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Research Article

Overpasses and Underpasses: Effectiveness of Crossing Structures for Migratory Ungulates

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ABSTRACT Maintenance of movement corridors is a fundamental component of the conservation of biological diversity, and is especially critical for terrestrial species that migrate extended distances. Highways and interstate freeways fragment corridors and often result in increased mortality of terrestrial migrants from collisions with vehicles. Wildlife crossing structures are an important tool in multiple ecosystems to allow safe passage for wildlife across roadways. Indeed, crossing structures have been used extensively in Europe and with increasing frequency in North America to reconnect fragmented habitats for numerous species. Few projects, however, have documented responses to >1 structure type simultaneously that are close to one another. We used mule deer (*Odocoileus hemionus*), a widespread species across diverse bioregions in western North America, to test hypotheses about efficacy of 2 different types of crossing structures for ungulates. We documented behavioral responses and use of overpasses and underpasses by mule deer. Our metrics to evaluate success included passage rates and the number of animals that crossed each structure. Crossing structures were used by mule deer immediately following construction and although all of the crossing structures were used, we observed greater passage rates at overpasses than underpasses. Wildlife crossing structures reduced habitat fragmentation and enhanced connectivity by allowing safe passage across US 93. More importantly, those structures succeeded in removing a large number of mule deer from the roadway making US 93 safer for wildlife and motorists. © 2016 The Wildlife Society.

KEY WORDS crossing structure, migration, mortality, mule deer, *Odocoileus hemionus*, overpass, passage rate, underpass.

Long-distance migration has been described as one of the most stunning biological phenomena, yet many of the massive overland treks by large mammals have been lost from Africa, Asia, and North America (Berger 2004). Indeed, one of the fundamental challenges to conservation is how best to devise strategies that retain long-distance migration as part of a rich biological heritage (Berger 2004). Migratory species, including ungulates, show high fidelity to migration routes (Alerstam et al. 2003, Berger et al. 2006, Sawyer et al. 2009, Bischof et al. 2012). When barriers or obstacles intersect migratory pathways, animal movements are impeded and migratory pathways may disappear or require detours to circumvent obstacles (Alerstam et al. 2003, Berger 2004, Seidler et al. 2015). Those changes in movement patterns may result in increased expenditure of energy and potentially lower survival (Alerstam et al. 2003, Berger 2004, Seidler et al. 2015).

Roads are a leading cause of habitat fragmentation, loss of migratory corridors, and loss of connectivity among populations in many ecosystems around the world (Beckmann and Hilty 2010). Changes in landscape composition and configuration often have negative effects on ecological processes, species survival, and human safety when wildlife are forced to cross roads (Forman et al. 2003, Clevenger 2005, Dingle and Drake 2007, Corlatti et al. 2008). Indeed, roads span over 6.4 million km, >1% of the land cover, in the United States (Beckmann et al. 2010). As road networks expand and traffic volumes increase with increasing human populations, loss of migratory corridors, declines in landscape connectivity, and increased risk of wildlife-vehicle collisions are likely to continue to rise (Groot Bruinderink and Hazebroek 1996, Hawbaker et al. 2006, Neumann et al. 2012).

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Collisions with vehicles are one of the major causes of mortality for many species of wildlife in human-dominated landscapes (Forman et al. 2003). The probability of vehicle collisions with wildlife is dependent on patterns of animal movement, physical features of landscapes, traffic volume, and placement of roads (Dussault et al. 2007, Lewis et al. 2011, Neumann et al. 2012). Nearly all species of wildlife are susceptible to vehicle collisions, but collisions with ungulates may result in human injuries and property damage in addition to mortality to the animal. Annually, thousands of ungulates are killed, and hundreds of humans are injured or killed by vehicle collisions in areas where large-bodied mammals cross roads (Groot Bruinderink and Hazebroek 1996, Huijser et al. 2009, Williams and Wells 2005). Moreover, the likelihood of collisions with ungulates during migratory events is elevated at spatially and temporally specific intervals because large numbers of animals cross roads where they intersect migratory pathways and do so in a relatively short time (e.g., during migration).

