UNIVERSIDADE FEDERAL DE LAVRAS

ELLEN RODRIGUES FERMIN

ROAD- RELATED FEATURES THAT PROMOTE MAMMAL ROAD CROSSINGS

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-graduação em Ecologia Aplicada, área de concentração ecologia e conservação de recursos em paisagens fragmentadas e agrossistemas, para a obtenção do título de Mestre.

Prof ª Dra. Clara Grilo
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ELLEN RODRIGUES FERMIN

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CARACTERÍSTICAS DA ESTRADAS QUE PROMOVEM CRUZAMENTOS DE MAMÍFEROS

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-graduação em Ecologia Aplicada, área de concentração ecologia e conservação de recursos em paisagens fragmentadas e agrossistemas, para a obtenção do título de Mestre.

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RESUMO

A presente dissertação foi escrita em formato de artigo cientifico na língua inglesa. O objetivo foi avaliar quais características da estrada promovem uma maior incidência de cruzamentos de mamíferos de médio e grande porte, e se variam de espécie para espécie ou entre grupo de espécies (carnívoros e ungulados). Foram utilizados dados de telemetria de 14 espécies de mamíferos, fornecidos por diferentes pesquisadores, para identificar os trechos de 500m de estradas com maior e menor incidência de cruzamentos nas rodovias. Posteriormente foram descritas 12 características da estrada (número de faixas, presença de cerca, tipo de cerca, presença de cruzamento de curso d'água, distância de curso d'água, topografia da estrada, tipo de vegetação de beira de estrada, conectividade de áreas abertas e fechadas e porcentagem de áreas abertas e fechadas) em 2201 trechos, utilizando o Google Street View. Foram desenvolvidos dez modelos, sendo eles Linear Generalizado Misto de família binomial, ou Linear Generalizado (1 - todos os mamíferos, 2 - todos os ungulados, 3 - todos os carnívoros, 4 - urso-pardo do Canadá, 5 - urso-pardo da Grécia, 6 - guepardo, 7 - onça-parda, 8 - lince euroasiático, 9 - corça e 10 - cervo-canadense). A alta/baixa incidência de cruzamento foi a variável resposta e as características da estrada foram as variáveis explicativas e interação entre as espécies e área de estudo as variáveis aleatórias. Os resultados mostraram incidência de cruzamentos de mamíferos é menor quando há maior número de faixas de estradas e quando um curso d'água cruza o trecho os mamíferos enquanto que a maior incidência de cruzamentos ocorreu longe de curvas. Apesar de nenhuma característica ter sido significante para todos os modelos, algumas características apresentaram efeitos em mais do que um modelo. A distância da curva aumentou o número de cruzamentos em mamíferos, carnívoros e urso-pardo do Canadá, enquanto, o número de faixas diminuiu a incidência de cruzamentos de mamíferos, carnívoros e ungulados. Além disso, a distância do curso d'água apresentou efeito negativo para carnívoros e ungulados, e positivo para guepardo e cervo-canadense. E por fim, a conectividade de áreas abertas resultou em mais cruzamentos para urso-pardo da Grécia e corça, porém diminuiu para onça-parda e lince euroasiático. Por não haver unanimidade de efeitos que influenciam os cruzamentos, a sugestão é que a melhor alternativa é analisar os cruzamentos em rodovia por espécie.

PALAVRAS-CHAVE: Mamíferos. Carnívoros. Ungulados. Cruzamentos em estradas. Atropelamento.

ABSTRACT

This master's thesis was written in the format of a scientific paper in the English language. The aim was to evaluate which road-related features promote a higher incidence of mammal crossings, and if they vary among species or groups of species (carnivores and ungulates). Telemetry data from 14 mammal species, provided by different researchers, were used to identify 500m road segments with the highest and lowest incidence of crossings. Subsequently, twelve road-related features (number of lanes, presence of exclusion fence, exclusion fence height, presence of stream crossing, stream in parallel, road topography, distance to the nearest curve, road verge structure, connectivity of open and closed areas, and percentage of open and closed areas) were analyzed in 2201 road segments using Google Street View. We ran the results to ten Generalized Linear Mixed Models of binomial family, or Generalized Linear model in some cases (1 - all mammals, 2 - all ungulates, 3 - all carnivores, 4 - brown bear from Canada, 5 - brown bear from Greece, 6 - cheetah, 7 – cougar, 8 - Eurasian lynx, 9 - roe deer, and 10 - wapiti). The high/low incidence of crossings was the response variable, and road-related features were the explanatory variables, with species interaction and study area as random variables. The results showed that mammal crossing incidence is lower when there are more lanes on the road, and when a stream crosses the segment. The incidence of crossings was higher away from a curve. Although we did not find a rod feature that was significant for all models, some features had effects on few models. The distance to the nearest curve increased the number of crossings in mammals, carnivores, and brown bears from Canada, while the number of lanes decreased the incidence of crossings in mammals in general, carnivores and ungulates. Furthermore, the distance from the stream in parallel had a negative effect on carnivores and ungulates, and a positive effect on cheetahs and wapiti. Connectivity of open areas resulted in more crossings for brown bears from Greece and roe deer, but decreased for pumas and Eurasian lynx. Due to the lack of consistency in the road features related with high incidence of crossings, we recommend analyzing the effects of roads by species.

KEYWORDS: Mammals. Carnivores. Ungulates. Road crossings, Roadkill.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

As estradas são caminhos terrestres para circulação de pessoas, veículos e animais (OXFORD LANGUAGES, 2023), podem ser pavimentadas ou não, de mão dupla ou mão única com quatro faixas, duas ou apenas uma, entre outras características. Desde a década de 50, houve um aumento no número de estradas em todo o mundo e, consequentemente, cresceram as preocupações sobre os impactos que podem ser causados na vida selvagem (DOYLE e HAVLICK, 2009; MAZEROLLE *et al*., 2005). Elas são essenciais para o desenvolvimento socioeconômico e necessárias para uma variedade de atividades, desde o transporte de alimentos até viagens de lazer (ÁREVALO *et al*., 2017; VAN DER REE *et al.*, 2015). No entanto, causam impactos negativos na vida selvagem por meio da mortalidade, causada por colisões com veículos, efeito barreira, que limitam os movimentos dos animais (Jacobson et al., 2016), o aumento do acesso a áreas remotas e conservadas, o que pode causar perda e degradação de habitat por meio do desmatamento, poluição acústica e do ar (ARESCO, 2005; COFFIN, 2007; HOLDEREGGER e DI GIULIO, 2010; JAEGER *et al*., 2005; SEO *et al*., 2015; VAN DER REE *et al*., 2015).

Embora a literatura tenha estimado altas taxas de atropelamentos para muitas espécies (BARTHELMESS, 2014; TAYLOR *et al*., 2002), observaram-se cruzamentos bem-sucedidos de estradas (GAGNON *et al*., 2006; JAARSMA *et al*., 2006). São diversos fatores que influenciam nos atropelamentos e cruzamentos de animais, entre eles o limite de velocidade, o tráfego, tamanho do animal, comportamento de cada espécie, topografia, distância de área urbana, distância de curso d’água e características da paisagem (ASCENSÃO *et al*., 2017;CANAL *et al*., 2019; CLEVENGER *et al*., 2003; D'Amico *et al*., 2015, De Freitas *et al*., 2015; Laliberté e St-Laurent, 2020;Ranapurwala *et al*., 2016;; Silva *et al*., 2019; da Silva *et al*., 2022).

No presente estudo, utilizamos dados de 14 espécies de mamíferos de grande porte que é um grupo particularmente vulnerável à mortalidade por atropelamento (GRILO *et al*., 2021). O objetivo da dissertação foi avaliar quais as características da estrada têm efeito na incidência de cruzamentos dos mamíferos, e também se essas características têm efeito semelhante quando avaliado espécie por espécie, ou se variam.

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Road-related features that promote mammal road crossings

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ABSTRACT

Roads cause several impacts to wildlife mainly mortality due to collision with vehicles and isolation of populations through barrier effect. However, it is not clear which road-related features are more related with safe road crossings. The aim of this study was to analyze which road-related features may explain the high incidence of mammal road crossings, and whether they vary among orders or by species. We compiled radio-tracking from 14 mammal species from different regions worldwide and described 12 road-features identified in 500-m road segments with high and low incidence of road crossings for each species using Google Street View. We ran generalized linear mixed models with incidence of crossings as the response variable to analyze the relationship with road features, using species and study areas as random effects. We ran models for all mammals, all carnivores, all ungulates and for each species with more than 50 road segments with observed high and low incidence of road crossings. We found that larger roads and streams crossing a road decreased mammal crossings while the distance to the nearest curve increased crossings. Our study highlights the importance of some road-related features in promoting safe crossings which should be considered in road plan designs. Since none of features explained the incidence of crossings in all models, we recommend that the analysis should be species-specific.

Keywords: Mammals. Carnivores. Ungulates. Road effects. Road crossings. Roadkill

Introduction

Road network worldwide reach to more than 40 million km (CIA, 2023) and the trend is to increase in the coming decades (Dulac., 2013; Laurance et al., 2014). Roads are essential to socioeconomic development and necessary for a range of activities from food transport to leisure travel (Árevalo et al. 2017; Obregón-Biosca & Junyent-Comas.2011; Van der Ree et al. 2015.). However, roads can also have major impacts on wildlife through habitat fragmentation and degradation as a consequence of noise, light and air pollution and traffic volume (Barber et al. 2009; Coffin, 2007; Malcolm & Ray 2000) and additional mortality from collision with vehicles (roadkill) (Clarke et al. 1998; Coffin 2007; Dekker & Bekker 2010). Those impacts affect daily movements blocking the access to essential resources such as water, food, and refuge (Forman et al. 2003; Jerina 2012; Krofel et al. 2010; Laforge et al. 2019; Mader et al. 1984; Riley et al., 2006.) and also dispersal which can affect the genetic diversity of the populations and ultimately population persistence at medium long term (Jaeger et al., 2005) (Clarke et al., 1998; Van der Ree et al., 2007).

Roads and railroads are considered one of the threats to 34 mammals species classified as Critically Endangered by IUCN Red List (IUCN, 2023), and also to 68 Endangered and 83 Vulnerable mammal species. A study estimated over 100 species of mammals are considered particularly vulnerable to roadkill, such as, brown bear (*Ursus arctos)*, Iberian lynx (*Lynx pardinus)* and plains zebra (*Equus burchellii*) (Grilo et al., 2021). Furthermore, Quintana et al. (2022) showed that 30 of 36 species of apex predator are exposed to roadkill, with implications on their conservation due to low populations densities and reproductive rate, and large home-range.

