



Original Article

Mitigating Roadway Impacts to Migratory Mule Deer—A Case Study With Underpasses and Continuous Fencing

HALL SAWYER,¹ *Western EcoSystems Technology, Incorporated, 200 S 2nd Street, Suite B, Laramie, WY 82070, USA*

CHAD LEBEAU, *Western EcoSystems Technology, Incorporated, 200 S 2nd Street, Suite B, Laramie, WY 82070, USA*

THOMAS HART, *Wyoming Department of Transportation, 5300 Bishop Boulevard, Cheyenne, WY 82009, USA*

ABSTRACT Wildlife–vehicle collisions pose a major safety concern to motorists and can be a significant source of mortality for wildlife. Additionally, roadways can impede movements and reduce habitat connectivity. For migratory ungulates, these problems can be exacerbated when roadways bisect migration routes, as is the case in Southwest Wyoming, USA, where a 21-km section of U.S. Highway 30 overlaps with a critical winter range and migration route used by thousands of mule deer (*Odocoileus hemionus*). In an effort to reduce deer–vehicle collisions (DVC) and maintain migratory connectivity, the Wyoming Department of Transportation installed 7 concrete box-culvert underpasses with continuous game-proof fencing between each crossing structure. To evaluate the effectiveness of this mitigation project, we used remote cameras to quantify the number of mule deer that used the underpasses, estimate passage rates through time, and compare rates of DVCs before and after underpass construction. Through 3 years of monitoring (which encompassed autumn migration [2008, 2009, and 2010], winter use, and spring migration [2009, 2010, and 2011] for 3 migration cycles), we documented 49,146 mule deer move through the underpasses. Passage rates of deer approaching underpasses steadily increased from 54% in Year 1 to 92% in Year 3. Peak movements during the autumn migration occurred in mid-December, while peak spring movements were in mid-March and early May. Underpass and fence installation effectively reduced DVCs by 81%. Had fence gates remained closed and cattle guards clear of snow, DVCs could be eliminated altogether. Our results suggest that underpasses, combined with game-proof fencing, can improve highway safety for motorists while providing safe and effective movement corridors for large populations of migratory mule deer. © 2012 The Wildlife Society.

KEY WORDS connectivity, fencing, highways, migration, mitigation, mule deer, *Odocoileus hemionus*, underpass, wildlife–vehicle collisions (WVC), Wyoming.

Wildlife–vehicle collisions (WVC) are a serious safety concern for motorists and can be a significant source of mortality for affected wildlife (Romin and Bissonette 1996, Putman 1997, Forman et al. 2003, Langbein et al. 2011). Additionally, roadways can restrict animal movements and increase fragmentation (Forman and Alexander 1998, Trombulak and Frissell 2000). For ungulate populations, potential impacts can be especially problematic when roads intersect with migration routes (e.g., Berger 2004, Sawyer et al. 2005). A case in point is U.S. Highway 30 in western Wyoming, USA. This 2-lane rural highway extends 21 km through crucial winter range and a migration route used by thousands of mule deer (Fig. 1). Deer–vehicle collisions (DVC) have historically been high along this roadway, with an average of 130 deer killed/year between 1989 and

2001 (Plumb et al. 2003). Despite a variety of mitigation measures implemented through the 1990s aimed at slowing traffic and warning motorists of potential collisions with wildlife (e.g., signs, reflectors, flashing lights), dozens of DVCs continued to occur each year in this segment of highway (Reeve and Anderson 1993, Gordon et al. 2004). The high rates of DVCs created safety concerns for motorists and, as traffic volumes increased by 42% between 1990 and 2000, managers were also concerned with maintaining habitat connectivity across the highway for migratory mule deer. In an effort to move deer underneath the highway and reduce DVCs, the Wyoming Department of Transportation installed a concrete box culvert at the western edge of the highway segment in 2001 (Fig. 1). To facilitate mule deer use of the underpass, a 2.4-m-high fence extended approximately 5.5 km on either side of the underpass. Although several hundred deer used the underpass in subsequent years (Gordon and Anderson 2003), remaining portions of the 21-km roadway continued to have high rates of DVCs, and it was apparent that additional crossing structures were needed. Accordingly, 6 new underpasses

