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Mitigating bighorn sheep–vehicle collisions and habitat fragmentation with overpasses and adaptive mitigation

Jeffrey W. Gagnon, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85023, USA *jgagnon@azgfd.gov*
Chad D. Loberger, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85023, USA
Kari S. Ogren, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85023, USA
Scott C. Sprague, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85023, USA
Susan R. Boe, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85023, USA
Raymond E. Schweinsburg, Arizona Game and Fish Department (retired), 5000 W. Carefree Highway, Phoenix, AZ 85023, USA

Abstract: As transportation infrastructure expands to accommodate increasing human population growth, wildlife–vehicle conflicts (WVCs) are a growing concern for motorist safety and wildlife populations. In the case of large ungulates, minimal information exists on successful mitigation of WVCs involving bighorn sheep (*Ovis canadensis*) and habitat fragmentation. Too address this void, we evaluated the effectiveness of 3 new wildlife overpasses, 3 culverts, 2 bridges, and ungulate exclusionary fencing as potential desert bighorn sheep (*O. c. nelsoni*; sheep) crossing opportunities along US Highway 93 in Arizona, USA. We evaluated sheep movements using global positioning system (GPS) radio-transmitter collars and remote cameras for 4 years from March 2011 to March 2015 and sheep–vehicle collision data collected from 2011 to 2020. Although GPS determined pre- and post-mitigation passage rates of sheep that crossed US Highway 93 were initially similar, they increased every year and were on average 217% higher following inclusion of wildlife crossings and by year 4 had ultimately increased 633% from pre-construction rates. Cameras recorded 6,936 crossings by a dozen wildlife species with sheep accounting for 95% of all crossings. Sheep used the 3 overpasses (90% of all sheep crossings) disproportionately more than the 3 culverts and 2 underpasses (10% of all sheep crossings) in the same area, and use of the 3 overpasses increased 905% in the first year. Sheep initially used the 30-m-wide overpasses at 83% and 175% higher passage rates than 2 15-m-wide structures; however, by year 4 passage rates were similar across overpasses. From February 2011 through February 2020, we documented 0.8 sheep–vehicle collisions/year for an overall 93.3% reduction from the 12 collisions per year previously documented. Most of the collisions occurred immediately following completion of the project and gradually reduced as sheep access points were identified and addressed through an adaptive mitigation process to iteratively improve success. Overpasses appear to be the preferred wildlife crossing type for sheep and when properly located and linked with ungulate exclusion fencing successfully reduced collisions and habitat fragmentation. These findings add to our knowledge base of effective roadway mitigation for different species. Long-term monitoring informs species learning curves, preference of wildlife crossing structure type, and adaptive mitigation opportunities to increase effectiveness of mitigation measures on current and future projects.

Key words: adaptive mitigation, Arizona, connectivity, crossing structures, desert bighorn sheep, fence, fragmentation, global positioning system, overpass, *Ovis canadensis nelsoni*, wildlife–vehicle collisions

As transportation infrastructure expands to accommodate increasing human population growth, wildlife–vehicle conflicts are a growing concern for motorist safety and wildlife populations. Both wildlife and humans are at risk of injury and death through vehicular collisions, but wildlife is also impacted indirectly through habitat fragmentation, reduced gene flow, and other deleterious effects (van der Grift et al. 2013).

From a human perspective the cost to society can be substantial, as >1.3 million wildlife–vehicle collisions (WVCs) involving deer (*Odocoile-*

us spp.) alone are reported to insurance companies annually across the United States (Conover 2019). Reported deer–vehicle collisions range from 48 per year in Hawaii, USA, to 133,817 deer–vehicle collisions annually in Pennsylvania, USA, and account for 58,622 injuries and 440 fatalities to motorists nationwide (Conover 2019). More than a decade ago, the overall costs of WVCs to society were conservatively estimated to exceed $8 billion but are likely higher now given increasing WVC trends and associated costs (Huijser et al. 2008).

For some wildlife populations, a more serious concern than mortality from collisions may be the indirect effects of roads, including barriers to wildlife movement or habitat fragmentation (Forman and Alexander 1998, Forman 2000, Forman et al. 2003, van der Ree et al. 2015). As one would expect, smaller and less mobile species have difficulty crossing roads due to their physical inabilities and small home ranges (Keller and Largiader 2003, Hibbitts et al. 2017). However, even medium-sized and larger wildlife that would be considered highly mobile can be detrimentally affected by roads and their associated traffic volumes (Gagnon et al. 2007, Proctor et al. 2012, Poessel et al. 2014, Zhang et al. 2015). Habitat fragmentation caused by roads can limit daily and seasonal movements, inhibit dispersal, and reduce or eliminate normal gene flow, all of which can ultimately have long-term negative consequences on population viability (Beier 1995, Forman and Alexander 1998, Epps et al. 2005, Riley et al. 2006).

Abundant species of wildlife may be able to withstand high levels of mortality from vehicular collisions and fluctuations in gene flow with little effect on overall abundance. Rare or less abundant species tend to suffer greater direct and indirect impacts from roads. For example, a relatively minimal number of vehicle collision mortalities accounted for 49% of all mortalities for Florida panthers (*Puma concolor coryi*) and >50% of Florida Key deer (*O. virginianus clavium*) mortalities, which substantially affected those endangered populations (Foster and Humphrey 1995, Lopez et al. 2003).

Additionally, the negative genetic and demographic consequences of habitat fragmentation could accumulate more rapidly in smaller populations. American pronghorn (*Antilocapra americana*) in northern Arizona, USA, experienced a population bottleneck after a 1967 snowstorm estimated to have claimed 40% of Arizona's remaining pronghorn partially attributed to fenced right-of-ways that impeded pronghorn migration to lower elevations, ultimately leading to a reduction in gene flow (White 1969, van Riper and Ockenfels 1998, Dodd et al. 2011, Theimer et al. 2012).

Properly implemented wildlife crossing structures with exclusionary fencing reduces both vehicular collisions and habitat fragmentation by safely accommodating movements necessary for survival (Clevenger and Barrueto 2014, van der Ree et al. 2015, Rytwinski et al. 2016). Different species may have different preferences that can be important to consider when planning for successful wildlife crossing structures (Gagnon et al. 2011, Sawyer et al. 2016, Simpson et al. 2016). Additionally, proper placement of wildlife crossing structures in known movement corridors can increase the ability of animals to quickly find and start using them (Gagnon et al. 2011, Sawyer et al. 2012).

Roadkill data is a commonly used method to select a location for wildlife crossing structures (Smith 2012, Downs et al. 2014). Adequate roadkill data are often unavailable, inaccurate, or rare for some species, and information other than roadkill may be required for wildlife crossing structure placement. In situations where minimal roadkill data are available, wildlife movement data from global positioning system (GPS) radio-transmitter collars have been used for placement of wildlife crossings and fencing (Downs et al. 2014, Loraamm and Downs 2016). In addition to identifying locations of mitigation measures, GPS location data also elucidate how wildlife are using movement and migration corridors and other important areas. Additionally, these data can be used to evaluate wildlife movement before, during, and after construction of new roads or crossing structures to characterize effectiveness of mitigation measures (Dodd et al. 2007*a*, Sawyer et al. 2009, Gagnon et al. 2015, Sawyer et al. 2016, Simpson et al. 2016).

