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Road orientation affects the impact of roads on wildlife

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ABSTRACT

Context. Understanding the factors determining the impacts of roads and how they fragment landscapes limiting the movement of animals, is key to implement efficient mitigation measures. **Aims.** Here we investigate if road orientation in relation to limiting resources, a largely overlooked factor on road impact assessments, can influence the movement of animals within a landscape where water resources are spatially clustered. **Methods.** We evaluated movement by monitoring animal tracks on unpaved roads: two with a North–South orientation and two with an East–West orientation. **Key results.** Animals were more likely to follow roads leading to limiting resources (i.e. East–West orientation), confirming human linear structures can facilitate wildlife movements. Carnivores were more likely to follow roads with any orientation and for longer compared to ungulates, whereas ungulates followed roads mainly in the orientation of limiting resources. **Conclusions.** Road orientation affects how roads influence the movement of animals in landscapes where resources are distributed along a spatial gradient with different effects for ungulates and carnivores. **Implications.** The key implications of this work affect the planning and implementation of mitigation strategies and safety measures. Our results suggest road-crossing infrastructure and fences will be most important in roads traversing a gradient to allow wildlife movement while preventing collisions. For roads along a gradient, crossing structures may be less important, but fences or appropriate signage could be useful to prevent or warn drivers of animals travelling on the road.

Keywords: animal movement, habitat fragmentation, landscape connectivity, mitigation, road ecology, roadkill, track census, wildlife collisions.

Introduction

Roads fragment landscapes, contribute to ecosystem degradation and threaten biodiversity (Bennett 2017). These linear structures are expected to increase by more than 60% globally by 2050 (Meijer *et al.* 2018), therefore, understanding the factors determining their impact on wildlife before they are designed and built is crucial to minimise environmental impact and reduce human safety risks along with the financial implications of wildlife collisions (Diaz-Varela *et al.* 2011; Morelle *et al.* 2013; Rytwinski *et al.* 2016; Visintin *et al.* 2018; Ascensão *et al.* 2019*a*). The most studied road impacts for wildlife are roadkill and fragmentation, both consequences of an animal choice to cross or avoid a road (Grilo *et al.* 2012). Their interaction produces the so-called barrier effect, which contributes to subdivide and isolate animal populations (Grilo *et al.* 2012) eventually compromising their viability (Ceia-Hasse *et al.* 2017). How roads affect wildlife depends on which species are in an area, their characteristics, and their local abundance (Jacobson *et al.* 2016; Visintin *et al.* 2016; González-Suárez *et al.* 2018; Ascensão *et al.* 2019*a*; Duffett *et al.* 2020), as well as on traffic and road properties (e.g. road width, traffic speed) and the characteristics of the surrounding environment (Borkovcová *et al.* 2012; D'Amico *et al.* 2015; Visintin *et al.* 2016). While diverse factors related to road properties and surrounding environment have been studied, there is still a gap in the literature regarding how the spatial properties of roads, such as their orientation in relation with limiting resources for animals, can influence how roads impact wildlife.

The objective of this work was to fill this gap evaluating how a largely overlooked aspect of road design, orientation, affects the impact of these linear structures on wildlife. To achieve this goal, we conducted a study within a Mediterranean ecosystem, in which water is a limiting resource that shows strong spatial aggregation. Road orientation can be important because limiting resources for animals, such as water, are often associated to geographical features (e.g. rivers, mountain chains or coastlines) that form landscape gradients. These gradients result in periodic movements of animals to and from resources that may occur across different spatio-temporal scales, from individual daily movements connecting water/refuge/food to large seasonal migrations to track fresh pastures. Therefore, we predict that in landscapes with a resource gradient, such as our study area, animals will respond differently to roads that run along the gradient compared to those that intersect it. In general, we expect that animals could either avoid completely, or alternatively use as movement corridors, roads that run along the gradient, while roads that intersect the gradient, i.e. blocking their access to the resources, will have to be regularly crossed but will rarely be used as travel corridors.

Additionally, we anticipate that different species groups will be influenced differently by road orientation. To test this possibility, we studied two groups of mammals: large herbivores and carnivores for which we predict different responses. Herbivores, namely ungulates, are dependent on primary productivity and regularly move across the landscape water gradient, but previous work suggest they may avoid roads (D'Amico *et al.* 2016). Conversely, carnivores' movements are less influenced by water and pasture resources and previous work suggests they can be attracted to roads and use these for travelling and marking (Whittington *et al.* 2011). Thus, we predict carnivores will use and travel on roads more often and be less affected by their orientation as their movement across the landscape is not strongly directional. Large herbivores, which are those most often involved in deadly collisions (Bissonette *et al.* 2008), are expected to cross roads traversing the gradient and could either avoid or travel along those roads that link resources.