Received: 14 December 2011; Accepted: 20 April 2012
Published: 25 July 2012

¹E-mail: hsawyer@west-inc.com

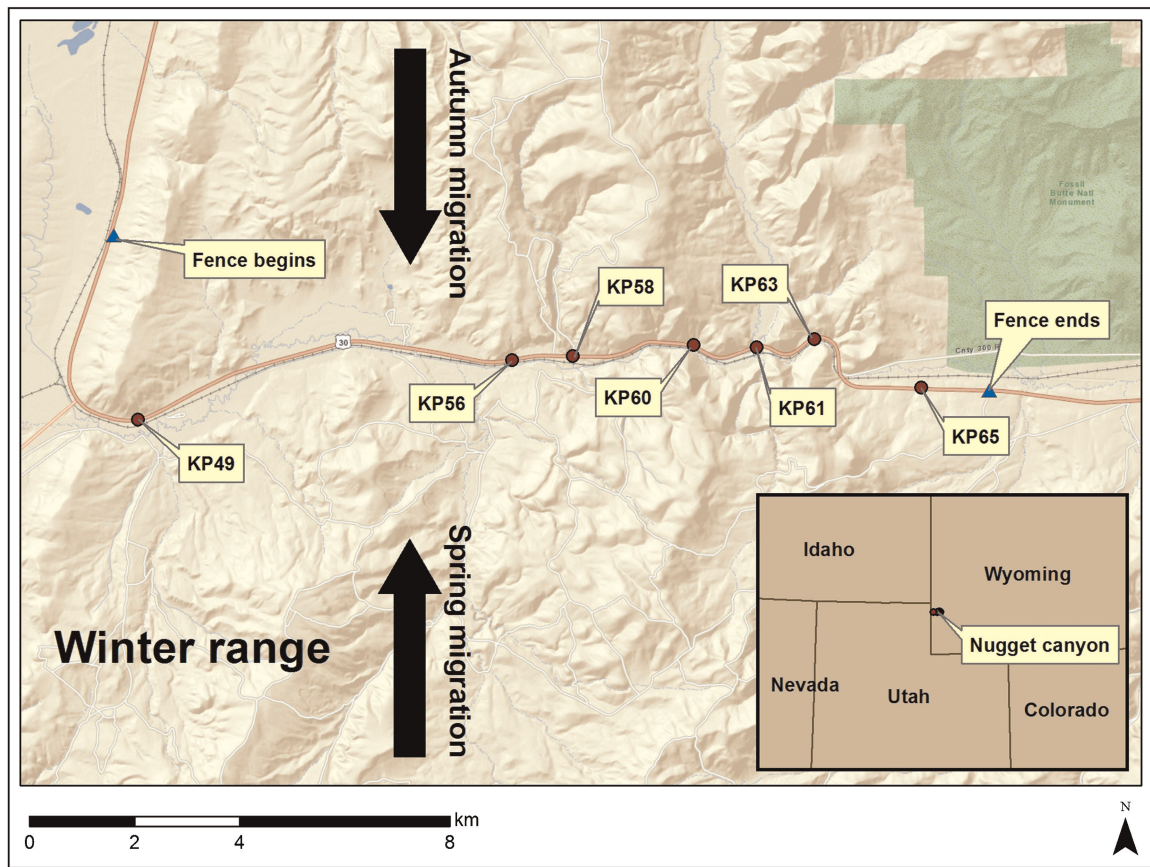


Figure 1. Location of game-proof fencing and 7 mule deer underpasses constructed along U.S. Highway 30 in Southwest Wyoming, USA.

and 10 km of fence were constructed in the summer of 2008.

Although previous studies have documented how many animals move through a particular underpass (Foster and Humphrey 1995, Ng et al. 2004, Kleist et al. 2007, McCollister and Van Manen 2010), none have focused on large migratory populations where animals can migrate at grade-level during one year, while the next year they cannot. Ungulates show strong fidelity to their migration routes (Berger et al. 2006, Sawyer et al. 2009, Sawyer and Kauffman 2011) and how they respond to fencing and underpasses is generally unknown. Our goal was to evaluate whether underpasses and associated fencing effectively reduced roadway impacts to this migratory deer population. First, we quantified the number of mule deer that used the underpasses. Second, we identified the seasonal and daily temporal patterns of deer movements through underpasses. Third, we estimated the passage rates of deer through underpasses to evaluate habituation through time. Finally, we evaluated DVCs before underpass construction (1990–2000), after construction of 1 underpass (2002–2007), and after construction of 6 additional underpasses (2009–2011). A clear understanding of whether underpasses and fencing can mitigate roadway impacts (i.e., DVCs, habitat connectivity) to migratory mule deer will improve the ability of wildlife and transportation agencies to sustain migratory ungulate populations and improve public safety on roadways.

