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Research article

Ungulate use of non-wildlife underpasses

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ABSTRACT

Wildlife crossing structures can provide safe passage for wildlife across transportation corridors, and can help mitigate the effects of highways and exclusion fencing on wildlife. Due to their costs, wildlife crossing structures are usually installed sparsely and at strategic locations along transportation networks. Alternatively, non-wildlife underpasses (i.e. conventional underpasses for human and domestic animal use) are usually abundant along major infrastructure corridors and could potentially provide safe crossing opportunities for wildlife. To investigate this, we monitored the use of 40 non-wildlife underpasses by roe deer (*Capreolus capreolus*), and moose (*Alces alces*) in south-central Sweden. We found that roe deer and moose use non-wildlife underpasses, and prefer underpasses that are at least 11.5 m wide and 5 m tall. Furthermore, roe deer used structures that had little human co-use and were in locations where the forest cover differed on both sides of the highway. In most cases, roe deer and moose were detected within 50 m of the underpass more than they were detected crossing under them. This suggests that animals often approach underpasses without crossing under them, however modifications to underpass design may improve non-wildlife underpass use. We recommend non-wildlife underpasses at gravel and minor roads, particularly those with little human co-use and with variable forest cover on both sides of the highway, be built wider than 11.5 m and taller than 5 m.

1. Introduction

Reducing the rate of wildlife-vehicle collisions is a priority for many road agencies around the globe. Common mitigation strategies include fencing, warning systems, and wildlife crossing structures (i.e. overpasses and underpasses; Dodd et al., 2007; Glista et al., 2009; Huijser et al., 2009; Huijser and McGowen, 2010; Huijser et al., 2008; Iuell et al., 2003; Smith et al., 2015; van der Ree et al., 2015a; Woltz et al., 2008). Although over- and underpasses are effective at providing connectivity for wildlife while reducing the risk of collision with vehicles (Beckmann et al., 2010; Clevenger et al., 2001b; Huijser et al., 2015; Iuell et al., 2003; van der Grift et al., 2016), they are costly investments and usually sparsely installed along transportation networks (Roberts and Sjölund, 2015; Seiler et al., 2016). Alternatively, non-wildlife underpasses (i.e. conventional underpasses where local-access roads pass under highways) are abundant throughout transportation networks and may complement wildlife over- and underpasses by providing additional locations for wildlife to cross a highway safely (e.g. Iuell et al., 2003; Mata et al., 2008; Rosell et al., 1997; van der Ree and van der Grift, 2015; Zhang et al., 2019).

Non-wildlife underpasses have been used by many animals such as: European badgers (*Meles meles*), red fox (*Vulpes vulpes*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), mountain lions *(Puma concolor),* and mule deer (*Odocoileus hemionus*), to name a few (Clevenger et al., 2001a; Mata et al., 2008; Ng et al., 2004; Seiler and Olsson, 2009; Sparks and Gates, 2012). In Sweden, there are more than 10,000 non-wildlife underpasses that may provide passage for large ungulates such as moose (*Alces alces*) and roe deer (*Capreolus capreolus*) (Seiler and Olsson, 2009; Seiler et al., 2015). Despite being relatively common along the road-network, and their apparent use by animals, non-wildlife underpasses are rarely studied, and thus their potential for providing safe crossing for wildlife is unknown.

The use of wildlife crossing structures (i.e. structure specifically designed for wildlife) depends on the structure design (e.g. dimensions), surrounding landscape features, and human disturbance (Ascensão and Mira, 2007; Cain et al., 2003; Chambers and Bencini, 2015; Clevenger and Waltho, 2000; Glista et al., 2009; Rodriguez et al., 1996; Smith et al., 2015; van der Grift et al., 2015). These same factors may influence non-wildlife underpass use, however, few studies have evaluated this (e.g. Mata et al., 2008). In this study, we aim to evaluate how passage

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dimensions, forest cover ratio, distance to nearest alternative passage, distance to nearest houses, frequency of vehicles and humans passing through the underpass, and the traffic on the highway above the underpass influence the use of non-wildlife underpasses by roe deer and moose throughout south-central Sweden. We provide recommendations to improve non-wildlife underpass use by roe deer and moose.