Identify where species are more likely to cross has been performed through roadkill and road crossing analysis. Roadkill studies show a relationship with intensity and speed of vehicles but there is no consensus on the type of association. For example, some studies showed that as the traffic increase the roadkill likelihood decrease (Driessen et al., 2021; Grilo et al., 2015; Seo et al., 2015.) while others showed an opposite association (Ramalho et al., 2021; Sadleir & Linklater, 2016; Saeki & Macdonald, 2004.). Also, the visibility to animal and to the driver seems to be an important driver of high roadkill likelihood (i.e. sinuosity make it difficult to observe and being observed when the individual is attempting to cross the road) (Dekker & Bekker, 2010; Meisingset et al., 2014; Putman et al., 2011; Zuberogoitia et al., 2014.). Studies on road crossings show that incidence of crossings is higher to American black bears (*Ursus americanus*) and moose (*Alces americanus*) in areas distant to urban areas (Zeller, et al., 2018, Zeller et al, 2020). Forested areas are used to cross roads by American black bears (Zeller et al., 2018), while bobcats (*Lynx rufus*) prefer to cross in secondary than in primary roads (Poessel et al., 2014). A review of 36 different studies showed crossings occur in less number of road lanes (Chen&Koprowski, 2019). However, little is known about the role of other road-related features on crossings at a fine scale (but see Popp & Donovan, 2016). A comprehensive analysis of the road features that may promote road crossings to different species and locations, are critical to guide road managers to define which measures should be applied promote a safe road crossing for wildlife.

In this study we aimed to identify the role of 12 road-related features that promote a high incidence of road crossings by medium and large mammals and whether they vary among orders or by species. We compiled radio tracking data from 14 mammal species, of different groups, carnivores (badger (*Meles meles*), cheetah (*Acinonyx jubatus*), cougar (*Puma concolor*), Eurasian lynx (*Lynx lynx*), genet (*Genetta genetta*), brown bear (*Ursus arctos*), grey Wolf (*Canis lupus*), and stone marten (*Martes foina*)) and ungulates (Asiatic wild ass (*Equus hemionus onager*), wapiti (*Cervus canadensis*), moose (*Alces americanus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*)) in several regions worldwide. Then, we compared high with low incidence of road crossings regarding the following road related-features: number of lanes, exclusion fence, exclusion fence height, stream crossing, stream in parallel, topography of road, distance to the nearest curve, road verge, connectivity of open and closed areas and percentage of open and closed areas. With this analysis we want to shed light to the general road related features that affect the incidence of road crossings and whether they differ by species to provide guidance road managers on which measures should be effective for target medium and large mammal species.

Methods

Data compilation

The data was obtained from published and unpublished radiotracking data shared by researchers (Table 3. in Appendix 1). Radio tracking data included 14 species (Asiatic wild ass, badger, cheetah, Cougar, Eurasian lynx, genet, brown bear, grey wolf, moose, red deer, roe deer, stone marten, wapiti, wild boar) from twelve countries (Iran, England, Namibia, Unites States of America, Norway, Spain, Canada, Greece, Poland, Germany, Switzerland and Portugal) (Figure 1). Since brown bear data were from Canada and Greece, we assumed as different species and we did not merge the data. We only selected radiotracking data with an interval of 1h which was the trade-off to use this minimum time interval between locations and maximum data to have the most accurate information on the location road crossings (e.g. Klar et al. 2009).

Road network for each country was obtained from Meijer et al. (2018) and for the missing roads we georeferenced using the Google Earth in the background. We divided the road network of each study area into 500m long segments. Consecutive locations ordered by date and time were converted into lines and overlapped with the road network to estimate the site of the road crossing. We estimated the number of road crossings in each 500m of road segments and selected the road segments with low incidence the ones that are in the 1st quantile and the road segments with high incidence the ones in the 4rd quantile, the number of crossings per quartile varies among species (Appendix 1.).

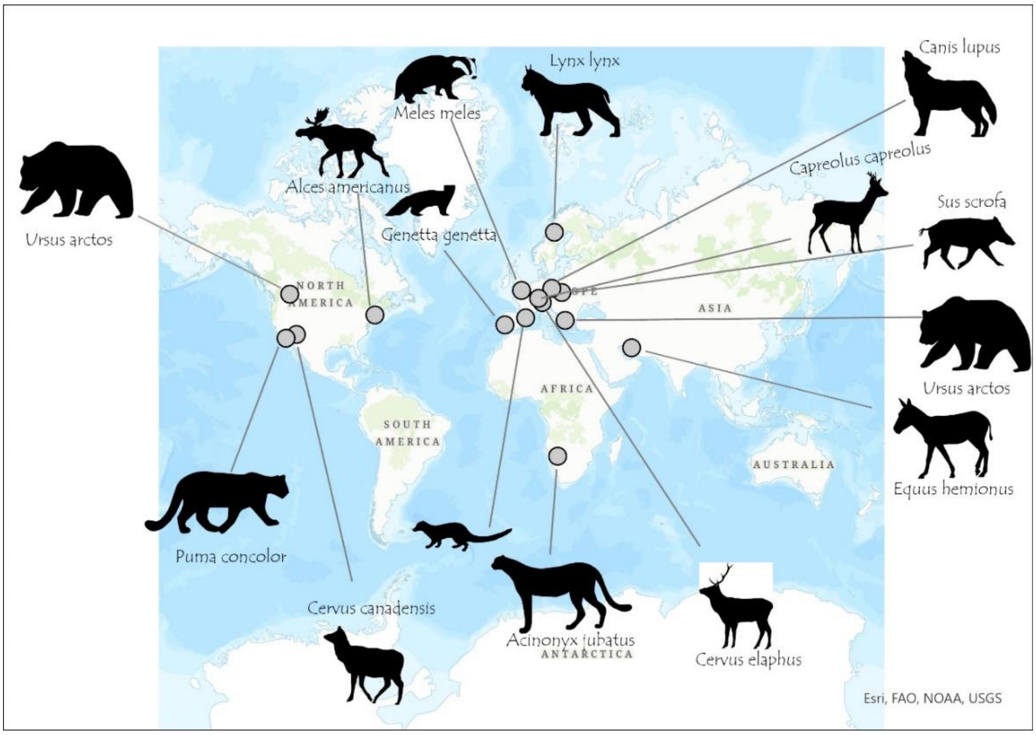

Figure 1 - Locations of study areas of each species.

Road-related features description

We used the coordinates of the centroid of each 500m segment selected to describe 12 road-related features using Google Maps and Google StreetView: number of lanes (one lane and two or more lanes), exclusion fence, exclusion fence height, road topography (flat or others), distance to the nearest curve, road verge (grassland and shrubs/trees), stream crossing the road, stream in parallel, percentage of closed areas, percentage of open areas, connectivity of closed areas and connectivity of open areas (Table 1).

Table 1. Characterization and unit of measure of road-related features.

	Feature	Description	Units
Barrier	Number of lanes	Number of lanes	0 (one lane) or 1(two or more lanes)
	Exclusion fence	Presence or absence of livestock fencing.	0/1
	Exclusion fence height	Height of fence, normal (livestock) or higher.	0 (with no fence or normal)/1(high)
	Stream crossing	Presence or absence of stream crossing a road segment.	0/1
	Stream in parallel	Distance to the nearest stream that runs parallel to the road	0 to 1000 meters
Perceptions of risk	Road Topography	Flat or others (below grade, above grade or mix below and above grade).	1 (flat)/ 0 (others)
	Distance to the nearest curve	Distance to the curve, more than 1000 meters was considered 1000.	0 to 1000 meters
	Road verge	Vegetation structure on the road verge (non-vegetation, grassland, shrubland or trees).	0 (with no vegetation or grassland), 1(shrubland or trees)
	Percentage of closed areas	Percentage of forest cover.	0 to 1
	Percentage of open areas	Percentage of grassland cover.	0 to 1
	Connectivity of closed areas	More than 50% of forest cover on both and complementary sides of the road means connectivity.	0 (no connectivity) 1 (connectivity)
	Connectivity of open areas	More than 50% of grassland areas on both and complementary sides means connectivity.	0 (no connectivity) 1 (connectivity

Data Analysis

We evaluated the factors that promote the road crossings, using R (R Core Team, 2022) using three approaches: A) all selected species; B) all carnivores or all ungulates; C) by species that presented more than 50 road segments with observed high and low incidence of road crossings. First, we standartized the variables that were outside the range between 0 and 1 using the formula: $z = \frac{\mathrm{x} - min(x)}{[\max{(x)} \ - min\ (x)]}$. Then, we tested multicollinearity among variables using the Spearman's rank correlation and variance inflation factor (VIF). Among the pairs of variables with correlation coefficient <-0.7 and >0.7, we selected the ones with more correlation with incidence of crossings. Thus, we excluded from futher analysis the following variables: exclusion fence height, connectivity of closed areas (except for cheetah), percentage of closed areas (except for cheetah), percentage of open areas (Appendix 2). We only included in the model variables with VIF lower than 3. Then we fitted a generalized linear mixed model (GLMM) that included the study area and species as the random effect for approach A and B. For the approach C we only used the study area as random effect when the species had different study areas. In each model, we ran a full model with all possible combinations of predictors and performed a model selection procedure to select the best-fit models as those with lowest Akaike information criterion values (ΔAICc < 2). We then apply model averaging to make inferences on how the road-related features influence the high incidence of crossings.

For analysis we used the following packages: Corrplot (Wei et al., 2017); lme4 (Bates et al., 2009; car (Fox et al., 2012); nlme (Pinheiro et al., 2017); MASS (Ripley et al., 2013); ggplot2 (Wickham et al., 2016); glmmTMB (Magnusson et al., 2017); MuMIn (Barton& Barton, 2019).

Results

Effect of road related features on mammals, carnivores and ungulates

Our data comprised 11,007 crossings for all target species. A total of 2201 road segments with high (25.8%) and low incidence of crossings (74.2%) were described in Google Street View. Carnivores represented 83,6% of the total road segments and ungulates represented 16,4%. The distance to the nearest curve had a significant positive association with incidence of mammal crossings (β= 0.5855 p=<0.001) (Table 2; Fig. 2) while the number of lanes and the presence of streams crossings had a significant negative effect (β= -0.626; p-value=<0.001; β =-0.361109, p-value=0.04601, respectively) (Table 2; Fig. 2).