Maintaining or re-establishing movement corridors, through use of crossing structures and other methods, have become a fundamental component of wildlife conservation (Corlatti et al. 2008). With anticipated growth of the human population and ongoing investment in highways, there is an increasing effort to exclude wildlife from roadways while maintaining landscape connectivity, especially with respect to migratory populations (Forman et al. 2003, Bissonette and Adair 2007). Previous studies have reported that installation of crossing structures, and exclusionary fencing to funnel wildlife to those structures, decreased wildlife-vehicle collisions up to 80% (Clevenger et al. 2001, Bissonette and Rosa 2012, Sawyer et al. 2012). Consequently, conservation biologists and transportation agencies have begun to incorporate crossing structures into road upgrades to reduce the risk of wildlife-vehicle collisions and to restore connectivity among habitats and movement corridors for animals (Clevenger and Waltho 2005, Jaarsma et al. 2007, Huijser et al. 2009, Sawaya et al. 2014).

We evaluated the use of crossing structures by mule deer (*Odocoileus hemionus*) during migratory periods at 2 sites, which included both overpasses and underpasses. Mule deer in eastern Nevada migrate >100 km between seasonal ranges and in doing so cross several major roadways (Wasley 2004, Blum et al. 2015). Our objective was to document the use of overpasses versus underpasses, when both types of structures were simultaneously available to the same migratory population of mule deer. We hypothesized that there would be no difference in numbers of animals crossing each structure type. Further, because numbers of animals crossing each site and structure varied, we also examined passage rates, the proportion of approaches that resulted in successful crossings, at both types of structures.

STUDY AREA

Our study area incorporated 2 sites located along US 93 in northeastern Nevada, USA, between the cities of Wells (41° 07′ N, 114° 58′ W) and Contact (41° 46′ N, 114° 45′ W). Those sites are located in areas where high numbers of deer-vehicle collisions had been documented by Nevada Department of Transportation (NDOT), and were verified by movement data from the Nevada Department of Wildlife (NDOW). Daily traffic volumes on US 93 from 2005 through 2014 ranged between 2,100 and 2,400 vehicles/day (NDOT 2014). Crossing structures were constructed where radio-collar data indicated many deer crossed US 93 during migration (T. Wasley, Nevada Department of Wildlife, personal observation). The first site was located at 10-Mile Summit (41° 21′ N, 114° 85′ W), about 16 km north of Wells at an elevation of 1,830 m. This site was completed in its entirety by August 2010 and consists of 1 overpass and 2 underpasses; and each structure was separated by about 2 km (Fig. 1). The second site was located at HD Summit (41.35° N, 114.81′), approximately 32 km north of Wells at an elevation of 1,920 m. This site consisted of 1 underpass and 1 overpass, separated by about 1.5 km (Fig. 1). The underpass at HD Summit was completed in August 2010, but the overpass was not completed until August 2011, a full year later.

Both overpasses were made of concrete arches that crossed over 2 lanes of US 93 (U.S. Department of Transportation 2011). Each overpass was covered with native soil, graded to match the natural elevation at the boundaries of the public right-of-way, and seeded with native vegetation. The overpass at 10 Mile Summit was 48.8 m wide by 20.1 m long, lower in elevation than most of the surrounding hills, and relatively flat on top of the structure. This structure allowed approaching wildlife a view of the 10 Mile Summit overpass and the land on the opposite side of the highway. The overpass at HD Summit is 30.5 m wide by 8.3 m long, and was located at the peak of the summit (i.e., higher in elevation than most of the surrounding hills). That location required steeper slopes over the crossing structure and did not allow for full view of the overpass or of the land on the opposite side of the highway until an animal reached the middle of the structure.

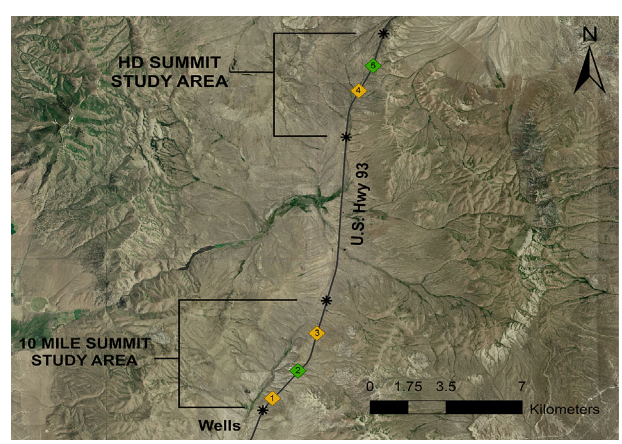

Figure 1. Study area used to examine crossings at wildlife crossing structures by mule deer. We studied crossing structures (diamonds) at 10-Mile and HD Summits on US 93 between Wells and Contact, Nevada, USA, 2010–2014; we examined overpasses (green) and underpasses (yellow). Distance between structures at 10-Mile Summit is about 2 km, and between structures at HD Summit is about 1.5 km. Each crossing is uniquely numbered and corresponds with Tables 1 and 2.