Desert bighorn sheep and roads

Desert bighorn sheep (*Ovis canadensis nelsoni*; sheep; Figure 1) in the southwest United States and Mexico occupy mountain ranges or rugged canyons characterized by sheer cliffs, ruggedness, high temperatures, and unpredictability of

Figure 1. Desert bighorn sheep (*Ovis canadensis nelsoni*) studied along US Highway 93 from 2011 to 2014, Arizona, USA (*photo courtesy of G. Andrejko, Arizona Game and Fish Department*).

rainfall and water availability (Leslie and Douglas 1979, McKinney et al. 2006). Although sheep can thrive in ecologically harsh conditions, their populations have declined through the last 200 years because of unregulated killing, disease from domestic livestock, habitat loss, and barriers to movement. Sheep populations were estimated at about 1 million in the nineteenth century with approximately 35,000 in Arizona and declining to as few as 2,500 animals in Arizona before restoration efforts began (Buechner 1960).

Sheep often exist in partially or fully isolated herds and are reliant on movement between mountain ranges, which in many cases are naturally fragmented by expanses of unsuitable landscapes. Anthropogenic barriers, including roads, can lead to the loss or obstruction of traditional corridors, and the severing of large intact habitat blocks into smaller, potentially less usable habitat blocks. The loss of corridors and fragmentation of large usable habitat blocks constitute a threat to persistence of viable sheep populations (Bleich et al. 1990, Epps et al. 2005). Although debates exist on the number of sheep needed for sustainable populations, in general, small and isolated sheep herds are more susceptible to local extinction and require additional management attention compared to larger herds (Berger 1990; Krausman et al. 1993, 1996; Berger 1999; Wehausen 1999). Besides the potential negative effects of isolation and random stochasticity, the inability of sheep to move between ranges bisected by roads reduces gene flow and can increase inbreeding levels. For example, Epps et al. (2005) found that roadways reduced the sheep genetic diversity within as few as 40 years. To ensure long-term persistence, small sheep populations that occupy marginal or comparatively poor habitat, or small suitable habitat patches, may require habitat and population management intervention (Berger 1990, Gross et al. 1997, McKinney et al. 2003, Turner et al. 2004).

Although relatively rare, vehicular related mortalities comprise a source of mortality for sheep in local areas. Cunningham and deVos (1992) documented that 50% of mortalities in the Black Mountains of northwestern Arizona were caused by vehicle collisions. Collisions with sheep also impose a monetary cost to society similar to those calculated for deer, elk (*Cervus canadensis*), and moose (*Alces* spp.; Huijser et al. 2009). Because of the limited number of hunting tags and a high desire for the opportunity to harvest them, single Arizona sheep tags have been auctioned for up to $380,000 with these funds being directed toward conservation (Arizona Game and Fish Department, unpublished data). Thus, loss of sheep due to vehicular collisions have an even higher monetary cost than many species.

Wildlife crossings are an option to restore sheep movement corridors, reconnect fragmented habitat blocks, and reduce collisions. Although wildlife crossings are no longer a novel approach to mitigating road effects, minimal information exists on proper wildlife crossing structure designs for some species, including sheep.

Research in Banff National Park, Canada, and surrounding parks maintains one of the longest-running wildlife crossing monitoring projects worldwide, and research has been continuous since 1996. Clevenger and Barrueto (2014) did not document sufficient Rocky Mountain bighorn sheep (*O. c. canadensis*) crossings in Banff to evaluate preference for different designs. In Arizona, the first wildlife crossing structures were underpasses built specifically for sheep along State Route (SR) 68 in 2002. Bristow and Crabb (2008) monitored sheep use of these 3 new underpasses with infrared motion-triggered cameras over a 20-month period and documented only 32 crossings by rams; only 12% of all radio-marked sheep (also all rams), successfully crossed SR 68. These results led them to recommend more open structures than the 50-m-wide and 20-m-high underpasses they studied (Bristow and Crabb 2008).

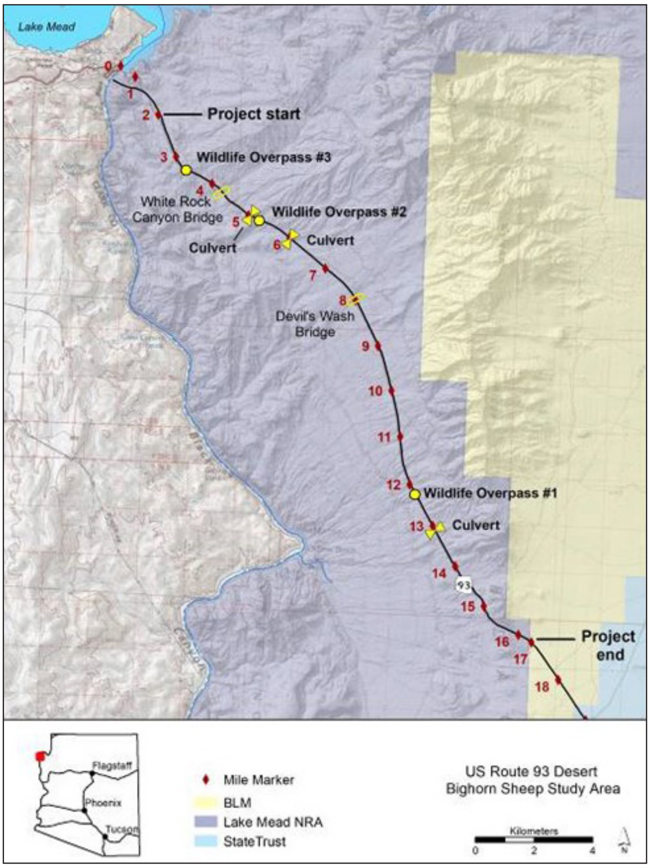

Figure 2. The US Highway 93 milepost 2–17 study area, including topography, land ownership, and location of structures monitored for desert bighorn sheep (*Ovis canadensis nelsoni*) use from 2011 to 2014, US Highway 93, Arizona, USA.