Our study provides new understanding regarding how wildlife is affected by road design, in particular orientation within the landscape. When designing a road, its orientation will largely be determined by the need to connect areas and relevant socioeconomic factors, yet, even if overall orientation is unlikely to be flexible, mitigation measures and safety guidance (e.g. speed limits and signage) could be adapted to reduce impact to wildlife and humans. Understanding how orientation influences the movement of wildlife can anticipate the probability of animals crossing roads or moving along them, behaviours which pose different challenges to wildlife and human safety. Here we offer insights to promote more effective mitigation strategies, with implications for sustainable road management and wildlife conservation.

Materials and methods

Study area

Our study was carried out in Doñana Biological Reserve, a management unit of 6794 ha with the highest level of environmental protection in the core of the Doñana Natural Area. The Doñana Natural Area (36°59′N, 6°26′W) comprises both National and Natural Parks, and is located in the Guadalquivir river estuary, in the Atlantic coast of South-western Spain (Fig. 1). The climate is Mediterranean sub-humid with marked seasons (i.e. hot dry summer and mild winter, with precipitations mainly during winter and spring). Doñana Biological Reserve hosts three main ecosystems: sandy dunes; Mediterranean shrubland/forest;

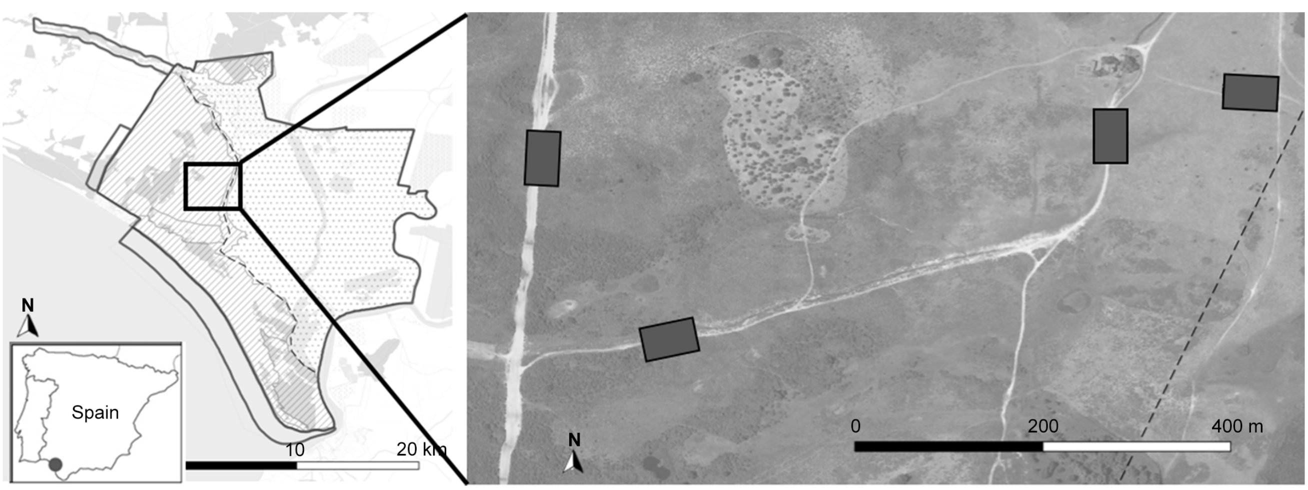

Fig. 1. Study area in Doñana National Park. Dark grey rectangles indicate the four sampled trails. The dashed black line indicates the ecotone, with water resources located towards East.

and marshland in the eastern area of the reserve (Fig. 1). During summer (June–September) most available water and pastures are concentrated along the ecotone between Mediterranean shrubland/forest and marshland, that runs mainly in a North–South direction within the Biological Reserve. Ungulate species in this area include wild boar *Sus scrofa*, feral cattle *Bos taurus*, red deer *Cervus elaphus*, feral horse *Equus caballus*, and fallow deer *Dama dama* (listed in approximate order of abundance; Castroviejo 1993). Carnivore species include red fox *Vulpes vulpes*, large grey mongoose *Herpestes ichneumon*, European badger *Meles meles*, feral dog *Canis lupus familiaris*, small-spotted genet *Genetta genetta*, feral cat *Felis silvestris catus*, Iberian lynx *Lynx pardinus*, Eurasian otter *Lutra lutra*, and European wildcat *Felis silvestris* (listed in approximate order of abundance; Castroviejo 1993). Doñana Natural Area has a heterogeneous road-network mostly composed by unpaved sandy roads that were built according to the transportation needs for humans (i.e. park management, historical reasons), with low traffic volume (~10 vehicles/day; Román *et al*. 2010).

