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PRONGHORN AND MULE DEER USE OF UNDERPASSES AND OVERPASSES ALONG US HIGHWAY 191, WYOMING

By:

Western EcoSystems Technology, Inc.
200 South 2nd St.
Laramie, Wyoming 82070

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Author(s)
Hall Sawyer and Patrick Rodgers

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Western Ecosystems Technology, Inc.
200 South 2nd St.
Laramie, Wyoming 82070

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5300 Bishop Blvd.
Cheyenne, WY 82009-3340
WYDOT Research Center (307) 777-4182

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Abstract: The seasonal migrations of ungulates are increasingly threatened by various forms of anthropogenic disturbance, including roads, fences, and other infrastructure. While roadway impacts (i.e., wildlife-vehicle collisions and landscape permeability) of two-lane highways to mule deer (*Odocoileus hemionus*) can largely be mitigated with underpasses and continuous fencing, similar mitigation may not be effective for pronghorn (*Antilocapra americana*) or other ungulate species that are reluctant to move through confined areas. The Wyoming Department of Transportation recently installed 6 underpasses and 2 overpasses along 20 km of US Highway 191 in western Wyoming, where we evaluated species-specific preferences by documenting the number of migratory mule deer and pronghorn that used adjacent overpass and underpasses for 3 years following construction. We also measured the amount of back and forth movement across the highway for each species through time. We documented 40,251 mule deer and 19,290 pronghorn migrate across the highway. Of those, 79% of mule deer moved under, whereas 93% of pronghorn moved over the highway. These strong species-specific differences were evident at both sites and support the notion that overpasses are more amenable to pronghorn than underpasses. Concurrently, we documented a sharp increase in the amount of back and forth movement of mule deer and pronghorn across the highway during migration periods. Such movement flexibility is presumed to improve their ability to respond to changing environmental conditions by easily accessing habitats on either side of the highway. Our results highlight that species-specific preferences are an important consideration when mitigating roadway impacts with wildlife crossing structures. Overpass and underpass construction reduced wildlife-vehicle collisions by approximately 81%.

Key Words
Connectivity, highway, migration, mitigation, mule deer, overpass, permeability, pronghorn, underpass.

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SI* (MODERN METRIC) CONVERSION FACTORS

APPROXIMATE CONVERSIONS TO SI UNITS

Symbol	When You Know	Multiply By	To Find	Symbol
		LENGTH		
in	inches	25.4	millimeters	mm
ft	feet	0.305	meters	m
yd	yards	0.914	meters	m
mi	miles	1.61	kilometers	km
		AREA		
in^2	square inches	645.2	square millimeters	mm^2
ft^2	square feet	0.093	square meters	m^2
yd^2	square yard	0.836	square meters	m^2
ac	acres	0.405	hectares	ha
mi^2	square miles	2.59	square kilometers	km^2
		VOLUME		
fl oz	fluid ounces	29.57	milliliters	mL
gal	gallons	3.785	liters	L
ft^3	cubic feet	0.028	cubic meters	m^3
yd^3	cubic yards	0.765	cubic meters	m^3
		NOTE: volumes greater than 1000 L shall be shown in m^3		
		MASS		
oz	ounces	28.35	grams	g
lb	pounds	0.454	kilograms	kg
T	short tons (2000 lb)	0.907	megagrams (or "metric ton")	Mg (or "t")
		TEMPERATURE (exact degrees)		
°F	Fahrenheit	5 (F-32)/9 or (F-32)/1.8	Celsius	°C
		ILLUMINATION		
fc	foot-candles	10.76	lux	lx
fl	foot-Lamberts	3.426	candela/m^2	cd/m^2
		FORCE and PRESSURE or STRESS		
lbf	poundforce	4.45	newtons	N
lbf/in^2	poundforce per square inch	6.89	kilopascals	kPa

APPROXIMATE CONVERSIONS FROM SI UNITS

Symbol	When You Know	Multiply By	To Find	Symbol
		LENGTH		
mm	millimeters	0.039	inches	in
m	meters	3.28	feet	ft
m	meters	1.09	yards	yd
km	kilometers	0.621	miles	mi
		AREA		
mm^2	square millimeters	0.0016	square inches	in^2
m^2	square meters	10.764	square feet	ft^2
m^2	square meters	1.195	square yards	yd^2
ha	hectares	2.47	acres	ac
km^2	square kilometers	0.386	square miles	mi^2
		VOLUME		
mL	milliliters	0.034	fluid ounces	fl oz
L	liters	0.264	gallons	gal
m^3	cubic meters	35.314	cubic feet	ft^3
m^3	cubic meters	1.307	cubic yards	yd^3
		MASS		
g	grams	0.035	ounces	oz
kg	kilograms	2.202	pounds	lb
Mg (or "t")	megagrams (or "metric ton")	1.103	short tons (2000 lb)	T
		TEMPERATURE (exact degrees)		
°C	Celsius	1.8C+32	Fahrenheit	°F
		ILLUMINATION		
lx	lux	0.0929	foot-candles	fc
cd/m^2	candela/m^2	0.2919	foot-Lamberts	fl
		FORCE and PRESSURE or STRESS		
N	newtons	0.225	poundforce	lbf
kPa	kilopascals	0.145	poundforce per square inch	lbf/in^2

*SI is the symbol for the International System of Units. Appropriate rounding should be made to comply with Section 4 of ASTM E380. (Revised March 2003)

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INTRODUCTION

The management and conservation of migratory ungulates is complicated by the long distances traveled across a mix of land uses, juristictional boundaries, and anthropogenic obstacles like roads and fences (Sawyer et al. 2005). Because migratory ungulates far outnumber their non-migratory counterparts (Fryxell et al. 1988), the conservation of migratory populations has become a top priority for wildlife and land management agencies. A key component of such management is ensuring roadways are safe and permeable to migratory species (Forman et al. 2003, Clevenger and Wierzchowski 2006). Grade-level crossings may be adequate along roads with relatively low traffic volumes, especially if right-of-way fencing is absent or designed as wildlife-friendly. However, maintaining functional migration routes across roads with high traffic volumes, multiple lanes, or impermeable right-of-way fencing requires careful transportation planning that incorporates wildlife crossing structures (e.g., underpasses or overpasses) into proposed or existing infrastructure (Gagnon et al. 2007*a*, Dodd and Gagnon 2011, Sawyer et al. 2012, Clevenger et al. 2015).

Wildlife crossing structures can provide an effective means to reduce wildlife-vehicle collisions (WVC) and maintain connectivity between seasonal ranges (Romin and Bissonette 1996, Clevenger et al. 2001, McCollister and Van Manen 2010, Sawyer et al. 2012). For ungulates, crossing structures typically consist of some sort of underpass (e.g., box culvert or span bridge) and adjacent fencing to funnel animals underneath the roadway. In general, underpasses are easier to install, significantly cheaper, and require less maintance than overpasses. While underpasses have proven effective for a variety of wildlife (Foster and Humphrey 1995, Clevenger and Waltho 2000, Forman et al. 2003), they may not be conducive for moving large numbers of pronghorn or other species (e.g., Mongolian gazelle) that live in open habitats and rely on vision to detect and avoid predators. Although pronghorn have been documented using underpasses on occasion (Plumb et al. 2003, Sawyer et al. 2012), it is presumed they would move more freely over roadways via overpasses where their vision is not impaired and movement is less constrained.

