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Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife-vehicle collisions and providing safe crossing opportunities for large mammals



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ABSTRACT

Wildlife fencing in combination with crossing structures is commonly regarded as the most effective and robust strategy to reduce large mammal–vehicle collisions while also maintaining wildlife connectivity across roads. However, fencing and associated measures may affect landscape esthetics and are sometimes considered costly and unpopular. Therefore fence length is often minimized. We investigated 1) whether short fenced road sections were similarly effective in reducing large mammal–vehicle collisions as long fenced road sections (literature review), and 2) whether fence length influenced large mammal use of underpasses (two field studies). We found that: 1) short fences (≤5 km road length) had lower (52.7%) and more variable (0–94%) effectiveness in reducing collisions than long fences (>5 km) (typically>80% reduction); 2) wildlife use of underpasses was highly variable, regardless of fence length (first field study); 3) most highway crossings occurred through isolated underpasses (82%) rather than at grade at fence ends (18%) (second field study); and 4) the proportional use of isolated underpasses (compared to crossings at fence ends) did not increase with longer fence lengths (up to 256 m from underpasses) (second field study). If the primary success parameter is to improve highway safety for humans by reducing collisions with large ungulates, the data suggest fence lengths of at least 5 km. While longer fence lengths do not necessarily guarantee higher wildlife use of underpasses as use varies greatly between locations, wildlife fencing can still improve wildlife use of an individual underpass.

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1. Introduction

Large mammal-vehicle collisions are abundant in many parts of the world (e.g. Groot Bruinderink and Hazebroek, 1996; Conover et al., 1995). Collisions with large ungulates typically result in the injury or death of the animals involved, substantial vehicle damage, and – in some cases – human injuries and fatalities (Allen and McCullough, 1976; Bissonette et al., 2008; Conover et al., 1995). Wildlife fencing in combination with wildlife crossing structures is commonly regarded as the most effective and robust strategy to reduce these types of collisions while also maintaining connectivity across highways for wildlife (review in Huijser et al., 2009). If wildlife fencing and crossing structures are designed based on the requirements of the target species,

and if they are implemented and maintained correctly, the measures can reduce large mammal–vehicle collisions by 80–97% (Clevenger et al., 2001; Gagnon et al., 2015; Sawyer et al., 2012). In addition, the number of animal movements across overpasses or through underpasses, as well as the percentage of animals out of a local population that use the structures, can be substantial (Clevenger and Waltho, 2000; Sawaya et al., 2013; Sawyer et al., 2012).

Despite the benefits described above, wildlife fences, wildlife crossing structures and associated measures can be a contentious issue. Wildlife fences for large ungulates are typically 2.4 m high and can affect landscape esthetics (Evans and Wood, 1980). In addition, some landowners may also object to associated measures such as gates, wildlife guards, or similar measures at access roads as they may be time consuming or unpleasant to drive across. Furthermore, despite the wildlife crossing structures that may be present, fences are sometimes a problem for wide ranging large mammal species such as mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) (Coe et al., 2015; Poor et al., 2012; Seidler et al., 2015). They can even be a

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source of injury and direct mortality for the animals (Jones, 2014). Finally, transportation agencies as well as the public may perceive wild-life fencing and associated measures as relatively expensive to construct and maintain.

Because of the issues described above highway managers tend to minimize the length of wildlife fencing associated with wildlife crossing structures (Ascensão et al., 2013; Ford et al., 2011; van Manen et al., 2012). Sometimes crossing structures are not accompanied by wildlife fencing at all. This occurs especially in multifunctional landscapes where fences, mitigation at access roads, and wildlife crossing structures are more likely to conflict with other land uses. However, even with short fenced road sections, planners and designers need to know how long the mitigated zone should be in order to obtain a substantial reduction in wildlife-vehicle collisions and, as a consequence, a substantial improvement in human safety (Rytwinski et al., 2015). They also need to know if wildlife fencing is required or how long the fencing should be in order to help guide wildlife to designated crossing structures rather than have them cross at grade on the road surface (Rytwinski et al., 2015). Currently, no study exists to provide fencelength recommendations with regard to either collision reduction or wildlife use of crossing structures. Therefore we conducted a literature review to investigate whether short fenced road sections were equally effective in reducing large mammal-vehicle collisions as long fenced road sections. In addition, we conducted two field studies to investigate large mammal use of underpasses that have no or very short fences. We were specifically interested if the use of isolated underpasses with no or very short fences (up to a few hundred meters) was similar to that of underpasses with longer sections of fencing (up to several kilometers) (first field study). In the second field study we investigated whether longer fence lengths (up to a few hundred meters from an underpass) were associated with increased wildlife use of the underpasses and reduced wildlife crossings at fence ends.