Data collection and variables definition

Within Doñana Biological Reserve, we selected a section of 50 m length in each of four unpaved roads (with sandy soil) close to the ecotone between Mediterranean shrubland/forest and marshland. Two of the surveyed roads run North–South (2° and 4°) perpendicular to the landscape water gradient. The other two roads run East–West (82° and 89°) in parallel with landscape water gradient (Fig. 1).

During 10 days in June–July 2019 we monitored ungulate and carnivore tracks on the selected road sections daily. The day before starting the data collection, we swept the sand in each road section using a heavy piece of wood pulled by a 4 × 4 vehicle to create a clean and homogeneous surface. Then, each road section was swept with a broom daily after tracks were recorded to avoid double counting them on subsequent days. Every sampling day, soon after sunrise, we surveyed the four road sections to record tracks starting each day on a different road section. For each track found we recorded: the species (when possible) or *species group* (i.e. ungulates or carnivores), the angle of the track where entering the road section and the angle where exiting it (recorded with a compass), *track length* within the road section (measured in metres with a tape), and described the *speed* of the animal that made the track as gait type: walk, trot, gallop. For each road section, we also visually estimated and recorded the percentage of *shrub coverage* in the band of 3 m adjacent to the roads because vegetation may affect animal movement.

Because not all tracks could be identified to species, our analyses focused on the two *species groups* (ungulates and carnivores). Track *speed* was also reclassified in two levels for analyses: slow for tracks that only showed gait = walk, and fast for all others. Track *movement type* was classified in two levels based on the entrance and exit angles and the road orientation: cross for tracks where the animal had entered the road from one side and exited from the other (regardless of track length) and follow for tracks of >3 m in length where entrance and exit occurred from the same side of the road or were beyond the 50 m section (entrance or exit angle were not recorded). We excluded nine tracks with a length <3 m that we could not clearly classify as 'cross' or 'follow'. Finally, track *movement direction* was defined as the travel direction (e.g. North–South or South–North) within the road for tracks with movement type = follow.

Data analyses

We fitted logistic mixed effects regression models using the glmer function from the lme4 package in R (R Foundation for Statistical Computing 2013) to:

1. Predict the *movement type* (cross vs follow) of each observed track as a function of three predictors: *road orientation*, *species group* and estimated *shrub coverage* in the adjacent terrain of each road.
2. Predict the *speed* (fast vs slow) of each observed track as a function of three predictors: *road orientation, species group* and *movement type*, (we expected animals crossing to move faster than those following roads).
3. Predict the *movement direction* for animals following roads (*movement type* = follow) for each *road orientation* (one model for each orientation) as function of two predictors: *species group* and *speed*.
4. Predict the *track length*, a proposed proxy for the duration of road travel, for animals following roads (*movement type* = follow) as a function of four predictors: *road orientation*, *species group*, movement *speed* and *shrub coverage*.

In models that included *road orientation* and *species group* as predictors, we tested for an interaction between these two predictors to explore differential responses. We report interaction terms if these were significant and otherwise report simpler additive models. In all fitted models we used observation *date* nested within *transect ID* (unique identifier for each of road sections) as a random factor to control for temporal and spatial non-independence of the track data.

Results

We analysed a total of 289 tracks (Table 1). Of these, 264 were made by ungulates including 24 by feral species (horses and cattle), 240 by wild species (wild boars, red and fallow deer) and 25 by carnivores (foxes, badgers, felids and other unidentified meso-carnivores). We found 132 tracks in

Table 1. Recorded tracks by animal species groups, movement type (cross vs follow) and road orientation.

Species group	Cross			Follow		
	East–West	North–South	Total	East–West	North–South	Total
Ungulates	42	114	156	82	26	108
Carnivores	2	5	7	6	12	18
Total	44	119	163	88	38	126

East–West roads and 157 in North–South roads. A total of 163 tracks crossed the road and 126 followed its trajectory.