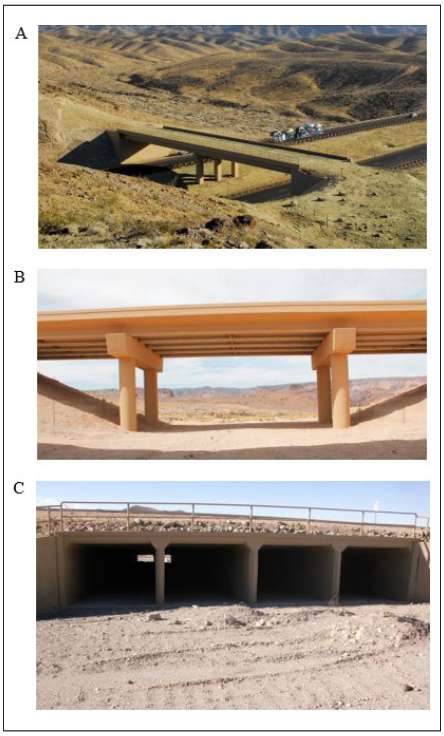

Figure 3. Examples of an overpass, underpass, and culvert linked with exclusionary fencing intended to allow desert bighorn sheep (*Ovis canadensis nelsoni*) movement across the highway corridor and reduce sheep–vehicle collisions. Examples are overpass #2 (A), Devils Wash Bridge (B), and culvert milepost 6.0 (C), 2011–2014, US Highway 93, Arizona, USA.

US Highway 93 planning

US Highway 93 (US 93) is a major roadway that connects Arizona to Canada and will be incorporated into the new Interstate-11 terminating at the Mexican and Canadian borders. In Arizona, planning to reconstruct US 93 at Hoover Dam began several decades ago with the intent to address increased traffic flows, motorist safety, and resident sheep concerns. The sheep population in the path of the proposed realignment was an important consideration in highway planning. Prior research (1989 to 1991) documented 24 vehicle collisions with sheep, or a mean of 12 sheep per year (Cunningham and Hanna 1992). Researchers suggested that without mitigation sheep would likely be unable to cross US 93 once construction was completed (Cunningham and deVos 1992, Cunningham and Hanna 1992).

The first phase of US 93 realignment (Hoover Dam Bypass; mileposts [MP] 0–2) started more abruptly than expected following the immediate shutdown of Hoover Dam to vehicular access following the 11 September 2001 terrorist attacks, detouring traffic to alternative routes. A delay in activities due to a partial bridge collapse during the realignment of Hoover Dam Bypass provided a window of opportunity to also begin construction on US 93 MP 2–17 with a goal of a simultaneous completion of both projects (Petroski 2010). To help determine the placement of wildlife crossing structures for US 93 MP 2–17, McKinney and Smith (2007) used data from sheep GPS collars to help identify placement of wildlife crossing structures. This data indicated that 82% of all highway crossings by sheep occurred at 5 major ridges. Three of the 5 ridges were ultimately prioritized for sheep crossing structures (McKinney and Smith 2007). These 3 overpasses were constructed, and exclusionary fencing encompassed the entire length of

Table 1. Name, location, and measurements of structures monitored with cameras to assess desert bighorn sheep (*Ovis canadensis nelsoni*) use following construction of US Highway 93 mileposts (MP) 2–17, 2011–2014, Arizona, USA. Overpasses (OP) are built to pass sheep over the roadway. Bridges and culverts are drainage structures that can also pass wildlife.

Structure name	Milepost	Width (m)*	Height (m)**	Length (m)***
Wildlife OP #3	3.3	30	NA	62
White Rock Canyon Bridge	4.2	26	7.6	66
Wildlife OP #2	5.2	15	NA	62
Culvert MP 5.2	5.2	2.4	2.4	68
Culvert MP 6.0	6.0	2.4	2.4	66
Devils Wash Bridge	8.0	26	7.6	65
Wildlife OP #1	12.2	15	NA	68
Culvert MP 13.1	13.1	2.4	2.4	78

* Measured as width of the smallest opening of the structure as they enter the crossing.
** Measured as the height of the opening of the structure perceived by bighorn sheep as they enter the crossing.
*** Length is the distance bighorn sheep have to travel to traverse the entire structure.

US 93 MP 2–17 also tying in 2 large bridges (e.g., underpasses) and multiple concrete box culverts designed for drainage (Figures 2 and 3; Table 1). US 93 was reopened to traffic October 20, 2010, and the final sections of wildlife exclusionary fencing linking the overpasses, underpasses, and culvert were completed in March 2011.

The objectives of our study were to determine if the combination of overpasses, underpasses, culverts, and fencing successfully mitigated sheep–vehicle collisions and habitat fragmentation. To complete this research, we compared pre- and post-construction GPS movement data from radio-marked sheep, camera monitoring of structures to determine sheep use to sheep–vehicle collision rates to those documented by Cunningham and Hanna (1992) prior to construction. Additionally, we used our long-term monitoring effort as an adaptive mitigation opportunity to improve upon mitigation installed for the stretch of US 93 we studied (MP 2–17) along with the adjacent US 93 Hoover Dam Bypass (MP 0–2) which was completed in 2004 to further reduce sheep–vehicle collisions along the entire 17-mile stretch of US 93 that passes through sheep habitat.

Study area

The 24-km US 93 project was located in northwestern Arizona, approximately 77 km southeast of Las Vegas, Nevada, USA (Figure 2). Elevations range from 197 m at the Colorado River to 1,511 m atop Mount Wilson. The topography includes rugged, mountainous terrain, steep talus slopes, cliffs, dry washes, and rolling hills. The annual average daily high and low temperatures are 30.4°C and 14.7°C, although temperatures during summer months exceed 38°C and rainfall events are rare and unpredictable. Vegetation across the study area is characteristic of the arid and sparse Mohave Desert Scrub Biotic Community and is dominated by the creosote-bursage association (Turner 1994). The 2011 to 2015 average annual daily traffic (AADT) once the highway was opened was 13,635 vehicles/day, which represented a 75% increase over the prior 5 years' (2005–2010) AADT of 7,793, with this latter figure consisting primarily of traffic associated with construction activities during the construction of Hoover Dam Bypass and MP 2–17 (Arizona Department of Transportation [ADOT], unpublished data).

Methods

Movements of GPS radio-marked sheep

We captured 70 sheep using a net gun fired from a helicopter along U.S. 93 from November 2010 through November 2012 and outfitted them with GPS satellite uplink radio-transmitters collars (Model NSG-D GlobalStar, North Star Science and Technology, LLC, King

George, Virginia, USA). The collars were programmed to receive 8 daily GPS locations for 24 months. To maximize data collection associated with movements near US 93, the collection of GPS locations were focused during daylight hours, every 2 hours from 0600–1800 hours when bighorn sheep, a primarily diurnal animal, are most active. We compared GPS data from this project to data collected by Gagnon et al. (2014) before and during construction (2008–2010). In cases where individual bighorn sheep wore a collar during both the pre- (2008–2010) and post- (2011–2014) construction phases, that individual's data were used separately in those 2 time periods.

To assess changes in movement across US 93, we compared crossing distribution, crossing rate, and passage rates using data collected pre- (2008–2010) and post- (2011–2014) construction. Crossing distributions were a comparison of where bighorn sheep crossed the highway in relation to final wildlife crossings and associated exclusionary fencing locations prior to and after construction. To quantify crossing distributions, we divided the study area into 0.16-km segments and tallied crossings where the lines between consecutive GPS fixes intersected a US 93 segment. Because individual sheep that cross more frequently than others can bias highway crossing distributions, we also calculated a Shannon-Diversity Indices (SDI) similar to that calculated for deer, elk, and pronghorn on other Arizona roadways (Shannon and Weaver 1949, Dodd et al. 2012, Gagnon et al. 2014). The SDI reduces the bias caused by individual sheep by placing a higher weight on segments that had more crossings by individual sheep.