Many types of underpasses have been used by transportation agencies, including those described as cylinders, concrete boxes, or bridge-type structures (Forman et al. 2003, Clevenger and Waltho 2005). The 3 underpasses in our study were the cylinder type, which are large cylindrical openings made from corrugated metal that pass below the roadway (Fig. 2). Each underpass was 8 m wide by 28 m long, and 6 m tall, and were located in natural drainages. At HD Summit, there also was a natural spring located near the entrance of the underpass. After installation, native soil was placed in the base of each metal cylinder and graded to match the natural elevations at the boundaries of the public right-of-ways to create natural pathways. All underpasses had a minimum $6\,m \times 4\,m$ clearance after all grading was completed (Fig. 2).

Exclusionary fencing was included to funnel wildlife to the entrance of each structure and to exclude animals from the roadway (Dodd and Gagnon 2010, Sawyer et al. 2012, Fairbank 2013, Sawyer et al. 2013). The fencing was 2.4 m tall and made of 12.5-gauge woven wire animal fencing. Escape ramps (i.e., jump-outs) were incorporated into the fencing, 6 at each study site, to allow individuals trapped within the fencing to jump out and away from the roadway (Sawyer et al. 2012). Fencing spanned the entire length of each study site between the structures to prevent wildlife from entering the roadway. At 10 Mile Summit, fencing spanned about 6.4 km, from 0.8 km south of the southern underpass to 1.6 km north of the northern underpass (Fig. 1). At HD Summit, the fencing spanned about 4.8 km and began 1.6 km south of the underpass and ended approximately 1.6 km north of the overpass.

Figure 2. Examples of wildlife crossing structures: overpass (top), and underpass (bottom). We investigated structure use by migratory mule deer at 10-Mile and HD Summits on US 93 between Wells and Contact, Nevada, USA, 2010–2014. Each underpass was 8 m wide by 28 m long, and 6 m tall; the vehicle in the underpass is a 1999 Toyota Tacoma to provide a visual indicator of size of the structure.

METHODS

Field Methods

The mule deer population we studied migrates between the Jarbidge Range and the Pequop Range, a distance of about 194 km. Mule deer move across US 93 from west to east during autumn migration (Oct–Nov) and from east to west during spring migration, which is a somewhat longer duration of crossings than autumn migration (Mar–May), and is partially dependent on timing of vegetation greenup (Bischof et al. 2012) but generally occurs between March and May. In addition, we maintained cameras throughout the first summer to estimate the crossings by resident deer, but we observed only 34 deer from 30 pictures using the structures outside of migrations. Thus, most mule deer that we observed using structures during migratory periods were migratory rather than residents.

We began data collection during the first migration that the structures were fully completed and available for use in September 2010 and continued through May 2014. At all structures at 10-Mile Summit and the underpass at HD Summit, we collected data during 8 migrations (autumn 2010 through spring 2014). The overpass and fencing at HD Summit were completed in August 2011; therefore, data collection at the HD overpass began 1 year later than at 10-Mile Summit and spanned 6 migrations (autumn 2011 through spring 2014). We monitored the structures for 10 weeks during each migration; observations for autumn migrations ranged from 15 September through 1 December, and for spring migrations ranged from 1 March through 15 May.

We used Reconyx PC800 HyperFire Semi-Covert IR Professional Cameras (Reconyx, Holmen, WI, USA; hereafter cameras) with infrared technology to document behavioral responses and use of each crossing structure by mule deer. Cameras were designed to trigger only when both motion and a change in temperature gradient were detected. This design helped to reduce the likelihood of false positives resulting from wind driven movement of vegetation, although false positives may occasionally occur (Reconyx 2013). We synchronized all cameras at the beginning of each migratory period. Cameras were set to rapidfire to capture quick movements and to prevent loss of movements between pictures. Pictures were collected in sets of 10 with no delay period to allow for continuous coverage. Thus, a series of photographs could be as short as 10 or >100 when individuals or large groups were in the camera range for extended periods of time. Those settings allowed for pictures to be taken in rapid succession without interruption, and when observed in order, are similar to viewing a video frame by frame (Fig. 3).