STUDY AREA

Our study site was a 21-km section of U.S. Highway 30 situated in Southwest Wyoming, in an area locally known as Nugget Canyon (Fig. 1). The canyon was characterized by steep sagebrush (*Artemisia tridentata*) canyons and open hill-sides. Elevations along the 2-lane roadway ranged from 1,890 m to 1,950 m, but the edges of the canyon reached elevations of 2,320 m. The Nugget Canyon area provided critical winter range to thousands of mule deer that migrated north each year to summer in the Wyoming Range. Because U.S. Highway 30 bisected this winter range, animals that wintered on the south side of Nugget Canyon must cross U.S. Highway 30 to complete their seasonal migrations. To reduce the number of DVCs, the Wyoming Department of Transportation installed 11 km of game-proof fence and 1 concrete box-culvert underpass (KP49) in 2001 (Fig. 1). In 2008, the fence was extended another 10 km, and an additional 6 underpasses (KP56, KP58, KP60, KP61, KP63, and KP65) were installed (Fig. 1). Underpass dimensions were approximately 6 m (width) × 18 m (length) × 3.0–3.5 m (ht), with an openness ratio of 1.10 (Fig. 2). We note that the openness ratio (opening width × ht/length of crossing) was calculated in metric units (Foster and Humphrey 1995). The height varied by as much as 0.5 m because of the amount of dirt fill used at each site. We refer readers to Reeve and Anderson (1993) and Gordon



Figure 2. Standard concrete-box underpass along U.S. Highway 30 in Southwest Wyoming, USA, with full-size pickup for reference (top). Mule deer moving through underpass (bottom).

et al. (2004) for detailed history of roadway mitigation efforts in Nugget Canyon, Wyoming.

METHODS

We installed 3 digital infrared Reconyx® (Holmen, WI) cameras in each of the 7 underpasses, including one at the entrance, one in the middle, and one at the exit. This camera configuration allowed us to count the number of deer that approached and passed through each underpass from either direction. Underpasses were equipped with cameras from 1 October through 31 May for 3 years. The study period encompassed autumn migration (2008, 2009, and 2010), winter use, and spring migration (2009, 2010, and 2011) for 3 migration cycles. We defined the autumn migration as 1 October through 31 December and spring migration as 1 March through 31 May. The winter period was January and February. We note that cameras were not installed the first year until 16 December, so only the later part of the autumn migration was documented that year. We refer to years 1, 2, and 3 as monitoring seasons 2008–2009, 2009–2010, and 2010–2011, respectively. We used digital photos to count the number of deer and other wildlife that used each underpass. We examined seasonal temporal patterns by calculating the number of deer that passed through each underpass each day. We examined the daily temporal

patterns by calculating the number of deer that moved through underpasses each hour of the day, during a 10-day sampling period that corresponded with the peak level of use during spring and autumn migrations.

When faced with a novel disturbance such as an underpass, ungulates may take some time to habituate before using it (e.g., Gagnon et al. 2011). We evaluated the passage rate success by calculating the proportion of animal approaches that resulted in successful crossings (Dodd et al. 2007). We defined an approach as any event in which animals moved to within 50 m of the underpass entrance (Gagnon et al. 2007b). The passage rate was then calculated by dividing the number of animals that successfully passed through the underpass by the number of animals that approached. This metric was intended to quantify the effectiveness of each underpass and help evaluate whether passage rate success improved over time (e.g., Xia et al. 2007, Gagnon et al. 2011). We calculated passage rates during the 10-day peak migration period of each season (autumn 2008 [17–26 Dec], autumn 2009 [08–17 Dec], autumn 2011 [21–30 Nov], spring 2009 [23 Apr 23–02 May], spring 2010 [17–26 Apr], spring 2011 [01–10 May]).

We used DVC data collected by the Wyoming Department of Transportation to assess how underpass and fence construction reduced DVCs. We compared the number of DVCs during 3 time periods: 1) 1 January 1990–1 October 2001, (141 months) prior to construction of the first underpass, 2) 1 October 2001–1 October 2008, (82 months) following construction of the first underpass, and 3) 1 October 2008–1 May 2011, (31 months) following construction of 6 additional underpasses. To make comparisons between the 3 periods that differed in temporal length, we standardized the number of DVCs by the number of months in each period.

RESULTS

Underpass Use by Mule Deer

We documented 49,146 mule deer that moved through the 7 underpasses between December 2008 and May 2011 (Table 1), including 12,483 during the 2008–2009 monitoring season, 13,403 during 2009–2010, and 23,260 during the 2010–2011 monitoring season. Overall, most deer movement occurred at the KP49 (47%; $n = 22,924$) and KP58 (28%; $n = 14,012$) underpasses (Table 1; Fig. 3). However, use at the other 5 underpasses steadily increased through the 3 years of study and accounted for the remaining 12%, 28%, and 34% of deer use during the 2008–2009, 2009–2010, and 2010–2011 monitoring seasons, respectively. Most underpass activity occurred during spring (37%; $n = 18,194$) and autumn (46%; $n = 22,569$) migrations, but deer crossings (17%; $n = 8,383$) also occurred on a regular basis throughout the winter period (Table 1).