Once an SDI was calculated, we graphed the weighted crossings and their relationship to overpasses, underpasses, and culverts. To calculate individual sheep crossing rates, we divided the total number of crossings by the total number of days the collar was affixed. Consistent with other Arizona studies, we calculated passage rates by dividing the number of roadway crossings by the number of times that sheep approached within 250 m of US 93 (Dodd et al. 2007*a*, Gagnon et al. 2007, Dodd and Gagnon 2011, Dodd et al. 2012). We compared crossing and passage rates using non-parametric Mann-Whitney U and Kruskal-Wallis tests (Sokal and Rohlf 2003).

Use of mitigation features

We evaluated 3 wildlife overpasses built specifically for sheep, along with 2 large underpasses and 3 culverts constructed primarily to facilitate drainage. We used a multi-camera custom video surveillance system backed up by Reconyx® rapid-fire still cameras (infrared motion triggered cameras; Holmen, Wisconsin, USA), that collected 3 photos per triggering event to document the total number of crossings by sheep at all mitigation structures and recorded sex and age class (ram, ewe, and juvenile). We evaluated passage rate (e.g., number of sheep crossings divided by the number of approaches to the structures) at the 3 overpasses and compared overpasses of different widths (2 at 15 m wide vs. 1 at 30 m wide) to help inform future overpass widths (Dodd et al. 2007*b*, Gagnon et al. 2011). To determine if width of overpasses influenced sheep crossings, we used logistic regression to calculate the odds of successful crossing once an animal approached (Agresti 1996).

We did not collect passage rates at the 2 underpasses due to the difficulty of placing cameras in a way that would capture all approaches. We were able to collect passage rates at the culverts to gather information on whether or not bighorn sheep would utilize culverts to cross roads.

Changes in sheep–vehicle collisions

Because no sheep–vehicle collisions were recorded while the road was closed and under construction (2001–2010), we relied on historical estimates of 12 vehicle-related mortalities per year (Cunningham and Hanna 1992) for our baseline collision rate. We conducted weekly roadkill surveys and worked with multiple local law enforcement and road maintenance entities that patrolled the area on a daily basis from February 2011 to 2020. We compared the reduction in percentage of annual collisions to the baseline level.

Use of adaptive mitigation to improve success

We used an iterative approach that incorporated results from our monitoring, or what we call adaptive mitigation, to improve the effectiveness of measures to reduce sheep–vehicle collisions along our project area (US 93 MP 2–17) and the previously constructed US 93 (MP 0–2). Even before US 93 (MP 0–2) ex-

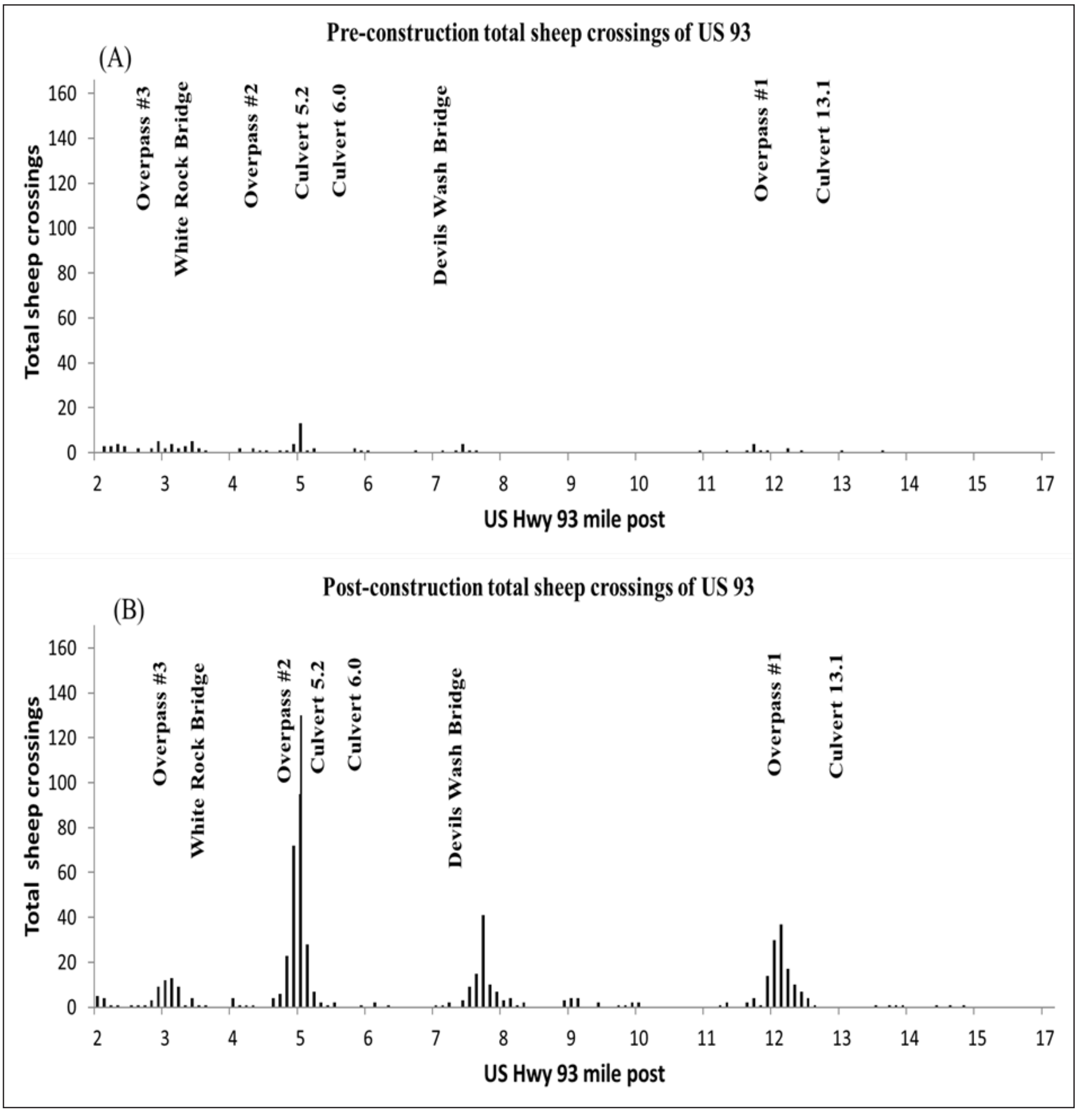

Figure 4. Distribution of desert bighorn sheep (*Ovis canadensis nelsoni*) crossings during pre-construction (A; 2008–2010) and post-construction (B; 2011–2014) by 0.16-km (0.1-mile) segment of US Highway 93 mileposts 2–17, Arizona, USA.

perienced restored traffic flows, maintenance staff reported sheep entering the right-of-way. Using a combination of reports of sheep presence in the right-of-way and sheep–vehicle collision records, we visually inspected areas where breaches may have occurred. When obvious breach locations were identified (e.g., cut fence or wash outs), they were repaired. At potential breach points that were not as obvious, we installed cameras to identify the point of entry onto the roadway and make improvements where necessary. Once these adaptations were complete, we continued camera monitoring at the cattle (*Bos taurus*) guards and escape ramps until 2019 to confirm the effectiveness of the modifications or make further improvements and monitored sheep–vehicle collisions for 1 more year through February 2020.

