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Research article

The road to success and the fences to be crossed: considering multiple infrastructure in landscape connectivity modelling

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Linear infrastructure represent a barrier to movement for many species, reducing the connectivity of the landscapes in which they reside. Of all linear infrastructure, roads and fences are two of the most ubiquitous, and are understood to reduce landscape connectivity for wildlife. However, what is often neglected consideration is a holistic approach of modelling the effects of multiple types of linear infrastructure simultaneously. Few studies have examined this, typically assessing the impacts of a singular kind of infrastructure on landscape connectivity. Therefore, the aim of this study is to address the relative importance of considering multiple kinds of linear infrastructure in landscape connectivity modelling. We utilised presence data of red deer *Cervus elaphus* and wild boar *Sus scrofa* in Doñana Biosphere Reserve (Spain) to generate a sequential approach of scenarios of landscape connectivity; firstly only with environmental variables, secondly with roads as the sole infrastructure, thirdly with the addition of fences, and finally with the further addition of fences and wildlife road-crossing structures. We found that the connectivity of the landscape was greatly affected by the addition of fences and wildlife road-crossing structures in both species, with fences in particular causing considerable alterations to estimated movement pathways. Our finding impresses a need to consider multiple different types of linear infrastructure when modelling landscape connectivity to enable a more realistic view of wildlife movement and inform mitigation and conservation measures more accurately.

Keywords: circuit theory, fence ecology, landscape ecology, road ecology, structural connectivity, wildlife road-crossing structures

Introduction

With the world becoming progressively urbanised to accommodate human population growth, transport and energy infrastructure is also expanding globally (Meijer et al. 2018, Emil et al. 2019), further encroaching on habitats suitable for wildlife

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(Laurance et al. 2009, Venter et al. 2016). Global increases in such infrastructure have rapidly reduced population abundance and persistence for a large amount of species, and consequently ecosystem functioning (Benítez-López et al. 2010, Haddad et al. 2015, Barrientos et al. 2021). Global infrastructure developments are predicted to continue to threaten biodiversity and wilderness hotspots (Ascensão et al. 2018, Rehbein et al. 2020), diminishing ecosystem services and human wellbeing (Tzoulas et al. 2007, Ghent, 2018).

Linear infrastructure such as roads, fences, powerlines, and railways pose many threats to wildlife, including mortality through collision (Harrington and Conover 2006, Kuvlesky et al. 2007), entrapment (Peris and Morales 2004, Budzik and Budzik 2014), or electrocution (Loss et al. 2014, D'Amico et al. 2018). Moreover, linear infrastructure indirectly damages the functioning of an ecosystem by increasing associated chemical pollutants (Leonard and Hochuli 2017) and encouraging invasive species introduction (Ascensão et al. 2020). Habitat fragmentation is also one of the more relevant indirect threats that linear infrastructure poses to wildlife (Madadi et al. 2017, D'Amico et al. 2018) with decreased landscape connectivity being a common consequence (Selva et al. 2015, Borda de Agua et al. 2017).

The connectivity of a landscape is often defined by the degree to which wildlife movement is restricted or facilitated between patches (Taylor et al. 1993), with linear infrastructure reducing this connectivity by creating physical and behavioural barriers (Jaeger et al. 2005, Burkholder et al. 2018). For example, concerning physical barriers, the introduction of wildlife-proof fencing prevented traditional movement pathways of migratory African elephants *Loxodonta africana* in Kenya and Tanzania (Osipova et al. 2018), and wildlife movement across canals in northern Spain was prevented by species such as roe deer *Capreolus capreolus* becoming entrapped or drowning (Peris and Morales, 2004). Moreover, the presence of energy infrastructure incited mass long-term avoidance by mule deer *Odocoileus hemionus* in Wyoming, USA (Sawyer et al. 2017), whereas high traffic volume on roads reduced the likelihood of ungulate crossing into new habitats in Sweden (Olsson et al. 2008). In a fragmented landscape, habitat patches become smaller and more isolated (Lees and Peres, 2009, Ceia-Hasse et al. 2018), leading to a lack of gene flow between patches (Delaney et al. 2010, Fenderson et al. 2014) and subsequently becoming more likely to suffer local extinction from genetic isolation (Corlatti et al. 2009, Koumoundouros et al. 2009).

Whilst the effects of linear infrastructure on wildlife connectivity are well documented for individual infrastructure (Crist et al. 2005, Jones et al. 2019), the additive effects of multiple types of infrastructure are often overlooked. Where multiple types of infrastructure are explored in combination, it is primarily avoidance of these structures which is considered, not the greater scale landscape connectivity. Among the few examples of avoidance with respect to multiple infrastructure are pronghorn *Antilocapra americana*, which avoid both roads and fences in Alberta, Canada (Jones et al. 2022), and reindeer *Rangifer tarandus*, which preferentially avoid the presence of powerlines and roads in combination in Norway (Nellemann et al. 2001). Therefore, whilst we may understand that wildlife avoids the presence of multiple linear infrastructure in a single landscape, the extent to which these alter connectivity and movement pathways remains largely unknown.

Among linear infrastructure, roads and fences are some of the most ubiquitous, and are often found in conjunction (van der Ree et al. 2015). Although roads have been extensively studied as barriers to connectivity, the importance of fences has only been recently acknowledged, despite having a greater extent than roads in many areas, such as in Alberta, Canada, where the extent of fences was double that of roads (Jakes et al. 2018). These infrastructure impede wildlife movement between habitat fragments physically, i.e. fences as impassable barriers (Sawyer et al. 2013), and behaviorally, i.e. avoidance of vegetation gaps provoked by roads (D'Amico et al. 2016). Therefore, wildlife needs to cross between habitat patches allowing them to obtain resources (Harrington and Conover, 2006, Wilkinson et al. 2021) and to prevent inbreeding (Olsson et al. 2008, Corlatti et al. 2009). However, the barriers roads and fences pose may force wildlife to shift to other habitats (Ballok et al. 2010, Osipova et al. 2018), disrupting natural migration and local movement pathways. The introduction of wildlife road-crossing structures (hereafter wildlife passages) may mitigate many of the negative side effects of these linear infrastructure (Ballok et al. 2010, van der Ree et al. 2015). Consequently, our hypothesis was that as all of these infrastructure will affect the connectivity of a landscape, they should be included as often as possible in connectivity models in order to comprehend a more realistic view of landscape connectivity.

The objective of our study is therefore to assess how the structural connectivity of a landscape changes when considering environmental variables alone and then subsequently adding roads, fences, and wildlife passages, using red deer *Cervus elaphus* and wild boar *Sus scrofa* as model species. Both of these species typically prefer to spend time away from roads and fences, and they may even have their movements impaired by these infrastructure (Burkholder et al. 2018, Laguna et al. 2022), including unpaved roads without traffic (D'Amico et al. 2016), but will cross boundaries if motivated by resources (Mulero-Pázmány et al. 2022), especially the wild boar which is less affected by anthropogenic disturbance (Frantz et al. 2012). As a consequence, both these ungulate species are likely to have connectivity affected by the combined presence of roads, fences, and wildlife passages, as we already know from literature focusing on only one or two of such infrastructure (Dodd et al. 2007, Frantz et al. 2012).