2. Material and methods

2.1. Site selection

We surveyed non-wildlife underpasses, built under 6 major highways in south-central Sweden. Underpasses were located in areas dominated by coniferous, nemo-boreal forest, were made primarily for forestry or agricultural local access roads which traverse under highways, and were used by fewer than 100 vehicles per day. The highway above each

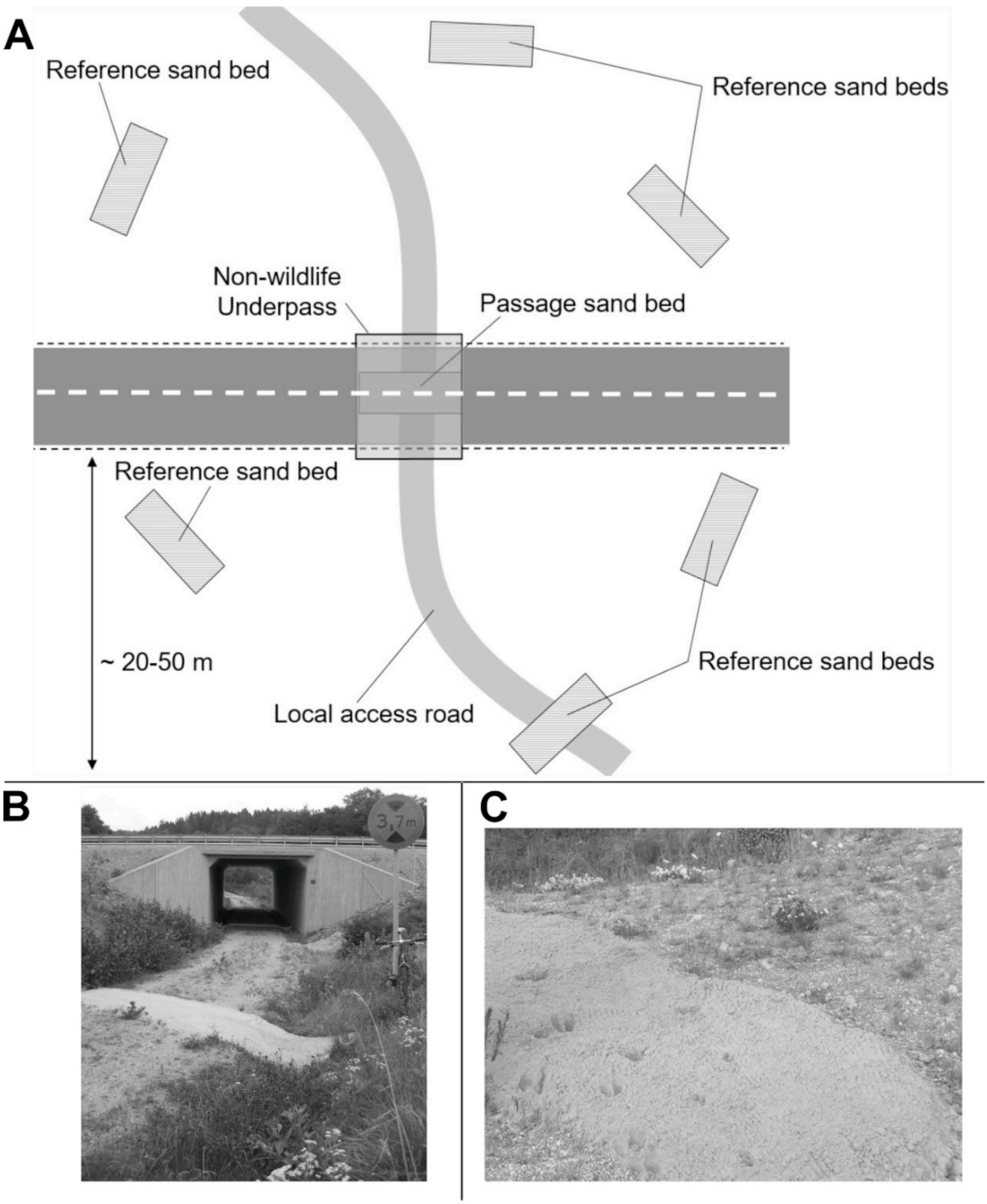

Fig. 1. A: Example site set-up, showing the fenced highway, local access road, non-wildlife underpass and passage/reference sand beds. In this example, there are 6 reference sand beds, but sites could have had between 3 and 6 reference sand beds depending on the topography, land use and vegetation, surrounding the underpass. B: A photo example of a reference sand bed outside the underpass entrance. The fenced highway is above the underpass. C: A photo example of moose tracks found on a sand bed. Photos by A. Seiler.

underpass was fenced against larger wildlife (i.e. fencing was 2.1 m in height), and carried an average traffic volume above 9000 vehicles per day (range 9101–59,822 vehicles per day). The underpasses were continuous, non-illuminated and dry; i.e. had no open gaps between highway lanes and lacked any other provisions for wildlife such as noise protection walls and visibility screens. We sought to maximize the variation in passage dimensions while reducing the variation in other confounding factors such as road characteristics, traffic volume, habitat composition, and species occurrences.

2.2. Data collection

2.2.1. Sand bed surveys for animal presence

We used sand beds to record animal presence within and nearby each underpass. The sand beds were 1.5 m in width, 5–10 cm deep, and their lengths spanned to the width of the underpass (Supplementary Information, Table S1). We placed 4–7 sand beds at each site: 1 sand bed was placed within the underpass (henceforth, “passage bed”), and 3–6 sand beds were placed in the area surrounding the underpass (henceforth, “reference beds”; Fig. 1). We placed reference beds 20–50 m away from the road to capture the activity of animals that approached the road/underpass, and thus had access to the underpass. These animals may or may not have crossed under the underpass (and thus over the passage bed). The number of reference beds and their placement at each site depended on the topography, land use and vegetation surrounding the underpass.

