therefore, we considered that the TM+AM was the model that worked best. In addition to traffic parameters, the degree of human disturbance also is important for the identification of potential wolf–vehicle collision points in our study region. This model includes speed, road fence presence and distance to anthropogenic elements as predictive variables, all of them positively correlated with collision occurrence. Odds ratio results ($e\beta$) show a 40% increase in roadkill probability for each 10-km increase in speed. It increases by 3.2% for each 100-m distance from an anthropogenic element. It is especially remarkable that the presence of road fences increases roadkill probabilities by 3.19 times (Table 5). AUC for the validation dataset (Fig. 2 and Table 6) is higher than the one obtained for calibration data. This is an unexpected result and perhaps consequence of the small sample size.

Type of road, the effect of fencing and roadkill concentration in time

The importance of road fences and traffic parameters can be verified by the index of the number of wolf mortalities per kilometre of road per year. This index is much higher for motorways (2.96±1.57 annual collisions/1,000 km, 30.0% of the total) and is significantly different from other roads

Table 5 Results of logistic regression models including rare event corrections generated to identify the spatial distribution in wolf–vehicle collisions

		Coefficient (*B*)	Std. error	Wald	*p* (>|z|)	Odds ratio
TM	Intercept α	−9.98	1.09	−9.19	<0.001	
	Speed	0.04	0.01	3.56	<0.001	1.043
	Sinuosity	−0.02	0.03	−0.79	0.427	0.980
	Fences	1.01	0.50	2.02	0.044	2.743
LM1000	Intercept α	−5.276	0.597	−8.83	<0.001	
	Unirrigated1000	0.004	0.005	0.94	0.350	1.004
	Irrigated1000	0.009	0.006	1.47	0.140	1.009
	ED1000	−0.004	0.006	−0.77	0.440	0.996
LM5000	Intercept α	−5.246	0.855	−6.13	<0.001	
	Forest5000	−0.003	0.011	−0.23	0.822	0.997
	Unirrigated5000	0.003	0.008	0.39	0.699	1.003
	Irrigated5000	0.017	0.009	1.82	0.068	1.017
	ED5000	−0.005	0.011	−0.5	0.614	0.995
AM	Intercept α	−1.963	0.282	−6.97	<0.001	
	Municbordi	−0.042	0.018	−2.31	0.021	0.958
	Popularea	0.018	0.012	1.44	0.151	1.018
TM+AM	Intercept α	−5.764	1.177	−4.9	<0.001	
	Speed	0.039	0.012	3.26	0.001	1.040
	Sinuosity	−0.022	0.026	−0.86	0.392	0.978
	Fences	1.160	0.511	2.27	0.023	3.191
	Municbord	−0.034	0.020	−1.7	0.089	0.967
	Popularea	0.031	0.014	2.18	0.029	1.032

The models have been calibrated using observed and random points

(γ^2=23.020, *df*=3, p<0.001). National roads have a lower index but still high (0.80±0.28 roadkills per year/1,000 km, 33.8%). For the regional road network (0.21±0.17 roadkills per year/1,000 km, 18.8%) and secondary roads (0.11± 0.05 roadkills per year/1,000 km, 17.5%), wolf–vehicle collisions are infrequent relative to total network length. The repeated-measures ANCOVA of the number of wolf roadkills per kilometre (controlled for traffic volume) demonstrated a significant main effect for fence presence ($F_{1,1}$=292.521, p=0.037). No effect for time was found in the repeated-measures analysis.