Recently, the Wyoming Department of Transportation completed a project in western Wyoming where 12 miles of game fencing, 6 underpasses, and 2 overpasses were constructed to reduce WVCs and allow large herds of migratory pronghorn and mule deer to safely cross US Highway 191 – an increasingly popular two-lane highway that leads to Grand Teton and Yellowstone National Parks. Because both overpasses were located in close proximity (< 0.5 mi, 0.8 km) to an underpass, this project provided an excellent opportunity to evaluate how migratory pronghorn and mule deer utilized overpasses and underpasses when both types of structures were available to them. Our primary objective was to document the proportion of mule deer and pronghorn that moved over and under the highway during migration. Additionally we examined daily temporal trends for species-specific differences in timing of highway crossings. Of secondary interest was whether the crossing structures altered movement behavior by allowing, or encouraging, back and forth movements across US Highway 191 during migration periods. Revealing species-specific differences and understanding how migratory pronghorn and mule deer utilize both overpasses and underpasses may benefit conservation efforts aimed at restoring migrations, maintaining landscape connectivity, and reducing WVCs. Given the cost differential between underpass and overpass construction, such information can help prioritize when and where overpass construction is warranted.

STUDY AREA

Our study site was a 12-mile section of US Highway 191 located in the upper Green River Basin of western Wyoming near the town of Pinedale (Fig. 1). The two-lane highway ranges in elevation from 7,000 to 7,400 ft. (2,133 to 2,255 m) and is surrounded by sagebrush (*Artemisia tridentata*) rangelands, riparian bottomland, and several irrigated hay meadows. Every spring, thousands of mule deer and pronghorn migrate north and west across US Highway 191 to their respective summer ranges (Sawyer et al. 2005). The mule deer typically migrate 25 to 60 miles (40 to 97 km) and summer in portions of four different mountain ranges, including the Gros Ventre, Snake River, Wyoming, and Salt River Ranges (Sawyer et al. 2005). Most pronghorn migrate 10 to 40 miles (16 to 64 km) to the upper Green River and Hoback Basins, but a small segment of the population (200-300 animals) migrates 100 miles (160 km) to Grand Teton National Park (Sawyer et al. 2005, Berger et al. 2006). Each autumn, mule deer and pronghorn follow the same migration routes to return to their winter ranges near Pinedale, Wyoming. Prior to the overpass and underpass construction, thousands of animals had to cross US Highway 191 at grade-level, posing a serious driving hazard for motorists and mortality risk to wildlife. During the 5-year period preceding construction, traffic volumes averaged approximately 2,000 vehicles per day and the number of WVCs nearly 100 per year (Wyoming Department of Transportation, unpublished data).

To reduce the number of WVCs and maintain connectivity of migration routes, the Wyoming Department of Transportation installed 12 miles of game-proof fence, 2 overpasses, and 6 underpasses. Although the exact location of these structures were influenced by engineering factors, they closely corresponded with known migration routes and road segments that experienced high levels of WVCs. Half of the structures (1 overpass and 3 underpasses) were installed north of Daniel Junction, where the highway runs north and south. We referred to this area as the North Section (Fig. 1). Here, the overpass was sited on Boroff Hill, where cut-banks on both sides of the road were amenable to overpass construction. The other crossing structures were installed east of Daniel Junction, where the highway runs east and west. We referred to this area as the East Section (Fig. 1). Here, the overpass was sited at Trapper's Point – a well-known migration bottleneck that has been used for thousands of years (Sawyer et al. 2005, Berger et al. 2006). Each overpass was approximately 150-ft. (45 m) wide. An especially important design feature of the overpasses was the 4-ft. (1.2 m) dirt berms that extend the length of both sides, such that animals cannot see the highway when traveling across the overpass (Fig. 2). Although the two overpasses were constructed 7 miles apart, each had an underpass located within 0.5 miles (0.8 km). Underpasses were constructed from simple span bridges that were approximately 20 m (width) × 13 m (length) × 4 m (height). Construction was completed in September 2012, just as the autumn migration was beginning.

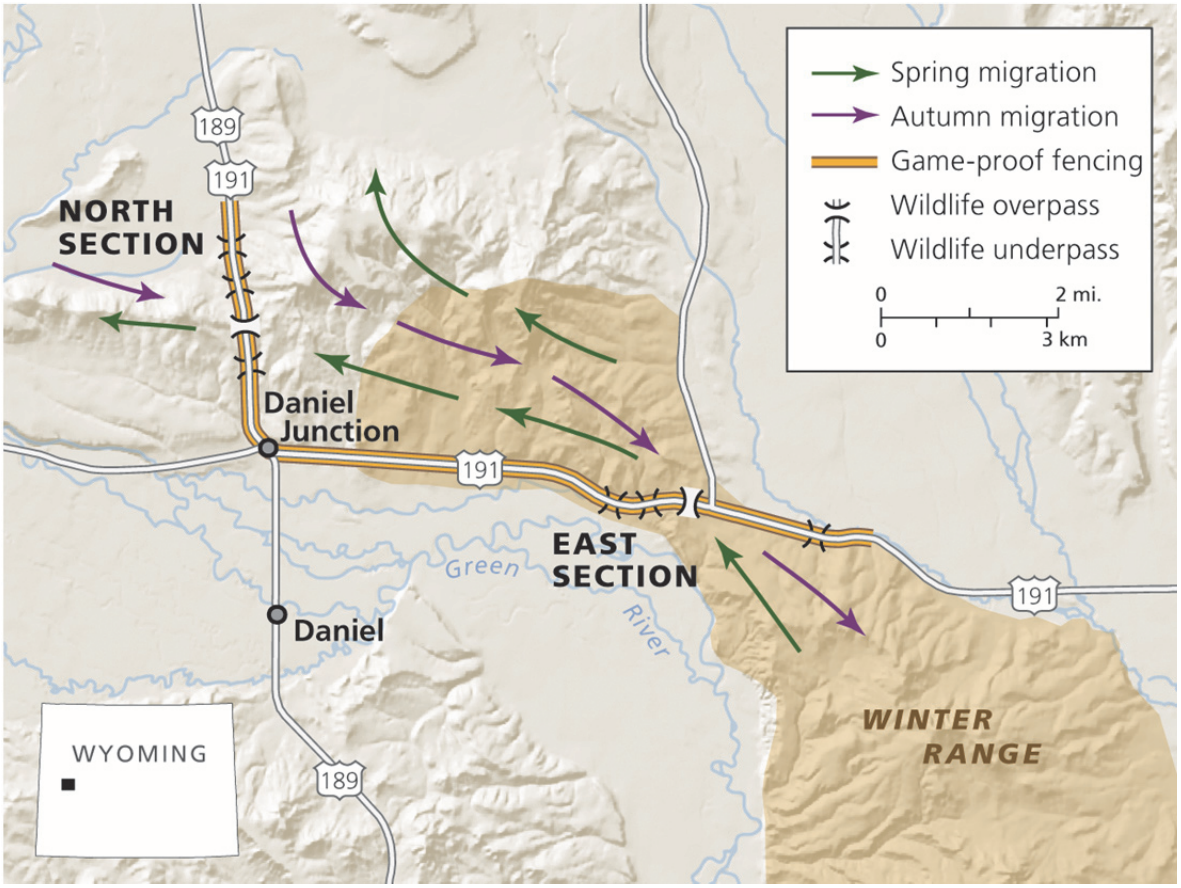

Figure 1. Approximate location of 6 underpasses and 2 overpasses constructed along US Highway 191 in western Wyoming to accommodate migratory mule deer and pronghorn. The North and East Sections each had 3 underpasses and 1 overpass. North Section includes Bridges 1-3 (north to south) and Boroff Overpass. East Section includes Bridges 4-6 (west to east) and Trapper's Point Overpass.