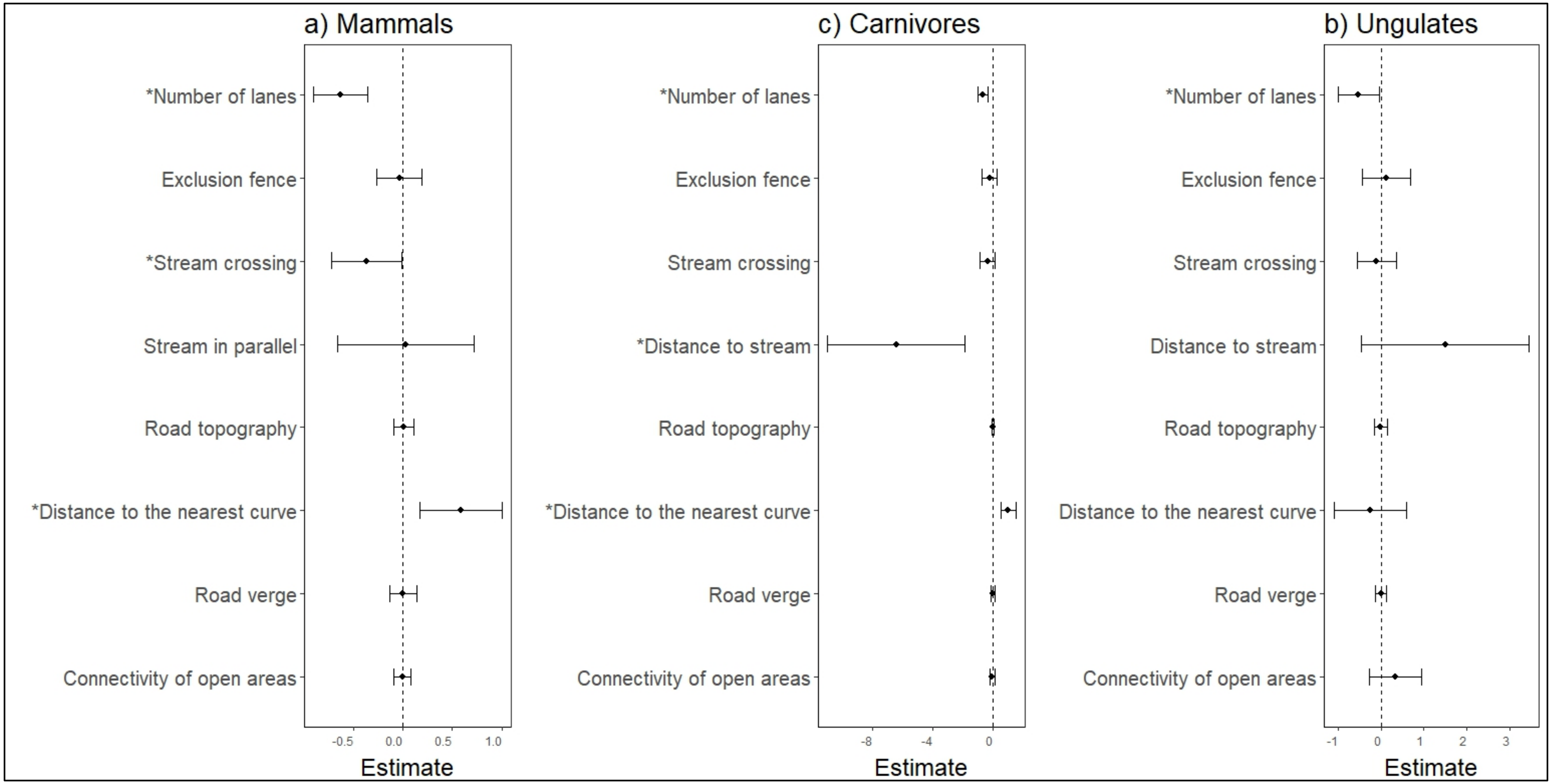

Fig. 2. Effect size and significance of road-related features on the incidence of crossings for a) all mammals b) all carnivores and c) all ungulates. *when the variable is significant.

We used 1841 road segments to model carnivores (77% low and 23% high incidence). Distance to the nearest curve presented a significant positive effect (β =1.036049; p-value=0.006) on the incidence of crossings while the number of lanes and the distance to stream in parallel had a significant negative effect on the incidence of crossing (β=-0.64; p-value=<0.001; β= -6.409; p-value=0.006, respectively). We used 360 road segments (60,5% low and 39,5 high) to model ungulate crossings. The probability of incidence of crossings significantly decreased with the number of lanes (β= -0.52, p-value=0.034) (Fig.2, Appendix 3).

Effect of road related features on each species

Brown bears - Distance to the nearest curve (β=1.03; p-value =0.02) and road topography (β= 1.00, p-value=1.03) had a significant positive effect on the incidence of road crossings in Canada (Table 2, Fig.3.) while exclusion fence (β=-1.055; p-value =0.008) and road verge (β=-1.958; p-value = <0.001) were significant negatively associated with high incidence of road crossings (Fig.3). In Greece, connectivity of open areas and the road verges had a significant positive effect on brown bear road crossings (β=0.614, p-value=0.026; β =3.368, p-value=0.001, respectively) (Fig.3.). Brown bears were less likely to cross when road topography was non-flat roads (β= 1.003, p = 0.01), in segments with stream crossing (β=-2.035; p-value=0.0312), and when the distance to stream in parallel was far away from roads (β=-20.764, p-value=<0.001) (Fig.3.).

Cheetah – Closed areas and distance to stream in parallel close were not associated with high incidence of crossings (β=-6.758, p-value =0.003; β= 16.25, p-value=0.005, respectively) (Fig.3.).

Cougar - the connectivity of open areas was the only significant variable in the model and was not related with the incidence of road crossings (β =-1.7695; p-value = 0.02) (Fig.3.).

Eurasian lynx - the connectivity of open areas was the only significant variable in the model and had a negative effect on the incidence of crossings (β=-0.685, p-value=0.021) (Fig.3.).

Roe deer - connectivity of open areas was the only significant variable in the model and was negatively related with incidence of crossings (β =1.028, p-value=0.0116) of the (Fig.3.).

Wapiti – the incidence of road crossings was associated with distance to stream in parallel (β=15.538; p-value = 0.0007) (Fig.3.).

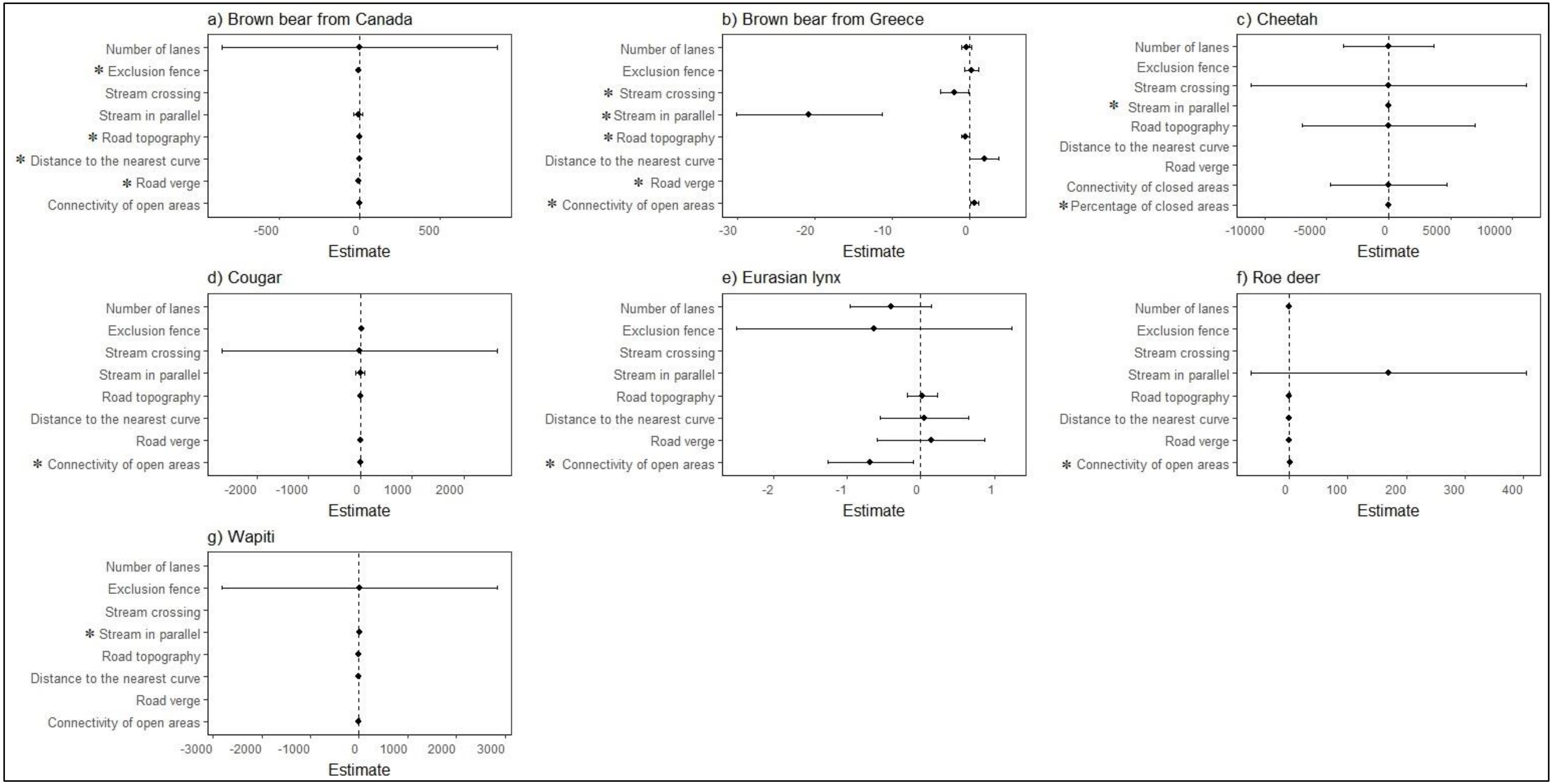

Fig.3. Effect size of road-related features on the incidence of crossings by each species: a) Brown bear from Canada; b) Brown bear from Greece; c) Cheetah; d) Cougar; e) Eurasian lynx; f) Roe deer; g) Wapiti. * when the variable is significant.