Animals moved differently on roads with different orientations being over five times more likely to follow and three times less likely to move fast on East–West roads compared to those with North–South orientation (Table 2, Figs 2, 3). Species differed in their use of roads, with carnivores being over seven times more likely to follow roads than ungulates and having a tendency (not significant) to move slower. However, groups did not differentially respond to road orientation: the interactions between *road orientation* and *species group* were not significant for *movement type* or *speed*. Finally, roads were used differently depending on the adjacent terrain and animals were more likely to follow roads in areas with more shrub coverage (Table 2).

There were no differences in *movement direction* associated with *species group* or movement *speed* (Table 3). However, several factors influenced *track length*, and thus, presumably the time animals followed roads. In particular, tracks were longer in North–South roads, if they belonged to carnivores, and when left by animals moving faster (Table 4, Fig. 3).

Table 2. Coefficient estimates (odds ratios (OR)) for models testing factors that influence how animals move on road (movement type and speed).

Variables	OR	95% CI
Movement type: follow/cross		
Intercept	0.348	0.106–1.353
Road orientation: East–West	**5.189**	**2.268–13.117**
Species group: ungulates	**0.139**	**0.034–0.398**
Shrub coverage	**1.037**	**1.024–1.053**
Speed: fast/slow		
Intercept	1.195	0.250–5.007
Road orientation: East–West	**0.266**	**0.055–0.932**
Species group: ungulates	0.299	0.079–1.073
Movement type: follow	0.477	0.171–1.195

We report the odds ratios for best estimates (OR) and their 95% bootstrapped confidence intervals. Predictors with 95% CI non-overlapping with one are highlighted in bold. Landscape direction is East–West.

Discussion

As predicted, our results showed that the movement of animals in relation to roads varies depending on the orientation of these structures, at least in landscapes where resources are spatially distributed along a gradient. We also found that ungulates and carnivores make different use of these structures, which suggests these groups could face different roadkill risk and fragmentation impacts.

Animals were more likely to follow roads along the environmental gradient that could be used to move to and from a key resource, which in this study area is freshwater. In semi-arid environments, wildlife depends highly on limited water (Kihwele *et al.* 2020), and many species travel daily to and from water and associated resources such as fresh pastures (Kasiringua *et al.* 2017). Our findings suggest that the animals may be taking advantage of existing roads for these movements, at least in the dry season when water is scarce. Several studies have described wildlife using roads, including some of the species we detected (e.g. wild boars and red foxes) (Macdonald 1979; Boughton *et al.* 2019). Roads can offer opportunities for foraging and marking behaviour (Monclús *et al.* 2009; Toger *et al.* 2018) and facilitate movement because they often present a flatter surface without vegetation or snow (Whittington *et al.* 2005; Brown *et al.* 2006). Indeed, we found that animals were more likely to follow unpaved roads in areas surrounded by more shrub coverage where movement may be hampered and left longer tracks when travelling faster because when flatter, obstacle-free terrain may be most important. However, wildlife may not use roads if these are heavily used by humans. In fact, wildlife are more likely to take advantage of roads with low traffic volume (Brown *et al.* 2006; Boughton *et al.* 2019), which is the case for our study area (10 vehicles/day; (Román *et al.* 2010). Similarly, wildlife can travel along heavily trafficked roads and associated roadsides during low-traffic periods, such as night-time for certain roads (Brown *et al.* 2006).

As hypothesised, the two species groups differed in their use of roads, with carnivores over seven times more likely to follow roads and doing so for longer compared to ungulates. Carnivore species have been shown to use roads for diverse purposes, including as travel corridors (Whittington *et al.* 2005), for territorial displays (Monclús *et al.* 2009), for hunting (Andersen *et al.* 2017) and