Manufacturer recommendations indicate the cameras were effective up to 15 m (Reconyx 2013). Nevertheless, we

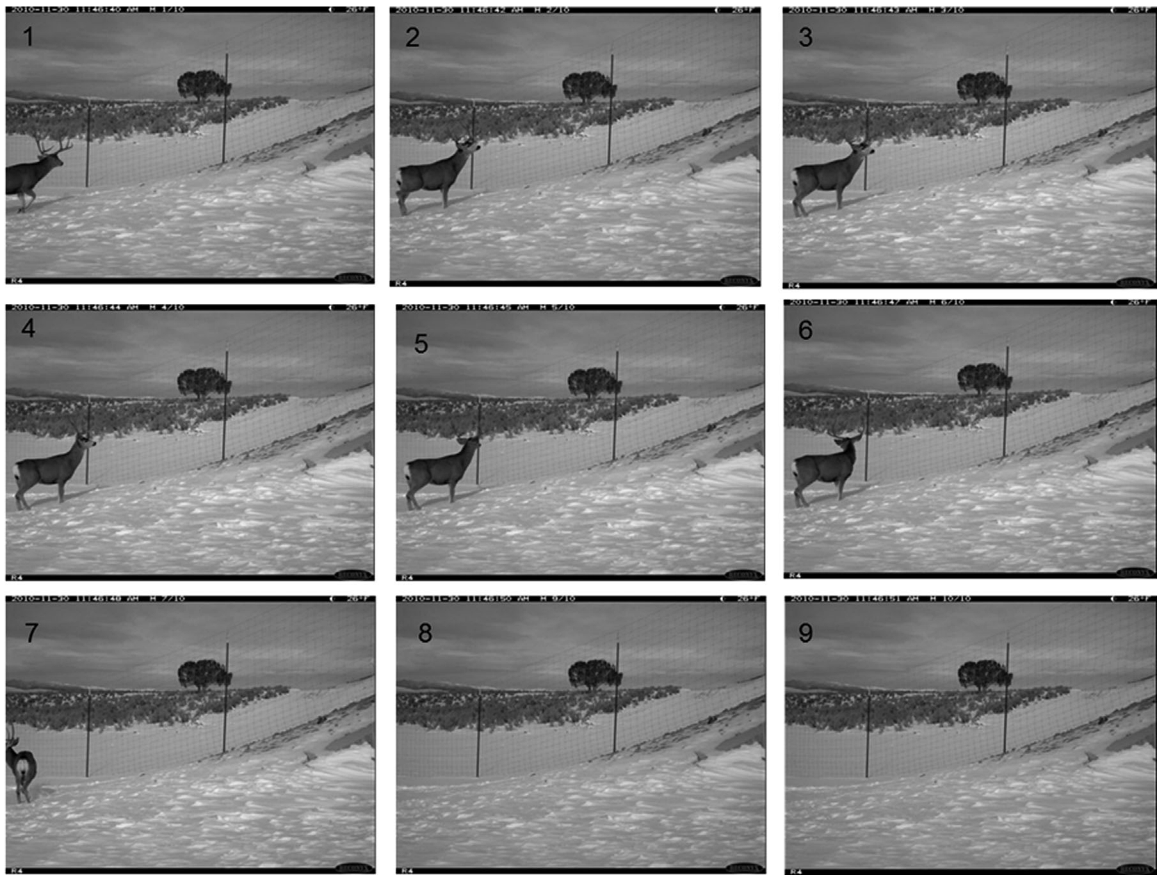

Figure 3. Series of photos indicating an unsuccessful crossing (retraction) at a wildlife crossing structure by a male mule deer at a10-Mile Summit underpass on US 93 between Wells and Contact, Nevada, USA, 2010–2014.

staggered cameras at intervals of 12 m to maximize clarity and consistency of photographs taken at night when infrared technology was required (Fig. S1, available online in Supporting Information). We placed cameras at the side of the wildlife crossing structures and fence ends to capture the approach of mule deer, and placement was dependent on the direction of seasonal movements. Cameras operated 24 hours a day and we did not document any camera failures during data collection (Simpson 2012). We grouped photographs in 5-minute increments, and carefully evaluated series of photos taken by multiple cameras to avoid double-counting individuals. All aspects of this research were approved by the Institutional Animal Care and Use Committee (Protocol #: 0500) at the University of Nevada Reno, and were in keeping with protocols adopted by the American Society of Mammalogists for field research involving mammals (Sikes et al. 2011). The property in which our research was conducted was owned by NDOT. Nevada Department of Wildlife and NDOT were collaborators on the project and no additional permissions or permits were required.