Figure 2. Aerial view of the Trapper's Point Overpass along US Highway 191 in western Wyoming, USA (top panel). Pronghorn crossing the overpass during fall migration 2013. Dirt berms provide visual barrier between animals and highway (bottom panel).

METHODS

We installed 2 digital infrared Reconyx® cameras on each overpass and one on each underpass (Fig 3). This camera configuration allowed us to determine the date, time, direction, and number of animals that passed over or under each crossing structure. The study period encompassed 3 years, including autumn migration (2012, 2013, and 2014), winter (2012-13, 2013-14, 2014-15), spring migration (2013, 2014, and 2015), and summer (2013 and 2014) . We defined autumn migration as 15 September through 30 November, winter as 1 December through 14 March, spring migration as 15 March through 15 May, and summer as 16 May through 14 September. We used digital photos to count the number of deer and pronghorn that used each underpass and overpass, where use was defined as animals that crossed completely over or under the highway. Each photo observation was entered into a database that recorded date, time, direction of movement, species, number of animals, and crossing structure.

We calculated the total number of animals that used each structure and plotted the proportional level of use observed at each structure by season. Because half of the crossing structures were built on the North Section of US Highway 191 and the other half along the East Section, we were also able to examine each section separately. Given the close proximity (< 0.5 mi, 0.8 km) of the overpasses and underpasses in each highway section, we assumed that animals had equal opportunity to move under or over the highway. To evaluate whether migratory mule deer or pronghorn preferred crossing the highway via underpass or overpass, and whether species-specific crossing patterns were consistent between sites, we simply calculated the proportion of each species that moved over and under the highway during migration periods. We calculated daily temporal trends by counting the number of mule deer and pronghorn that used underpasses and overpasses during each hour of the day during spring and autumn migrations.

Additionally, we examined whether the crossing structures increased the amount of back and forth movement across the highway by calculating the total number of non-directional movements (i.e., those in opposite direction of migration) that occurred each year. Here we defined years as complete migration cycles where one autumn and spring migration were included in each year, so Year 1 included migrations from autumn 2012 and spring 2013 and so on. We then used these non-directional movements as an index to the amount of back and forth movement that occurred across the highway through the first 3 years that animals used crossing structures. Lastly, we used WYDOT data (MP 101-117) to compare WVC rates of mule deer and pronghorn before (January 2005 – September 2012) and after (October 2012 – April 2015) construction of the crossing structures.

Figure 3. Cameras were installed at each crossing structure and checked approximately every 3 weeks.

RESULTS

Mule Deer

We documented 59,987 mule deer use the overpasses and underpasses between September 2012 and May 2015, including 18,033 during autumn migration, 19,130 during the winter period, 22,216 during spring migration, and 608 during the summer period (Table 1). Overall, most deer crossed at Bridge 5 (40 percent, *n*=23,699) and Bridge 3 (16 percent, *n*=9,595) (Table 1; Figs. 4-5). With the exception of Bridge 4 which was rarely used, the other crossing structures typically moved ~10 percent of the mule deer. These patterns were consistent across the 3-year study period (Fig 5). Mule deer crossings averaged 237 per day during autumn migration and 370 per day during spring migration (Table 1: Fig. 6). Surprisingly, a significant portion of mule deer crossings occurred during the winter (Table 1: Fig. 6). Peaks in deer movement corresponded with spring and autumn migrations in late-March and mid-November, respectively. Overall, more mule deer traveled under the highway (*n*=47,098; 79 percent) in both the North and East Sections of the study area (*n*=15,285 and *n*=31,813, respectively) whereas only 21 percent of mule deer crossed over the highway (*n*=12,889; Fig. 10).

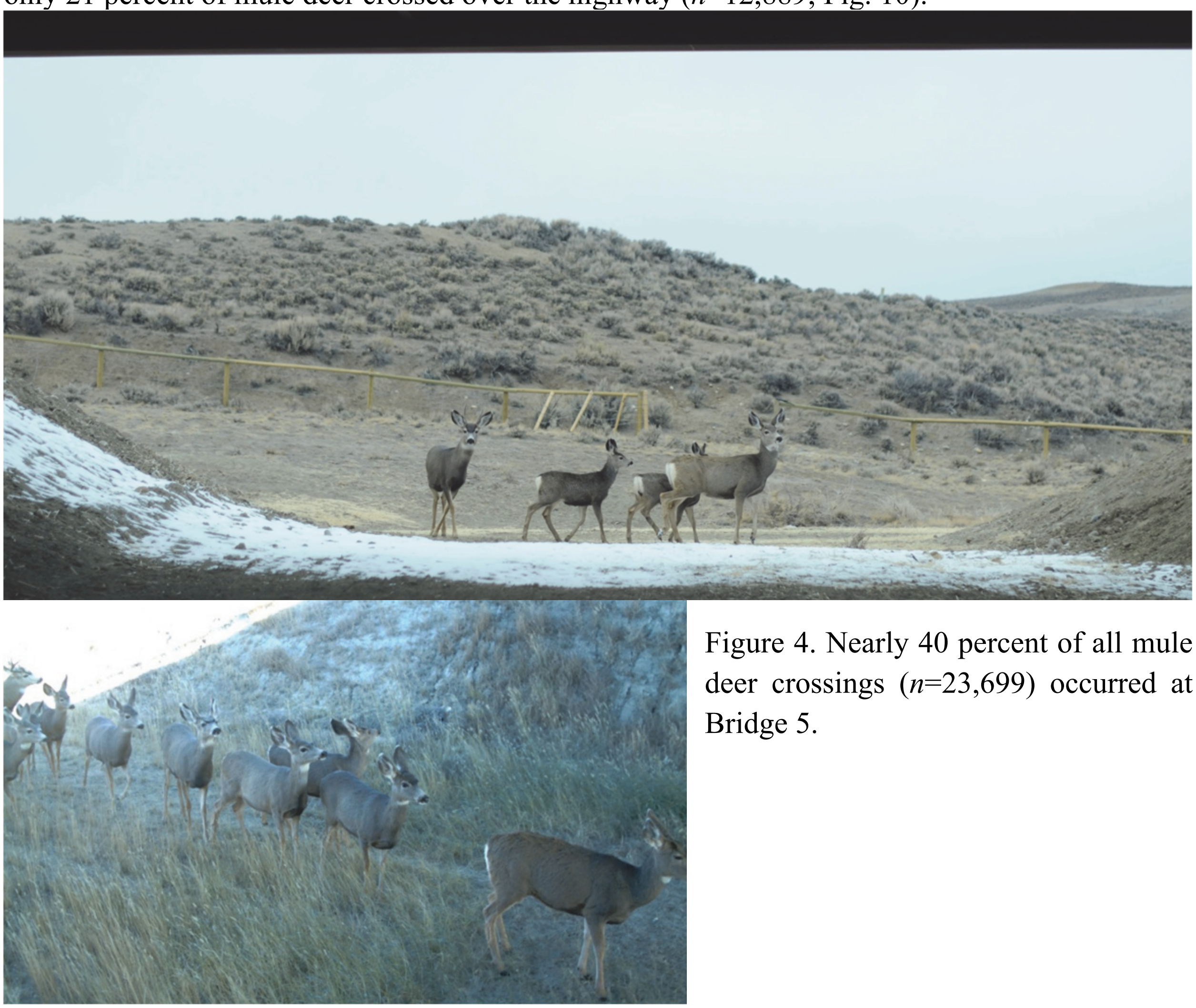

Figure 4. Nearly 40 percent of all mule deer crossings (*n*=23,699) occurred at Bridge 5.