In order to determine the impacts of differing infrastructure on the connectivity of these species, we utilised a sequential approach in which we produced a baseline connectivity model with solely environmental features, and compared it firstly to a model including the addition of roads, secondly to a model including roads and fences, and finally to a model considering all infrastructure including wildlife passages such as underpasses and overpasses. We predicted the addition of roads should significantly reduce the structural connectivity across our study area, and the further addition of fences should further reduce connectivity among areas which were permeable when roads were the only considered barrier to movement. Additionally, wildlife passages should at least partially restore connectivity by creating crossing opportunities through otherwise impermeable linear infrastructure.

Material and methods

Study area

Our study focused on Doñana Biosphere Reserve, an area around 1000 km^2 in the southwest of Spain (36°590′N, 6°260′W; Fig. 1). The climate of Doñana is typically Mediterranean, containing three main ecosystems: Mediterranean scrublands/woodlands, wetlands, and dunes. Doñana receives around 500 m of rainfall per annum, and has an average temperature of approximately 25°C (data by Doñana's Singular Scientific-Technical Infrastructure ICTS-RBD: http://icts.ebd.csic.es), with hot dry summers and mild winters. Doñana has varying levels of protection, with urban, rural, and natural environments scattered within the boundaries of the reserve. The reserve is characterised by a large road network of both paved and unpaved roads, with paved roads comprising of only 2% of the total (Román et al. 2010) (Fig. 1), which allows high-intensity agriculture, tourism, and scientific research, among other activities. Fences are found throughout the reserve (Fig. 1), with 2 m high road fences found along main paved roads to prevent wildlife moving across areas with high traffic, and livestock fences which aim to separate areas with differing protection degrees, management strategies, or owners. Road fences are 2 m high and made of single wire mesh (5 cm span), whereas livestock fences are predominantly, but not always, 1.50 m high and made of horizontal wooden poles (20 cm span among poles). Overall, natural areas are concentrated in the core of the Biosphere Reserve, and the density of more anthropised environments increases towards the surroundings. As a consequence, Doñana's natural areas represent a biodiversity island surrounded by a highly anthropised matrix, with only the Guadiamar Green Corridor (i.e. a riparian protected area recently established along a minor river in the northern area of Doñana) connecting it to the nearest natural areas, in western Sierra Morena (approx. 50 km).

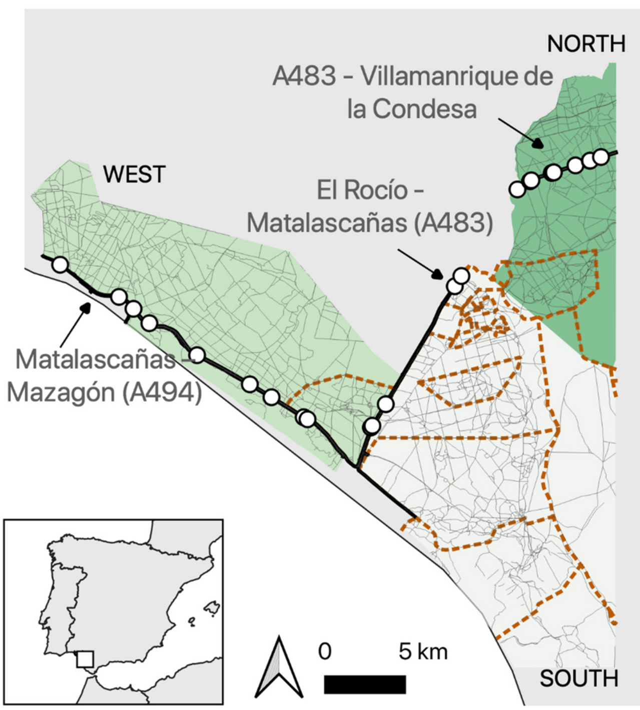

Figure 1. Study area of Doñana. Shown are the location of road fences in black with corresponding road names, and livestock fences in dotted brown. Our study area is divided into three sub-areas: North in dark green, West in light green, and South in white. Locations of wildlife road-crossing structures are indicated by white circles.

Data collection

Species occurrence information

Red deer and wild boar are ungulates commonly found in our study area. Presence–absence data used here was collected by D'Amico et al. (2016) using 40 randomly distributed transects, each 200 m long, perpendicular to and beginning from major paved or unpaved roads. The transects were positioned a minimal distance of 2 km apart and were divided into twenty 10 m-long segments. Presence of the focal species was determined by walking along the transect and georeferencing pellets found within a 1 m-wide buffer zone. For more detail, see methods in D'Amico et al. (2016).

Infrastructure information

All roads were georeferenced in our study area (D'Amico et al. 2016). Fences were mapped using remote sensing, and subsequently validated in the field to allow for assignment of differing types (i.e. road fencing and livestock fencing). Wildlife under- and overpasses were mapped along all roads with road fences in our study area by direct field observation, their location georeferenced, and their width and length recorded. Height was also measured for underpasses and was determined to be the distance from the ceiling of the underpass to the ground. An Openness Index, hereafter OI (Clevenger and Waltho, 2005), was calculated for each underpass to determine the suitability as a wildlife passage for each species using the formula OI = (Width × Height) / Length.

Modelling landscape connectivity

Landscape connectivity models were built using CIRCUITSCAPE software (McRae et al. 2008). CIRCUITSCAPE relies on electrical circuit theory, creating multiple random movement pathways between focal nodes over a landscape permeability map. D'Amico et al. (2016) calculated the probability of occurrence of both species to the entire study area, using first environmental variables alone, and then environmental and road-related variables together. Here, we used the probability of occurrence maps from D'Amico et al. (2016) in CIRCUITSCAPE (i.e. we assumed that higher likelihood of occurrence is related to higher landscape permeability).

The first layers of presence probability from D'Amico et al. (2016) (without considering roads) fed the baseline scenario of connectivity (i.e. environmental variables only), where movement was assumed to be conditioned by habitat quality, without considering roads, fences or passages. We then created three other scenarios for each species, where in the first one we overlaid roads (hereafter road scenario), in the second one we overlaid both roads and fences (hereafter fence scenario), and a third scenario where we overlaid roads, fences and wildlife passages (hereafter mitigated fence scenario).

The second layers of presence probability from D'Amico et al. (2016) (also considering roads) fed the road scenario, where movement was assumed to be conditioned by environmental variables and roads. For the fence scenario, we assumed that fences bordering main roads were impermeable to our study species, functioning as a barrier. Well managed fences, such as those paralleling roads, are highly impermeable to ungulates, whereas livestock fences can be more readily permeable (Burkholder et al. 2018, Laguna et al. 2022). In fact, throughout seven years of roadkill fieldwork in this region, we have recorded no roadkills of these species in fenced roads (D'Amico et al. 2015), suggesting that road fences do prevent access by ungulates. As for the livestock fences, scattered throughout the study area, we assumed that they represent a less restrictive movement filter. As there is no detailed information on the degree of barrier they represent, we assumed, based on personal observations, a conservative value in which they reduce the permeability value of the habitat they cross by 20%.

The mitigated fence scenario is similar to the fence scenario, except that we increase the permeability in places where wildlife passages exist, allowing movement through these areas. Overpasses were assumed to be completely permeable, but underpasses are likely to differ in their level of permeability. Nevřelová et al. (2022) defined levels of usability for red deer and wild boar to underpasses based on their OI, but otherwise there is limited evidence as to the level of underpass permeability to ungulates. Therefore, we assigned permeability values for road underpasses and red deer and wild boar based on their OI (Table 1).

Table 1. Openness Index and Relative Ungulate Permeability of Underpasses where OI = (Width × Height) / Length.