Statistical Analyses

We documented mule deer behaviors as approaches, retractions, and successful crossings. We defined approaches as the numbers of individuals that entered the frame of the camera. Retractions were the number of individuals that turned around and returned in the direction from which they originated. Finally, we defined a successful crossing as the number of individuals that moved through the picture frames (i.e., further into the structure), and did not return in the direction from which they originated. Because we staggered cameras at the entrances of each structure to achieve full coverage, and reviewed pictures in 5-minute increments, we are confident that animals did not return in the direction from where they originated but successfully crossed the structure. Because deer that crossed in the opposite direction of the migration already may have crossed the structures, we excluded crossings in the opposite direction of that migratory period for all statistical analyses. Because few individuals inhabit the study area throughout the entire year, we assumed that most movements were in the direction of the migration. After we reviewed all pictures, we calculated the passage rate for each structure by dividing the number of successful crossings by the number of approaches to each structure for each individual structure, season, and year (Gagnon et al. 2011).

We used a model selection procedure incorporating generalized linear models with a maximum likelihood approach with dependent variables of number of deer that crossed a structure and passage rates in R 3.1.1 (R Development Core Team 2014). We used a categorical variable defined as subsequent migration to determine if use of a structure changed with familiarity, such that a number from 1–8 indicated the time that the structure was used (e.g., 1 = first migration that structure was used, 2 = sec migration that structure was used, through 8 migrations). Using this categorical variable, we could account for the overpass at HD Summit becoming available later than the other structures and identified it as novel the first time the structure was encountered by mule deer. We investigated the influence of the following predictor variables on our models: site (10-mile or HD Summit), year, season, structure type (overpass or underpass), subsequent migration, structure × site interaction, or year × structure interaction (R Development Core Team 2014). We tested all combinations of models using the MuMIn package in R 3.1.1 (R Development Core Team 2014). We used an information-theoretic approach for model selection, using Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, and Akaike weight (ω_i; Burnham and Anderson 2010). We chose the most parsimonious model by reviewing competitive models within 0–2 ΔAIC_c values of the top model for uninformative parameters; such models only differ by a small amount because of the addition of a single parameter and often the additional parameter has confidence intervals that overlap 0 (Arnold 2010, McKee et al. 2015). Following selection of the most parsimonious model, we examined pairwise comparisons of means for numbers of deer crossing the structures and passage rates between each site and structure (Zar 2010).

RESULTS

We accrued about 1,000,000 photos between 8 migrations and 16 cameras located at the crossing structures and ends of the exclusionary fencing. Approximately 30% of the photos contained no wildlife, 20% contained various species of wildlife, and 50% contained mule deer. We documented 35,369 mule deer that successfully crossed over or through ≥1 of the crossing structures during 8 migratory periods (Table 1). We documented 3 elk (*Cervus canadensis*) approaching the underpasses on US 93, but we documented only 1 successful crossing. Conversely, 3 elk approached and crossed an overpass. Other mammal species that we observed in photos using the crossing structures included American badger (*Taxidea taxus*), American pronghorn (*Antilocapra americana*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), blacktailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), red fox (*Vulpes vulpes*), and domestic cattle, horses, dogs, and cats.

During autumn migrations, most mule deer crossed the structures between 15 October and 15 November, although migratory mule deer crossed from 1 October through 30 November. During spring migrations, however, the duration of migratory movement was longer than that of autumn migration and occurred between 1 March and 31 May (Fig. 4). We recorded 30,259 mule deer that used the crossing structures at 10 Mile Summit and 5,110 mule deer used the crossing structures at HD Summit (Table 1). Thus, when both sites were available for use, 85.6% of the mule deer documented used a structure at 10 Mile Summit and 14.4% crossed at HD Summit (Table 1). We observed a high passage rate (>0.94) at the overpasses the first migration they were open for use, and their passage rate remained high (≥0.89) throughout the duration of the study (Table 1). Passage rates for mule deer at the underpasses were low the first year and increased with each subsequent migration to about 0.60, although the passage rate remained lower than that of the overpasses (Table 1).