2. Methods

2.1. Literature review: impact of fence length on reducing large mammal–vehicle collisions

We conducted a literature review to investigate whether short fenced road sections were equally effective in reducing large mammal-vehicle collisions as long fenced road sections. We searched for all publications (peer-reviewed and non-peer reviewed) that reported on the effectiveness of wildlife fencing designed for large mammals. We used search engines such as BIOSIS for peer-reviewed scientific articles, and we conducted internet searches (Google Scholar, Google) for gray literature. We specifically searched for effectiveness data that related to large ungulates including deer (e.g. Odocoileus spp.; Capreolus capreolus); elk (Cervus spp.) and moose (Alces spp.). Other search terms related to highways, infrastructure, mitigation measures, roads, wildlife fences, wildlife crossing structures, wildlife underpasses, and wildlifevehicle collisions, crashes and carcasses. We only included data from road sections that had wildlife fencing on both sides of the highway. Many of the publications not only related to wildlife fences but also to crossing structures. We included data that related to fences and wildlife underpasses and overpasses. However, we excluded data from mitigated road sections with at-grade crossing opportunities (e.g. a gap in the fence on opposite sides of the highway) as these specifically allowed for the continued presence of animals on the roadway in a mitigated road section. The latter was not consistent with the objectives of our study.

The effectiveness of the fences and associated measures was sometimes based on wildlife-vehicle crash data (collected by law enforcement personnel). In other cases effectiveness was calculated based on carcass removal data (collected by road maintenance personnel or by employees of natural resource management agencies) or carcass observations (collected by researchers or the public). We included all

effectiveness data, regardless of who had collected the data, unless we had reason to believe that the search and reporting effort was not constant for the road section(s) concerned (based on the description in the original publication). If multiple data sources for wildlife-vehicle collisions were reported for a road section we calculated the average of these data sources and used this value in our analyses rather than multiple values that related to the same mitigated highway section. If one overall value was reported for the effectiveness in the original publication we used this value in our analyses. However, if the wildlife-vehicle collision data (any source or combination of sources) showed an increase in collisions in the mitigated road sections rather than a decrease, the effectiveness value for the fence and associated measures was set at zero (i.e. no reduction in wildlife-vehicle collisions).

Data from studies that only reported on the combined effectiveness for different road sections of different lengths were excluded from the analyses as we could not tell what the effectiveness was of the individual fenced road sections. However, we applied one exception to this rule related to one publication (Clevenger et al., 2001). This paper reported on the combined effectiveness of three road sections, but each section was at least 10 km long. In this case we included one data point in our analyses and we assigned it to the shortest of the three road sections (10 km long).

When the data allowed, the potential reduction in wildlife-vehicle collisions was calculated based on a before-after-control-impact analysis (BACI) rather than only a before-after analysis (BA) or a controlimpact analysis (CI) (Roedenbeck et al., 2007; van der Grift et al., 2013). In addition to the effectiveness data and the study design we also noted the length of the road section with wildlife fencing, fence height, target species, potential presence of fence-end and fence-gap treatments (including gates, cattle or wildlife guards, electric mats etc.), potential wildlife or multifunctional crossing structures (i.e. underpasses or overpasses), and escape opportunities from the fenced road corridor for wildlife (i.e. jump-outs, escape ramps, or one-way gates) (Appendix A). For examples of these measures see Clevenger and Huijser (2011), Huijser et al. (2015a) and Parker et al. (2008). Descriptions and characteristics of the mitigated highway sections were obtained from the original publications. In some cases additional information was obtained through communication with the authors or from satellite images.

2.2. Field studies: large mammal use of underpasses with no or very short fences

We conducted two field studies along highways in western Montana, USA to investigate if the length of wildlife fencing associated with wildlife underpasses influenced large mammal use of the underpasses. In the first field study we measured large mammal use of underpasses with no or very short fences and compared the use to that of underpasses that were associated with longer sections of wildlife fencing (up to a few kilometers). In the second field study we investigated whether longer fence lengths (up to a few hundred meters from an underpass) were associated with increased wildlife use of the underpasses and reduced wildlife crossings at fence ends.