Results

We recovered location data from 48 sheep collars affixed for an average of 454.4 days/animal resulting in 167,300 locations post-construction. Pre- and post-construction GPS movement data from 14 sheep that were collared both prior to and after highway construction were split ac-

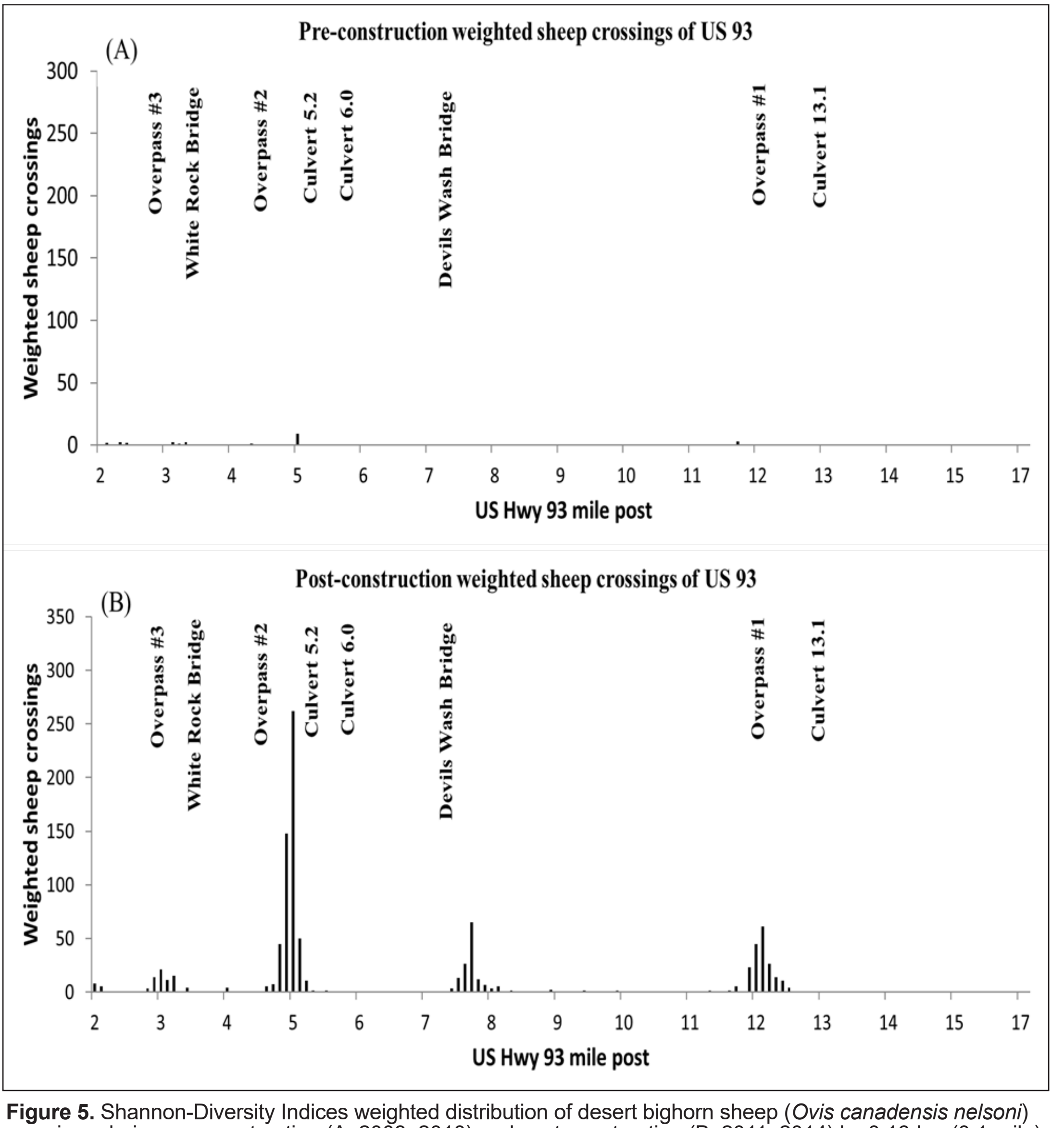

Figure 5. Shannon-Diversity Indices weighted distribution of desert bighorn sheep (*Ovis canadensis nelsoni*) crossings during pre-construction (A; 2008–2010) and post-construction (B; 2011–2014) by 0.16-km (0.1-mile) segment of US Highway 93 mileposts 2–17, Arizona, USA.

cordingly and represented both groups. Pre-construction GPS data included the 14 sheep collared during both phases and an additional 19 sheep collared during pre-construction.

Acclimation to overpasses and fencing: GPS movement data

Our GPS data documented a gradual acclimation to the crossings for 4 years after highway construction. We noted a shift in the location of GPS determined crossings along US 93. Actual and SDI-weighted crossing distributions as determined by GPS movement data showed minimal sporadic crossings of US 93 MP 2–17 pre-construction and definite peaks in crossings at the overpass and underpasses post-construction (Figures 4 and 5).

Crossings of US 93 ultimately increased over time following an initial learning period. Compared to pre-construction, the highway crossing rate per GPS collared sheep was the lowest in year 1 post-construction (1.40 crossings ± 0.50/sheep) as sheep adjusted to the exclusionary fencing and located crossing opportunities at the overpasses. However, crossing rate increased steadily from 7.65 ± 1.52/sheep in year 2, before peaking in year

Table 2. Crossings, crossing rates, passage rates, and number of radio-marked desert bighorn sheep (*Ovis canadensis nelsoni*) pre- and post-construction, US Highway 93 mileposts 2–17, Arizona, USA, 2011–2014.

Parameter	Pre-construction (2008–2010)	Post-construction (2011–2014)
No. collared bighorn sheep used for analysis	33	48
No. highway crossings	91	545
Mean days bighorn sheep collared (±SE)	357.2 (±36.3)	454.4 (±29.5)
Mean crossings/ bighorn sheep (±SE)	2.8 (±1.1)	11.4 (±2.7)
Mean crossing rate (crossings/ day; ±SE)	0.01 (±0.01)	0.03 (±0.01)
Mean passage rate (crossings/ approach; ±SE)	0.05 (±0.02)	0.19 (±0.03)

3 at 13.3 ± 2.17/sheep and appearing to level off around 11.80 ± 0.88/sheep in year 4.