We visited sites every 3 days on average (range 1–10 days). At each visit, we identified tracks found on the sand bed to roe deer or moose and recorded the total number of tracks left by each species. It was not possible to determine the number of individuals that crossed each bed, only overall number of tracks. We did not collect data if sand beds had been heavily disturbed by, for example, heavy rain, vehicles or passage of domestic animals. After each visit, the sand beds were raked smooth in preparation of the next visit. All sites were not monitored simultaneously. Monitoring periods lasted 95 days on average (range 28–168 days) per site. The total sampling period spanned over 12 years, with data collection occurring in 1997, 1998, 2003, 2005, and 2009. Details on sampling periods for each site and number of inventories collected for each species are provided in Supplementary Information Table S2.

2.2.2. Data selection for quality control

To ensure the quality of the data collected across different years and by different field personnel, we only used data collected from underpasses that were inventoried at least 9 times between June and November (the period of year where we have data from all sites). Underpasses that were inventoried fewer than 9 times were visited too infrequently to provide reliable data (i.e. they were inventoried 4 times or fewer). Furthermore, underpasses that were not visited by roe deer or moose at least three times in the monitoring period, as evidenced by tracks found on either passage or reference beds, were excluded as the underpasses were likely not in suitable locations or near a population to offer a fair comparison of underpass use. To further control for the reliability of tracks, roe deer data were only included if inventories occurred within 5 days of each other, and moose data were only included if inventories occurred within 10 days of each other. Tracks become harder to identify over time, and any more time between inventories would have made identification unreliable. Through this data quality control, we excluded 13 sites. Thus, our dataset consisted of 40 sites, of which roe deer were present at 33 and moose at 23 sites (13 sites where both were present).