Openness index	Red deer permeability	Wild boar permeability
< 0.10	0.00	0.00
0.10–0.50	0.00	0.30
0.51–1.00	0.30	0.60
1.01–1.50	0.60	0.90
1.51–2.00	0.90	0.99
> 2.00	0.99	0.99

We utilised CIRCUITSCAPE using the wall-to-wall omnidirectional approach (Pelletier et al. 2014) for producing regional-scale maps of connectivity. Omnidirectional methods use the circuit theory algorithm to model the flow of electric current across a resistance grid from all directions, originating from the perimeter of the study area (Koen et al. 2014, Pelletier et al. 2014). The wall-to-wall models allow the flow of electrical current between thin, parallel source and ground strips placed on opposite sides of a buffered study region. Here, we used a buffer distance of 10 km, where the land use outside our study area was randomly assigned for each grid cell, to allow the diffusion of current before entering the study area. The area occupied by the ocean was ignored (NA value).

The flow of current is modelled using the 'advanced mode' in CIRCUITSCAPE across the region from North to South, South to North, East to West and West to East. The resulting current maps in each of the four directions are then averaged together for a final map of current density, which we used as maps of expected use intensity. Each map of use intensity was scaled to range between 0 and 100, to allow comparisons across species and scenarios of use intensity.

Patterns of landscape connectivity were visually inspected considering the use intensity across the landscape and the different scenarios (i.e. considering the role of the roads, fences and passages). Additionally, in order to better visualise the results, we divided our study area into three distinct sub-areas: the North sub-area (i.e. north of the El Rocío lagoon, including both National and Natural Park), the South sub-area (i.e. the core of the National Park, south of the El Rocío lagoon and east of the paved road road A-483 El Rocío-Matalascañas), and the West sub-area (i.e. mostly including Natural Park, west of the paved road A-483 El Rocío-Matalascañas, Fig. 1). A two-way analysis of variance (ANOVA) was employed to determine whether there were significant differences in estimated use intensity among areas and among scenarios, for each focal species. Tukey's honestly significant difference (HSD) test was applied to identify the specific groups that differed significantly from one another.

Results

We created four scenarios of structural connectivity throughout Doñana, for each of the two ungulate species. Both the baseline scenario considering only environmental variables and the road scenario also considering road presence showed that landscape connectivity is predominantly channelled from the South sub-area (i.e. the core of the National Park) to the West one (Fig. 2A–B). For both species, the West sub-area was potentially the most intensively used (Fig. 3), whereas the usage of the North sub-area was minimal (Fig. 2A–B, 3). The introduction of fences, however, prevented all potential ungulate movement between the South and West sub-areas, with landscape connectivity subsequently being channelled from the South to North sub-areas through El Rocío lagoon (Fig. 2C). Potential usage of the West sub-area, blocked by

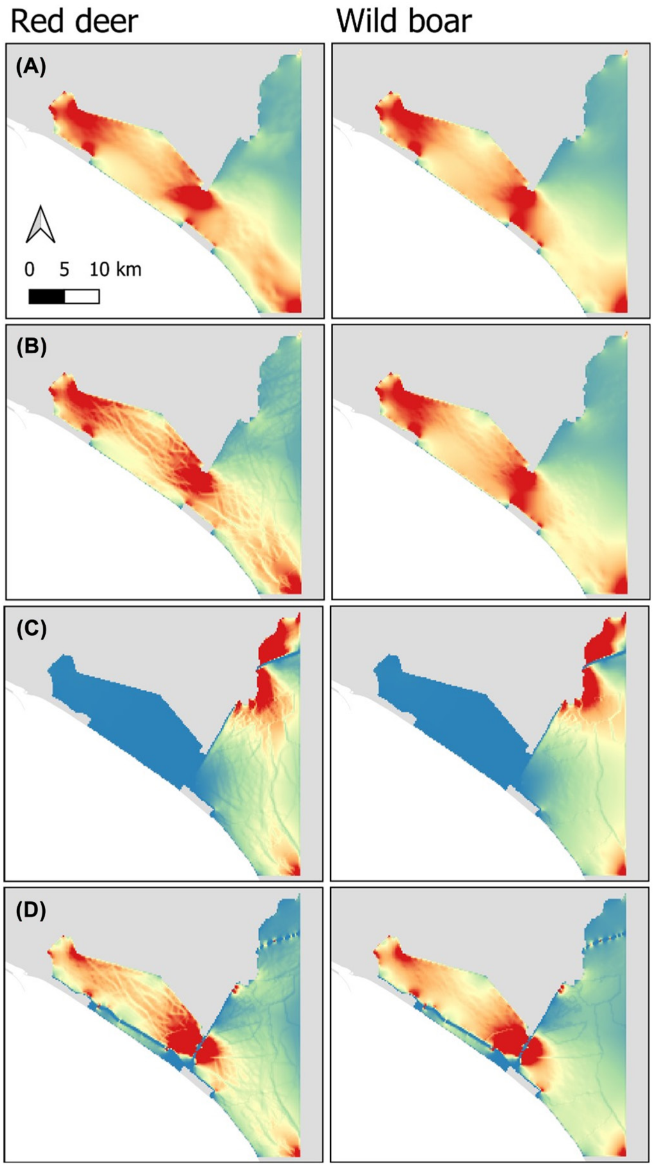

Figure 2. Landscape connectivity for red deer and wild boar when considering the three scenarios of landscape permeability: (A) baseline assuming that connectivity is conditioned by environmental variables solely (no barriers); (B) road scenario assuming that movement is further conditioned by roads; (C) fence scenario, where, additionally, road fences impede animal movement and livestock fences restrict movement by 80%; and (C) mitigated fence scenario, where fences have similar effects to (B), but wildlife passages are permeable (according to their Openness Index) for movement. Colour gradient stands for the probability of movement with red/blue colour representing higher/lower values.

impermeable road fences, was reduced to low levels for both species (Fig. 3), essentially removing this connectivity corridor (Fig. 2C). In our final scenario, the addition of wildlife passages provided for connectivity breaks in infrastructure, providing new potential movement pathways. There were thirty-three underpasses in our study area, all with differing values of openness, and two overpasses, which were completely permeable for both species. For red deer, seven underpasses were impermeable (OI < 0.50), and ten passages having permeability above 0.6 (OI > 1.00). For wild boar, all underpasses were permeable, and twenty-six passages had permeability of 0.6 or above (OI > 0.50). Here, both red deer and wild boar could predominantly utilise passages between the South and West sub-areas of Doñana (Fig. 2D), with potential usage, and consequently a connectivity corridor, being restored to similar levels as our baseline scenario (Fig. 3). At the same time, potential use of the North sub-area for both species returned to similar levels to our baseline scenario (Fig. 3). When comparing the estimated use intensity across areas and scenarios, we found significant differences in all pairwise comparisons, except for baseline and road scenarios (Fig. 4).

Discussion

This study provided, to the best of our knowledge, a first assessment into how multiple linear infrastructure may affect the connectivity of a landscape. Addition of a secondary type of infrastructure to our model, more specifically adding fences to roads, potentially reduced or even erased the connectivity between areas of Doñana that were previously accessible. However, with the addition of a third infrastructure (i.e. wildlife passages), connectivity was partially restored to these areas. Our study, therefore, highlighted the complexities of wildlife connectivity where multiple linear infrastructure are present. This impresses the need to consider as many infrastructure as possible (i.e. roads, fences, powerlines, railways, etc.) in connectivity modelling to ensure a more holistic and robust understanding into landscape connectivity.