Overall, following highway construction, the 48 sheep crossed US 93 between MP 2–17 on 545 occasions, or 11.4 (±2.7) crossings/sheep for a crossing rate of 0.03 crossings/day (±0.01). This represented a 200% and 300% increase in crossings/day and crossings/sheep, respectively. The GPS-collared sheep crossed the same stretch of US 93 91 times prior to construction, or 2.8 (±1.1) crossings/sheep at a crossing rate of 0.01 crossings/day (±0.01; U = 6.30, df = 1, $P = 0.01$). Because the number of approaches per sheep within 250 m of US 93 prior to construction did not differ from those following construction (U = 0.13, df = 1, $P = 0.71$), changes in passage rates (crossings/approaches) were driven primarily by this increase in crossings. The increase in crossings led to an overall passage rate increase of nearly 217% from 0.06 (±0.02) crossings/approach to 0.19 crossings/approach (SE ± 0.03 crossings/approach; U = 7.70, df = 1, $P < 0.01$; Table 2).

This difference in pre- and post-construction passage rates was more pronounced over time, especially following the initial 0.02 crossings/approach drop in passage rate in year 1 to 0.04 (±0.03) crossings/approach as sheep became acclimated to the new fencing and crossings. Passage rates for years 2, 3, and 4 were all significantly higher than pre-construction. In year 2, passage rates increased to 0.24 crossings/approach (SE ± 0.03; U = 12.79, df = 1, $P < 0.01$) and then to 0.34 (SE ± 0.04; U = 12.95, df = 1, $P < 0.01$) in year 3, and ultimately to 0.44 (SE ± 0.04; U = 12.29, df = 1, $P < 0.01$) in year 4 (Figure 6). Although there was a gradual increase in passage rates over time, years 2, 3, and 4 did not differ (K-W = 2.10, df = 2, $P = 0.35$), and ultimately, year 4 passage rates were 10-fold higher than year 1 (U = 11.77, df = 1, $P < 0.01$). Ewe and ram passage rates did not differ from each other pre-construction or in any of the 4 years post-construction and followed a similar acclimation trend with a pre-construction rate of 0.04 (±0.01) crossings/approach for ewes and 0.07 (±0.01) crossings/approach for rams.

This was followed by a small drop in passage rates in year 1 to 0.04 crossings/approach for rams and 0.03 crossings/approach for ewes to ultimately 0.32 (±0.02) crossings/approach for ewes and 0.52 (±0.06) crossings/approach for rams in year 4 (Figure 6).

Acclimation to crossing structures and fencing

Our camera data confirmed GPS data were consistent with findings that bighorn sheep appeared to acclimate to the crossings over time. From March 15, 2011 to March 15, 2015, we logged 11,680 total camera monitoring days at 8 structures that could potentially function as wildlife crossings (3 overpasses, 2 underpasses, and 3 culverts). The cameras recorded 6,903 crossings by various wildlife species, but sheep accounted for 95% of all animals documented using all structures combined (Table 3; Figure 7).

Overall, we documented 6,530 crossings by sheep at the 8 structures we monitored. Initially in year 1, 80.0% of crossings occurred at the overpasses and only 20.0% and <1% of crossings occurred at the underpasses and culverts, respectively. Crossings by sheep at the structures we monitored appeared to shift away from the underpasses, and in year 4, 90.0% of sheep crossings occurred at the overpasses and only 8.8% and <1% of crossings occurred at the underpasses and culverts, respectively. Overall, 89.9% of crossings occurred at the 3 over-

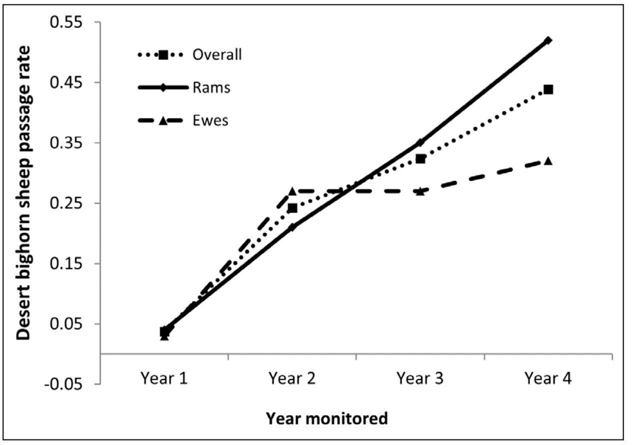

Figure 6. Desert bighorn sheep (*Ovis canadensis nelsoni*) passage rate (crossings/approaches) for rams and ewes, during a 4-year period (2011–2014) following reconstruction, US Highway 93 mileposts 2–17, Arizona, USA.

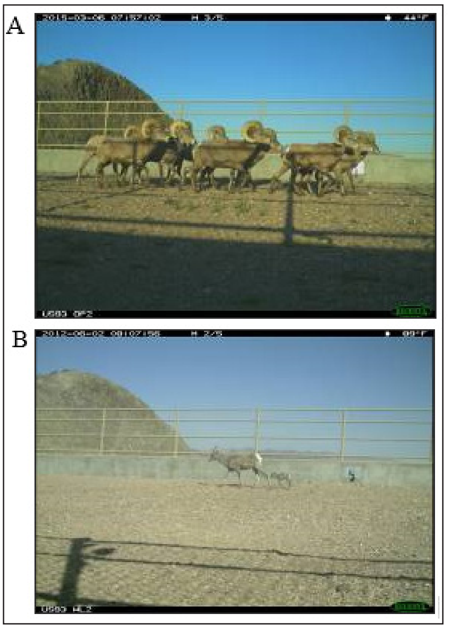

Figure 7. Bachelor herd of desert bighorn sheep (*Ovis canadensis nelsoni*) rams (A) and ewe and newborn lamb (B) using overpasses along US Highway 93 mileposts 2–17, Arizona, USA.

Table 3. Wildlife crossings at 8 structures (3 overpasses, 2 bridges, and 3 culverts), 2011–2014, along US Highway 93, mileposts 2–17, Arizona, USA.

Structure	Milepost	Bighorn sheep	Deer	Coyote	Bobcat	Fox	Other	All species
Overpass #3	3.3	1,407	2	75	0	52	6	1,542
White Rock Canyon Bridge	4.0	84	0	0	0	0	0	84
Overpass #2	5.2	2,286	0	3	0	15	11	2,315
Culvert	5.2	97	0	12	0	7	1	117
Culvert	6.0	96	0	8	1	15	1	121
Devils Wash Bridge	8.0	390	0	0	0	0	0	390
Overpass #1	12.2	2,168	0	33	0	57	45	2,303
Culvert	13.1	2	0	13	1	15	0	31
Total		6,530	2	144	2	161	64	6,903

passes compared to 2 underpasses (7.2%) and 3 culverts (3.0%; Figures 8 and 9; Table 3).