2.2.3. Site-level variables for underpasses

To identify which factors of the underpass or site influenced its use by roe deer and moose, we included the relative amount of vehicle-traffic through the underpass, underpass dimensions (length, width, height), the ratio of forest cover on each side of the highway, distance to the nearest alternative passage, distance to nearest house, and the average daily traffic on the highway above the underpass. Vehicular traffic passing through the underpass was calculated based on the number of crossing vehicles during the inventories, averaged as number of vehicles per daytime hour. At low traffic volumes (approximately <1 vehicle/day) it was also possible to estimate the number of vehicles based on tire tracks on the sand beds. Both traffic measures were summarized as a ‘Co-Use’ value, and was given a category of high or low depending on if it was above the median vehicle-traffic volume or below, respectively (ranged from 0 to 5.8 vehicles per hour, per underpass; for the sites roe deer were present at, the median was 1.6 vehicles per hour, per underpass and for the sites the moose were present at, the median was 0.04 vehicles per hour). Forest cover ratio, the distance to nearest house, and distance to nearest alternative passage considered suitable for wildlife (i.e. similar underpasses or fence openings) were quantified from topographic satellite maps (Swedish Land Survey; https://www.geodata.se) and the national bridge database of the Swedish Transport Administration (https://batman.trafikverket.se/). Forest cover ratio represents the uniformity of forest cover on both sides of the highway, centred on the underpass, and calculated within a 200 m radius. Forest cover ratios of 1 mean both sides of the highway had the same level of forest cover, whereas a low ratio indicates the forest cover was different on each side. We chose to include forest ratio in the analysis because animals may be crossing underpasses to access habitat not available on their side of the road (i.e. sites with low forest ratios; e.g. Clevenger and Waltho, 2005; Sparks and Gates, 2012). We used a 200 m radius around each underpass in order to assess the habitat animals would occupy and traverse in order to use the underpasses, while reducing overlap between habitat assessments of adjacent sites (average forest cover: 70%, ranging 17–100%). Road and road traffic data was obtained from the National Road Database of the Swedish Transport Administration (http://www.nvdb.se/en). Detailed information on each underpass is provided in Supplementary Information Table S2.

2.3. Statistical analysis

To compare the difference in underpass use, we fitted Poisson regression models, using the number of tracks per inventory as the response variable. Models were fit separately for roe deer and moose. We used site-level variables as the explanatory variables: length, width, and height of the underpass, forest cover ratio, distance to nearest alternative passage, distance to nearest house, average daily traffic on the highway. Data came from sand beds from three categories: reference sand beds, sand beds in passages with high human co-use, and sand beds in passages with low human co-use. Thus, we used this categorization as the intercept, in place of a global intercept, to compare between the three conditions. To account for natural variation in species presence and activity between inventories and between sites, we also included a random effect for site, and a random effect for inventory number nested within site. To account for differences in sampling effort, the models were offset by the number of beds present at each site (i.e. 1 for passage beds, 3–6 for reference beds), and the number of days between subsequent inventories. We used the ‘bobyqa’ optimiser to increase the number of iterations and assist with convergence (Powell, 2009). All continuous predictors were standardized around the mean. We interpreted covariates with 95% bootstrapped (1000 simulations) confidence intervals that did not overlap zero as significant. All analyses were performed using R (v.3.5.3, R Core Team, 2019). Poisson regression models were fit using ‘glmer’ from the ‘lme4’ package (Bates et al., 2015).

For variables identified as significant predictors of the number of tracks per inventory, we used a change point analysis to identify the threshold to the change in response variable. We did so using the identified variable as the explanatory variable for number of tracks (‘chngpt’ package; Fong et al., 2017). In change point analysis, we only used data from passage beds and not from reference beds.

3. Results

Of the 33 sites where roe deer were present, they used 29 underpasses (i.e. roe deer tracks were found on the passage bed at least once; at the remaining 4 sites, tracks were only found on reference beds). On average, there were more roe deer tracks on reference beds than on passage beds (reference beds: average 2.9 tracks per inventory per site, ranging 0–7.5 tracks per inventory per site; passage beds: average 0.6 tracks per inventory per site, ranging 0–3.3 tracks per inventory per site). Furthermore, there were significantly fewer roe deer tracks at sites with high human co-use (>1.6 vehicles/hour) compared to sites with little human co-use (<1.6 vehicles/hour; high co-use: average 0.29 tracks per inventory per site, ranging 0–3 tracks per inventory per site; low co-use: average 1.07 tracks per inventory per site, ranging 0–8 tracks per inventory per site). Number of tracks increased significantly with underpass width and height, and decreased significantly with distance to nearest alternative passage, forest ratio (Fig. 2). Change point analyses revealed threshold levels for width, height, forest ratio and distance to passages (the significant predictors for number of roe deer tracks) are: 11.5 m, 5 m, 0.89, and 343 m respectively.