The greatest change to connectivity in our modelling focusing on Doñana's ungulates was caused by the addition of fences, and especially road fences. This difference among fence type is a direct consequence of their permeability, and was already described in other areas for several ungulates (Dodd et al. 2007, Laguna et al. 2022), and also other species (Pirie et al. 2017, Wilkinson et al. 2021). The first implication of this finding is that implementing livestock fences in protected areas does not necessarily affect landscape connectivity for wild ungulates, but this may be dependent on their body size (Harrington and Conover 2006, Epps et al. 2013). A second implication is the confirmation that road fences can be a major issue affecting wildlife movement and ultimately the segregation of animal populations (Jaeger and Fahrig, 2004, Corlatti et al. 2009, Holderegger and Di Giulio, 2010). Concerning the comparison between roads and fences, it is known that the former, even when unpaved, usually trigger avoidance by ungulates (D'Amico et al. 2016, Mulero-Pázmány et al. 2016), but including fences into our modelling created much greater consequences for wildlife movement and landscape connectivity here. Namely, the addition of road fences to our road scenario (i.e. considering only habitat and roads) caused a potential reduction in almost all movement between the South sub-area of the region (i.e.

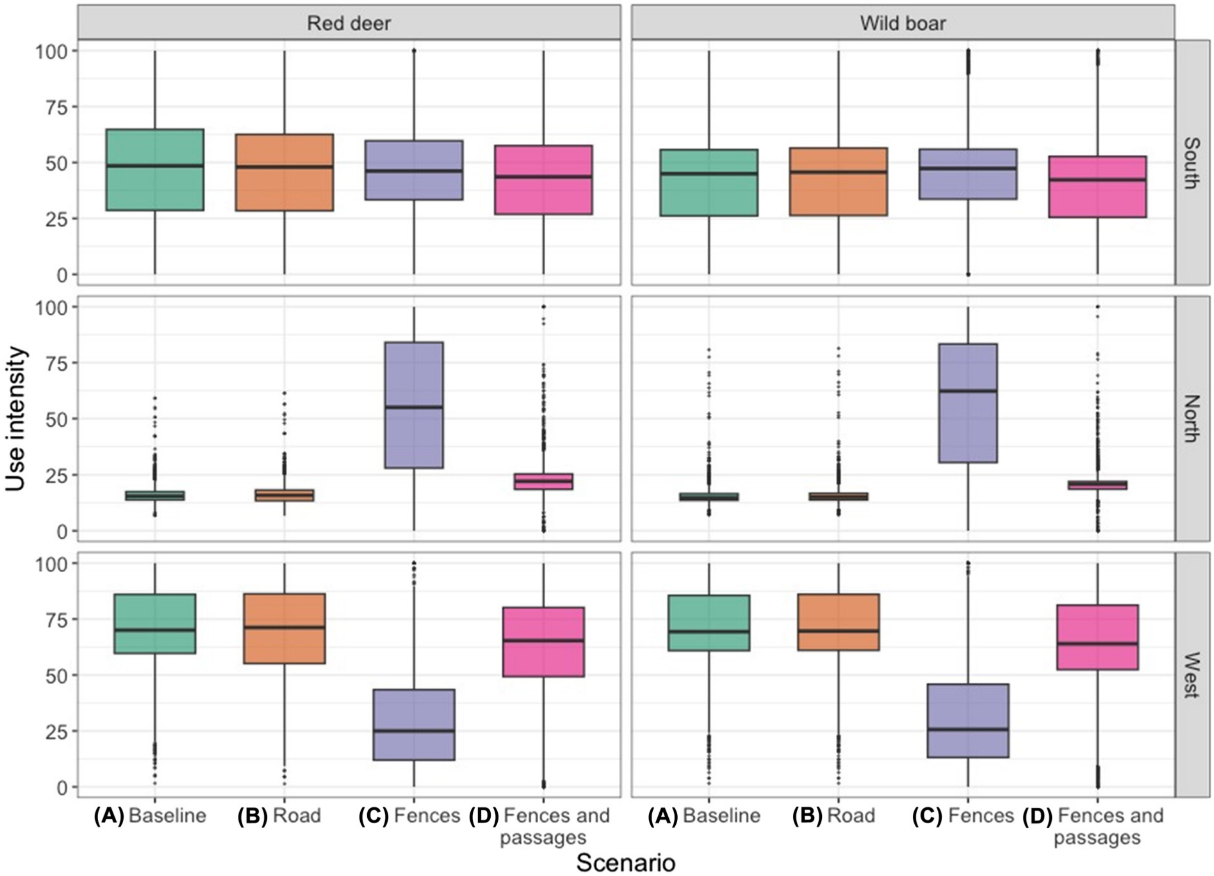

Figure 3. Use intensity of Doñana's North, South, and West sub-areas by red deer and wild boar across four scenarios of landscape permeability: (A) baseline scenario, where movement is conditioned by solely environmental variables; (B) road scenario, with roads added to the baseline scenario; (C) fence scenario, where the addition of road fences impede potential ungulate movement and livestock fences restrict it by 80%; and (D) mitigated fence scenario, with addition of wildlife passages.

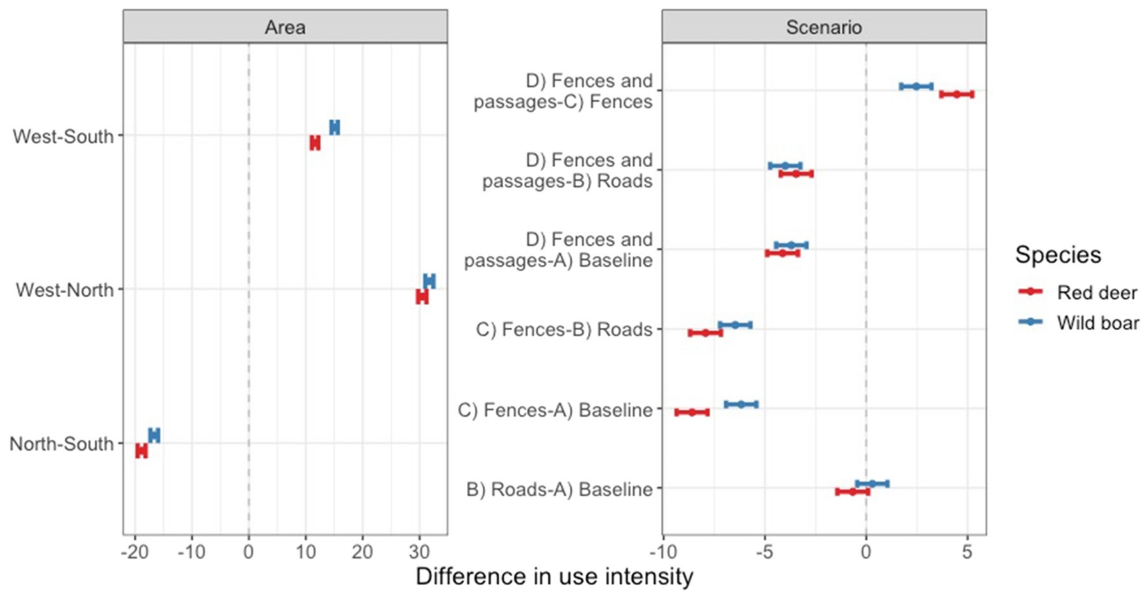

Figure 4. Confidence intervals on the differences between the means of use intensity across areas (left panel) and scenarios (right panel), for each focal species. The intervals are based on the Studentized range statistic from Tukey's Honest Significant Difference method. Treatments with an interval overlaping zero (vertical dashed line) are not significantly different.