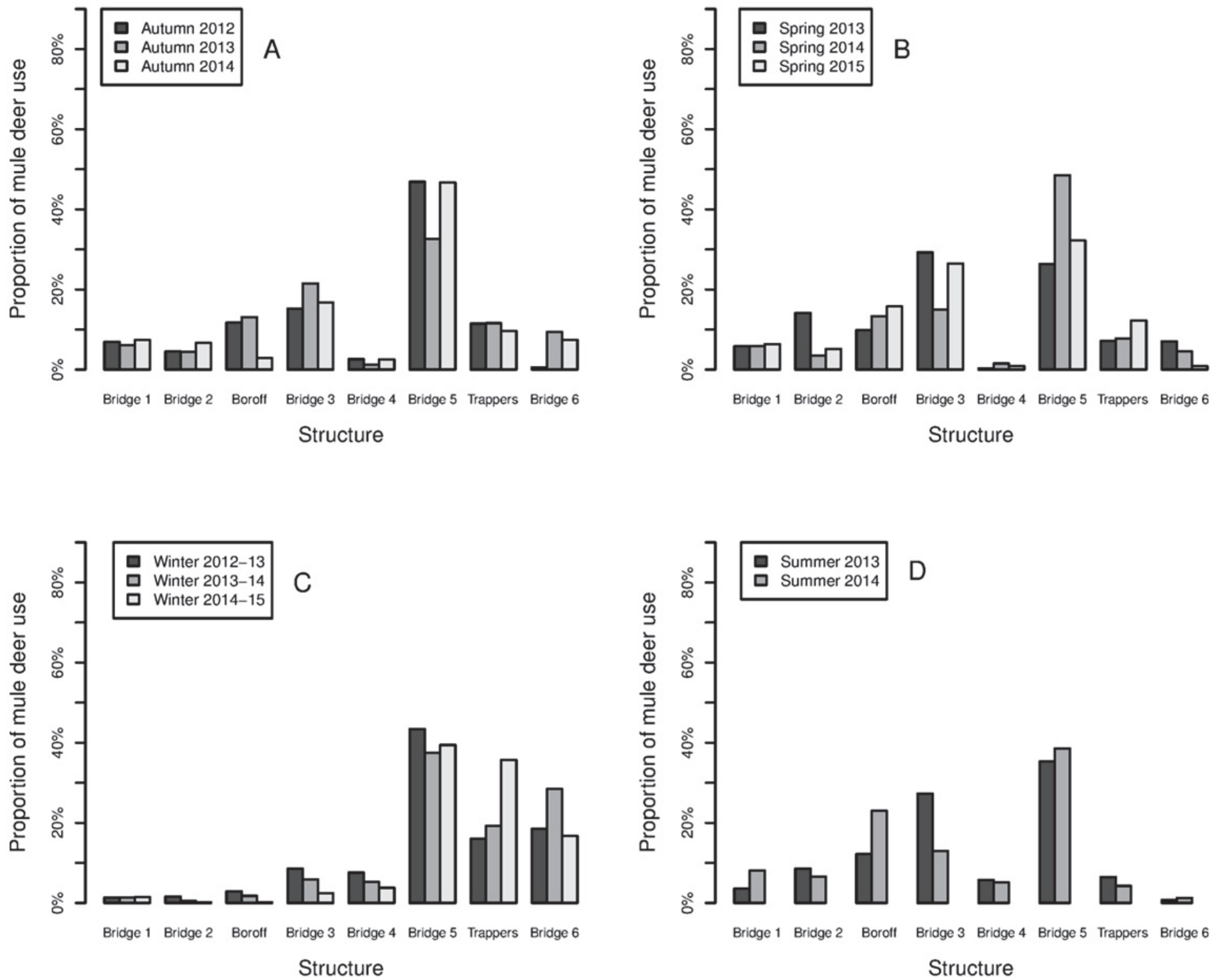

Figure 5. Proportional level of mule deer use at each crossing structure during (A) the autumn migration, (B) spring migration, (C) winter, and (D) summer, September 2012 through May 2015.

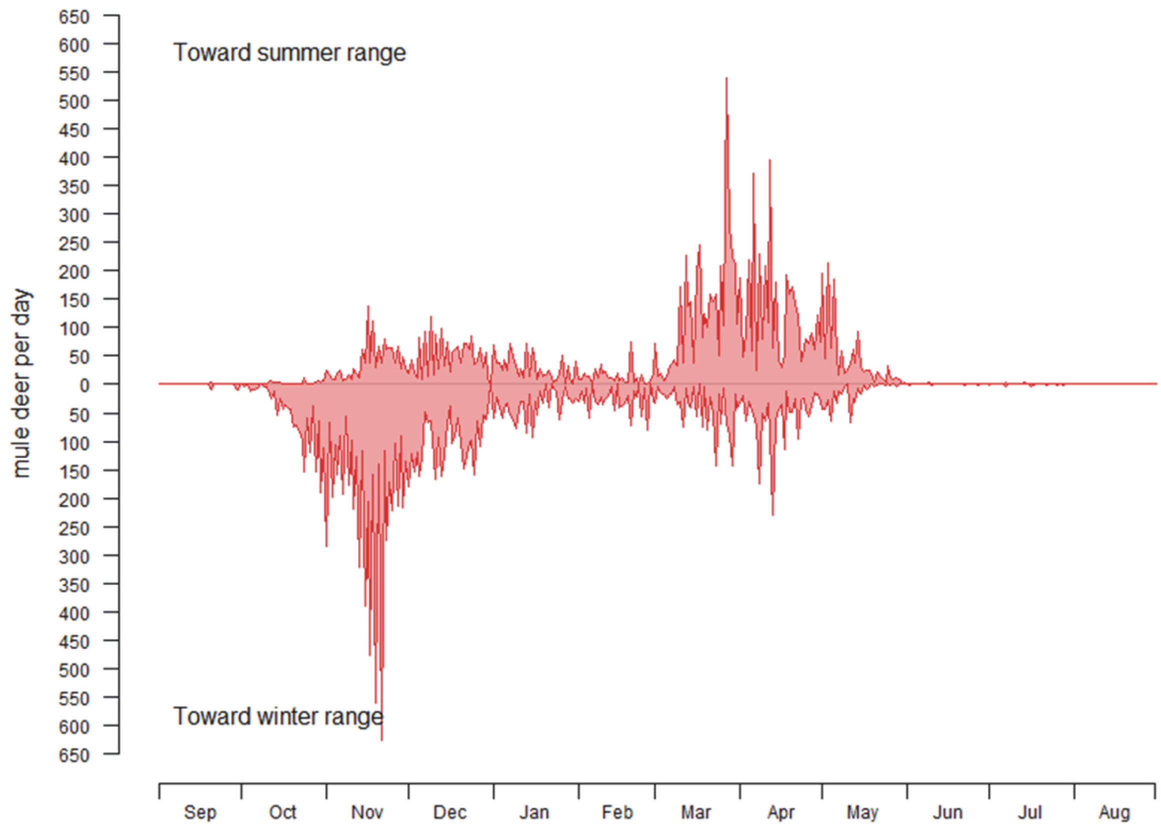

Figure 6. Average number and direction of mule deer that moved through crossing structures along US 191 in western Wyoming, 2012 through 2015. The peaks represent spring and autumn migrations.