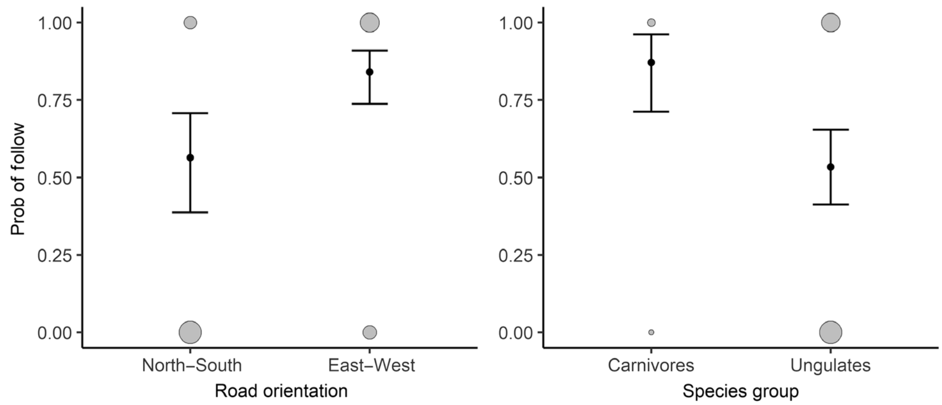

Fig. 2. Model predictions (median shown as black symbols and 95% CI as error bars) showing changes in the probability of movement type being 'follow' for roads with different orientations and for different species groups. Plots also display the observed occurrence of 'follow' movements (grey circles positioned at $y = 1$) and cross movements (grey circles at $y = 0$) for each road orientation and species group. The size of the grey circles is proportional to the number of observations (e.g. we observed more 'follow' movement on East–West than on North–South roads).

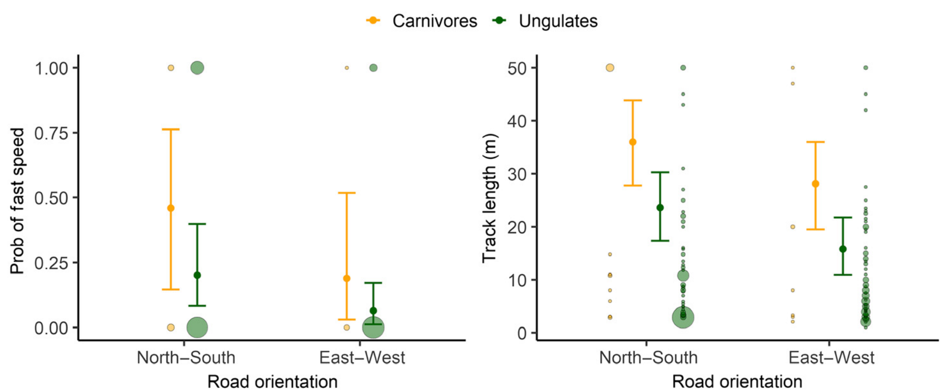

Fig. 3. Model predictions (median shown as small symbols with 95% CI error bars) showing the probability of *movement speed* being fast (left panel) and estimated *track length* for movement type = 'follow' (right panel) across species group and roads with different orientations. Plots also display the observed occurrence of fast movements (circles positioned at $y = 1$) and slow movements (circles at $y = 0$) in the left panel and the observed track lengths (right panel) for each road orientation and species group. The size of these circles is proportional to the number of observations. There were more slow than fast movements on ungulates following East–West roads.

scavenging (Barrientos *et al.* 2018). In our study area, red foxes are known to actively select roads for defecation, probably as a marking behaviour (Suárez-Esteban *et al.* 2013). Conversely, prey species, such as ungulates in our case study, are more likely to exhibit road-gap avoidance as part of their anti-predator behaviour (Laurance *et al.* 2004; Chen and Koprowski 2016). In agreement with a previous study in this area (D'Amico *et al.* 2016), we found that ungulates do sometimes use roads, with a tendency to follow East–West roads more than those oriented North–South. This suggests road use may be an acceptable risk when there is a benefit such as easier travel to and from limiting resources.

Previous studies have evaluated how road design and some related characteristics influence wildlife impacts. Road design depends on road alignment, profile and section (Garber and Hoel 2019). Regarding road alignment, both the presence of curves and road sinuosity can affect roadkill risk (Grilo *et al.* 2011; D'Amico *et al.* 2015). Similarly, regarding road profile, road slope can have an effect on roadkill probability (D'Amico *et al.* 2015; Kang *et al.* 2016). Many road features related to road section have been often considered as predictors of different road impacts, such as roadkill and fragmentation, for example road size and the presence of road shoulders or ditches (Matos *et al.* 2012; D'Amico *et al.* 2015; Jacobson *et al.* 2016). Our study is the

Table 3. Coefficient estimates for models testing factors that influence the *movement direction* in animals that follow roads (*movement type* = follow).