the core of the protected area) and West sub-area (which actually represents a suboptimal but important area, entailing a large extent of suitable habitats for the persistence of local ungulate populations; D'Amico et al. 2016). As a consequence of including fences into our modelling, the remaining movement of both species was channelled towards North through the large lagoon in El Rocío, likely due to the fact that waterbodies can provide points of weakness to fenced areas (Laguna et al. 2022). Importantly, our modelling identified this large waterbody as a suboptimal landscape corridor for our study species, but the actual situation of prolonged drought and groundwater overexploitation is now causing a chronic lack of water in Doñana lagoons (Camacho et al. 2022, de Felipe et al. 2023), so landscape connectivity through El Rocío lagoon could currently be higher than modelled. With landscape connectivity being potentially channelled from the West to the North sub-area of the reserve, both study species could increase their movement towards the Guadiamar Green Corridor, which currently is the only possible connection to western Sierra Morena, the nearest natural area in the region (Blazquez-Cabrera et al. 2019). We believe this is an interesting example, and to the best of our knowledge the first one in the scientific literature, explicitly showing that considering one or two infrastructure types can modify the output of landscape connectivity scenarios.

However, both the landscape connectivity scenarios produced by considering one or two infrastructure types cannot be considered completely realistic without including a third infrastructure type: wildlife passages. One approach to reduce the negative effects of roads and fences on connectivity is the implementation of wildlife passages such as overpasses (Olsson et al. 2008, Corlatti et al. 2009) and underpasses (Dodd et al. 2007, Mysłajek et al. 2020). The addition of wildlife passages to our landscape connectivity modelling restored the potential flow of movement between the core of the reserve (i.e. South sub-area) and West sub-area (i.e. a suboptimal area with suitable habitats but without a clear connection to other natural areas). However, wildlife passages did not completely restore landscape connectivity to potential levels estimated by considered in our baseline or road scenarios. Additionally, this fourth scenario including wildlife passages (i.e. the mitigated fence scenario) entailed again relatively poor landscape connectivity between the core of the protected area and the North sub-area, just as in the baseline and road scenarios. As a consequence, the mitigated fence scenario was affected by two main issues: a relative isolation of ungulate sub-populations of Doñana (especially between the South and North sub-areas), and consequently a poor connectivity for the study species between Doñana and the Guadiamar Green Corridor (especially South and West sub-populations). This limited connectivity for our study species can be due to several wildlife passages being not completely permeable, with ungulates being channelled through a few defined passages. Indeed, based on underpass Openess Index (i.e. OI), many underpasses were not suitable for crossing by ungulates. For wild boar, all underpasses were permeable, as already highlighted by the available literature (Mata et al. 2008, Ważna et al. 2020). Conversely for the red deer many underpasses were completely impermeable, and only a few had enough permeability, so wildlife passages' usage for red deer in Doñana was therefore heavily restricted, as previously observed in other areas (Bhardwaj et al. 2020, Ważna et al. 2020). Doñana's road underpasses were built for usage by the endangered Iberian lynx *Lynx pardinus* (Ferreras et al. 2010) and not specifically for large ungulate usage, therefore it is unsurprising that several wildlife passages may impose movement restrictions.

As a consequence of the limited connectivity among sub-populations and also with the Guadiamar Green Corridor, the genetic viability of our study species could be locally affected in the long term, due to reductions in gene flow and consequent inbreeding, as already described for both species in Doñana (Landi et al. 2011, Queiros et al. 2014) and previously observed in similar situations for other species, including ungulates in Sweden and California (Olsson et al. 2008, Rudnick et al. 2012, Fraser et al. 2019). However, both study species are globally listed as 'Least Concern' by the IUCN (Lovari et al. 2018, Keuling and Leus 2019), as well as at the national scale (Palomo et al. 2007), and they are very abundant in Doñana (data by Doñana's Singular Scientific-Technical Infrastructure ICTS-RBD: http://icts.ebd.csic.es). Nevertheless, the genetic viability of Doñana's populations of red deer and wild boar should not be overlooked, since local populations here include some of the most ancestral lineages for both species (Landi et al. 2011, Fernández-García et al. 2014, Galarza et al. 2015) which in the remainder of their distribution have been largely hybridised with other subspecies, domestic varieties and even other species (Scandura et al. 2008, Delibes-Mateos and Delibes 2013, Queiros et al. 2014, Smith et al. 2018). As a consequence, improving the connectivity among Doñana's sub-areas and also the Guadiamar Green Corridor should be a priority for increasing gene flow and conserving genetic viability in the long term. This goal can be achieved by implementing two widely utilised measures aimed at improving the effectiveness of wildlife passages by decreasing the associated road and fence avoidance. The first measure is installing acoustic and visual barriers on the road fences located in correspondence with wildlife passages (Jackson and Griffin 2000, Sawyer et al. 2016), and the second is promoting habitat continuity from the surrounding environments to the passages (Bhardwaj et al. 2020, Nevřelová et al. 2022). These measures can be applied to all the wildlife passages in Doñana, prioritising the structures with suitable OI for ungulate movement (Nevřelová et al. 2022). The overpasses showed a relatively high effectiveness in our case study, but they could be improved too, probably even with more success, by implementing both suggested measures (Jackson and Griffin 2000, Sołowczuk 2020).

Furthermore, changes in landscape connectivity are likely to have impacts beyond red deer and wild boar populations. Whilst neither species is of conservation concern, other interacting species may be indirectly impacted by changes to landscape connectivity. For instance, red deer can be a seed disperser of native species in Doñana (Castañeda et al.

2018), as well as a herbivore contributing to the overgrazing recorded in some environments (Giralt-Rueda and Santamaria 2021), finally affecting secondary successions and the community composition of the vegetation (Muñoz-Reinoso 2017). Moreover, road avoidance locally observed for this species has been described to positively affect fleshy-fruited shrub recruitment and establishment along roadsides (Suárez-Esteban et al. 2013, Suárez-Esteban et al. 2014). As a consequence, changes in landscape connectivity and therefore red deer density in different Doñana's sub-areas are likely to have a considerable impact on vegetation and ultimately on habitat structure. Additionally, fawns and juveniles are also an important prey for the endangered Iberian lynx in Doñana (Delibes 1980). An improved connectivity for red deer, then, could also have positive effects on Iberian lynxes too. Similar examples can be found for wild boar too. This species can influence soil structure and natural successions by their trampling and rooting behaviours (Sandom et al. 2013), which in the case of Doñana has been documented to impact the locally endangered cork oak *Quercus suber* recruitment (Herrera 1995) and also herbaceous communities (Fernández-Llario et al. 1996), some of them listed in the 'Habitats Directive'. They can further negatively impact populations that they opportunistically prey on, such as several species of amphibians (Díaz-Paniagua et al. 2007), and ground-nesting waterbirds (Santoro et al. 2010). All these potential impacts of wild boar on biodiversity will spread in parallel to the improved connectivity for this species, so they should be taken into account and properly mitigated.