Deer use varied between underpasses, with most use occurring at KP49 and KP58 (Fig. 3). Additionally, the amount of deer use varied between spring and autumn migrations at several of the underpasses (Fig. 3). For example, the proportion of deer use was higher at underpass KP49 during the

Table 1. Number of mule deer that moved through underpasses during the autumn migration (Oct–Dec), the winter period (Jan–Feb), and the spring migration (Mar–May), December 2008 through May 2011, Nugget Canyon, Wyoming, USA.

Underpass	2008–2009	2009–2010	2010–2011	Total
Autumn migration				
KP49	1,552	3,308	5,553	10,413
KP56	83	274	855	1,212
KP58	638	885	4,242	5,765
KP60	149	1,062	1,529	2,740
KP61	18	151	298	467
KP63	3	199	943	1,145
KP65	47	374	406	827
Sub-total	2,490	6,253	13,826	22,569
Winter period				
KP49	2,112	1,228	1,527	4,867
KP56	69	40	1,782	1,891
KP58	233	104	379	716
KP60	56	110	371	537
KP61	16	22	55	93
KP63	5	48	104	157
KP65	37	75	10	122
Sub-total	2,528	1,627	4,228	8,383
Spring migration				
KP49	3,496	2,298	1,850	7,644
KP56	258	136	900	1,294
KP58	2,957	1,786	1,613	6,356
KP60	96	557	423	1,076
KP61	95	179	68	342
KP63	400	314	287	1,001
KP65	163	253	65	481
Sub-total	7,465	5,523	5,206	18,194
Total	12,483	13,403	23,260	49,146

autumn compared with the spring, whereas deer use at underpass KP58 was higher during the spring compared with autumn. With the exception of KP49 and KP58, the proportion of deer use generally increased throughout the study period (Fig. 3).

The timing of peak movements during the autumn migrations occurred in mid-December, with a maximum of 284 animals/day (Fig. 4). Spring migrations were characterized by multiple peaks of deer movement that generally occurred in mid-March and early May, with a maximum of 223 animals/day (Fig. 4). On a daily basis, peak levels of underpass use occurred in the mornings (0600–0800 hours) and evenings (1800–2000 hours; Fig. 5). Morning use was more prominent during the spring, whereas evening use was more common in the autumn.

Passage Rates

Passage rates averaged 54% among all 7 structures during the first year of study and increased to 72% during the second year and 92% in the third year (Fig. 6). The oldest underpass (KP49) had a relatively high success rate to begin with, presumably because it had been in place already for 7 years. Passage rates observed at the 6 new underpasses steadily increased through the 3-year study period, further suggesting that it may take mule deer up to 3 years to habituate to underpasses before using them without hesitation.

Mule Deer–Vehicle Collisions

Prior to underpass construction, the average number of DVCs in the 21-km study area was 9.75/month.

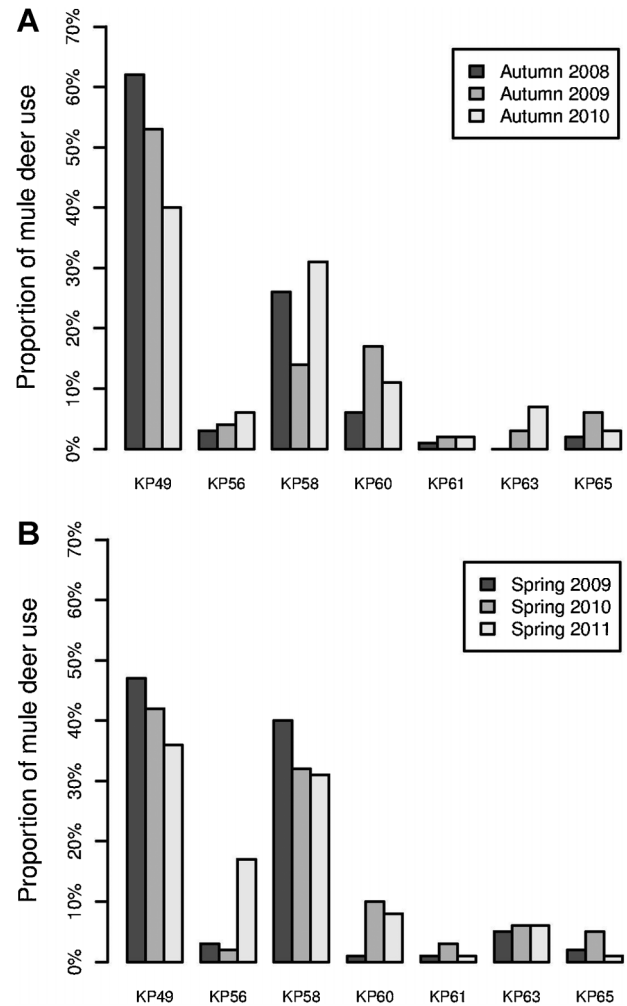


Figure 3. Proportional level of mule deer use at each underpass during spring and autumn migrations, December 2008 through May 2011, Nugget Canyon, Wyoming, USA.