Table 1. Number of mule deer that used overpasses (Boroff and Trappers) and underpasses (Bridges 1-6) during autumn migration (Sep 15 - Nov 30), winter (Dec 1 - Mar 14), spring migration (Mar 15 - May 15), and summer (May 16 - Sep 14), 2012 - 2015.

	Structure	2012-13	2013-14	2014-15	Total
Autumn Migration	Bridge 1	275	321	649	1,245
	Bridge 2	179	234	589	1,002
	Boroff	464	689	254	1,407
	Bridge 3	603	1,131	1,477	3,211
	Bridge 4	103	67	224	394
	Bridge 5	1854	1714	4118	7,686
	Trappers	454	610	852	1,916
	Bridge 6	22	494	656	1,172
	sub-total	**3,954**	**5,260**	**8,819**	**18,033**
Winter Period	Bridge 1	95	117	57	269
	Bridge 2	112	44	7	163
	Boroff	201	148	8	357
	Bridge 3	589	487	97	1,173
	Bridge 4	521	434	150	1,105
	Bridge 5	2984	3114	1559	7,657
	Trappers	1100	1595	1413	4,108
	Bridge 6	1272	2363	663	4,298
	sub-total	**6,874**	**8,302**	**3,954**	**19,130**
Spring Migration	Bridge 1	376	483	476	1,335
	Bridge 2	916	289	385	1,590
	Boroff	639	1102	1,180	2,921
	Bridge 3	1891	1,237	1,984	5,112
	Bridge 4	20	128	66	214
	Bridge 5	1703	4010	2413	8,126
	Trappers	462	644	920	2,026
	Bridge 6	456	373	63	892
	sub-total	**6,463**	**8,266**	**7,487**	**22,216**
Summer Period	Bridge 1	5	38	N/A	43
	Bridge 2	12	31	N/A	43
	Boroff	17	108	N/A	125
	Bridge 3	38	61	N/A	99
	Bridge 4	8	24	N/A	32
	Bridge 5	49	181	N/A	230
	Trappers	9	20	N/A	29
	Bridge 6	1	6	N/A	7
	sub-total	**139**	**469**	**N/A**	**608**
	Total	**17,430**	**22,297**	**20,260**	**59,987**

Pronghorn

We documented 25,256 pronghorn cross US Highway 191 between September 2012 and May 2015, including 10,219 during autumn migration, 4,084 during the winter period, 3,071 during spring migration, and 1,882 during the summer period (Table 2). Overall, most pronghorn movement (80 percent, *n*=20,230) occurred at Trapper's Point Overpass (Table 2; Figs. 7-8). Approximately 10 percent (*n*=2,480) of pronghorn crossed at Boroff Hill Overpass and the remaining 10 percent of crossings were distributed among the six underpasses (Table 2; Fig. 8). Peaks in pronghorn movement corresponded with spring and autumn migrations in late-March and mid-October, respectively. Overall, 90 percent of pronghorn traveled over the highway (n=22,710) and only 10 percent moved under (*n*=2,546; Fig. 10).

Figure 7. Pronghorn use at the Trapper's Point Overpass (*n*=20,230), was much higher than any of the other structures and comprised 80 percent of all pronghorn crossings.

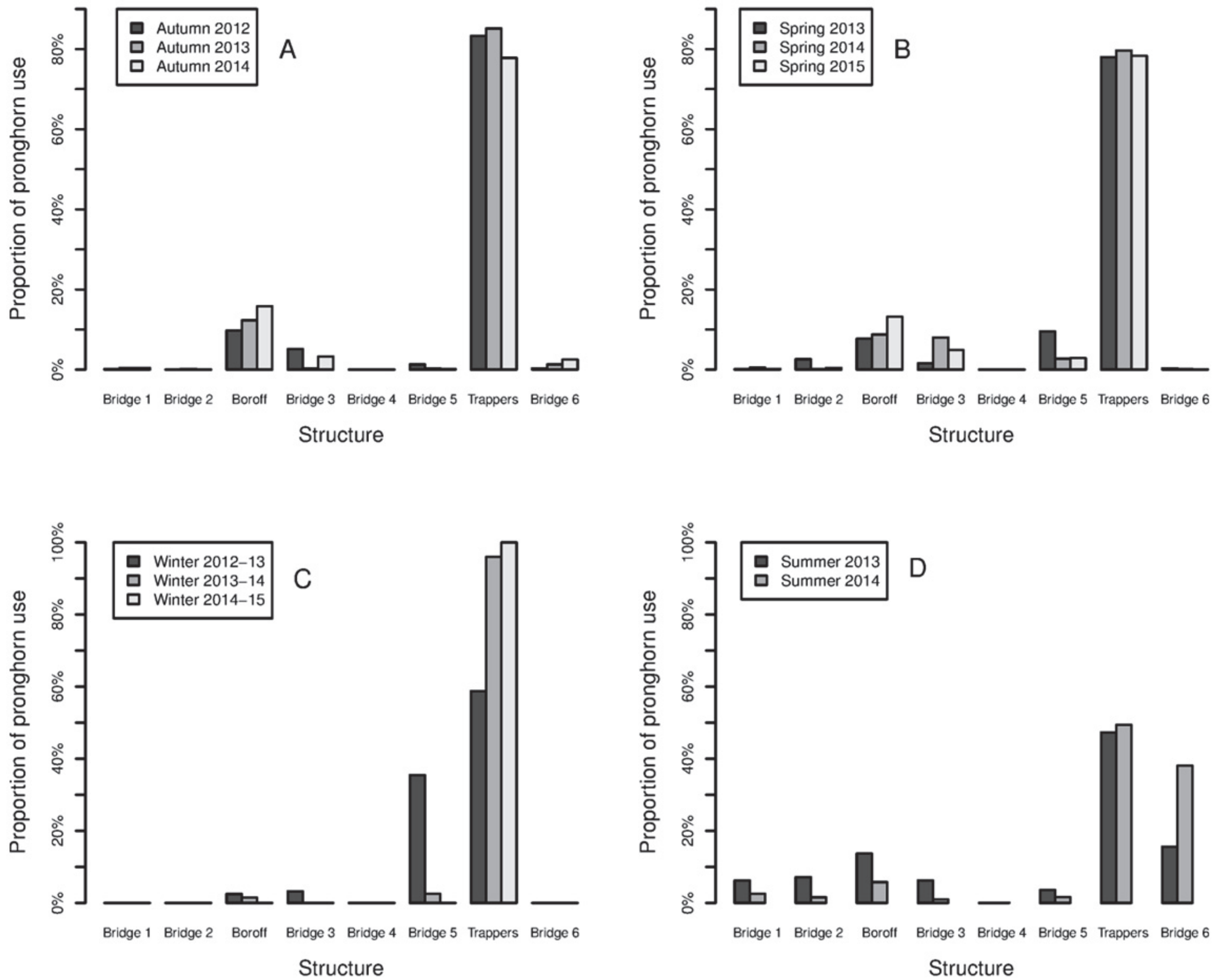

Figure 8. Proportional level of pronghorn use at each crossing structure during (A) the autumn migration, (B) spring migration, (C) winter, and (D) summer, September 2012 through May 2015.