We found no significant annual pattern (γ^2=17.794, *df*= 11, p=0.086), but roadkill frequencies were higher from November to April, which coincided with the breeding

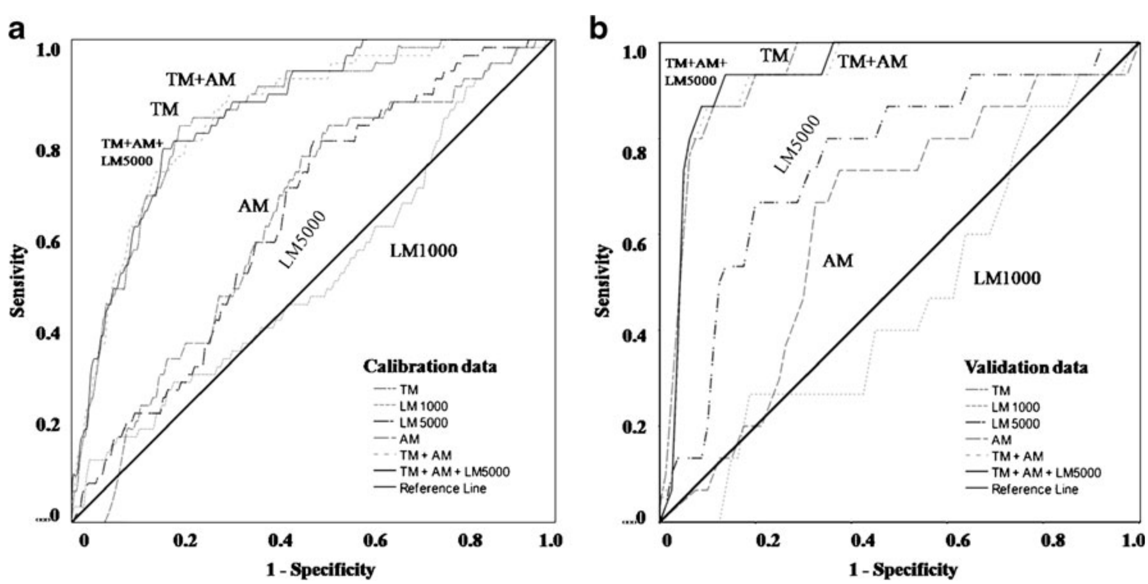

Fig. 2 Receiver operating characteristic (ROC) curves obtained for each model with both **a** calibration and **b** validation data

Table 6 Comparison among models using the Akaike information criterion and area under the ROC curve (AUC) for both calibration and validation data

	AIC	AUC calibration	AUC validation
TM	289.2	0.841	0.935
LM1000	341.4	0.518	0.463
LM5000	340.0	0.631	0.752
AM	335.3	0.634	0.626
TM+AM	284.3	0.843	0.928
TM+AM+LM5000	288.7	0.847	0.933

season and hunting period (Fig. 2). Nevertheless, the daily pattern is significant (γ^2=66.299, df=23, p<0.001). Peaks occur during maximum activity periods that coincide with high traffic intensity. The result is a bimodal curve with two peaks: one at dusk and the first hours of the night and the other at sunrise (Fig. 3).

Discussion

The best predictive model for wolf roadkills includes not only traffic parameters but also the degree of human presence. Landscape variables hardly improve models. The results are different from those reported in models for large ungulate collisions where landscape variables play important roles (Puglisi et al. 1974; Bashore et al. 1985; Finder et al. 1999). Forest proximity and traffic parameters are the main explanatory variables in elk collisions (Seiler 2005). These variables were similar to those found in Soria Province, included in our study region, where hotspots of ungulate–vehicle collisions are located in forested areas with quite low agricultural cover, certain landscape diversity and low human presence (Malo et al. 2004). Moreover, wolves are large carnivores that can adapt to different kinds of habitat, with extensive home ranges and long daily movements in which they move through a mosaic of patch types. Thus, predictive modelling with coarse, general landscape variables used in this study did not add to the model. Neither land uses nor landscape structure indices, regardless of the analysis of scale, have been useful in logistic models. Nonetheless, it could be possible to find differences with a larger sample size.