Our most parsimonious model ($\omega_i = 0.288$) for number of crossings by mule deer included site, structure type, and a site × structure interaction (Table 2). Two other models were within 2 AIC_c of the top model, but those other models contained uninformative parameters because additional variables had confidence intervals that overlapped 0 and did not appreciably improve the models (Table 2). Overall, most mule deer crossed the overpass at 10-Mile Summit, which differed from all of the other structures and locations in number of crossings (Fig. 5). We observed an effect of site ($\beta = -2{,}757.3$, 95% CI = −3,036.3 to −2,478.3), structure ($\beta = -2{,}980.0$, 95% CI = −3,203.7 to −2,756.3), and an interaction between study site and structure ($\beta = 2{,}823.0$, 95% CI = 2,465.4–3,180.6); we observed greater numbers of

Table 1. Number of approaches (AP), successful crossings (C), and passage rates (PR) for wildlife crossing structures during migratory periods by mule deer on US 93 between Wells and Contact, Nevada, USA, 2010–2014. We calculated passage rates by dividing the successful crossings by approaches for each migration and structure.

		10 Mile Summit									HD Summit[a]					
		Underpass[b] (1)			Overpass (2)			Underpass (3)			Underpass (4)			Overpass (5)		
Year	Season	AP	C	PR	AP	C	PR	AP	C	PR	AP	C	PR	AP	C	PR
2010	Autumn	431	148	0.34	2,967	2,853	0.96	1,227	330	0.27	790	179	0.23			
2011	Spring	387	215	0.56	2,760	2,716	0.98	955	476	0.50	64	44	0.68			
2011	Autumn	181	116	0.64	3,228	3,043	0.94	513	253	0.49	921	418	0.45	505	477	0.94
2012	Spring	229	78	0.34	3,447	3,242	0.94	1,021	403	0.39	525	320	0.61	243	234	0.96
2012	Autumn	152	116	0.76	4,193	4,007	0.96	364	287	0.79	741	629	0.85	654	625	0.96
2013	Spring	329	207	0.63	3,465	3,440	0.99	682	348	0.51	266	185	0.70	321	318	0.99
2013	Autumn	149	96	0.64	3,880	3,767	0.97	314	215	0.68	644	425	0.66	748	682	0.91
2014	Spring	118	76	0.64	2,953	2632	0.89	506	356	0.70	216	185	0.86	416	395	0.95

[a] The overpass at HD Summit was completed during the summer of 2011.
[b] Each crossing structure has a unique identifier (structure no.) that is consistent with Figure 1.

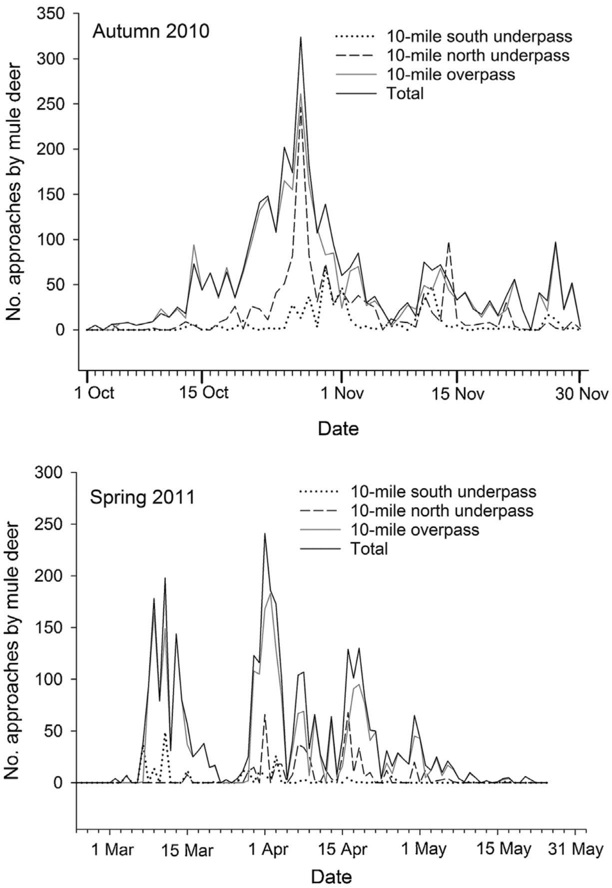

Figure 4. Documented number of approaches of mule deer by date during autumn 2010 migration (top) and spring 2011 migration (bottom) at wildlife crossing structures on US 93 between Wells and Contact, Nevada, USA.

deer crossing the overpass at 10 Mile Summit compared with underpasses, but no statistical difference in crossings between the structures at HD Summit (Fig. 5). Our top model for passage rate by mule deer included only year and structure type (Table 3). We observed an effect of year ($\beta = 0.0573$, 95% CI $= 0.0245$–0.0902) in which passage rates increased through the duration of the study with habituation to the structures. In addition, we observed a higher passage rate ($\beta = -0.0361$, 95% CI $= -0.4425$ to -0.02789) by mule deer at the overpasses (0.95 ± 0.036, mean $\pm$ SE) compared with the underpasses (0.60 ± 0.036) irrespective of location.