For the first field study we selected 23 underpasses along US Hwy 93 North on the Flathead Indian Reservation (Appendix B). All underpasses had dimensions considered suitable for large mammals (Appendix B). The underpasses were constructed between 2005 and 2010 (median age at time of this research was 6 years). The fenced road length associated with the underpasses varied between 0.0 and 6.2 km (Appendix B), and fence height was 2.4 m. We placed wildlife cameras (Reconyx Hyperfire PC900) at the entrances of the 23 underpasses and kept them in operation for a full year (1 January 2013–31 December 2013) (Huijser et al., 2015b). For underpasses wider than 12 m we used multiple cameras as the maximum range of the cameras at night (with infrared flash IR flash) was about 12 m. We analyzed the images and counted the number of large mammals (deer (Odocoileus spp.)

size and larger) that used the underpasses to access the other side of the highway. Our crossing data only related to successful crossings. Events where animals entered the underpass but turned around within 5 min were not included in our analyses.

The second field study was designed for white-tailed deer (Odocoileus virginianus). This species was expected to be by far the most common large mammal species to use the structures (Cramer et al., 2012; Huijser et al., 2015b). We selected 10 large mammal underpasses (constructed 2005–2012, median age at the time of the research 6-7 years) along two highways (US Hwy 93 and State Hwy 206) (Appendix C). These crossing structures were known to be used by white-tailed deer (Cramer et al., 2012; Huijser et al., 2015b), they were 1.9-4.9 m high, 4.0-39.9 m wide (width is equal to road length in this context), and the wildlife fencing was designed for large ungulates (2.4 m high). We only selected isolated underpasses for which the fences did not connect to other crossing structures, which would have complicated the interpretation of the data. As a consequence, the fence lengths were always relatively short; the maximum fence length we encountered (measured from an underpass) was 256 m (Appendix C). The short fence lengths meant that a white-tailed deer that had the center of its home range on the road anywhere in the fenced road section always had access to both the underpass and at least one of the associated fence ends (radius home range 399–618 m (Foresman, 2012)). In other words, it was reasonable to assume that an individual deer that approached a mitigated road section had a choice to cross the highway at either an underpass or at one of the fence ends. Note that fence lengths were measured as "road length fenced" excluding potential additional fence length as a result of zig-zagging rather than running perfectly parallel to the highway. Some of the underpasses had no wildlife fencing at all, but the wing walls associated with the structure still resulted in a barrier that was at least 2.4 m tall for at least a few meters from the opening of the underpass.

The second field study included 10 "sites". Each site consisted of an underpass and four fence ends. We placed a minimum of five wildlife cameras (Reconyx Hyperfire PC900) at each site: one at an entrance of the wildlife underpass, and one at each of the four fence ends. Underpasses with openings wider than 12 m had multiple cameras installed as 12 m was the maximum distance at which we could reliably identify large mammals at night (aided by infrared flash). Cameras at fence ends were located at the last fence post and faced away from the wildlife fence. These cameras were angled slightly away from the road to reduce the likelihood of vehicles triggering the cameras. We only recorded crossings that occurred within the first 12 m of a fence end (marked with a stake for reference). Cameras were placed at an approximate height of 1 m. The cameras were programmed to take 10 photos in rapid succession (in <10 s) each time they were triggered, with zero lag time before the next series of images was taken. The cameras remained at a site until 14 full days (days of 24 h) of data were collected from all cameras. The data from the 10 sites (10 underpasses and their 40 fence ends) was collected between June 2012 and October 2013.

For this second field study we created a record each time a large mammal was detected by a camera at either an underpass or within the first 12 m from a fence end. For each record we identified the species involved and evaluated the animal's behavior for a potential road crossing. For a successful highway crossing the animal had to enter or exit the underpass or enter or leave the highway at a fence end and it could not return for at least 3 min. Returns within 3 min were considered unsuccessful highway crossings and were not included in our analyses. Images for fence ends across from one another were viewed at the same time to ensure that if the same highway crossing event was captured on more than one camera (i.e. seen both entering and exiting the roadway), it would be counted as only one crossing event. In these cases the crossing was assigned to the fence end where the animal entered the road. If an animal was only detected entering or leaving the roadway, the crossing was assigned to the fence end where the animal was actually detected. We did not speculate what the animal may or may not have done on the other side of the road as some of the fence ends on opposite sides of the road were staggered. In addition, for all animals that were recorded, we evaluated if they were, at any moment, present in the right-of-way (i.e. between the right-of-way fences on either side of the road) and whether they were foraging.