Moose were present at 23 underpasses, and used 12 of the them (i.e. moose tracks were found on the passage bed at least once; at the remaining 11 sites, tracks were only found on reference beds). On average, there were more moose tracks on reference beds than on passage beds (reference beds: average 2.4 tracks per inventory per site, ranging 1–5.6 tracks per inventory per site; passage beds: average 0.4 tracks per inventory per site, ranging 0–1.7 tracks per inventory per site). Number of moose tracks increased significantly with underpass width but no other variable had a significant effect on the number of moose tracks (Fig. 2). Although not significant, moose tended to use underpasses at least 5 m in height, and only used four underpasses shorter than 5 m in height (they were 4, 4.15, 4.2, and 4.8 m tall; Supplementary Information Table S1). Change point analyses revealed the threshold level for width is 11.5 m for moose.

4. Discussion

4.1. Improving non-wildlife underpass use

Non-wildlife underpasses are largely available throughout most road networks and may support wildlife connectivity across the landscape. However, their use is not usually quantified, so this potential goes largely unnoticed. To address this gap, we monitored 40 non-wildlife underpasses, and found that 29 of 33 underpasses were used by roe deer, and 12 of 23 underpasses were used by moose. We provide evidence that non-wildlife underpasses can be used to aid habitat connectivity for ungulates, if current designs are improved to promote underpass use. Here, we provide three recommendations to improve underpass designs for wildlife use of non-wildlife underpasses.

Firstly, we propose that non-wildlife underpasses, under fenced highways and planned for limited human use (i.e. fewer than 100 vehicles per day as in this study), should be built as wide and tall as possible to promote their use by ungulates. In this study, we found that underpass use by roe deer and moose decreased when underpasses were narrower than 11.5 m in width. Moose, as the larger species, were generally more reluctant than roe deer to cross through underpasses, however both species showed a preference towards larger underpasses (Fig. 2). Furthermore, roe deer were more likely to use underpasses that were at least 5 m in height. Although we did not find a significant influence of height on moose-use of underpasses, moose only used four underpasses that were less than 5 m in height, suggesting they may also have a tendency to use underpasses more if the underpasses are at least 5 m tall (Supplementary Information Table S1). Our findings are in line with earlier studies that suggest that ungulates generally prefer crossing structures that are wider, taller and shorter in length, than the smaller structures that facilitate movements of small and medium sized mammals such as lagomorphs (*Lepus* spp. and *Oryctolagus* spp.), badgers, genet (*Genetta genetta*) or red fox (Ascensão and Mira, 2007; Clevenger and Waltho, 2005; Ng et al., 2004; Olbrich, 1984; Rodriguez et al., 1996; Rosell et al., 1997; Zhang et al., 2019). Previous study has also showed that migratory moose in northern Sweden were more likely to break through road fences rather than use a narrow road underpass that were built to reconnect their migration routes (Seiler et al., 2003). Ungulates likely prefer wide underpasses due to their body size and to their anti-predator behaviour, where open areas pose less of a threat of predation (Clevenger and Waltho, 2000, 2005; Ng et al., 2004; Olbrich, 1984; Sparks and Gates, 2012). Of the variables we tested, width is the only design features that can be easily modified, since underpasses that are designed for human-use are constrained by traffic safety, road standard or technical requirements. Therefore, modifications to length