Following construction of the first underpass in 2001, the average number of DVCs declined by 12% to 8.58/month. After construction of 6 additional underpasses and fencing in 2008, the average number of DVCs was further reduced to

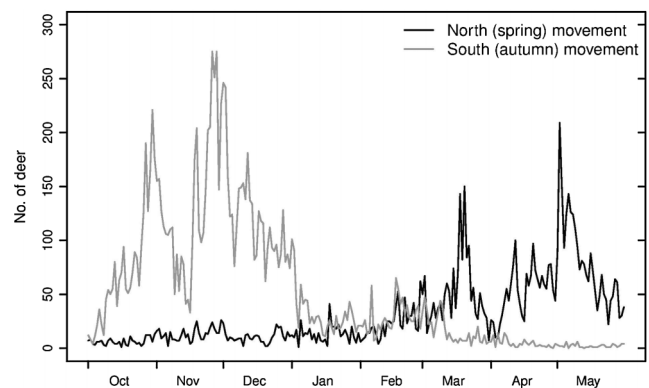


Figure 4. Mean number of mule deer moving south to north (spring migration) and north to south (autumn migration) underneath U.S. Highway 30, Nugget Canyon, Wyoming, USA.

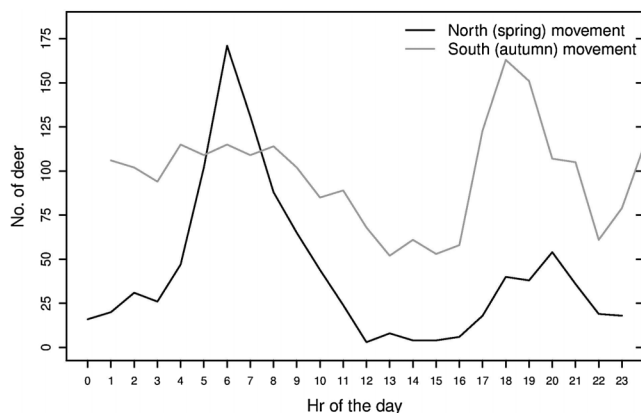


Figure 5. Number and time of day that mule deer moved through underpasses during the spring and autumn migrations, December 2008 through May 2011, Nugget Canyon, Wyoming, USA.

1.82/month. Overall, the construction of 7 underpasses and associated fencing reduced mule DVCs by 81%.

Underpass Use by Other Wildlife

In addition to mule deer, we recorded 1,953 elk (*Cervus elaphus*), 201 pronghorn (*Antilocapra americana*), 13 coyotes (*Canis latrans*), 77 bobcats (*Lynx rufus*), 9 badgers (*Taxidea taxus*), 13 moose (*Alces alces*), 3 raccoon (*Procyon lotor*), and 1 cougar (*Puma concolor*) as they moved through the underpasses.

DISCUSSION

Reducing DVCs is needed across wide regions of North America to improve highway safety and minimize deer mortality (Romin and Bissonette 1996, Putman 1997, Forman et al. 2003, Langbein et al. 2011). We found underpass and fence construction reduced DVCs by 81% in a 21-km stretch of U.S. Highway 30, where thousands of animals must cross the highway to complete their seasonal migrations. Previous studies have shown that game-proof fencing used in conjunction with underpasses can effectively move animals underneath roadways and reduce WVCs (Romin and

Bissonette 1996, Clevenger et al. 2001, McCollister and Van Manen 2010). Our study broadens support of these findings and suggests that this mitigation approach can effectively move thousands of migrating mule deer underneath roadway segments that extend >20 km. Importantly, DVCs did not increase in areas immediately adjacent to the fence ends, where deer were free to move across the highway at grade-level (Sawyer and LeBeau 2011). Rather than shift their migration routes and move around the fencing, deer moved underneath the highway, presumably through the underpass closest to their original migration route. We note that DVCs were not completely eliminated from the project area. Deer occasionally accessed the roadway through cattle guards filled with snow or gates left open by recreational users. Fortunately, both of these problems are correctable and if the fence infrastructure (i.e., cattle guards, gates) is managed properly, especially during the peak movement periods during spring and autumn migrations, then DVCs could be eliminated altogether.