2.3. Analyses

Based on our literature review we calculated by what percentage individual fenced road sections reduced the number of collisions with large mammals (Appendix A). We plotted the data points, examined the scatter plot, and then selected a Michaelis-Menten function. This forced the curve through the origin which was consistent with the fact that without fencing the effectiveness in reducing collisions is zero. It also forced the curve to approach an asymptote. This was also a logical choice as fencing and associated measures could, at a maximum, reach an effectiveness of 100%. We also calculated a 95% confidence interval associated with the curve (bootstrap percentile-based intervals). If the effectiveness of fencing and associated measures was independent of the length of the mitigated road section, we would expect the curve to "hug" the vertical axis, increasing very quickly to a "stable" level of effectiveness independent of the mitigated road length. If the effectiveness was dependent on the length of the mitigated road section we would expect the curve to climb at a reduced angle and not to parallel the ver-

For the first field study we categorized the 23 underpasses in three groups: no or very short fences (0.0–0.4 km mitigated road length, 11 isolated underpasses with fence not connected to other structures), several kilometers of fencing (1.4–2.7 km, 7 underpasses with fence typically connected to other structures), and about 6 km of fencing (6.1–6.2 km, 5 underpasses with fence always connected to other structures) (Appendix B). For each underpass we calculated the number of successful large mammal crossings per day (24 h). The number of large mammal crossings per day was summarized in a box plot for each of the three fence length categories.

For the second field study we calculated the total number of highway crossings by large mammals through the 10 underpasses as well as at the 40 fence ends (Appendix C2). In addition we calculated the proportional highway crossings for each underpass as the number of highway crossings at an underpass divided by the total number of highway crossings at the site (i.e. the underpass concerned and its four fence ends). The proportional highway crossings at each fence end were calculated as the number of highway crossings at the fence end divided by the total number of highway crossings at the site. We summarized these data in a box plot. Finally, we conducted a weighted linear regression analysis and investigated the potential effect of the length of wildlife fencing (measured from the edge of the opening of an underpass to each fence end) on the proportion of highway crossings at fence ends. Each of the 40 data points was weighted by the total number of highway crossings at a site. Should fence length have influenced the proportion of highway crossings at fence ends we expected this to be a negative effect. We expected fewer large mammals to cross the highway at grade at a fence end with increasing fence length and we expected more large mammals to use the nearby underpass instead.

3. Results

3.1. Literature review: impact of fence length on reducing large mammal–vehicle collisions

We identified 21 fenced road sections for which effectiveness data were available (Appendix A). All but one of the road sections were located in North America. The fenced road lengths (range 0.6–33.8 km) as well as effectiveness (range 0–97%) varied greatly (Fig. 1, Appendix A). The average effectiveness of the road sections with fencing and associated measures in reducing collisions with large mammals was 70.7%

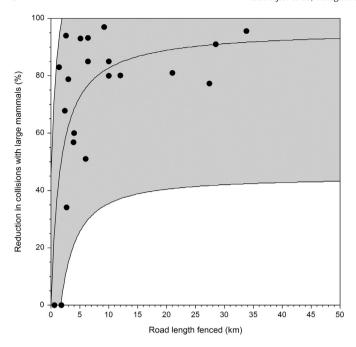


Fig. 1. The effectiveness of the 21 mitigated road sections with varying fence lengths in reducing collisions with large mammals. A Michaelis–Menten function (black line) was fitted to the data (Y = 96.07 * X / (1.62 + X)) with associated 95% confidence interval (grav area).

(SD = 28.5). However, the curve (Fig. 1) did not parallel the vertical axis indicating that the effectiveness increased with the length of a mitigated road section. This was consistent with the underlying scatter plot. In addition, the scatter plot and the 95% confidence interval associated with the curve also showed that shorter mitigated road sections were more variable in reducing collisions with large mammals than longer sections (Fig. 1). The average effectiveness for mitigated road sections longer than 5 km was 84.1% (SD = 12.4, range 51–97%). Mitigated road sections shorter than 5 km were less effective (52.7% on average) and more variable (SD = 34.5, range 0–94%) (Fig. 1).