DISCUSSION

All of the crossing structures effectively enhanced connectivity of migratory corridors that were bisected by US 93. In general, the overpass at 10-mile Summit was the most successfully crossed in terms of numbers of deer than any of the other structures that we observed. Although we observed no difference in numbers of individuals crossing underpasses and overpasses at HD Summit, the underpass at HD Summit was available to mule deer 1 full year prior to completion of the overpass. Thus, mule deer that traveled through HD Summit when both structures were available likely had some familiarity with the underpass, which may explain the lack of difference in numbers of animals crossing the 2 types of structures at that site. Nevertheless, our hypothesis that passage rates were greater at overpasses irrespective of location was supported. Most mule deer that approached an overpass continued over the structure, versus the greater proportion of individuals that hesitated and retreated from the underpasses.

We observed some differences among study sites including the proximity of resources, distribution of movements, surrounding topography, visibility of the structures, or width and steepness of the structures. The overpass at 10-Mile Summit is located along a flat stretch of highway and allowed mule deer approaching the overpass to view the structure and terrain on the opposite side of the highway, creating a relatively flat bridge above the roadway. The overpass at HD Summit is located at the peak of a summit and has a steep grade, which does not allow for full view of the structure or of the terrain on the opposite side of the highway until an animal reaches the middle of the structure. In addition, the overpass at 10-Mile Summit was wider and shorter than the overpass at HD Summit, which also may have contributed to higher numbers of individuals crossing that structure. Van Wieren and Worm (2001) reported that width of overpasses was an important factor in use by large ungulates, and they observed that wider structures were more successful. Finally, there was a natural spring located near the entrance of the underpass at HD Summit. This resource may attract deer to this structure and may confound our results because there are no water sources near the underpasses at the study site at 10-Mile Summit.

Ungulates have been reported to habituate to use of underpasses after about 3 years (Forman et al. 2003, Clevenger 2005, Clevenger and Waltho 2005, McCollister

Table 2. Results of a model-selection procedure evaluating number of crossings for wildlife crossing structures during migratory periods by mule deer on US 93 between Wells and Contact, Nevada, USA, 2010–2014. The most parsimonious model is indicated with an asterisk.

Model[a]	df[b]	AIC_c[b]	ΔAIC_c[b]	ω_i[b]
Site + structure + site × structure + season	6	538.5	0.00	0.394
Site + structure + site × structure*	5	539.1	0.63	0.288
Site + structure + site × structure + year + season	7	539.5	0.99	0.241
Site + structure + site × structure + year	6	541.8	3.26	0.077
Site + structure + subsequent migration + site × structure	12	553.8	15.25	0.000

[a] Variables include season (spring or autumn migration), site (HD or 10 Mile Summit), structure (overpass or underpass), subsequent migration (migrations numbered in order of occurrence), and year (calendar year of migration). All models include intercept from regression analysis.
[b] Degrees of freedom (df), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weight (ω_i).

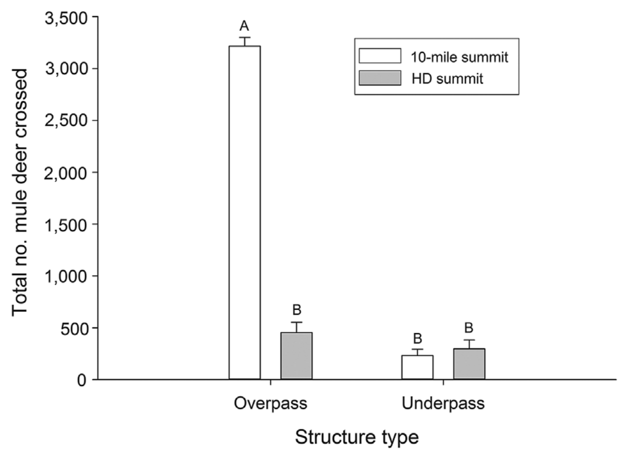

Figure 5. Least squared mean (± SE) number of mule deer that crossed each structure. We observed an interaction between study site and structure when modeling number of mule deer crossing wildlife crossing structures at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, USA, 2010–2014. Different letters indicate significant ($P < 0.001$) differences.