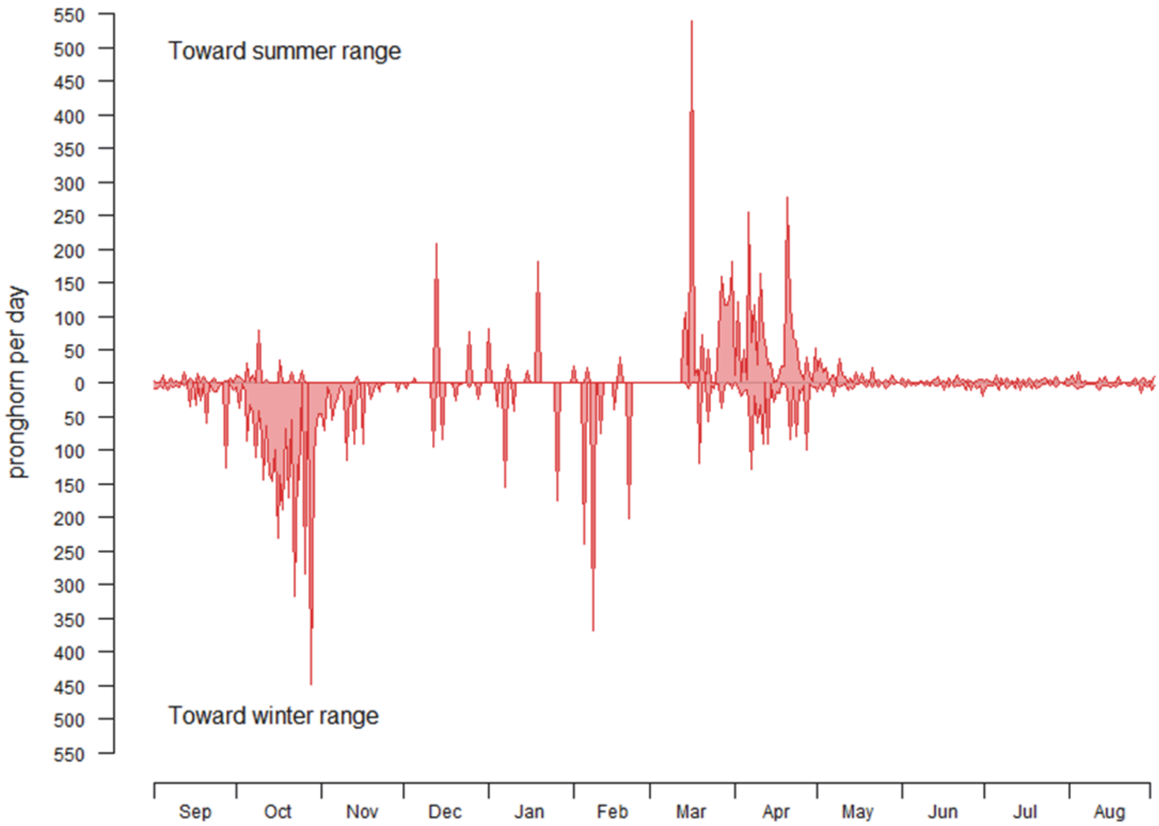

Figure 9. Average number and direction of pronghorn that moved through crossing structures along US 191 in western Wyoming, 2012 through 2015.

Table 1. Number of pronghorn that used overpasses (Boroff and Trappers) and underpasses (Bridges 1-6) during autumn migration (Sep 15 - Nov 30), winter (Dec 1 - Mar 14), spring migration (Mar 15 - May 15), and the summer (May 16 - Sep 14), 2012 May 2015.

	Structure	2012-13	2013-14	2014-15	Total
Autumn Migration	Bridge 1	4	13	19	36
	Bridge 2	0	6	1	7
	Boroff	234	370	764	1,368
	Bridge 3	122	8	157	287
	Bridge 4	0	0	0	0
	Bridge 5	31	10	10	51
	Trappers	1986	2557	3759	8,302
	Bridge 6	8	39	121	168
	sub-total	***2,385***	***3,003***	***4,831***	***10,219***
Winter Period	Bridge 1	0	0	0	0
	Bridge 2	0	0	0	0
	Boroff	7	41	0	48
	Bridge 3	9	0	0	9
	Bridge 4	0	0	0	0
	Bridge 5	99	69	0	168
	Trappers	164	2624	1071	3,859
	Bridge 6	0	0	0	0
	sub-total	***279***	***2,734***	***1,071***	***4,084***
Spring Migration	Bridge 1	3	18	6	27
	Bridge 2	53	8	15	76
	Boroff	157	324	441	922
	Bridge 3	32	296	163	491
	Bridge 4	0	0	1	1
	Bridge 5	194	101	96	391
	Trappers	1583	2946	2619	7,148
	Bridge 6	7	6	2	15
	sub-total	***2,029***	***3,699***	***3,343***	***9,071***
Summer Period	Bridge 1	26	37	N/A	63
	Bridge 2	30	23	N/A	53
	Boroff	57	85	N/A	142
	Bridge 3	26	14	N/A	40
	Bridge 4	0	1	N/A	1
	Bridge 5	15	24	N/A	39
	Trappers	197	724	N/A	921
	Bridge 6	65	558	N/A	623
	sub-total	***416***	***1,466***	**N/A**	***1,882***
	Total	**5,109**	**10,902**	**9,245**	**25,256**

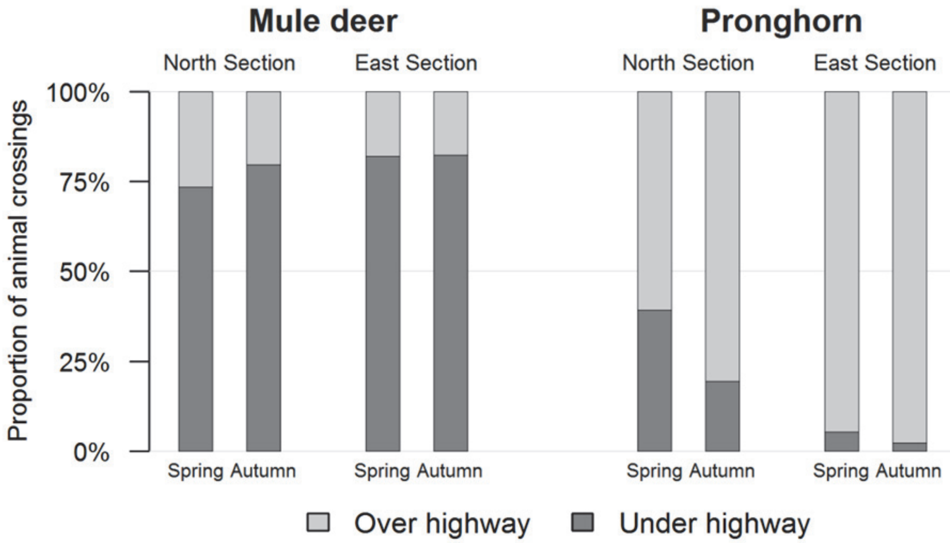

Figure 10. Proportion of mule deer and pronghorn moving over and under the North (Boroff) and East (Trapper's Point) Sections of US Highway 191 in western Wyoming during spring migration (Mar15-May15) and autumn migrations (Sept 15 –Nov 30), 2012 through 2015.