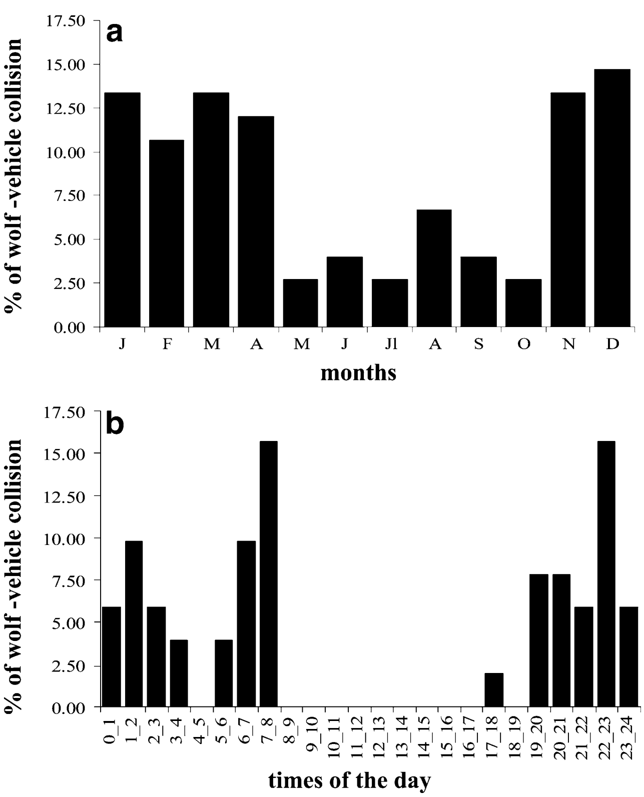

Fig. 3 Temporal distribution of wolf–vehicle collisions: **a** months and **b** times of the day

Collisions with wolves tend to occur along roads where high speeds and traffic intensity exist, as has been reported for accidents involving ungulates (Seiler 2005). It is noteworthy that fences along roads play an important role in wolf roadkills. Many of them occur on fenced roads, mainly motorways. The number of collisions per kilometre and year on unfenced major roads is proportionally lower, although they have dense traffic at high speeds. Repeated-measured ANCOVA results showed that it not a confounding effect of traffic volume. The effectiveness of Spanish motorway fences is insufficient for the well-being of the wolf populations. Moreover, the absence of animal-escape mechanisms in the older motorways for wolves to escape the right-of-way away from the road aggravates the situation. Another possible interpretation of the results is that the lower roadkill rates in unfenced roads with heavy traffic volumes could be related to wolf behaviour. Wolves may select positively the right moment to cross the road and avoid the collision. Future research should focus on wolf behaviour when a vehicle is coming down the road. The results about the fence effectiveness are different from other studies which showed that road fences contribute to a decrease in road mortality but also increase barrier effect (Jaeger and Fahrig 2004). Ward (1982), Lavsund and Sandegren (1991) and Clevenger et al. (2001) found that fencing and wildlife crossing structures can reduce ungulate collisions by 80%. Moose collisions are more frequent on unfenced medium-traffic roads (Seiler 2005). Fences act as selective filters but do not have the same effectiveness for all species. Some carnivore species can occasionally overcome road fences due to their strength or jumping and climbing abilities. When wildlife gains access to a motorway, fences have the opposite effect to that desired, increasing the time the animal stays on the road and the probabilities of being killed. We are not saying that fences are not useful but that construction failures and lack of maintenance favour wildlife access to the road and diminish fence effectiveness. Clevenger et al. (2001) reported that only two of the six deaths of wolves took place after fencing, but the sample size was so small that no conclusions could be drawn. Black bears *Ursus americanus*, grizzly bears *Ursus arctos* and cougars *Puma concolor* were capable of climbing fences. Coyotes *Canis latrans* reached the road through holes between the fences and ground. The Iberian lynx can easily penetrate fences with a large mesh size, not fixed to the ground and without overhangs (Guzmán et al. 2004). It is necessary to investigate the efficacy of different types of fences for carnivores. Furthermore, it is necessary to focus on escape mechanisms that allow carnivores inside fenced roads to reach the exterior again. Several designs have been proposed, e.g. lateral doors of escape or ramps built with different materials and designs (Iuell et al. 2003).