It is important to note that roads and fences are not the only kinds of linear infrastructure found in Doñana, and most of them can impact animal behaviour in different ways. For example, another infrastructure which can affect ungulate movement is powerlines (Nellemann et al. 2001). Corona discharge from powerlines (i.e. an electrical process which emits UV light) can be detectable by some ungulate species such as reindeer (Bartzke et al. 2014), and causes increased alertness and avoidance of this infrastructure (Tyler et al. 2016). We did not include this potential effect as we were uncertain of the effect of powerlines on our study species, but not taking into account the presence of powerlines or other infrastructure may modify our understanding about landscape connectivity for ungulates in Doñana. For this reason, here we want to acknowledge for this potential study limitation in order to emphasize again about the necessity to create overarching approaches that not ignore the presence of all potential affecting factors.

Conclusions

Our study showed that modelling a single linear infrastructure, such as roads, may not be a sufficient enough metric to understand how wildlife move throughout a landscape in reality. In our case study, landscape connectivity for ungulates was dramatically impacted by the addition of a second linear infrastructure, fences, to our modelling, and prevented movement throughout large portions of the study area. These reductions of movement to our study species' evidenced the significant impact fences play in reducing wildlife connectivity, but also provided insight into how we may approach modelling a landscape dominated by linear infrastructure in the future. By considering a holistic approach where not one type of infrastructure, but as many as possible, are modelled, we may begin to better understand how linear infrastructure impede wildlife movement, and consequently improve management practices of these areas.

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Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c59zw3rfg (Botting et al. 2023).

References

Ascensão, F., Fahrig, L., Clevenger, A. P., Corlett, R. T., Jaeger, J. A. G., Laurance, W. F. and Pereira, H. M. 2018. Environmental challenges for the belt and road initiative. – Nat. Sustain. 1: 206–209.

Ascensão, F., Latombe, G., Anadón, J. D., Abellán, P., Cardador, L., Carrete, M., Tella, J. L. and Capinha, C. 2020. Drivers of compositional dissimilarity for native and alien birds: the relative roles of human activity and environmental suitability. – Biol. Invas. 22: 1447–1460.

Ballok, Z., Náhlik, A. and Tari, T. 2010. Effects of building a highway and wildlife crossings in a red deer (*Cervus elaphus*) habitat in Hungary. – Acta Silvatica Lignaria Hung. 6: 51–58.

Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C. and Pereira, H. M. 2021. The lost road: do transportation networks imperil wildlife population persistence? – Perspect. Ecol. Conserv. 19: 411–416.

Bartzke, G., May, R., Bevanger, K., Stokke, S. and Røskaft, E. 2014. The effects of power lines on ungulates and implications for power line routing and rights-of-way management. – Int. J. Biodivers. Conserv. 6: 647–662.

Benítez-López, A., Alkemade, R. and Verweij, P. A. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. – Biol. Conserv. 143: 1307–1316.

Bhardwaj, M., Olsson, M. and Seiler, A. 2020. Ungulate use of non-wildlife underpasses. – J. Environ. Manage. 273: 111095.

Blazquez-Cabrera, S., Ciudad, C., Gastón, A., Simón, M. Á. and Saura, S. 2019. Identification of strategic corridors for restoring landscape connectivity: application to the Iberian lynx. – Anim. Conserv. 22: 210–219.

Borda-de-Água, L., Barrientos, R., Beja, P. and Pereira, H. 2017. Railway ecology. – Springer.

Botting, I., Ascensão, F., Navarro, L. M., Paniw, M., Tablado, Z., Román, J., Revilla, E. and D'Amico, M. 2023. Data from: The road to success and the fences to be crossed: considering multiple infrastructure in landscape connectivity modeling. – Dryad Digital Repository, https://doi.org/10.5061/dryad.c59zw3rfg.

Budzik, K. and Budzik, K. 2014. A preliminary report of amphibian mortality patterns on railways. – Acta Herpetol. 9: 103–107.

Burkholder, E. N., Jakes, A. F., Jones, P. F., Hebblewhite, M. and Bishop, C. J. 2018. To jump or not to jump: mule deer and white-tailed deer fence crossing decisions. – Wildl. Soc. Bull. 42: 420–429.

Camacho, C., Negro, J. J., Elmberg, J., Fox, A. D., Nagy, S., Pain, D. J. and Green, A. J. 2022. Groundwater extraction poses extreme threat to Doñana world heritage site. – Nat. Ecol. Evol. 6: 654–655.

Castañeda, I., Fedriani, J. M. and Delibes, M. 2018. Potential of red deer (*Cervus elaphus*) to disperse viable seeds by spitting them from the cud. – Mamm. Biol. 90: 89–91.

Ceia-Hasse, A., Navarro, L. M., Borda-de-Água, L. and Pereira, H. M. 2018. Population persistence in landscapes fragmented by roads: disentangling isolation, mortality, and the effect of dispersal. – Ecol. Modell. 375: 45–53.

Clevenger, A. P. and Waltho, N. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. – Biol. Conserv. 121: 453–464.

Corlatti, L., Hackländer, K. and Frey-Roos, F. 2009. Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. – Conserv. Biol. 23: 548–556.

Crist, M. R., Wilmer, B. O. and Aplet, G. H. 2005. Assessing the value of roadless areas in a conservation reserve strategy: biodiversity and landscape connectivity in the northern Rockies. – J. Appl. Ecol. 42: 181–191.

D'Amico, M., Román, J., Reyes, L. D. L. and Revilla, E. 2015. Vertebrate road-kill patterns in Mediterranean habitats: who, when and where. – Biol. Conserv. 191: 234–242.

D'Amico, M., Périquet, S., Román, J. and Revilla, E. 2016. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. – J. Appl. Ecol. 53: 181–190.

D'Amico, M., Catry, I., Martins, R. C., Ascensão, F., Barrientos, R. and Moreira, F. 2018. Bird on the wire: landscape planning considering costs and benefits for bird populations coexisting with power lines. – Ambio 47: 650–656.

De Felipe, M., Aragonés, D. and Díaz-Paniagua, C. 2023. Thirty-four years of Landsat monitoring reveal long-term effects of groundwater abstractions on a World Heritage Site wetland. – Sci. Total Environ. 880: 163329.

Delaney, K. S., Riley, S. P. and Fisher, R. N. 2010. A rapid, strong, and convergent genetic response to urban habitat fragmentation in four divergent and widespread vertebrates. – PLoS One 5: e12767.

Delibes, M. 1980. Feeding ecology of Spanish lynx in the Coto Doñana. – Acta Theriol. 25: 309–324.

Delibes-Mateos, M. and Delibes, A. 2013. Pets becoming established in the wild: free-living Vietnamese potbellied pigs in Spain. – Anim. Biodivers. Conserv. 36: 209–215.

Díaz-Paniagua, C., Portheault, A. and Gómez-Rodríguez, C. 2007. Depredadores de los anfibios adultos de Doñana: análisis cualitativo. – Munibe 25: 148–157.

Dodd, N., Gagnon, J. W., Boe, S. and Schweinsburg, R. E. 2007. Role of fencing in promoting wildlife underpass use and highway permeability . – In: Proceedings of the 2007 International Conference on Ecology and Transportation (ICOET), pp. 475–487.

Emil, S. O. S., Utamiputri, P., Bennun, L., Edwards, S. and Bull, J. W. 2019. The role of "no net Loss" policies in conserving biodiversity threatened by the global infrastructure boom. – One Earth 1: 305–315.