Variables	β/OR	95% CI
Direction in East–West roads		
Intercept	0.828	0.050–11.302
Species group: ungulates	0.894	0.121–5.417
Speed: slow	1.247	0.189–7.962
Direction in North–South roads		
Intercept	1.354	0.258–11.420
Species group: ungulates	0.447	0.036–2.376
Speed: slow	2.615	0.468–44.418

We report odds ratios (OR) and their 95% bootstrapped confidence intervals. Landscape direction is East–West.

Table 4. Coefficient estimates for models testing factors that influence the *track length* in animals that follow roads (*movement type* = follow).

Variables	β	95% CI
Intercept	39.548	30.223 to 49.686
Road orientation: East–West	**−7.796**	**−13.835 to −1.370**
Species group: ungulates	**−11.893**	**−19.115 to −4.841**
Speed: slow	**−8.739**	**−15.544 to −1.278**
Shrub coverage	0.006	−0.102 to 0.109

We report best estimates and their 95% bootstrapped confidence intervals. Relevant predictors with 95% CI non-overlapping with zero are highlighted in bold.

first assessment of how road orientation in relation to key resources affects animal movement, which can ultimately influence landscape connectivity and direct impacts to wildlife and humans, but our approach had some limitations. First, we did not monitor animal tracks outside roads; thus, we could not test whether the studied species used roads differently from the natural landscape. However, our study design allowed us to compare the use on roads running both across and along the environmental gradient, testing the hypothesis that road use by animals could differ when both orientations are available. Second, our study area is small (<1 km^2) and did not allow us to confirm that the patterns found here will apply to larger geographical scales. Studies addressing the consequences of animal movement on landscape connectivity are usually performed at a larger scale (landscape or regional, up to global) involving high economic costs (e.g. tagging or radio-marking several individuals of the target species; Blazquez-Cabrera *et al.* 2016) or complex modelling efforts (e.g. Ascensão *et al.* 2019*b*). Here, we used a smaller-scale approach that can represent a valuable first step to assess landscape connectivity with a relatively small effort, both economically and analytically. Third, the low traffic levels and the lack of pavement of the studied roads seem to facilitate animal movement along them, but effects may be different for busy or paved roads. Future research would be necessary to understand how different types of roads facilitate or prevent access of wildlife to spatially aggregated limiting resources and how this may affect landscape connectivity and ultimately the persistence of animal populations.

Our results have potential implications for the conservation and management of species and areas, and for human safety by helping in understanding the mechanisms potentially reducing wildlife-vehicle collisions. Roadkills occur when wildlife use roads, which we show can be influenced by road orientation, suggesting this aspect of road design should be considered as a factor affecting collision probability. Road orientation seems to influence particularly large ungulates, which due to their size pose the greatest risk to humans in case of a collision (Conover 2019). We recommend that mitigation measures should be prioritised for roads paralleling resource gradients as these may be preferably used by large ungulates to access limiting resources. Fenced roadsides could be designed to act as suitable corridors for ungulates, allowing for required movements to essential resources but limiting collision risks (Jakes *et al.* 2018). For roads that transverse the environmental gradient, wildlife road-crossing structures will be essential to ensure access to limiting resources. Finally, while road orientation may be primarily driven by human requirements (i.e. which areas need to be connected), whenever possible the construction of new roads in directional landscapes should consider road orientation in relation to key resources for wildlife to reduce the impact on animals movement and landscape connectivity.

Conclusion

The main finding of our study is that road orientation affects how these linear structures influence animal movement in landscapes where resources are distributed along a spatial gradient with distinct effects for ungulates and carnivores. When a road is planned and designed its orientation will be primarily determined by human needs and costs, although environmental impact assessments will also take into consideration aspects that we studied here such as animal movement and critical resources (Stokes 2015; Broniewicz and Ogrodnik 2020). However, we consider the key implications of our work affect the planning and implementation of mitigation strategies and safety measures. Our results suggest road-crossing structures and fences will be most important for roads traversing a gradient to allow wildlife movement while preventing collisions. For roads along a gradient, crossing structures may be less important, but fences or appropriate signage could be useful to prevent or warn drivers of animals travelling on the road.

Future work will be necessary to expand on our research by covering different areas with varying resource gradients, representing different species, and comparing roads with higher levels of traffic and other features (e.g. paved, multiple lanes). Additional work should also consider overcoming some of the limitations of our study, by including off-road data on animal movement and covering a wider region. Despite its limitations, our study expands our knowledge of how largely overlooked aspects of how roads are designed can affect animal movement and ultimately landscape connectivity.

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