As traffic volumes increase and roadways are widened, it also becomes more difficult to maintain habitat connectivity (Forman et al. 2003). Our study suggests that underpass and fence construction did not affect the permeability of U.S. Highway 30 to migratory mule deer. Rather, underpasses provided mule deer with a safe means to cross the 2-lane highway and maintain connectivity with their distant seasonal ranges. We documented 49,146 mule deer that moved underneath U.S. Highway 30 during a 3-year period and 83% of those animals were in the process of migrating. During peak migration periods, >200 deer/day moved through the underpasses, with most use occurring in morning and evenings. Other studies suggest that underpass and fence construction may actually improve highway permeability because animals are less affected by traffic volume when moving underneath the roadway, compared with crossing at grade-level (Gagnon et al. 2007a, Dodd and Gagnon 2011).

Across the globe, migratory ungulates tend to outnumber their nonmigratory counterparts (Fryxell et al. 1988). Mule deer are no exception (e.g., Garrott et al. 1987, Brown 1992) and typically migrate 15–150 km between their seasonal ranges (Sawyer et al. 2005, Sawyer and Kauffman 2011). Sustaining these herds will require that mule deer safely cross roadways that overlap with established migration routes. Given the strong fidelity that mule deer show to their migration routes (Thomas and Irby 1990, Sawyer et al. 2009), maintaining routes across roadways with high traffic volume will likely require some form of crossing structure (e.g., underpass or overpass). In general, structures with high openness ratios are considered more appealing to wildlife (Foster and Humphrey 1995, Clevenger and Waltho 2000, Gordon and Anderson 2003). Yet, regardless of the openness ratio of a structure, some habituation period for animal use should be expected. For example, Gagnon et al. (2011) recently showed that elk may take up to 4 years to habituate to open-span bridge underpasses. Similarly, we found mean passage rates of mule deer through concrete-box underpasses steadily increased from 54% in Year 1 to 92% in Year 3, suggesting that mule deer habituation may also take several

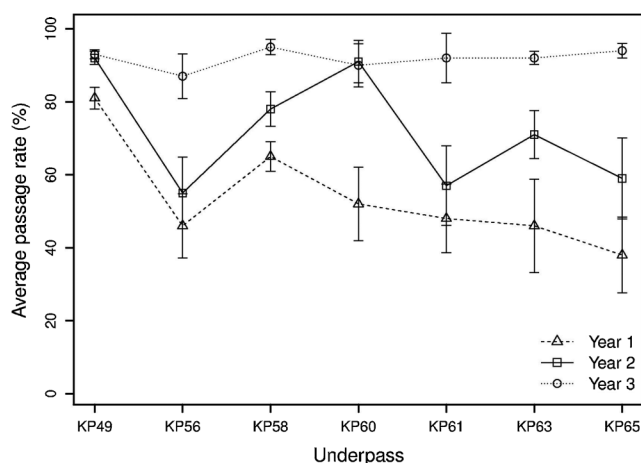


Figure 6. Average passage rates ($\pm$ SE) of mule deer at each underpass during 3 years of study, December 2008 through May 2011, Nugget Canyon, Wyoming, USA.

years. Passage rates are likely influenced by a variety of factors including structure design, traffic levels, and species of animal (Clevenger and Waltho 2000; Gagnon et al. 2007*a, b*). Nonetheless, having some knowledge of the expected habituation period will help refine expectations and public perceptions of mitigation projects, especially in high-profile areas where animal movements are visible from the roadway.

Of the 7 underpasses we monitored, most deer use occurred at KP49 and KP58. Given that each underpass was the same size, it is of interest why those two were used more than others. Certainly, factors such as vegetation, human activity, and topography may influence the effectiveness of underpasses (Clevenger and Waltho 2000, 2005; Ng et al. 2004). Although we did not conduct any formal analysis to evaluate how these factors differ between the 7 underpasses, we suspect that the location of the underpasses relative to established migration routes was the most likely explanation for the differential use. In other words, because underpasses KP49 and KP58 were situated in close proximity to existing migration routes, they received the highest levels of deer use. Although we do not have telemetry data to document where established migration routes occurred before construction, we do know that road segments with the highest levels of DVCs closely corresponded with the locations of KP49 and KP58 (Sawyer and LeBeau 2011), which suggests that higher numbers of deer historically crossed the highway in these areas. It has long been recognized that wildlife-crossing structures should be situated along existing movement corridors or migration routes to increase the effectiveness of the structure (Singer and Doherty 1985, Bissonette and Adair 2008). New methods to identify migration routes and prioritize sites for crossing structures are quickly emerging (e.g., Sawyer et al. 2009, Lewis et al. 2011) and will improve the ability of transportation planners to ensure underpasses are located within existing movement corridors. Collecting migratory data prior to designing a mitigation project can improve the effectiveness of underpasses by ensuring they are sited correctly, and potentially reduce costs by determining the minimum number of underpasses needed. For example, Bissonette and Adair (2008) recommend underpasses be spaced every 1.6 km in areas with high DVCs. The average spacing in Nugget Canyon was 2.7 km, and it is possible that our mitigation project would have been equally successful with even fewer underpasses, provided we had spatially explicit migration data to refine planning and determine the number and location of underpasses.