and Van Manen 2010), and we observed some habituation to the underpasses during our study. After 3 years of use, however, passage rates by mule deer at the underpasses remained substantially lower than that of the overpasses, which remained high from first encounter throughout duration of our study. Our data were specific to migratory ungulates and use of crossing structures is temporally specific and of lower frequency compared with resident populations that use the structures year around (Dodd et al. 2007, Gagnon et al. 2011). Migratory mule deer encounter crossing structures about twice per year during seasonal migrations, whereas resident individuals encounter those crossings regularly throughout the year. If migratory deer take longer to habituate to underpasses than resident deer, the lower passage rates of migratory mule deer in our study, even 4 years after completion of the structures, may reflect that outcome.

We evaluated one type of underpass, cylindrical structures made of corrugated metal; therefore, our results for comparing underpasses with overpasses may not be applicable to other types of underpasses. Moreover, dimensions of underpasses including openness, line-of-sight, height, and other environmental variables may affect use of those structures by ungulates, and often differ substantially between locations and types of underpasses (Dodd et al. 2007, Gagnon et al. 2011). Sawyer et al. (2012) reported high use of concrete box underpasses by mule deer, but there were no direct comparisons with overpasses. Underpasses resulting from bridge-type structures may be as effective as overpasses, because of the height, wide range of view typically observed with that type of crossing structure, and the presence of natural vegetation beneath the structure (Dodd et al. 2007; Gagnon et al. 2007, 2011). Underpasses we investigated in eastern Nevada, are substantially different than the bridge-type underpasses used in Arizona (Dodd et al. 2007, Gagnon et al. 2011), especially relative to height and openness of the structures. Heights of the structures we studied were about 6 m, whereas bridge-type underpasses are often much taller (Gagnon et al. 2011). Responses to underpasses likely vary dependent on the type of underpass constructed and the target species for the structure. For example, elk used the large bridge-type underpasses in Arizona with much higher success than we observed using the underpasses in our study (Dodd et al. 2007, Gagnon et al. 2011).

MANAGEMENT IMPLICATIONS

Mule deer in our study used all crossing structures extensively during migration and those structures effectively enhanced connectivity of migratory corridors bisected by US 93. Crossing structures helped reduce negative effects of US 93 as an obstacle to movements of migratory mule deer, and reduced vehicle-related mortalities of mule deer (Simpson 2012). Moreover, crossing structures in our study were in several locations because of multiple sites where migratory deer crossed US 93; in a large stretch of highway, provision for multiple crossing structures rather than a single structure is certainly desirable (Sawyer et al. 2012).

Although the overpasses had a higher passage rate by mule deer than the cylinder type of underpasses in our study, both types of crossing structures are important tools for restoring connectivity of landscapes, and reducing deer-vehicle collisions (Clevenger et al. 2001, Sawyer et al. 2012). Not all crossing structures are created equal, however, and managers should consider what kind of structure will provide the best outcome for the target species. The type, width, and length of underpasses constructed affect responses by wildlife (Van Wieren and Worm 2001). Moreover, the time for habituation to underpasses may vary depending on whether the target population is migratory or resident. Because

Table 3. Results of a model-selection procedure evaluating passage rates across wildlife crossing structures during migratory periods by mule deer on US 93 between Wells and Contact, Nevada, USA, 2010–2014.

Model[a]	df[b]	AIC_c[b]	ΔAIC_c[b]	ω_i[b]
Year + structure	4	−44.95	0.00	0.264
Year + structure + season	5	−43.45	1.50	0.124
Year + structure + site	5	−42.95	2.00	0.097
Year + site + structure + site × structure	6	−41.80	3.15	0.087
Year + season + site + structure	6	−41.24	3.71	0.066
Year + season + site + structure + site × structure	7	−40.09	4.86	0.037

[a] Variables include season (spring or autumn migration), site (HD or 10 Mile Summit), structure (overpass or underpass), subsequent migration (migrations numbered in order of occurrence), and year (calendar year of migration). All models include intercept from regression analysis.

[b] Degrees of freedom (df), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weight (ω_i).

migratory populations encounter the crossing structures with lower frequency than residents, we hypothesize that time to habituation to underpasses for migratory ungulates may be extended. Crossing structures in this study were effective at preserving migratory corridors, reducing fragmentation of habitats throughout human altered landscapes, and making roadways safer for wildlife and motorists.

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