Epps, C. W., Castillo, J. A., Schmidt-Küntzel, A., Du Preez, P., Stuart-Hill, G., Jago, M. and Naidoo, R. 2013. Contrasting historical and recent gene flow among African buffalo herds in the Caprivi strip of Namibia. – J. Hered. 104: 172–181.

Fenderson, L. E., Kovach, A. I., Litvaitis, J. A., O'brien, K. M., Boland, K. M. and Jakubas, W. J. 2014. A multiscale analysis of gene flow for the New England cottontail, an imperiled habitat specialist in a fragmented landscape. – Ecol. Evol. 4: 1853–1875.

Fernández-García, J. L., Carranza, J., Martínez, J. G. and Randi, E. 2014. Mitochondrial D-loop phylogeny signals two native Iberian red deer (*Cervus elaphus*) Lineages genetically different to western and eastern European red deer and infers human-mediated translocations. – Biodivers. Conserv. 23: 537–554.

Fernández-Llario, P., Carranza, J. and Hidalgo De Trucios, S. 1996. Social organization of the wild boar (*Sus scrofa*) in Doñana National Park. – Misc. Zool. 19: 9–18.
Ferreras, P., Rodríguez, A., Palomares, F. and Delibes, M. 2010. Iberian lynx: the uncertain future of a critically endangered cat. – In: Macdonald, D. W. and Loveridge, J. A. (eds), Biology and conservation of wild felids. Oxford Univ. Press.
Frantz, A. C., Bertouille, S., Eloy, M. C., Licoppe, A., Chaumont, F. and Flamand, M. C. 2012. Comparative landscape genetic analyses show a Belgian motorway to be a gene flow barrier for red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*). – Mol. Ecol. 21: 3445–3457.
Fraser, D. L., Ironside, K., Wayne, R. K. and Boydston, E. E. 2019. Connectivity of mule deer (*Odocoileus hemionus*) populations in a highly fragmented urban landscape. – Landsc. Ecol. 34: 1097–1115.
Galarza, J. A., Sanchez-Fernandez, B., Fandos, P. and Soriguer, R. 2015. The genetic landscape of the Iberian red deer (*Cervus elaphus* hispanicus) after 30 years of big-game hunting in southern Spain. – J. Wildl. Manag. 79: 500–504.
Ghent, C. 2018. Mitigating the effects of transport infrastructure development on ecosystems. – Consilience 19: 58–68.
Giralt-Rueda, J. M. and Santamaria, L. 2021. Complementary differences in primary production and phenology among vegetation types increase ecosystem resilience to climate change and grazing pressure in an iconic Mediterranean ecosystem. – Remote Sens. 13: 3920.
Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. – Sci. Adv. 1: e1500052.
Harrington, J. L. and Conover, M. R. 2006. Characteristics of ungulate behavior and mortality associated with wire fences. – Wildl. Soc. Bull. (1973–2006) 34: 1295–1305.
Herrera, J. 1995. Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.). – Forest Ecol. Manage. 76: 197–201.
Holderegger, R. and Di Giulio, M. 2010. The genetic effects of roads: a review of empirical evidence. – Basic Appl. Ecol. 11: 522–531.
Jackson, S. and Griffin, C. 2000. A strategy for mitigating highway impacts on wildlife. – In: Messmer, T. A. and West, B. (eds), Wildlife and highways: seeking solutions to an ecological and socio-economic dilemma. The Wildlife Society.
Jaeger, J. A. G. and Fahrig, L. 2004. Effects of road fencing on population persistence. – Conserv. Biol. 18: 1651–1657.
Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. and Tluk, K.. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. – Ecol. Modell. 185: 329–348.
Jakes, A. F., Jones, P. F., Paige, L. C., Seidler, R. G. and Huijser, M. P. 2018. A fence runs through it: a call for greater attention to the influence of fences on wildlife and ecosystems. – Biol. Conserv. 227: 310–318.
Jones, P. F., Jakes, A. F., Telander, A. C., Sawyer, H., Martin, B. H. and Hebblewhite, M. 2019. Fences reduce habitat for a partially migratory ungulate in the Northern Sagebrush Steppe. – Ecosphere 10: e02782.
Jones, P. F., Jakes, A. F., Vegter, S. E. and Verhage, M. S. 2022. Is it the road or the fence? Influence of linear anthropogenic features on the movement and distribution of a partially migratory ungulate. – Movem. Ecol. 10: 37.
Keuling, O. and Leus, K. 2019. *Sus scrofa*. The IUCN red list of threatened species 2019. e.T41775A44141833. – The IUCN Species Survival Commission.
Koen, E. L., Bowman, J., Sadowski, C. and Walpole, A. A. 2014. Landscape connectivity for wildlife: development and validation of multispecies linkage maps. – Methods Ecol. Evol. 5: 626–633.
Koumoundouros, T., Sumner, J., Clemann, N. and Stuart-Fox, D. 2009. Current genetic isolation and fragmentation contrasts with historical connectivity in an alpine lizard (*Cyclodomorphus praealtus*) threatened by climate change. – Biol. Conserv. 142: 992–1002.
Kuvlesky, W. P., Brennan, L. A., Morrison, M. L., Boydston, K. K., Ballard, B. M. and Bryant, F. C. 2007. Wind energy development and wildlife conservation: challenges and opportunities. – J. Wildl. Manage. 71: 2487–2498.
Laguna, E., Barasona, J. A., Carpio, A. J., Vicente, J. and Acevedo, P. 2022. Permeability of artificial barriers (fences) for wild boar (*Sus scrofa*) in Mediterranean mixed landscapes. – Pest Manage. Sci. 78: 2277–2286.
Landi, V., Negro, J. J., Vega-Pla, J. L., Gortázar, C., García-Aznar Navajas, J. M., Delgado Bermejo, J. V. and Martínez Martínez, A. 2011. Caracterización genética del jabalí de la estación biológica de Doñana. – Arch. Zootec. 60: 373–376.
Laurance, W. F., Goosem, M. and Laurance, S. G. 2009. Impacts of roads and linear clearings on tropical forests. – Trends Ecol. Evol. 24: 659–669.
Lees, A. C. and Peres, C. A. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. – Oikos 118: 280–290.
Leonard, R. J. and Hochuli, D. F. 2017. Exhausting all avenues: why impacts of air pollution should be part of road ecology. – Front. Ecol. Environ. 15: 443–449.
Loss, S. R., Will, T. and Marra, P. P. 2014. Refining estimates of bird collision and electrocution mortality at power lines in the United States. – PLoS One 9: e101565.
Lovari, S., Lorenzini, R., Masseti, M., Pereladova, O., Carden, R. F., Brook, S. M. and Mattioli, S. 2018. *Cervus elaphus* (errata version published in 2019). The IUCN Red List of Threatened Species 2018. e.T55997072A142404453. – The IUCN Species Survival Commission.
Madadi, H., Moradi, H., Soffianian, A., Salmanmahiny, A., Senn, J. and Geneletti, D. 2017. Degradation of natural habitats by roads: comparing land-take and noise effect zone. – Environ. Impact Assess. Rev. 65: 147–155.
Mata, C., Hervás, I., Herranz, J., Suárez, F. and Malo, J. E. 2008. Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. – J. Environ. Manage. 88: 407–415.
McRae, B. H., Dickson, B. G., Keitt, T. H. and Shah, V. B. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. – Ecology 89: 2712–2724.
Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J. and Schipper, A. M. 2018. Global patterns of current and future road infrastructure. – Environ. Res. Lett. 13.
Mulero-Pázmány, M., D'Amico, M. and González-Suárez, M. 2016. Ungulate behavioral responses to the heterogeneous road-network of a touristic protected area in Africa. – J. Zool. 298: 233–240.
Mulero-Pázmány, M., Rollán, L., D'Amico, M. and González-Suárez, M. 2022. Road orientation affects the impact of roads on wildlife. – Wildl. Res. 50: 39–46.
Muñoz-Reinoso, J. C. 2017. Effects of deer browsing in a Mediterranean coastal juniper stand. – Forestry 90: 304–311.
Mysłajek, R. W., Olkowska, E., Wronka-Tomulewicz, M. and Nowak, S. 2020. Mammal use of wildlife crossing structures