The benefits of reduced DVCs and migratory connectivity across U.S. Highway 30 were not limited to mule deer. We documented a variety of other ungulates, carnivores, and small mammals that moved through the underpasses. Of particular interest was use by pronghorn, moose, and elk. Use of concrete-box underpasses by all 3 species is considered relatively rare (Forman et al. 2003), but our results suggest these types of underpasses may benefit them as well as mule deer.

Given the ability of underpasses in Nugget Canyon to reduce DVCs and maintain permeability to thousands of animals across U.S. Highway 30, it may be of interest to

consider the economic and logistical challenges for a construction project of this type. The 6 new underpasses and 10 km of fencing constructed in 2008 cost approximately US\$ 4.1 million, with \$2.8 million used for underpasses and \$1.3 million for fencing. Four million dollars is a sizable amount, but when we consider that each DVC has an estimated cost of US\$ 8,388 (Huijser et al. 2008) and the underpasses effectively eliminate 95 DVCs/year, the savings per year is \$796,860. Thus, the 4.1 million could be realized in approximately 5 years. Of additional concern are construction time and traffic delays. Construction of the 6 underpasses in 2008 began in May and was completed in September, outside of the migratory time period. Two underpasses were constructed at a time, such that traffic lights could be placed at each end and a pilot car directed traffic through a 1-lane dirt detour on the side of the road. Each set of 2 underpasses took approximately 50 days to complete. In short, it is possible to complete underpass projects such as Nugget Canyon in one construction season with minimal traffic delays.

MANAGEMENT IMPLICATIONS

Ideally, mitigation measures aimed at reducing WVCs should also maintain habitat connectivity by encouraging animals to travel underneath or over the roadway via crossing structures. Installation of underpasses and continuous fencing can effectively reduce DVCs and maintain habitat connectivity for migratory mule deer populations that number in the thousands. However, careful maintenance of fence infrastructure (e.g., gates and cattle guards) is needed to ensure that animals stay off the roadway, especially during periods of peak animal movements. Similar to elk (Gagnon et al. 2011), mule deer may take up to 3 years to habituate to underpasses and move through them with no hesitation. For migratory ungulates, underpasses should be located as close to existing migration routes as possible. Collection of migratory data prior to project design can help ensure that the correct number of underpasses is constructed and that they are placed in the best location. Although some ungulates are believed to prefer overpasses (Forman et al. 2003), our results suggest that underpasses may be a viable option for moving a variety of ungulates, including mule deer, elk, moose, and pronghorn, underneath 2-lane highways.

ACKNOWLEDGMENTS

We thank R. Bingham, J. Eddins, T. Carpenter, J. Hoffman, N. Hymas, M. Zornes, S. Lockwood, and B. Rudd for administrative and logistical support. This study was funded by the Wyoming Department of Transportation. Comments from 2 anonymous reviewers improved the manuscript.

LITERATURE CITED

- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Berger, J., S. L. Cain, and K. M. Berger. 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters* 22:528–531.