3.2. Field studies: large mammal use of underpasses with no or very short fences

White-tailed deer were by far the most numerous species that used the 23 crossing structures included in the first field study (n = 9892, 94.37%). Other species included mule deer (n = 359, 3.42%), American black bear (*Ursus americanus*) (n = 162, 1.55%), mountain lion (Puma concolor) (n = 35, 0.33%), unidentified deer species (Odocoileus spp.) (n = 27, 0.26%), grizzly bear (Ursus arctos) (n = 5, 0.05%), elk (n = 1, 0.01%), and unidentified bear species (*Ursus* spp.) (n = 1, 0.01%). The number of large mammal crossings through the underpasses varied greatly between the individual structures, regardless of the length of the fenced road section (Fig. 2). There was no indication that the number of large mammals that used the isolated underpasses with no or very short fences (0.0-0.4 km) was consistently different from underpasses associated with longer fenced road sections (1.4-2.7 or 6.1-6.2 km) (Fig. 2). The median number of crossings per day for the three fence length categories was 0.22 (0.0-0.4 km), 0.77 (1.4-2.7 km) and 0.44 (6.1–6.2 km) (Fig. 2).

In our second field study we recorded 997 large mammals at either the underpasses or the fence ends. Of these detections, 727 (73%) resulted in the animal crossing the highway corridor. Over 99% of the recorded highway crossings by large mammals (721 out of 727) related to white-tailed deer. The remaining 6 crossings were by bears (3 American black bears and 3 either black bears or grizzly bears). For all sites combined, 599 of the 727 recorded highway crossings (82%) occurred at

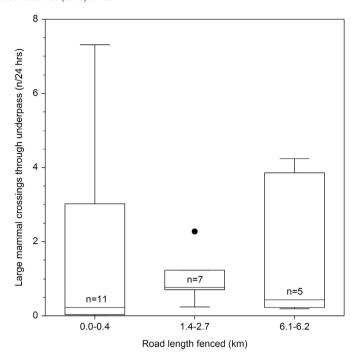


Fig. 2. Box plot of the number of large mammal crossings through the 23 underpasses per day in 2013. The underpasses were divided into three categories based on the fenced road length associated with the underpasses. Box: middle 50% of the data (25–75 quartile); horizontal line: median; whisker boundaries: 1.5 times inter-quartile range; severe outliers: 3.0 times inter-quartile range.

underpasses, and the remaining 18% of the highway crossings were at grade at the fence ends. The proportion of highway crossings varied substantially between the underpasses with a median of 85.5% (Fig. 3). The proportion of highway crossings at fence ends also varied greatly with a median of 3% (Fig. 3).

We plotted the proportion of highway crossings at each of the 40 fence ends as a function of the length of the fence to the associated underpass (Fig. 4). The proportion of highway crossings at fence ends did

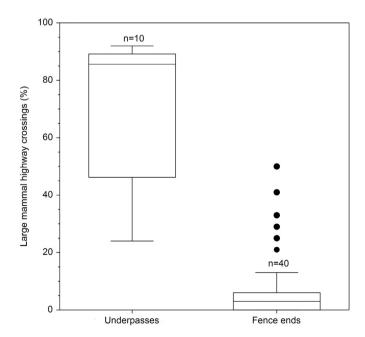


Fig. 3. Box plot of the percentage of highway crossings through the 10 underpasses and at grade at the 40 fence ends. Box: middle 50% of the data (25–75 quartile); horizontal line: median; whisker boundaries: 1.5 times inter-quartile range; severe outliers: 3.0 times inter-quartile range.

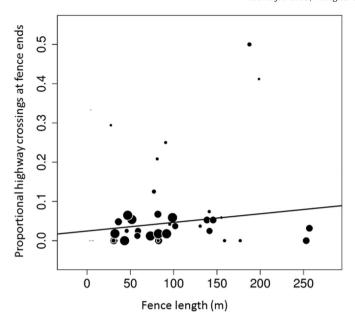


Fig. 4. The proportion of highway crossings at each fence end (n=40) as a function of fence length (measured from the edge of the opening of an underpass to the fence end). The size of the "bubbles" is proportional to the weight of each data point which is based on the total number of highway crossings at each underpass and its four fence ends.

not increase or decrease across the range of fence lengths sampled (minimum fence length = 3.2 m, maximum = 256.7 m) (n = 40; $R^2 = 0.0297$; p-value = 0.2878; slope = 0.0002). In other words, for fence lengths up to a few hundred meters from an isolated underpass, longer fences were not associated with fewer highway crossings at fence ends (proportionally) or more highway crossings through the associated underpasses (proportionally).