Table 2. Summary of road-related features with significative effects on the incidence of crossings for mammals, carnivores, ungulates and for each species.

	≥2 lanes	Exclusion fence	Stream crossing	Stream in parallel	Topography of roads	Distance to the nearest curve	Road verge	Connectivity of open areas	Percentage of closed area
MAMMALS	↓		↓			↑			
Carnivores	↓			↓		↑			
Brown bear (Canada)		↓			↑	↑	↓		
Brown bear (Greece)			↓	↓	↓		↑	↑	
Cheetah (Namibia)				↑					↓
Cougar (USA)								↓	
Eurasian lynx (Norway)								↓	
Ungulates	↓								
Roe deer (Germany)								↑	
Wapiti (USA)				↑					

Discussion

Our main results showed that mammals seemed to have a higher incidence of crossings far from curves, but they avoided crossing road segments with two or more lanes and where roads are crossed by streams. However, we found no consistency in features explaining incidence of crossings when the analysis focused on carnivores and ungulates or by species with some exceptions.

Distance to the nearest curve was the road-feature that explained more incidence of safe crossings in opposition with the documented unsuccessful crossings that result in mortality in curved roads (Grilo et al. 2009; Grilo et al. 2011; Jakubas et al. 2018). The straight road increase animal and driver visibility (Montgomery et al. 2012, Ranapurwala et al. 2016) and promote the ability to cross the roads safely.

Wider roads were less crossed by mammals, carnivores and ungulates (Teodorović & Janić, 2017). These types of roads are in general associated with high traffic volume and vehicle speed (Tang et al., 2014; Xiao-bao&Ning, 2007) which may prevent individuals to try to cross them (Graham et al 2010; van Langevelde & Jaarsma 2005; Zeller et al. 2021). For example, some mammals such as bank vole (*Clethrionomys glareolus*), brown bear, black bear (*Ursus americanus*) (Graham et al 2010; Rico et al. 2007, Zeller et al 2021) were observed to select narrow roads to cross which is in line with our results.

Unexpectedly, we found that streams crossing roads were negatively associated with mammal crossing. Streams and associated riparian vegetation are considered corridors of movement for many species (Brum et al. 2017; Dickson et al. 2005; Jensen et al. 2022; Naiman & Decamps 1997) since they have more availability of refuge and prey (Ascensão et al. 2017; Darveau et al 2001; Serieys et al. 2021). Thus, the occurrence of streams close to roads should approach individuals to these infrastructures being more likelihood trying to cross them. However, we observed that streams in parallel close to roads seemed to be related to high incidence of crossings for carnivores, in general, and brown bear. The high distance of streams in the study areas of cheetah and wapiti may led to the model output being a high incidence of crossings in roads far away from streams (on average, 6.4 kilometers for cheetah and 9.7 kilometers for wapiti). In their study areas, they probably were using other places to use water, such as sazonal pan, water to domestic animals and perennial stream and they were less attracted to the natural streams close to the road (Rostro-Garcia et al. 2015, Strohmeyer & Peek 1996).

Low incidence of cougar and Eurasian lynx crossings occurred in open areas on both sides of the road which is in line with their habitat preferences that select forest areas to home range (Belotti et al. 2013; Gantchoff et al 2021; Suel 2009). Brown bear in Greece and roe deer crossed more in open areas, maybe because there is more visibility although they are more forest dwelling species (Benhaiem et al. 2008; Parsons et al., 2021).

Based on our findings we highlight the fact that each taxon has a unique set of resource requirements. For example, deer feed mostly on tree leaves, seedlings, and forbs (Latham, 1999) and inhabit closed areas. In contrast, brown bears are omnivores and movements to search of food (Bojarska & Selva, 2012; Selva et al., 2017), while cougars seek closed areas to stalk prey (Coon et al., 2020). Our results are consistent with the ecology of these species, as road-related features were related with their habitat preferences in general and varied among species. For example, the model with all mammals only had one road-related feature in common with ungulate, roe deer, and wapiti models, suggesting that it is not a good model to explain ungulate behavior on roads. Similarly, the ungulate model was not consistent with the roe deer and wapiti models. Mammal and carnivores model had two road-related features in common. Comparing the group carnivore with carnivore species, the distance to stream in parallel only have the same negative effect in brown bear from Greece whereas the distance to a curve only appears in brown bear to Canada, the others groups or had contrary effect or were not significative. Therefore, it is best to evaluate each species individually (Find'o et al., 2019).

In conclusion, our findings suggest there are some road features relatively consistent across species (distance to the nearest curve and number of lane) that should be indicators of incidence of road crossings when data is scarce on species road crossings. However, species has different requirements analysis should be performed by species individually to find the best locations for mitigation and therefore be more effective in reducing the roadkill likelihood and promote the connectivity of their habitat across the road. Furthermore, fine-scale analysis are essential to understand how road characteristics affect crossings and therefore how mitigation should be applied.

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Appendix 1.

Table 3. Telemetry data with information on the species, number of individuals, number of data, Q1 minimum number of crossings in a road segment, Q2 maximum number of crossings in a road segment, period of survey, country and data owners.

	Family	Scientific name	Common name	N ind	N locations	Q1 (min crossings)	Q4 (max crossing)	Period	City/State/ Country	Data owners
Carnivores	Canidae	*Canis lupus**	Grey wolf	2	19	1	4	2015-2016	Poland	Hernryk Okarma/Katarzina
	Felidae	*Acinonyx jubatus*	Cheetah	36	132	6	153	2012-2019	Namibia	Ruben Portas
		Lynx lynx	Eurasian lynx	49	999	1	15	2008-2016	Norway	Jenny Mattison
		Puma concolor	Cougar	8	56	1	16	2001-2016	USA	Kathy Zeller/ Winston Vickers
	Mustelidae	*Martes foina**	Stone marten	5	10	1	15	2003-2008	Portugal	Clara Grilo
		*Meles meles**	Badger	9	7	1	22	2016-2017	England	Maren Huck/Sarah Perkins
	Ursidae	*Ursus arctos*	Brown bear	16	427	1	80	2003-2009	Greece	Alexandros Kalamandris
		Ursus arctos	Brown bear	40	185	1	23	2015-2019	Canada	Clayton Lamb
	Viverridae	*Genetta genetta**	Genet	10	8	1	4	1999-2002	Spain	Camps Munuera
Ungulates	Cervidae	*Alces americanus*	Moose	3	105	1	33	2007-2010	USA	Kathy Zeller/ Winston Vickers
		Cervus canadensis	Wapiti	39	80	1	61	2006-2010	USA	Jeff Gagnon
		*Cervus elaphus**	Red deer	15	18	1	26	2017-2018	Switzerland	Thomas Rempfler/Christian Rossi
		Capreolus capreolus	Roe deer	44	27	1	4	2010-2014	Germany	Falko Brieger/Matteo Bastianelli
		Capreolus capreolus	Roe deer	79	103	1	402	2009-2012	Germany	Marco Heurich/Matteo
	Equidae	*Equus hemionus onager**	Asiatic wild ass	58	21	1	4	2017-2018	Iran	Mohammadi
	Suidae	*Sus scrofa**	Wild boar	3	8	1	15	2013-2015	Poland	Hernryk Okarma/Katarzina

Appendix 2.

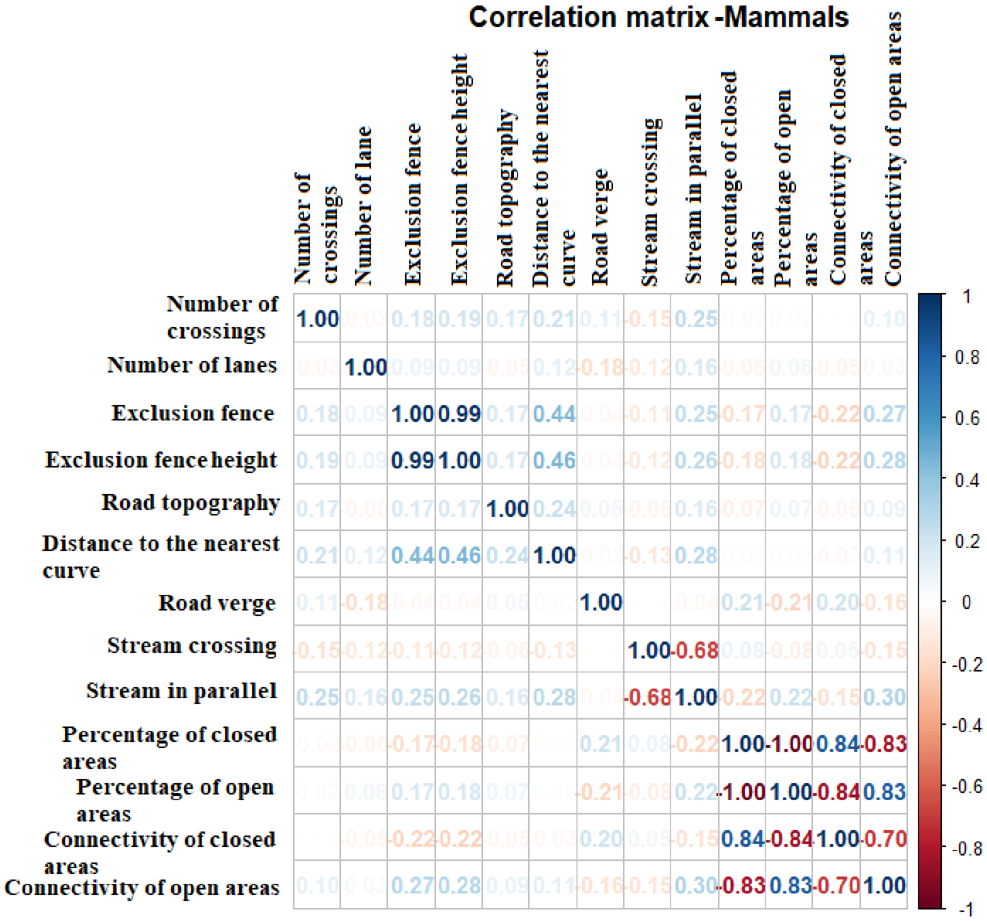

Fig 4. Correlation matrix of mammals in general.