Researchers have also included in roadkill modelling some indicators of the degree of anthropogenic disturbance. Like other species (Bashore et al. 1985;Clevenger et al. 2003), wolves positively select undisturbed areas. In this way, municipal limit closeness and human settlement remoteness are good indicators. Administrative borders are historically tranquil areas with low human presence. Clevenger and Waltho (2000) found that carnivores selected road-crossings far from anthropogenic elements and with low human disturbance. Rodríguez et al. (1997) verified the same behaviour for red foxes *Vulpes vulpes* and wild cats *Felis silvestris*. Wolves accustomed to human presence may frequent the vicinity of small villages. Blanco et al. (2005) indicated that radio-marked wolves used road-crossing structures placed closer than 200 m to inhabited houses. It is probable that wolves accustomed to human presence would be less reluctant to cross motorways than populations established in remote areas (Blanco et al. 2005).

Although they did not contribute to improve model fit, landscape variables in roadkill localities differed slightly from random sites. Wolf–vehicle collisions tended to be located in agricultural areas. On the agricultural plateau, wolf density (2.4–3.0 wolves/100 km^2) is not as high as in other undisturbed forest areas of the mountainous periphery (maximum density in the northwest Zamora Province with 6.0–7.2 wolves/100 km^2; Blanco and Cortés 2002). Carrion abundance can be the main factor to explain the permanent presence of wolves in an atypical area, such as the plains with their cereal crops. Because of carrion, wolves do not have to attack livestock as often which is why do not come into conflict with humans and persecution is less intense (Barrientos 2000). The higher number of wolf–vehicle collisions on the plateau could be explained not only by higher densities of roads with intense traffic but also by the proportion of roaming individuals. Wolf movement characteristics may be even more important than population density. It is probable that a low quality habitat and a large quantity of food provided by dumps favour a high percentage of non-territorial individuals (Blanco and Cortés 2002). This has been shown in coyotes (Todd and Keith 1976). Roaming individuals undergo higher rates of mortality because they wander around areas influenced by humans (Blanco and Cortés 2002). Wolves, radio-marked by Blanco and Cortés (1999), on the steppes cultivated with cereal crops spent 40.8% of the time as peripheral and roaming individuals. Dispersed wolves suffer a higher proportion of deaths (Fuller 1989; Waser 1996; Pletscher et al. 1997). Blanco and Cortés (2002) measured the annual rate of dispersion on the plateau at 48.6%. Several roadkills have taken place in areas where the species is not well established, which may coincide with the young dispersing or roaming individuals. Although we could not obtain data about the ages and sexes of road-killed wolves, according to Lovari et al. (2007), it is more probable that the young suffer the highest roadkill frequencies.

In conclusion, it is difficult to obtain good models for the roadkills of large carnivore species such as wolves because of their small population sizes, large home ranges and long daily movements. They use different habitats, so landscape variables are not very useful for the prediction of collision locations. These results suggest that it is difficult to focus permanent mitigation structure locations, e.g. underpasses or overpasses within the road network. Perhaps with a bigger sample size, it would be possible to find patterns, but wolf–vehicle collisions can be considered as rare events, so larger samples are difficult to encounter for suitable spatio-temporal scales. Only variables relative to traffic and road parameters and the degree of anthropogenic disturbance can partially explain spatial distribution. Therefore, the importance of road fences should be taken into account. Future research should focus on the specific specs of fences and animal-escape mechanisms to be effective. Roadkill minimisation also requires the correct installation and maintenance of the fences. Wolf roadkills in the region of study are proportionally more common in agricultural zones, where wolf densities are lower. This fact might be explained by the higher density of roads with intense traffic and the longer daily movements of the animals. Furthermore, the ecological characteristics of this area imply a high percentage of roaming individuals, which are more frequently killed on the roads. If roaming individuals were the principal victims of roadkills, the consequences for population viability might be lower.

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