A total of 357 large animals were recorded at fence ends of which 164 (46%) entered the road or vegetated right-of-way. Of the large mammals recorded at a fence end 128 (36%) ended up crossing the highway, 126 (35%) related to deer (*Odocoileus* spp.) foraging, and 62 (17%) related to deer foraging within the road corridor (i.e. on the road side of the right-of-way fence).

4. Discussion

4.1. Short fences are less effective in reducing collisions

Our literature review showed that wildlife fencing and associated measures implemented along short road sections (<5 km) were, on average, less effective in reducing collisions with large mammals than fencing implemented along long road sections (>5 km). Mitigated road sections that were at least 5 km long reduced collisions with large mammals by 84.1% on average whereas mitigated road sections that were shorter than 5 km only reduced these collisions by 52.7% on average. In addition, the effectiveness of mitigated road sections shorter than 5 km was extremely variable. This meant that the effectiveness of wildlife fencing was highly unpredictable for any specific mitigated road section shorter than 5 km in length. On the other hand, mitigated road sections that were at least about 5 km long were almost always at least 80% effective in reducing collisions with large mammals. To our knowledge this is the first quantitative evidence that the effectiveness of wildlife fencing depends on the length of the mitigated road section. When large mammals, specifically large ungulates, are the target species, reducing the length of wildlife fencing to less than about 5 km can substantially limit effectiveness.

4.2. Why are short fences less effective and more variable in reducing collisions?

Based on the literature we argue that road sections at and near fence ends tend to have a concentration of wildlife–vehicle collisions which reduces the effectiveness of the mitigated road section near a fence end. When a fenced road section is very short (≤5 km), it is either under partial or full influence of fence-end effects, which can suppress the effectiveness of the fence for the entire mitigated road section. However, the results of our literature review suggest that when a fenced road section is longer than about 5 km, the fence-end effects are sufficiently diluted to achieve at least 80% reduction in collisions with large mammals.

Fence-end effects can include a concentration of animal crossings at fence ends, animals entering the fenced right-of-way at fence ends, and spatial inaccuracies of the collision data. We explain these issues here based on the literature. When animals approach a fenced section of highway they may follow the fence (LeBlond et al., 2007) until they encounter a suitable crossing structure or an at-grade crossing opportunity at a fence end. The latter can result in a higher concentration of atgrade crossings and collisions at fence ends compared to other unfenced road sections that are further away from a fence end (e.g. Clevenger et al., 2001; Parker et al., 2008; Gulsby et al., 2011). This phenomenon is sometimes referred to as a "fence-end run". However, fence-end runs may not always be present (e.g. Craighead et al., 2011; Bissonette and Rosa, 2012). Fence-end runs do not necessarily impact the effectiveness of fenced road sections, but since the spatial precision of crash and carcass data is typically only 0.1 mile or 0.1 km at best (Huijser et al., 2007), some of the animals that are hit just outside the fenced road section are likely to be mistakenly assigned to the fenced road section. In addition, some of the animals at the fence ends may end up wandering into the fenced road corridor. Ungulates that are attracted to the vegetation in the right-of-way may be particularly interested in accessing the fenced road section (e.g. Carbaugh et al., 1975). Such intrusions into the fenced road corridor can result in collisions in the mitigated road section, especially near fence ends (Siemers et al., 2015).

Short fenced road sections were, on average, not only less effective in reducing large mammal–vehicle collisions than longer fenced road sections, but their effectiveness was also far more variable. This can be related to variations in spatial accuracy of the collision data and thus varying levels of errors when assigning the collisions to either the mitigated or unmitigated highway section. In addition, differences in local topography and habitat, as well as the presence or absence of fenceend treatments (see next section) likely have a substantial impact on wildlife movements and thus collisions near fence ends. This type of variation also exists for longer fenced road sections. However, fenceend effects, including variations in fence-end effects, appear to be substantially diluted if the fenced road sections are at least 5 km long.