Use at the 3 overpasses, where most sheep crossings occurred (5,861 crossings), increased 905% from year 1 (214 crossings; 0.28 crossings/approach) through year 2 (2,151 crossings; 0.78 crossings/approach) before slowing slightly and leveling out in year 3 (1,734 crossings; 0.89 crossings/approach) and year 4 (1,762; 0.87 crossings/approach; Figure 10). This increase in the proportion of a successful crossing from years 1 through 4 differed across years ($\chi^2 = 550.5$, df = 3, $P < 0.01$), and the chance of a successful crossing increased incrementally with each additional year, with years 1 versus 2 (OR = 9.15; 95% CI = 7.03 – 11.91, $P < 0.01$) and year 2 versus 3 (OR = 2.44; 95% CI = 1.89 – 3.13, $P < 0.01$), but leveled out and was not significant from year 3 to 4 (OR = 0.79; 95% CI = 0.58 – 3.13, $P < 0.12$).

Although sheep use of underpasses and cul-

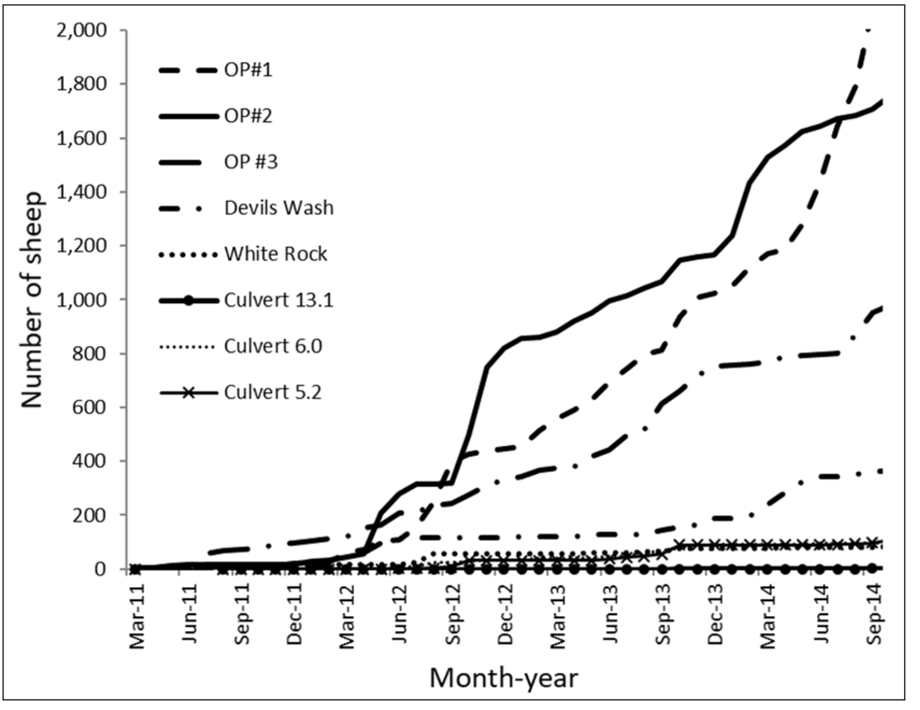

Figure 8. Cumulative desert bighorn sheep (*Ovis canadensis nelsoni*) crossings by month and by individual structure monitored following reconstruction of US Highway 93 mileposts 2–17, Arizona, USA, 2011–2014.

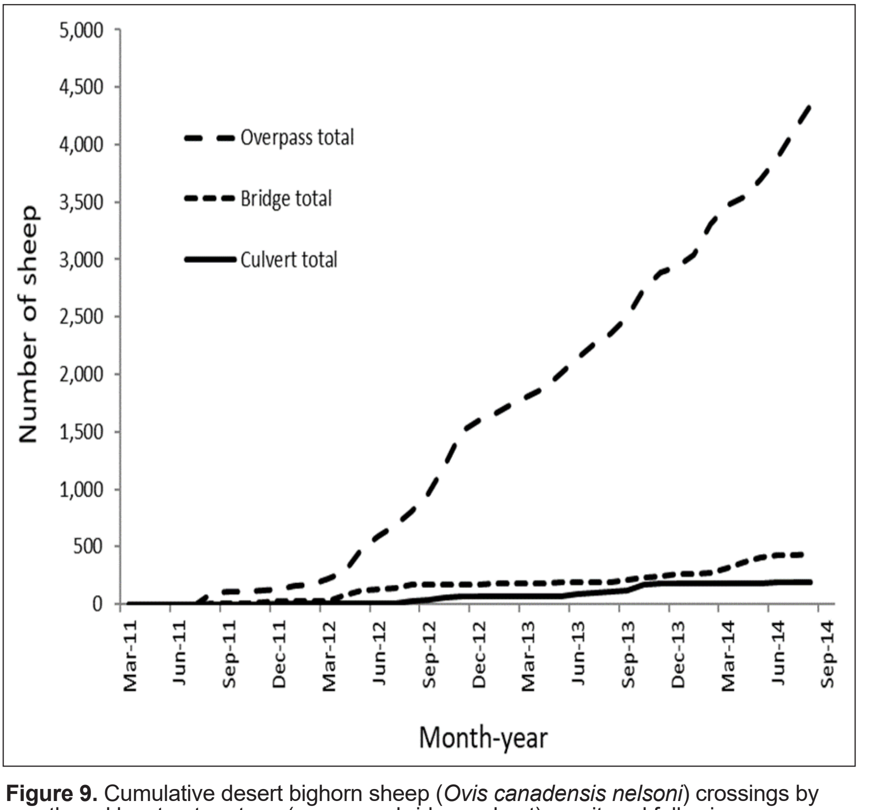

Figure 9. Cumulative desert bighorn sheep (*Ovis canadensis nelsoni*) crossings by month and by structure type (overpass, bridge, culvert) monitored following reconstruction of US Highway 93 mileposts 2–17, Arizona, USA, 2011–2014.