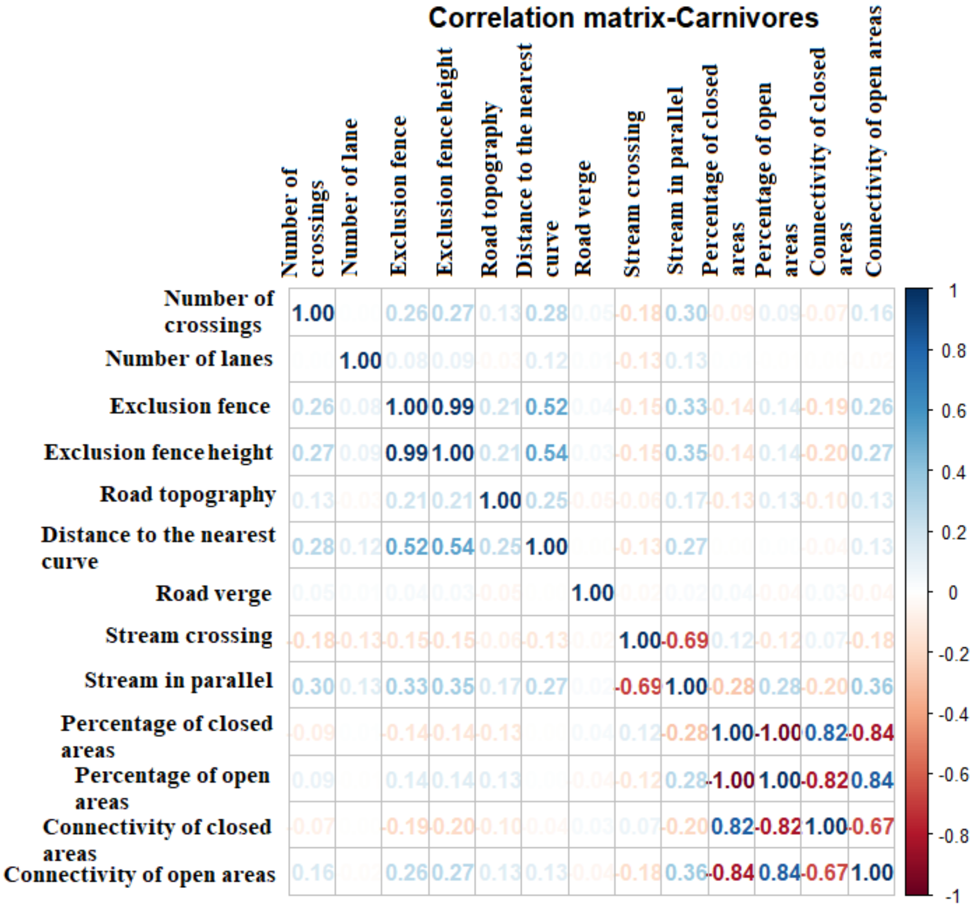

Fig 5. Correlation matrix of carnivores.

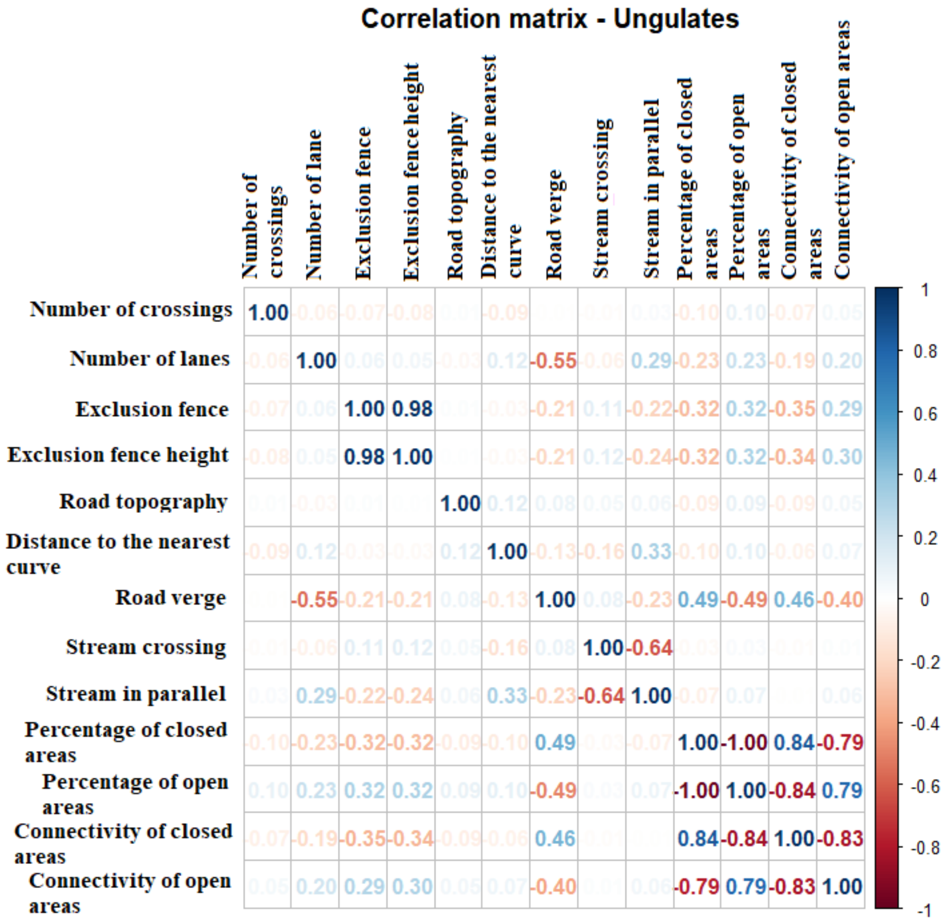

Fig 6. Correlation matrix of ungulates.

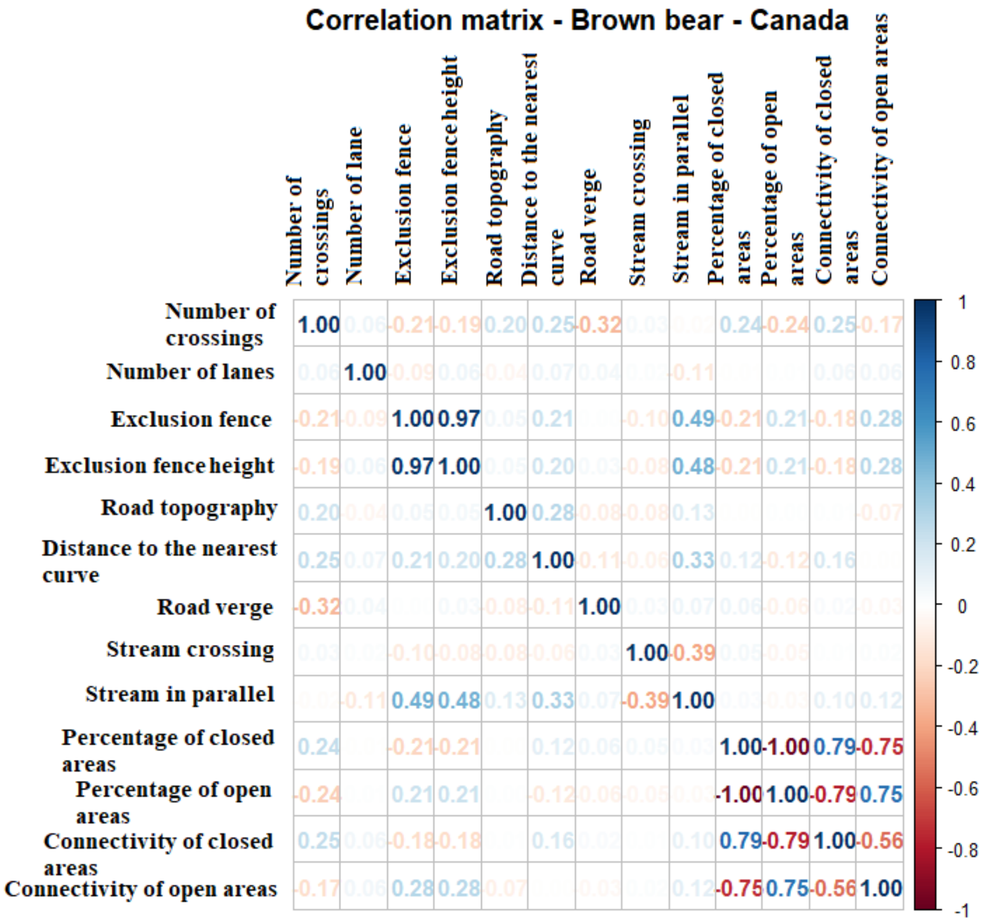

Fig 7. Correlation matrix of brown bear from Canada.

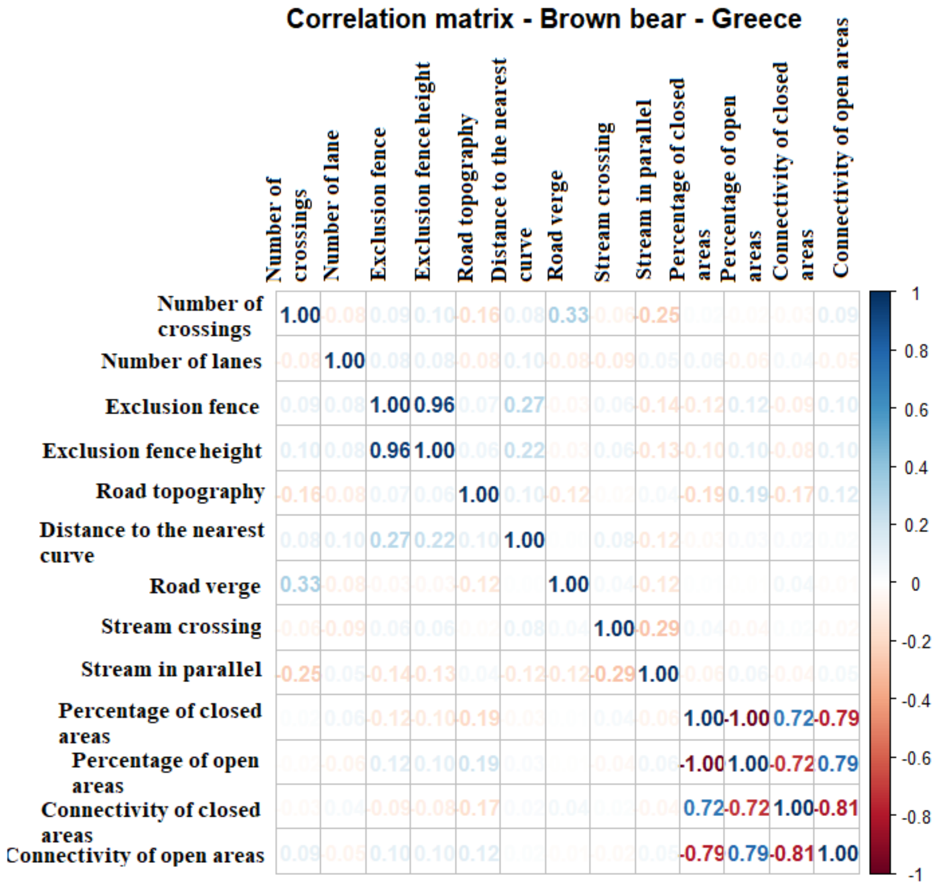

Fig 8. Correlation matrix of brown bear from Greece.