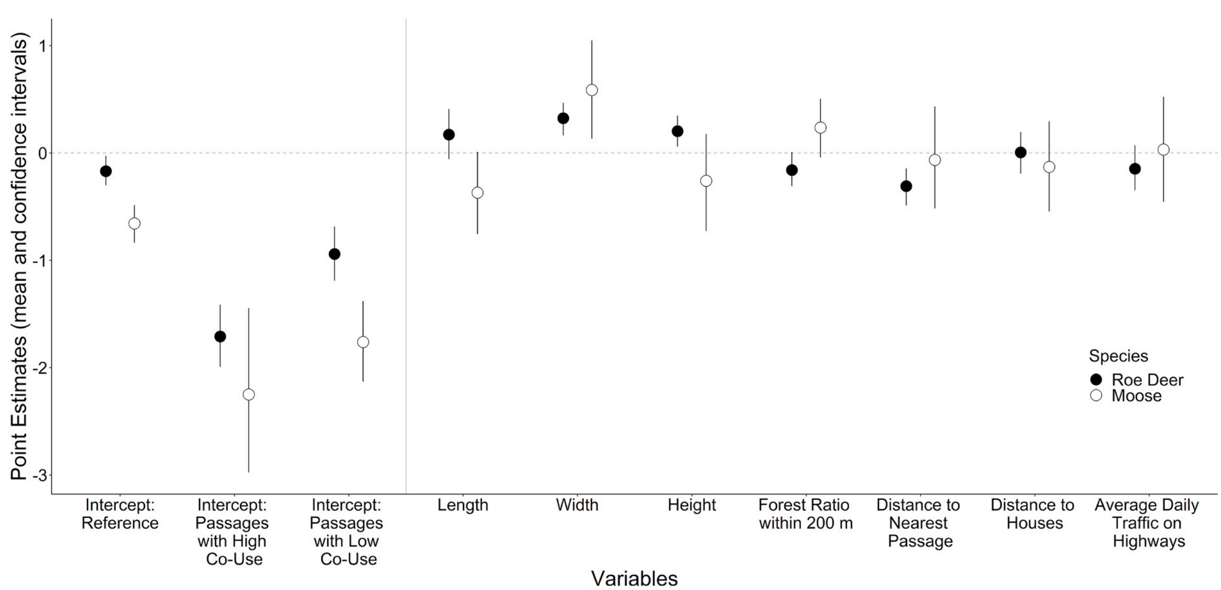

Fig. 2. Estimates of beta coefficients for each variable from the model using roe deer (black circles) and moose (white circles) data. Points show the mean estimates, while the error bars indicate the 95% confidence intervals. Confidence intervals overlapping 0 (dashed line) indicate no significant effect. The three variables on the left of the plot show the three intercepts: reference, passages with high human co-use, and passages with low human co-use.

and height are more difficult and expensive to be controlled for in underpass construction. Due to this limitation and the trends which suggest that large ungulates use larger structures, we propose that non-wildlife underpasses (with limited human co-use) should be built at least 11.5 m in width, in order to promote their use by roe deer and moose.

Our second recommendation is to pay extra attention to wildlife at underpasses where the forest cover varies on both sides of the highway (i.e. low forest ratio), since ungulates tend to prefer such sites (Fig. 2). Where forest cover varies on both sides on the road, individuals may cross the road more, as they seek shelter over low-activity periods (for example during the days), and open areas during high-activity foraging periods (such as dawn and dusk; Ager et al., 2003; Beier and McCullough, 1990). Non-wildlife underpasses may help to facilitate the natural movement patterns of these species in landscapes with a mix of forest cover and agricultural lands such as those in which our study was conducted.

Finally, our last recommendation is to provide underpasses in close proximity to one another, where possible. Underpasses more than 343 m away from the nearest alternative passage were used less by roe deer (Fig. 2), however this is likely an artefact of our data as there are few sites closer than 343 m to another passage in our study (Supplementary Information Table S1). Nevertheless, providing safe crossing opportunities in close proximity to on another may reduce the barrier effect of the road network on wildlife, by ensuring more passages within the home range of the species, or by allowing individuals to maintain their home range on either side of the road (Bissonette and Adair, 2008; Clevenger and Huijser, 2011; De Montis et al., 2018; Karlson et al., 2017; Zhang et al., 2019). With the evidence from the present study, we propose that non-wildlife underpasses can fill the gaps between purpose-built wildlife crossing structures when they are designed appropriately for wildlife-use. Building purpose-built wildlife crossings structures is an expensive endeavour, which would become exponentially more expensive if agencies had to build them in close proximity to one another throughout the entire transportation network. Therefore, non-wildlife underpasses could complement purpose-built wildlife crossing structures in providing permeability across transportation networks.