Daily Temporal Patterns

The number of mule deer underpass crossings peaked in the morning (0500 – 1000 hrs) and evening (1700 – 2000 hrs; Fig. 11). A similar crepuscular pattern was evident with mule deer overpass crossings, but the morning peak was shorter (0500 – 0800 hrs). In contrast, most pronghorn crossings occurred throughout daylight hours (0600 – 2000 hrs; Fig. 11).

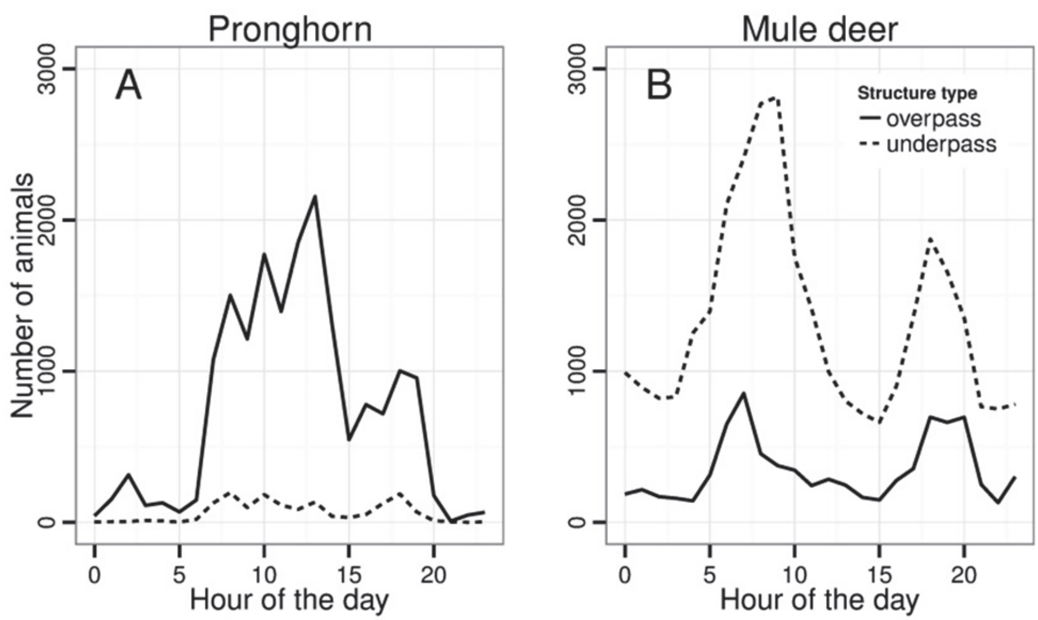

Figure 11. Number of animals and time of day that mule deer and pronghorn used underpasses and overpasses during spring and autumn migrations, 2012 – 2015.

Non-directional Movement During Migration

Non-directional movement during migration increased dramatically from Year 1 to Year 2 and then appeared to stabilize at Year 3 (Fig. 12). We recorded 2,055, 3,367, and 3,417 non-directional movements of mule deer during migrations of Years 1, 2, and 3, respectively. For pronghorn, we documented 283, 1,150, and 1,151 non-directional movements in migrations of Years 1, 2, and 3. Between Year 1 and Year 2, the number of non-directional movements for mule deer and pronghorn increased 64 percent and 306 percent, respectively (Fig. 12).

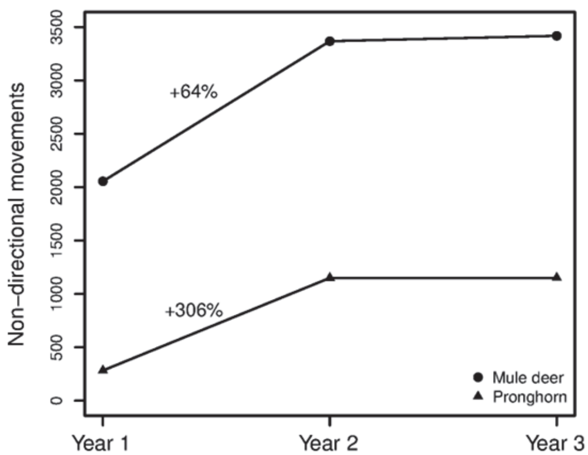

Figure 12. Total number of non-directional movements (i.e., opposite direction of migration) of mule deer and pronghorn during migrations of Year 1 (Autumn 2012 and Spring 2013), Year 2 (Autumn 2013 and Spring 2014), and Year 3 (Autumn 2014 and Spring 2015) along US Highway 191 in western Wyoming, USA.

Wildlife-Vehicle Collisions

Prior to overpass and underpass construction (2005 – 2012), the total number of mule deer and pronghorn WVC's was 662, with an average of 85 per year. Of those, most (91 percent) were mule deer and only 9 percent involved pronghorn. By the third year following overpass and underpass construction, the number of WVCs dropped by 81 percent, to an average of 16 per year. Pronghorn-vehicle collisions were completely eliminated while mule deer-vehicle collisions were reduced by 79 percent.

Other Wildlife Crossings

We documented 10 other wildlife species crossing U.S. Highway 191 via overpasses or underpasses, including: 343 coyotes (*Canus latrans),* 257 sage grouse (*Centrocercus urophasianus*), 66 moose (*Alces alces*), 30 elk (*Cervus elaphus),* 29 badger (*Taxidea taxus*), 5 red fox (*Vulpes vulpes*), 5 geese (*Branta canadensis*), 4 white-tailed deer (*Odocoileus virginianus*), 2 bobcat (*Lynx rufus*), and 2 skunk (*Mephites mephitis*) (Table 3; Fig. 13).

Table 3. Number of other wildlife species that moved through overpasses and underpasses along US Highway 191, September 2012 through May 2015.

	Other Wildlife Crossings									
Structur e	**Coyot e**	**Sage Grous e**	**Moos e**	**El k**	**Badge r**	**Fo x**	**Canad a Goose**	**White -tailed deer**	**Bobca t**	**Skun k**
Boroff	104	0	3	1	0	3	0	0	0	0
Bridge 1	11	257	2	0	11	0	0	3	0	0
Bridge 2	13	0	2	0	4	2	0	0	0	0
Bridge 3	4	0	2	0	1	0	0	0	0	1
Bridge 4	5	0	25	2	1	0	5	0	0	0
Bridge 5	41	0	9	7	2	0	0	1	1	0
Bridge 6	97	0	18	0	10	0	0	0	0	1
Trappers	68	0	5	20	0	0	0	0	1	0
Total:	**343**	**257**	**66**	**30**	**29**	**5**	**5**	**4**	**2**	**2**

Figure 13. Photos of other wildlife, including Sage Grouse at Bridge 1 (top left), elk at Bridge 5 (top right), and coyote and moose at Trapper’s overpass (bottom left and bottom right).