4.3. Fence-end treatments and other design considerations can improve the effectiveness of fences

Fence-end treatments are designed to discourage wildlife from crossing the highway at fence ends and to discourage wildlife from entering the fenced road corridor at a fence end. Fewer animals crossing the highway at fence ends and fewer intrusions into the fenced road section should result in fewer collisions, both within and outside the mitigated section. Fence-end treatments designed to discourage wildlife from crossing the highway at fence ends include angling fences away from the road or ending fences at a bridge or steep slope (Huijser et al., 2015a). Fence-end treatments designed to discourage wildlife from entering the fenced road corridor at a fence end include fences angled towards the road, boulder fields that block access into the fenced vegetated right-of-way, or wildlife guards or electric mats embedded in the travel lanes (Huijser et al., 2015a).

When designing mitigation measures and deciding on where fences should start and end, it is important to consider the location of potential collision hotspots, the surrounding landscape and the size of the home range of the target species. Tailoring the design of the mitigation measures to local conditions can greatly improve the effectiveness of fences in reducing wildlife-vehicle collisions. Obviously the mitigated road section should cover the entire length of a wildlife-vehicle collision hotspot that may have been identified based on wildlife-vehicle collision data. However, in real world settings this does not always happen (Cramer et al., 2014). In addition, the fences should also include "buffer zones" on either side of a hotspot (Ward, 1982; Huijser et al., 2015a). If a fence ends exactly where the hotspot ends, the animals that approach the road at the edge of the hotspot can simply step to the side and cross the highway at grade at a fence end. Such fence-end runs are less likely if the fences extend further than the actual hotspots. In this context it is useful to consider the home range size of the target species. Note that the diameter of the home range for most large Cervidae is a few hundred meters up to about 8 km. If an animal has the center of its home range at the edge of a hotspot it can be expected to be able to travel a distance equivalent to the radius of its home range. This provides an indication of the appropriate length of the buffer zones. Local topography and habitat can also help guide decisions on where wildlife fences should start and end. It is also important to consider the spatial accuracy of the wildlife-vehicle collision data (typically only 0.1 mile or 0.1 km at best) (Huijser et al., 2007). If mitigation measures are proposed for very short road sections, e.g. only a few hundred meters, it would be relatively easy to partially or fully miss a hotspot (Ford et al., 2011). Wildlife fencing is likely most effective if the supporting wildlife-vehicle collision data are spatially accurate, if the mitigation measures cover the actual hotspots as well as adjacent buffer zones, and if the designs are tailored to the local conditions, including topography and habitat. Consulting experts and people with local knowledge and expertise, including road maintenance personnel, is likely to improve the effectiveness of the mitigation measures.

4.4. Large mammal use of underpasses can be high regardless of fence length

Our first field study showed that large mammal use of underpasses designed for large mammals varied greatly between the structures. The use was similar for isolated structures with no or limited fencing, structures connected to a few kilometers of fencing, and structures connected to more than 6 km of fencing. The data showed that the presence of wildlife fencing and longer fence lengths did not necessarily guarantee higher wildlife use. Similarly, the absence of fencing or the presence of very short sections of fencing did not always result in low use of an underpass by large mammals. This suggests that large mammal use of underpasses is heavily influenced by other factors. These factors likely include the location of the structure in relation to the surrounding habitat, wildlife population density, and wildlife movements.

Our findings may seem to contradict other studies that clearly showed that connecting crossing structures to wildlife fencing can result in a very substantial increase in wildlife use (Dodd et al., 2007; Gagnon et al., 2010). However, while our data showed great variability in wildlife use of underpasses regardless of the presence and length of wildlife fencing, our data do not necessarily contradict studies that showed the importance of fencing. In our study we did not manipulate the presence or length of wildlife fencing at the structures. We simply compared wildlife use of different structures that happened to have or not have wildlife fencing. However, Dodd et al. (2007) and Gagnon et al. (2010) were able to record wildlife use of crossing structures both before and after wildlife fencing was installed and connected to particular structures. Thus, while wildlife use of underpasses is highly variable—probably mainly because of differences between locations—, an individual underpass may still have higher wildlife use if that

underpass is connected to wildlife fencing and if the fence length is long rather than short.