along a new motorway in an area recently recolonized by wolves. – Eur. J. Wildl. Res. 66: 1–14.
Nellemann, C., Vistnesb, I., Jordhøyc, P. and Strandc, O. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. – Biol. Conserv. 101: 351–360.
Nevřelová, M., Lehotská, B. and Ružičková, J. 2022. Methodology of wildlife underpasses attractiveness assessment. – Ekológia (Bratislava) 41: 172–182.
Olsson, M. P. O., Widén, P. and Larkin, J. L. 2008. Effectiveness of a highway overpass to promote landscape connectivity and movement of moose and roe deer in Sweden. – Landsc. Urban Plan. 85: 133–139.
Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., Balkenhol, N. and Struebig, M. 2018. Fencing solves human-wildlife conflict locally but shifts problems elsewhere: a case study using functional connectivity modelling of the African elephant. – J. Appl. Ecol. 55: 2673–2684.
Palomo, L. J., Gisbert, J. and Blanco, J. C. (eds). 2007. Atlas y Libro Rojo de los Mamíferos terrestres de España. – Organismo Autónomo de Parques Nacionales.
Pelletier, D., Clark, M., Anderson, M. G., Rayfield, B., Wulder, M. A. and Cardille, J. A. 2014. Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. – PLoS One 9: e84135.
Peris, S. and Morales, J. 2004. Use of passages across a canal by wild mammals and related mortality. – Eur. J. Wildl. Res. 50: 67–72.
Pirie, T. J., Thomas, R. L. and Fellowes, M. D. E. 2017. Game fence presence and permeability influences the local movement and distribution of South African mammals. – Afr. Zool. 52: 217–227.
Queiros, J., Vicente, J., Boadella, M., Gortázar, C. and Alves, P. C. 2014. The impact of management practices and past demographic history on the genetic diversity of red deer (*Cervus elaphus*): an assessment of population and individual fitness. – Biol. J. Linn. Soc. Lond. 111: 209–223.
Rehbein, J. A., Watson, J. E. M., Lane, J. L., Sonter, L. J., Venter, O., Atkinson, S. C. and Allan, J. R. 2020. Renewable energy development threatens many globally important biodiversity areas. – Global Change Biol. 26: 3040–3051.
Román, J., Barón, A. and Revilla, E. 2010. Evaluación de los efectos del tránsito a motor sobre especies y comunidades de interés en el Espacio Natural de Doñana [Evaluation of the effects of motorized traffic on species and communities of interest within Doñana Natural Area]. Technical report for the Ministry of Environment of the Andalusian Regional Government. – Doñana Biological Station (CSIC).
Rudnick, D., Ryan, S., Beier, P., Cushman, S., Dieffenbach, F., Epps, C., Gerber, L., Hartter, J., Jenness, J., Kintsch, J., Merenlender, A., Perkl, R., Preziosi, D. and Trombulak, S. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. – Issues Ecol. 16: 1–20.
Sandom, C. J., Hughes, J. and Macdonald, D. W. 2013. Rooting for rewilding: quantifying wild boar's *Sus scrofa* rooting rate in the Scottish Highlands. – Restor. Ecol. 21: 329–335.
Santoro, S., Máñez, M., Green, A. J. and Figuerola, J. 2010. Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. – Bird Study 57: 515–524.
Sawyer, H., Kauffman, M. J., Middleton, A. D., Morrison, T. A., Nielson, R. M., Wyckoff, T. B. and Pettorelli, N. 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. – J. Appl. Ecol. 50: 68–78.
Sawyer, H., Rodgers, P. A. and Hart, T. 2016. Pronghorn and mule deer use of underpasses and overpasses along U. S. Highway 191. – Wildl. Soc. Bull. 40: 211–216.
Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L. and Strickland, D. 2017. Mule deer and energy development – Long-term trends of habituation and abundance. – Global Change Biol. 23: 4521–4529.
Scandura, M., Iacolina, L., Crestanello, B., Pecchioli, E., Di Benedetto, M. F., Russo, V., Davoli, R., Apollonio, M. and Bertorelle, G. 2008. Ancient vs. recent processes as factors shaping the genetic variation of the European wild boar: are the effects of the last glaciation still detectable? – Mol. Ecol. 17: 1745–1762.
Selva, N., Switalski, A., Kreft, S. and Ibisch, P. L. 2015. Why keep areas road-free? The importance of roadless areas. Handbook of road ecology. – John Wiley & Sons Ltd.
Smith, S. L., Senn, H. V., Pérez-Espona, S., Wyman, M. T., Heap, E. and Pemberton, J. M. 2018. Introgression of exotic *Cervus* (*nippon* and *canadensis*) into red deer (*Cervus elaphus*) populations in Scotland and the English Lake District. – Ecol. Evol. 8: 2122–2134.
Sołowczuk, A. 2020. Effect of landscape elements and structures on the acoustic environment on wildlife overpasses located in rural areas. – Sustainability 12: 7866.
Suárez-Esteban, A., Delibes, M. and Fedriani, J. M. 2013. Unpaved road verges as hotspots of fleshy-fruited shrub recruitment and establishment. – Biol. Conserv. 167: 50–56.
Suárez-Esteban, A., Delibes, M. and Fedriani, J. M. 2014. Unpaved roads disrupt the effect of herbivores and pollinators on the reproduction of a dominant shrub. – Basic Appl. Ecol. 15: 524–533.
Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. – Oikos 68: 571–573.
Tyler, N. J. C., Stokkan, K. A., Hogg, C. R., Nellemann, C. and Vistnes, A. I. 2016. Cryptic impact: visual detection of corona light and avoidance of power lines by reindeer. – Wildl. Soc. Bull. 40: 50–58.
Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., KaŹmierczak, A., Niemela, J. and James, P. 2007. Promoting ecosystem and human health in urban areas using green Infrastructure: a literature review. – Landsc. Urban Plan. 81: 167–178.
van Der Ree, R., Gagnon, J. W. and Smith, D. J. 2015. Fencing: a valuable tool for reducing wildlife-vehicle collisions and funnelling fauna to crossing structures. Handbook of road ecology. – John Wiley & Sons Ltd.
Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A. and Watson, J. E. M. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. – Nat. Commun. 7: 12558.
Ważna, A., Kaźmierczak, A., Cichocki, J., Bojarski, J. and Gabryś, G. 2020. Use of underpasses by animals on a fenced expressway in a suburban area in western Poland. – Nat. Conserv. 39: 1–18.
Wilkinson, C. E., Mcinturff, A., Kelly, M. and Brashares, J. S. 2021. Quantifying wildlife responses to conservation fencing in East Africa. – Biol. Conserv. 256.