DISCUSSION

Most ungulates in western North America are migratory and rely on discrete seasonal ranges to meet their annual nutritional requirements. Although the importance of migration routes are widely recognized, conserving them presents serious challenges because of the long distances that animals travel across a mix of land ownership and jurisdictional boundaries (Sawyer et al. 2009). While roadways are only one type of impediment to migration, mitigating their impacts with the installation of wildlife crossing structures holds great promise for reducing mortality and maintaining landscape connectivity for migratory ungulates (Huijser et al. 2007, Gagnon et al. 2011, Bissonette and Rosa 2012, Sawyer et al. 2012). However, given the various life-history characteristics and predator avoidance strategies within the suite of ungulate species, crossing structures that are suitable for one species (e.g., mule deer) may not be for others (e.g., pronghorn). Our study helps refine species-specific preferences of crossing structures (see Clevenger and Waltho 2000, Clevenger et al. 2005) and shows that when given the choice between underpasses and overpasses, mule deer tend to move underneath roadways and pronghorn prefer to travel over.

There is a growing literature that evaluates underpass use by the more well-studied ungulates like white-tailed deer (Romin and Bissonette 1996, McCollister and Van Manen 2010, Dodd and Gagnon 2011), mule deer (Sawyer et al. 2012), and elk (Clevenger and Waltho 2005, Gagnon et al. 2007*b*, 2011). Until now, no such information existed for pronghorn (but see Plumb et al. 2003, Sawyer et al. 2012), even though they occur in every western state of the US (Yoakum 2004). While fewer pronghorn chose to move over US Highway 191 in the North Section (71 percent) compared to the East Section (96 percent), the vast majority of pronghorn in both areas moved over the highway. We speculate that these relatively small differences in pronghorn use were associated with the approaches of crossing structures, where some combination of environmental variables (e.g., slope, topography, or fencing) lessened the appeal of the North Section overpass to pronghorn, or possibly made the underpass approaches more attractive. Regardless, the overall trends in pronghorn use were consistent for both North and East Sections, further suggesting that they preferred overpasses to underpasses. We note too, that the East overpass was located immediately adjacent to pronghorn winter range and therefore received much higher levels of use (15,450 crossings) than the North Section overpass (2,290 crossings).

Increasingly, state wildlife and transportation agencies are investing in wildlife crossing structures to reduce WVCs and increase landscape permeability (Forman et al. 2003, Bissonette and Adair 2008, Clevenger and Wierzchowski 2006). Underpasses remain the most common type of crossing structure because of their relatively low cost. For example, in our study area the average cost per underpass was $400,000 US dollars, whereas each overpass cost in excess of $2,000,000 US dollars. Given the large cost differential between underpass and overpass structures, it is critical that agencies have the information they need to make informed decisions about when and where each type of structure is warranted. Our study suggests that overpasses are not needed to mitigate impacts of two-lane highways to mule deer in open sage brush regions. Rather, underpasses in conjunction with game-proof fencing appear adequate for reducing deer vehicle-collisions and maintaining connectivity of seasonal ranges (Sawyer et al. 2012). In contrast, pronghorn showed a strong preference for overpasses and rarely moved underneath the highway. Absent the overpasses, it is possible that pronghorn would have eventually moved underneath the roadway and continued their migrations. However, given that 92 percent of all pronghorn moved over rather than under the highway, our results suggest that overpasses are much more amenable to pronghorn movements than underpasses. Thus, the investment and construction of overpasses in regions that support pronghorn appear warranted. When we consider that WVCs were reduced by 81% (69 animals per year) and that each WVC carries an estimated cost of US$ 8,388 (Huijser et al. 2008), the cost savings $578,772 per year could surpass the cost of one overpass in approximately four years.

Mitigating roadway impacts requires that crossing structures be properly designed and located for the species of interest (Clevenger and Waltho 2000, Clevenger et al. 2005, Bissonette and Adair 2008). Temperate ungulate generally migrate along moisture gradients associated with elevation and topography (Hebblewhite et al. 2008, Sawyer and Kauffman 2011, Bischoff et al. 2012). Our observation of non-directional movements increasing by >60 percent for mule deer and >300 percent for pronghorn suggest that the crossing structures may enhance movement options and encourage behavioral plasticity that was not feasible before overpass and underpass construction, when animals had to cross the highway at grade level. Clearly, the level of back and forth movements increased the last 2 years of study, and previous telemetry work in the area with both mule deer and pronghorn suggest that back and forth movements across the highway were uncommon prior to underpass and overpass construction (Sawyer et al. 2005, Sawyer and Kauffman 2011). Providing migratory ungulates with the means to move back and forth across highways during migration should improve their ability to track vegetation phenology or respond to other environmental cues that influence seasonal movements. At the very least, such flexibility allows animals to utilize habitats that were previously difficult to access. Anecdotally, we also noted that non-directional movements by adult males were common during portions of the autumn migrations that coincided with breeding, as they roamed about searching for females. Additional study is needed to better understand how non-directional movements mediated by crossing structures, i.e., the ability to safely move back and forth across roadways, might benefit migratory ungulates in terms of tracking phenology, responding to environmental cues, or breeding.

Currently, wildlife overpasses are uncommon in the US and the novelty of them in our study area led to several unanticipated management issues that had to be addressed. First was pronghorn hunting on or in close proximity of the East Section overpass. The hunting season overlapped with autumn migration when hundreds of pronghorn were funneling through the overpasses. Unfortunately, some hunters were tempted by the predictable movements and easy access to these animals. Given the ethical and road safety issues with shooting animals as they exit the crossing structures, the Wyoming Game and Fish Department quickly made it illegal to hunt within 0.5 mi (800 m) of an overpass. The second issue involved the 4 ft. (1.2 m) dirt berms installed on the overpasses to visually screen the highway from the animals as they cross. As it turned out, these dirt berms were also attractive to ATV and motorcyclists (Fig. 14). Recognizing that human disturbances like this can reduce the effectiveness of crossing structures (Clevenger and Waltho 2000, Barrueto et al. 2014) and damage vegetation reclamation efforts to stabilize soils and attract wildlife, the Bureau of Land Management posted signs to deter motorized use. Such disturbances could be particularly disruptive to pronghorn because they utilized the overpasses during all hours of the day. The final issue was figuring out what entity or entities were responsible for opening and closing fence gates that run perpendicular to each of the crossings structures for livestock containment (Fig. 15). The area is a mix of private and federal lands used by an assortment of livestock operators. Coordination of the fence gates to ensure they are open during migration is generally a collaborative effort among agencies and livestock growers, but proved to be a difficult task when cattle drives or other livestock activity overlapped with wildlife movements.

Figure 14. Motorcycles and ATVs on Trapper's Point Overpass.

Figure 15. Fence gates at east approach to Boroff Hill Overpass.

MANAGEMENT IMPLICATIONS

- Continuous fencing used in conjunction with underpasses and overpasses can effectively mitigate roadway impacts (i.e., habitat fragmentation, wildlife-vehicle collisions) to migratory mule deer and pronghorn. Here, WVCs involving pronghorn were completed eliminated, while those involving mule deer were reduced by 79 percent. Reducing WVCs further will require careful maintenance of fence infrastructure (e.g., cattle guards and gates), especially during periods of peak mule deer movement.

- Pronghorn strongly preferred overpasses to underpasses. In contrast, most mule deer moved underneath the two-lane highway rather than over. Investment in overpass construction appears warranted in regions that support pronghorn, but may not be necessary in areas inhabited only by mule deer.

- Snow fencing or earth work that minimizes snow drifting on the west side of Boroff Overpass could improve the permeability during spring migration (Fig. 16).

Figure 16. Deep snow drifts on west side of Boroff Overpass make it difficult for mule deer and pronghorn to cross the structure in early spring.

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