4.5. Highway crossings occurred primarily through underpasses rather than at fence ends

Our second field study showed that, despite the very short fence lengths associated with the isolated underpasses, the vast majority (82%) of all large mammal highway crossings occurred at the underpasses. Only 18% of the highway crossings occurred at grade at the fence ends. This suggests that relatively few animals choose to cross within the first 12 m from a fence end, even if there is no or very short fencing present. Of course we do not know how many animals may have crossed the road beyond 12 m from the fence ends. Note that the fact that relatively few animals crossed at grade at a fence end does not necessarily mean that fence-end effects (see Section 4.2) were small or absent. Fence-end effects include, but are not restricted to highway crossings at fence ends.

We found that the proportional use of isolated underpasses (compared to crossings at fence ends) did not increase with longer fence lengths (up to 256 m from underpasses). Thus, within the range of fence lengths sampled there was no disproportionate benefit of increasing the length of wildlife fencing adjacent to an isolated underpass. As previously stated, this does not necessarily mean fence-end effects (see Section 4.2) were small or absent, nor do we know how many animals may have crossed the highway beyond 12 m from the fence ends. These results specifically apply to isolated crossing structures with short sections of fencing. If multiple crossing structures are connected to continuous fencing spanning many kilometers of road, individual animals are less likely to have access to a fence end. Therefore long fenced road sections (many kilometers) with multiple crossing structures are likely to have a higher proportion of animals using crossing structures (compared to the proportion of animals crossing the highway at grade at the two fence ends).

Our study showed that large mammals, specifically deer (*Odocoileus* spp.), approached the highway for multiple reasons. They not only approached the highway with the intention to cross, but they also approached the road to forage. Of all large mammals detected at the fence ends in our study, 35% related to deer (*Odocoileus* spp.) foraging, and 17% related to deer foraging within the road corridor (i.e. on the road side of the right-of-way fence). Foraging close to the travel lanes is risky as the animals spend more time close to traffic and they may also be less alert. Foraging in the vegetated right-of-way near fence ends may also result in animals wandering into the fenced road corridor. Our data on the behavior of large mammals near fence ends confirm that fence-end treatments (see Section 4.4) may be important to keep large ungulates from wandering into the fenced road corridor.

5. Conclusions

Wildlife fencing for large ungulates is most effective at reducing collisions (at least about 80% reduction) if the fencing and associated measures are installed over road lengths of at least 5 km. If fencing is implemented over relatively short road lengths (< 5 km), the average effectiveness in reducing collisions with large mammals may drop to about 50%. The effectiveness of wildlife fencing was highly unpredictable for any specific mitigated road section shorter than 5 km in length. Furthermore, the associated economic benefits (i.e. fewer collisions and lower costs) will decrease disproportionally compared to the costs associated with the mitigation measures. Improving the spatial precision of collision data; proper placement of fences in relation to hotspots, buffer zones, and local topography and habitat; as well as fence-end treatments can help improve the effectiveness of short sections of wildlife fencing in reducing collisions. These factors can also help reduce the variation in the effectiveness of short fences. Because we reviewed all available publications that reported on the effectiveness of wildlife

fencing for large mammals, we believe the results of our literature review are generally applicable, especially for large ungulates in North America. In the context of wildlife use of underpasses, our first field study showed that isolated underpasses with no or very short fences have very variable use by large mammals; similar to that for crossing structures connected to sections of wildlife fencing up to 6 km long. Furthermore, our second field study showed that longer fence lengths (up to a few hundred meters from an underpass), did not result in an increase in the proportion of highway crossings through the isolated underpasses compared to at-grade crossings at fence ends. The data suggest that if the primary success parameter is improving highway safety for humans through a substantial reduction in collisions with large ungulates, the road length fenced may have to be at least 5 km. However, longer fence lengths do not necessarily guarantee higher absolute wildlife use of underpasses, as use appears to be heavily influenced by the location of a crossing structure. Nonetheless, existing literature showed that inclusion of wildlife fencing may still improve the use of individual underpasses.

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Appendixes. Supplementary data

The supplementary data include a table with the characteristics of the highway sections included in our literature review to investigate the effect of the length of a fenced road section on the reduction in collisions with large mammals (Appendix A), a table with the locations, characteristics and wildlife use of the 23 underpasses included in our first field study (Appendix B), and tables of the locations and characteristics of the 10 underpasses 40 fence ends (Appendix C1) and the large mammal highway crossings at these underpasses and fence ends (Appendix C2). Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.02.002.

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