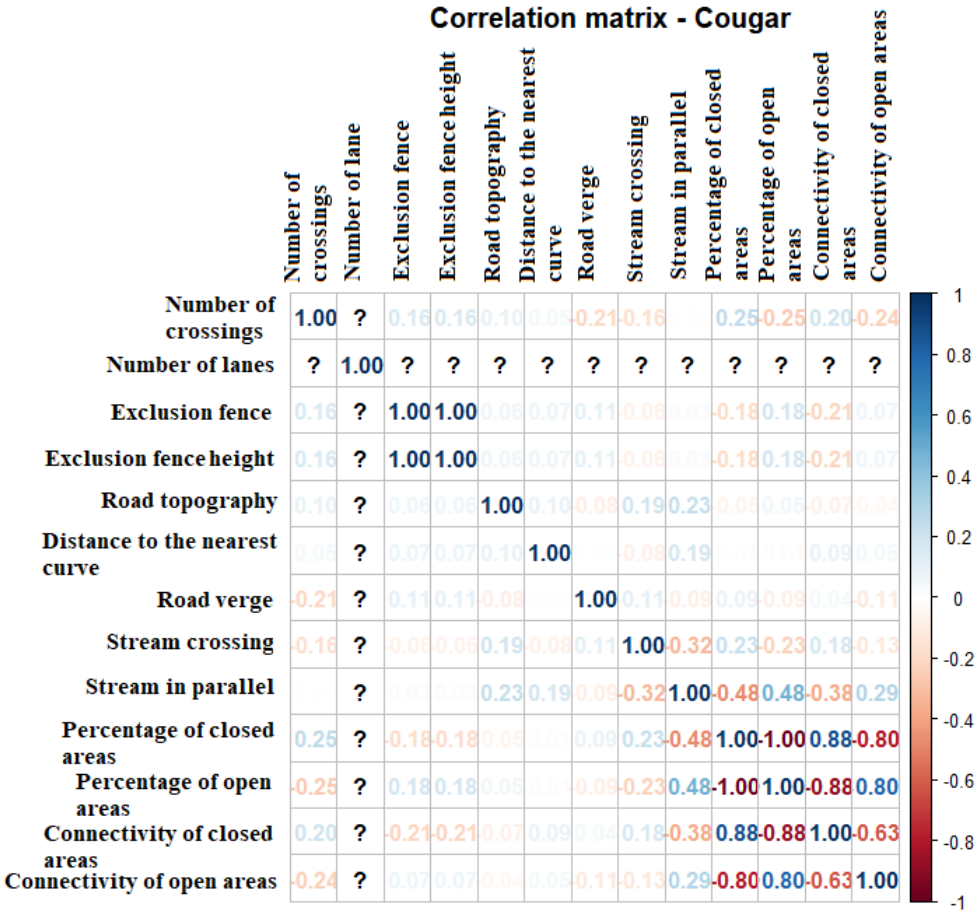

Fig 9. Correlation matrix of cougar.

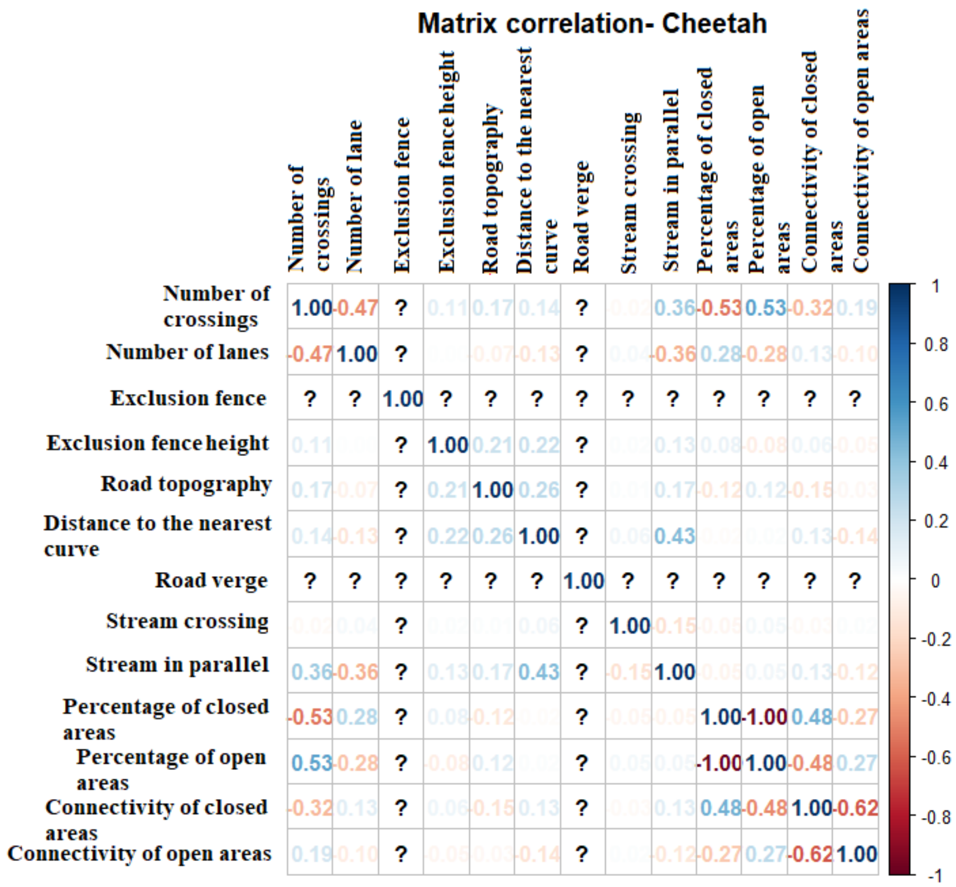

Fig 10. Correlation matrix of cheetah.

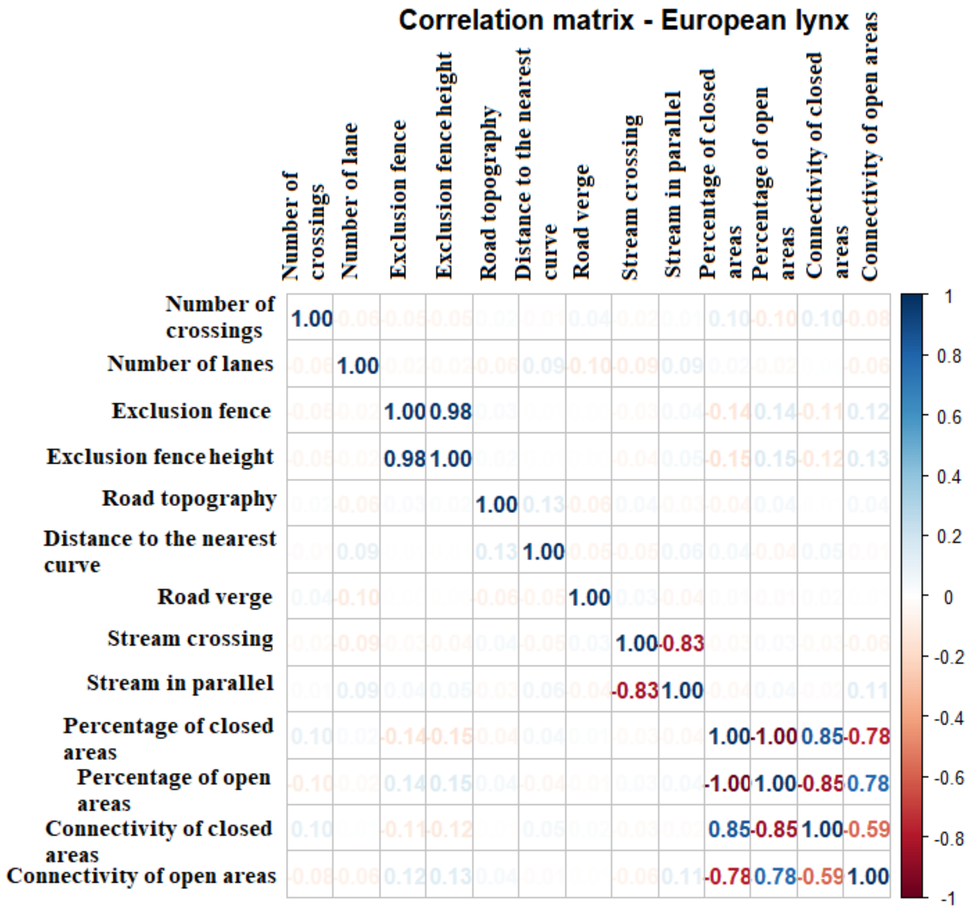

Fig 11. Correlation matrix of European lynx.