4.2. Future directions

Improving the attractiveness of non-wildlife underpasses may increase their use and thus their potential to support landscape connectivity for wildlife. Large underpasses – at least 11.5 m wide, and at least 5 m tall – can accommodate the road they serve, as well as habitat features such as creeks and a vegetated road verge, which may improve underpass use by smaller terrestrial animals in addition to roe deer and moose (Ascensão and Mira, 2007; Clevenger and Huijser, 2011; Lesbarreres and Fahrig, 2012; Zhang et al., 2019). Borrowing standards from wildlife crossing structure design, vegetation throughout underpasses increases the probability that wildlife will use them (Bhardwaj et al., 2017; Clevenger and Huijser, 2011; Smith et al., 2015), and shields or earth berms can help reduce the exposure of wildlife to noise, light and movement of the vehicles passing by on the highway above the underpasses (Clevenger and Huijser, 2011; Parris, 2015). Wildlife often have access to underpasses but do not use the underpasses (as evidenced in this study). Thus, it stands to reason that some external factors may be disrupting them from crossing through the underpasses. Future studies into the feasibility and effectiveness of modification strategies to improve underpass attractiveness will be valuable in order to create optimal and cost-effective designs to make the road network more permeable for wildlife.

In our study, we found that human co-use has a negative impact on wildlife use of underpasses. Although the underpasses in this study are primarily designed for human-use, it is evident that underpasses with little human-use are more likely to be used by wildlife (Fig. 2), and therefore may be better to prioritize for modifications for wildlife-use rather than structures with high human co-use. Additionally, to understand the extent to which non-wildlife underpasses are effective in promoting habitat connectivity for wildlife, it is essential to compare their use and effectiveness to purpose-built wildlife underpasses. Developing a successful, and cost-effective permeability plan will likely require a combination of structure designs that are accessible by humans and/or wildlife. Future study into the comparison of use between wildlife and non-wildlife underpasses are necessary and will be valuable in improving our understanding of the role of non-wildlife crossings in landscape connectivity.

5. Conclusions

Increasing the permeability of road networks is not likely to come from a single solution. Several effective methods may need to be distributed across the road network (Bissonette and Adair, 2008; Clevenger and Huijser, 2011; Karlson et al., 2017). This may include building strategically placed wildlife over- or underpasses (Beckmann et al., 2010; Clevenger and Huijser, 2011; van der Ree et al., 2015b), building openings in exclusion fences coupled with automated warning systems (Huijser et al., 2008; van der Ree et al., 2015a), and calming traffic in problematic segements of the road network (Jaarsma and Willems, 2002). However, these options will depend on practical, economic and political constraints. Strategies to reduce the impacts of habitat fragmentation caused by transportation corridors should not disregard the potential of non-wildlife underpasses to provide landscape connectivity (Seiler et al., 2015, 2016). Installing large wildlife crossing structures more frequently throughout road networks will be costly, and take many years to implement, and non-wildlife underpasses may supplement existing mitigation methods. Furthermore, new non-wildlife underpasses are bound to be constructed to allow for access of people, goods and services throughout the landscape. The cost of adapting non-wildlife underpasses for increased use by wildlife may be outweighed by the benefit of improved landscape connectivity for said wildlife. The creation of a well-integrated and effective de-fragmentation approach in transport and landscape planning is within our grasps. The only requirement is that we remain adaptive in our approaches, and try to improve our designs in each planning phase to incorporate new knowledge about wildlife and crossing structures in each step. Through a combination of strategies and design modifications, it may be possible to create a landscape permeable to humans and wildlife.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Manisha Bhardwaj: Formal analysis, Writing - original draft, Writing - review & editing. **Mattias Olsson:** Conceptualization, Methodology, Writing - review & editing. **Andreas Seiler:** Conceptualization, Methodology, Writing - review & editing.

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Appendix A. Supplementary data

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