- Bissonette, J. A., and W. Adair. 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation* 141:482–488.
- Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. *Journal of Wildlife Management* 56:246–253.
- Clevenger, A. P., B. Chruszcz, and K. E. Gunson. 2001. Highway mitigation fencing reduces wildlife–vehicle collisions. *Wildlife Society Bulletin* 29:646–653.
- Clevenger, A. P., and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology* 14:47–56.
- Clevenger, A. P., and N. Waltho. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation* 121:453–464.
- Dodd, N. L., and J. W. Gagnon. 2011. Influence of underpasses and traffic on white-tailed deer highway permeability. *Wildlife Society Bulletin* 35:270–281.
- Dodd, N. L., J. W. Gagnon, A. L. Manzo, and R. E. Schweinsburg. 2007. Video surveillance to assess highway underpasses by elk in Arizona. *Journal of Wildlife Management* 71:637–645.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology & Systematics* 29:207–231.
- Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. *Road ecology—science and solutions*. Island Press, Washington, D.C., USA.
- Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. *Wildlife Society Bulletin* 23:95–100.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? *The American Naturalist* 131:781–798.
- Gagnon, J. W., N. L. Dodd, K. S. Ogren, and R. E. Schweinsburg. 2011. Factors associated with use of wildlife underpasses and importance of long-term monitoring. *Journal of Wildlife Management* 75:1477–1487.
- Gagnon, J. W., T. C. Theimer, N. L. Dodd, S. Boe, and R. E. Schweinsburg. 2007a. Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management* 71:2318–2323.
- Gagnon, J. W., T. C. Theimer, N. L. Dodd, A. L. Manzo, and R. E. Schweinsburg. 2007b. Effects of traffic use on elk use of wildlife underpasses in Arizona. *Journal of Wildlife Management* 71:2324–2328.
- Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. *Journal of Wildlife Management* 51:634–643.
- Gordon, K. M., and S. H. Anderson. 2003. Mule deer use of underpasses in western and southeastern Wyoming. Pages 309–318 in C. L. Irwin, P. Garrett, and K. P. McDermott, editors. *Proceedings of the International Conference on Ecology and Transportation*. Center for Transportation and the Environment, North Carolina State University, Raleigh, USA.
- Gordon, K. M., M. C. McKinstry, and S. H. Anderson. 2004. Motorist response to a deer-sensing warning system. *Wildlife Society Bulletin* 32:565–573.
- Huijser, M. P., P. McGowen, J. Fuller, A. Hardy, A. Kociolek, A. P. Clevenger, D. Smith, and R. Ament. 2008. *Wildlife–vehicle collision reduction study*. Report to Congress. Federal Highway Administration, Washington, D.C., Virginia, USA.
- Kleist, A. M., R. A. Lancia, and P. D. Doerr. 2007. Using video surveillance to estimate wildlife use of a highway underpass. *Journal of Wildlife Management* 71:2792–2800.
- Langbein, J., R. J. Putman, and B. Pokorny. 2011. Road traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. Pages 215–250 in R. J. Putman, M. Apollonio, and R. Andersen, editors. *Ungulate management in Europe: problems and practices*. Cambridge University Press, Cambridge, England, U.K.
- Lewis, J. S., J. L. Rachlow, J. S. Horne, E. O. Garton, W. L. Wakkinen, J. Hayden, and P. Zager. 2011. Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. *Landscape and Urban Planning* 101:99–107.
- McCollister, M. F., and F. T. Van Manen. 2010. Effectiveness of wildlife underpasses and fencing to reduce wildlife–vehicle collisions. *Journal of Wildlife Management* 74:1722–1731.
- Ng, S. J., J. W. Dole, R. M. Sauvajot, S. P. D. Riley, and T. J. Valone. 2004. Use of highway undercrossings by wildlife in southern California. *Biological Conservation* 115:499–507.
- Plumb, R. E., K. M. Gordon, and S. H. Anderson. 2003. Pronghorn use of a wildlife underpass. *Wildlife Society Bulletin* 31:1244–1245.
- Putman, R. J. 1997. Deer and road traffic accidents: options for management. *Journal of Environmental Management* 51:43–57.
- Reeve, A. F., and S. H. Anderson. 1993. Ineffectiveness of Swareflex reflectors at reducing deer–vehicle collisions. *Wildlife Society Bulletin* 21:127–132.
- Romin, L. A., and J. A. Bissonette. 1996. Deer–vehicle collisions: status of state monitoring activities and mitigation efforts. *Wildlife Society Bulletin* 24:276–283.
- Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. *Journal of Animal Ecology* 80:1078–1087.
- Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* 19:2016–2025.
- Sawyer, H., and C. LeBeau. 2011. Evaluation of mule deer crossing structures in Nugget Canyon, Wyoming. Wyoming Department of Transportation FHWA-WY-11/02F, Cheyenne, USA.
- Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.
- Singer, F. J., and J. L. Doherty. 1985. Managing mountain goats at a highway crossing. *Wildlife Society Bulletin* 13:469–477.
- Thomas, T., and L. R. Irby. 1990. Habitat use and movement patterns by migrating mule deer in southeastern Idaho. *Northwest Science* 64:19–27.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- Xia, L., Q. Yang, Z. Li, Y. Wu, and Z. Feng. 2007. The effect of the Qinghai–Tibet railway on the migration of Tibetan antelope *Pantholops hodgsonii* in Hoh-xil National Nature Reserve, China. *Oryx* 41:352–357.

Associate Editor: Ruckstuhl.