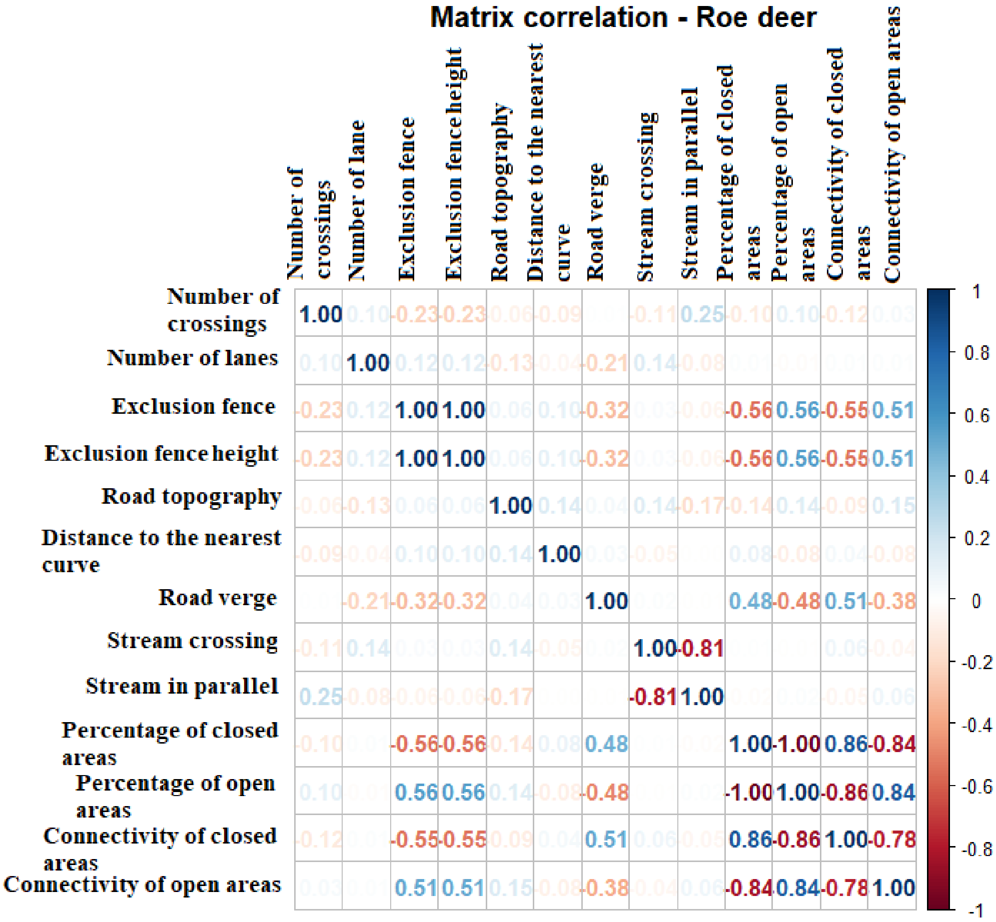

Fig 12. Correlation matrix of roe deer.

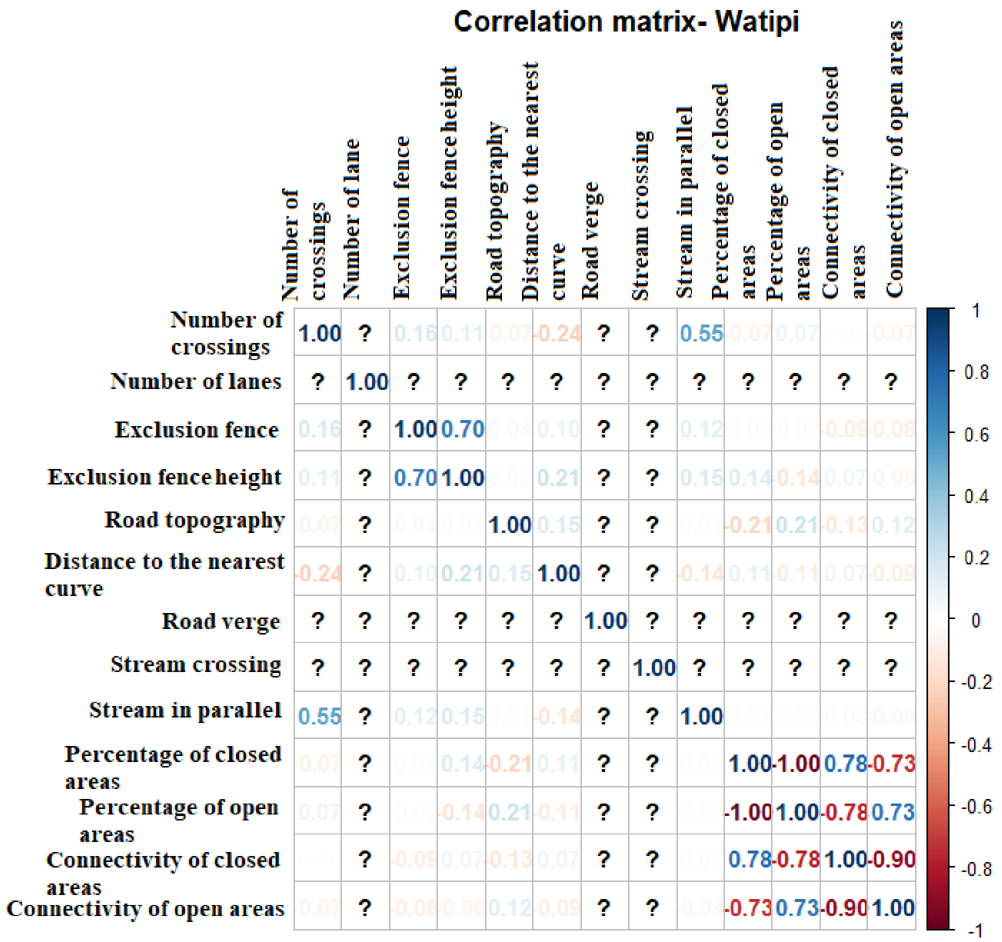

Fig 13. Correlation matrix of wapiti.

Appendix 3.

All mammals - Results of averaging of the best-fitted mixed-effects models (ΔAICc< 2) analyzing the effects of road-related feature variables on the incidence of crossings

	β	SE	Adjusted SE	z Value	p-value
(Intercept)	-0.060	0.230	0.230	0.262	0.793
Number of lanes	-0.626	0.138	0.138	4.533	<0.001
Exclusion fence	-0.033	0.116	0.116	0.284	0.777
Stream crossing	-0.361	0.180	0.181	1.995	0.046
Stream in parallel	0.029	0.350	0.350	0.083	0.934
Road topography	0.008	0.052	0.052	0.156	0.876
Distance to the nearest curve	0.585	0.212	0.212	2.757	0.006
Road verge	0.004	0.068	0.068	0.066	0.947
Connectivity of open areas	-0.004	0.046	0.046	0.080	0.936

All carnivores - Results of averaging of the best-fitted mixed-effects models (ΔAICc< 2) analysing the effects of road-related feature variables on the incidence of crossings by.

	β	SE	Adjusted SE	z Value	p-value
(Intercept)	-0.056957	0.364403	0.364638	0.156	0.87588
Number of lanes	-0.645573	0.160716	0.160821	4.014	5.96E-05
Exclusion fence	-0.213176	0.257653	0.257745	0.827	0.40819
Stream in parallel	-6.409570	2.318856	2.320380	2.762	0.00574
Road topography	0.004391	0.043727	0.043753	0.1	0.92005
Distance to the nearest curve	1.036049	0.254713	0.254877	4.065	<0.001
Road verge	-0.004889	0.07411	0.074156	0.066	0.94743
Connectivity of open areas	-0.023181	0.079964	0.08	0.29	0.77199

All ungulates - Results of averaging of the best-fitted mixed-effects models (ΔAICc< 2) analyzing the effects of road-related feature variables on the incidence of crossings by.

	β	SE	Adjusted SE	z Value	p-value
(Intercept)	-0.238258	0.218289	0.218994	1.088	0.277
Number of lanes	-0.523627	0.246224	0.247054	2.119	0.034
Exclusion fence	0.12613	0.290511	0.29099	0.433	0.665
Stream in parallel	1.499109	0.998997	1.000.846	1.498	0.134
Road topography	-0.005259	0.08135	0.081604	0.064	0.949
Distance to the nearest curve	-0.256121	0.428542	0.42923	0.597	0.551
Road verge	0.003771	0.067127	0.067342	0.056	0.955

Connectivity of open areas	0.335565	0.313108	0.313617	1.070	0.285

Each species - Results of averaging of the best-fitted mixed-effects models (ΔAICc< 2) analyzing the effects of road-related feature variables on the incidence of crossings by.

	β	SE	Adjusted SE	z Value	p-value
Brown bear in Canada					
(Intercept)	-3.9336	437.9689	440.9584	0.009	0.99288
Number of lanes	3.4468	437.9686	440.9581	0.008	0.99376
Exclusion fence	-1.0555	0.3989	0.4015	2.629	0.00856
Stream in parallel	-5.8257	13.5773	13.6283	0.427	0.66904
Road topography	1.0039	0.432	0.435	2.308	0.021
Distance to the nearest curve	1.0310	0.4619	0.465	2.217	0.02662
Road verge	-1.9580	0.4972	0.5005	3.912	<0.001
Connectivity of open areas	-0.2752	0.3766	0.3778	0.728	0.46637
Brown bear in Greece					
(Intercept)	-0.06294	0.40846	0.40936	0.154	0.8778
Number of lanes	-0.4332	0.33791	0.33844	1.280	0.20055
Exclusion fence	0.19106	0.46839	0.46919	0.407	0.68385
Stream crossing	-2.03467	0.94135	0.94407	2.155	0.03115
Stream in parallel	-20.76395	4.80786	4.82176	4.306	<0.001
Road topography	-0.57251	0.24024	0.24093	2.376	0.01749
Distance to the nearest curve	1.83245	0.93356	0.93622	1.957	0.05031
Road verge	3.36790	1.06550	1.06859	3.152	0.00162
Connectivity of open areas	0.61417	0.27488	0.27567	2.228	0.02589
Cheetah					
(Intercept)	10.522	4018.651	4058.050	0.003	0.99793
Number of lanes	-17.528	1854.581	1872.730	0.009	0.99253
Stream crossing	8.285	5688.743	5744.667	0.001	0.99885
Stream in parallel	16.255	5.814	5.870	2.769	0.00562
Road topography	8.460	3565.122	3600.093	0.002	0.99813
Connectivity of closed areas	-17.942	2398.760	2422.231	0.007	0.99409
Percentage of closed areas	-6.758	2.294	2.317	2.917	0.00353
Cougar					
(Intercept)	0.2369	0.5255	0.5348	0.443	0.6578
Exclusion fence	22.674	12.581	12.883	1.760	0.0784
Stream crossing	-11.7541	1358.8952	1392.2369	0.008	0.9933
Stream in parallel	-1.7189	45.364	45.879	0.375	0.7079
Road topography	0.4389	0.6752	0.6823	0.643	0.52
Road verge	-0.9937	0.9441	0.9557	1.040	0.2984
Connectivity of open areas	-1.7695	0.7636	0.7817	2.263	0.0236
Eurasian lynx					
(Intercept)	-1.97435	0.23393	0.23415	8.432	<0.001
Number of lanes	-0.40652	0.2802	0.28042	1.450	0.1472
Exclusion fence	-0.6331	0.95709	0.95778	0.661	0.5086

Road topography	0.02299	0.10635	0.10645	0.216	0.829
Distance to the nearest curve	0.05194	0.3074	0.30771	0.169	0.866
Road verge	0.13717	0.37171	0.37194	0.369	0.7123
Connectivity of open areas	-0.68523	0.29685	0.29721	2.306	0.0211
Roe deer					
(Intercept)	-0.66226	0.75396	0.75761	0.874	0.382
Number of lanes	0.17201	0.33293	0.33453	0.514	0.6071
Stream in parallel	169.91232	120.53496	121.30780	1.401	0.1613
Road topography	-0.5877	0.67467	0.67795	0.867	0.386
Distance to the nearest curve	-0.67231	1.25771	1.26452	0.532	0.595
Road verge	0.01366	0.12624	0.12724	0.107	0.9145
Connectivity of open areas	1.02834	0.40377	0.40759	2.523	0.0116
Wapiti					
(Intercept)	-2.31287	0.76427	0.77555	2.982	0.002862
Exclusion fence	12.91803	1449.27843	1473.04110	0.009	0.993003
Stream in parallel	15.53826	4.52909	4.60243	3.376	0.000735
Road topography	0.07934	0.4606	0.46614	0.17	0.864854
Distance to the nearest curve	-0.67414	0.89693	0.90455	0.745	0.456108
Connectivity of open areas	-0.10056	0.37248	0.37682	0.267	0.789567

Appendix 4.

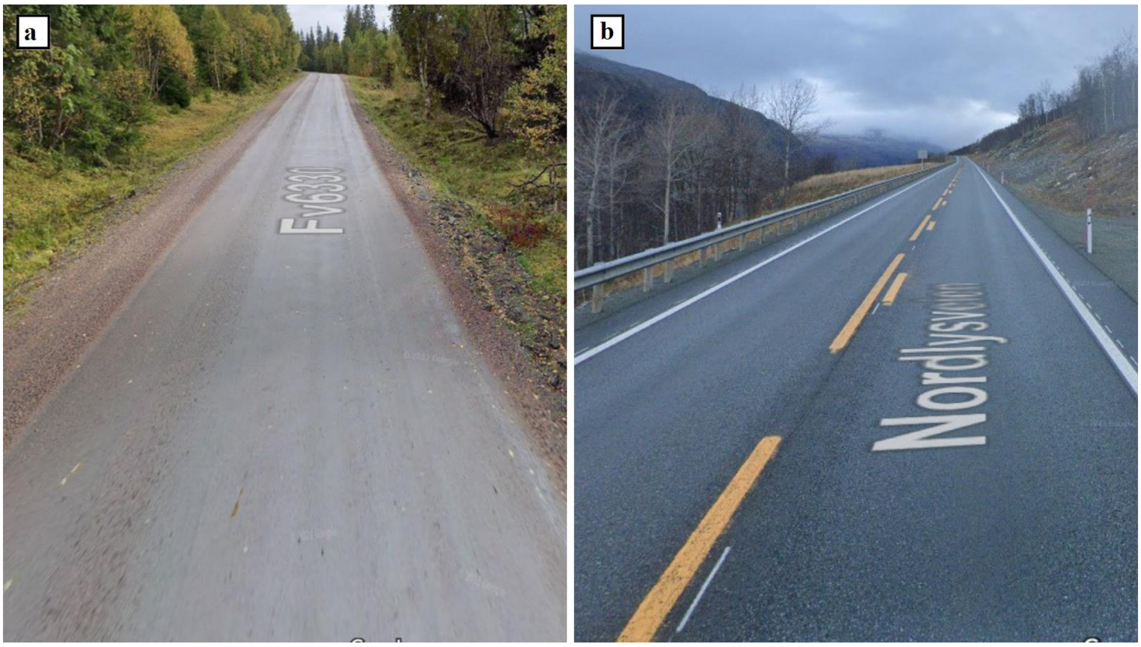

Fig 14. Number of lanes: a) one-lane (0); b) two-lanes (1).

Fig 15. Exclusion fence and exclusion fence height: a) no exclusion fence (0); b) Presence of exclusion fence (1) and normal for livestock (1); c) Presence of exclusion fence (1) and high (1).

Fig 16. Stream crossings. Example of: a) absence of a stream crossing in 500m of segment in Google Street View (0); b) absence of a stream crossing in 500m of segment in Google Satellite (0); c) absence of a stream crossing in Google Maps in 500m of segment (0); d) presence of a stream crossing in 500m of segment in Google Street View (1); e) presence of a stream crossing in Google Satellite (1); f) presence of a stream crossing in 500m of segment in Google Maps (1).

Fig 17. Stream in parallel. Example of a stream at 162m distant from the centroid.

Fig 18. Road topography. Example of: a) other type of road (0); b) flat road (1).

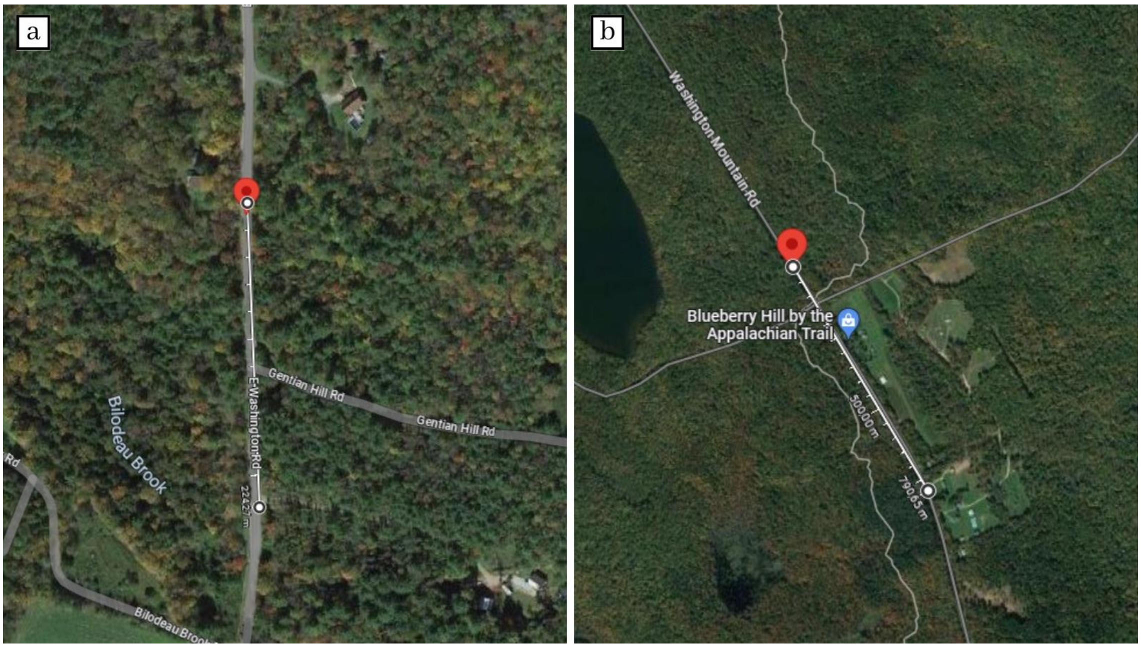

Fig 19. Distance to the nearest curve. Example: a) a curve in the segment of 500m than the value was 0; b) a curve at 790m distant from the centroid.

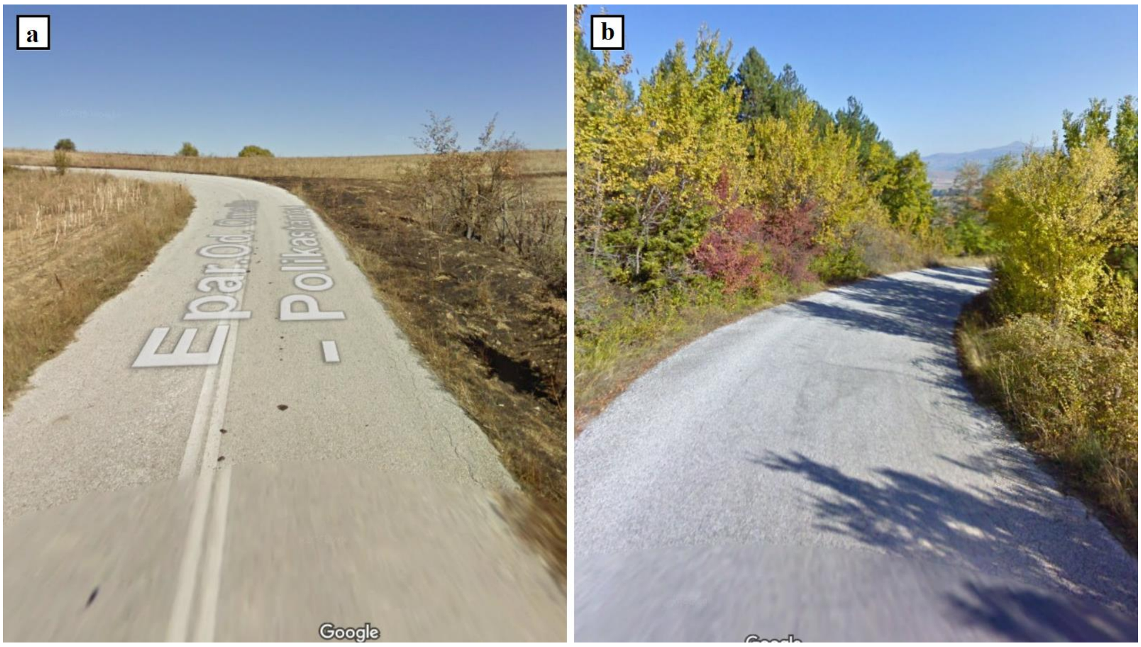

Fig 20. Road verge. Example of: a) a grassland (0); b) trees (1).

Fig. 21. Percentage of open areas. Example of: a)25% of open area; b) 90% of open area.

Fig 22. Percentage of closed areas. Example of: a)80% of closed are; b)100% of closed area.

Fig 23. Connectivity of closed areas. Example of: a) less than 50% connectivity of closed areas (0); b) more than 50% connectivity of closed areas (1).

Fig 24. Connectivity of open area. Example of: a) less than 50% of connectivity of open areas (0); b) more than 50% connectivity of open areas (1).