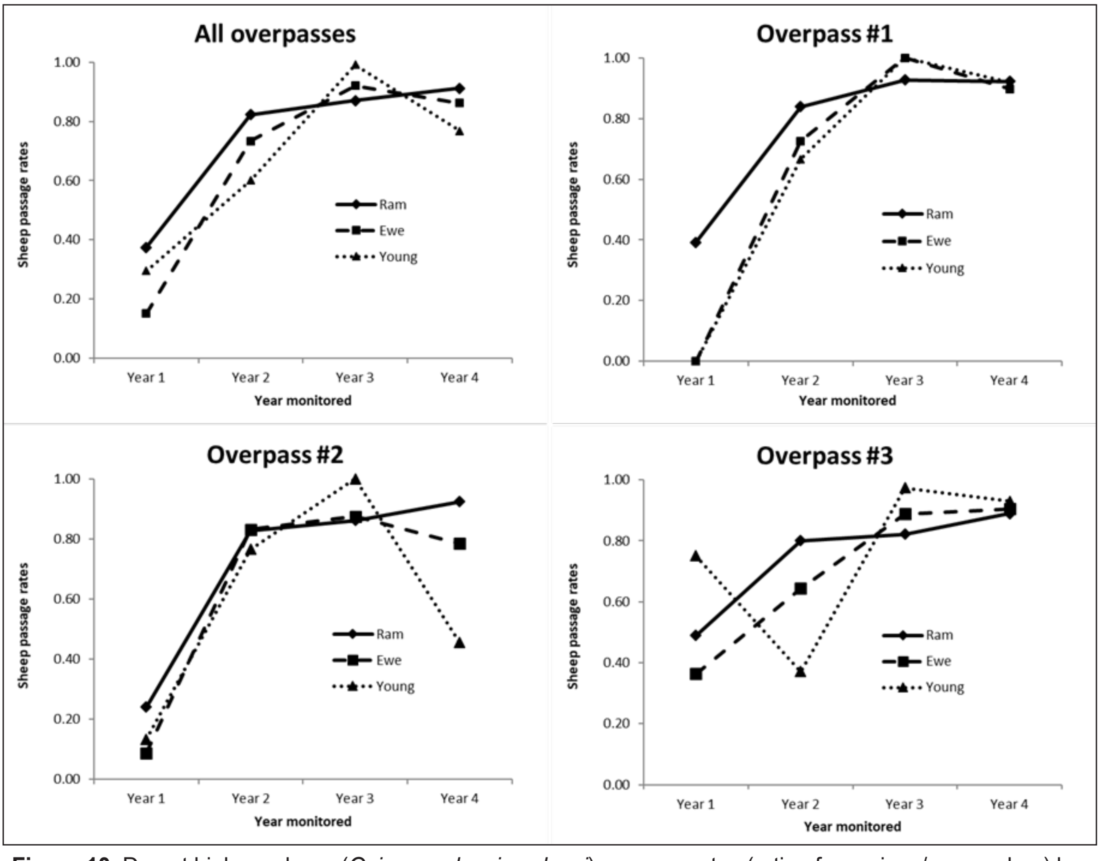

Figure 10. Desert bighorn sheep (*Ovis canadensis nelsoni*) passage rates (ratio of crossings/approaches) by sex and age at all overpasses (A) combined, at the 15-m-wide overpass #1 (B) and #2 (C), and at the 30-m-wide overpass #3 (D) for 4 years following completion of overpasses and fencing (2011–2014), US Highway 93 mileposts 2–17, Arizona, USA.

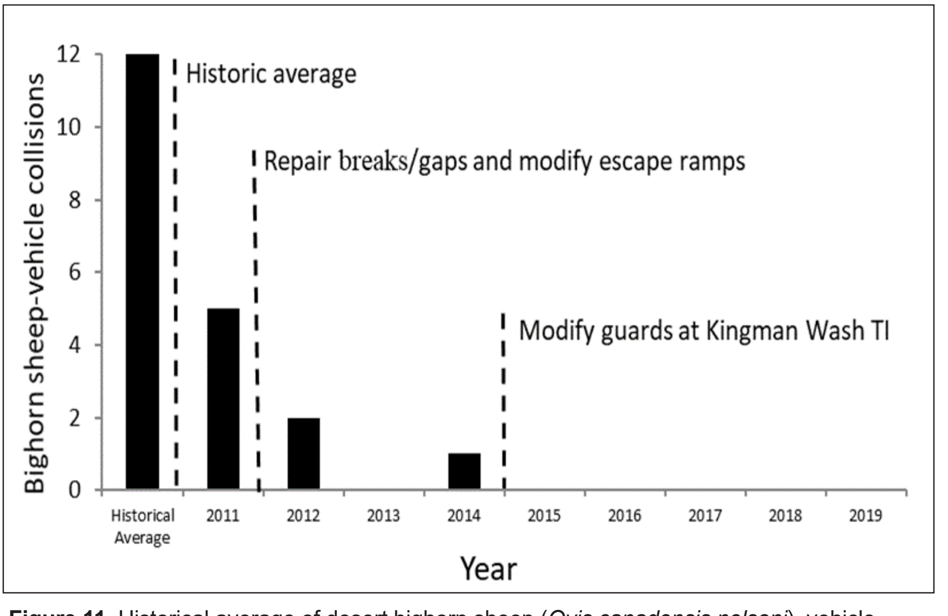

Figure 11. Historical average of desert bighorn sheep (*Ovis canadensis nelsoni*)–vehicle collision rates (Cunningham and Hanna 1992) compared to years 2011–2019, an additional 5 years beyond our wildlife crossing structure and global positioning system collar monitoring, and timeline of adaptive mitigation modifications made to improve project effectiveness, US Highway 93 mileposts 2–17, Arizona, USA. TI = Transportation Interchange.

Table 4. Desert bighorn sheep (*Ovis canadensis nelsoni*) overpass (OP) crossings and passage rates compared by sex and age class, and width (OP #1 and #2 are 15 m wide and OP #3 is 30 m wide), US Highway 93, Arizona, USA, 2011–2014.

Overall bighorn sheep crossings*						Overall bighorn sheep passage rates					
OP	Year 1	Year 2	Year 3	Year 4	Total	OP	Year 1	Year 2	Year 3	Year 4	Total
#1	53	576	661	878	2,168	#1	0.24	0.78	0.94	0.91	0.72
#2	41	1,094	684	467	2,286	#2	0.16	0.82	0.86	0.80	0.66
#3	120	481	389	417	1,407	#3	0.44	0.65	0.89	0.90	0.72
Total	214	2151	1734	1762	5,861	Mean	0.28	0.75	0.90	0.87	0.70
Ram crossings						Ram passage rates					
OP	Year 1	Year 2	Year 3	Year 4	Total	OP	Year 1	Year 2	Year 3	Year 4	Total
#1	53	342	437	317	1,149	#1	0.39	0.84	0.93	0.92	0.77
#2	29	220	173	106	528	#2	0.24	0.83	0.86	0.92	0.71
#3	46	131	60	95	332	#3	0.49	0.80	0.82	0.89	0.75
Total	128	693	670	518	2,009	Mean	0.37	0.82	0.87	0.91	0.74
Ewe crossings						Ewe passage rates					
OP	Year 1	Year 2	Year 3	Year 4	Total	OP	Year 1	Year 2	Year 3	Year 4	Total
#1	0	211	181	413	805	#1	0.00	0.73	1.00	0.90	0.66
#2	8	826	452	339	1,625	#2	0.09	0.83	0.87	0.78	0.64
#3	61	317	264	224	866	#3	0.36	0.64	0.89	0.90	0.70
Total	69	1,354	897	976	3,296	Mean	0.15	0.73	0.92	0.86	0.67
Juvenile crossings						Juvenile passage rates					
OP	Year 1	Year 2	Year 3	Year 4	Total	OP	Year 1	Year 2	Year 3	Year 4	Total
#1	0	23	39	143	205	#1	0.00	0.67	1.00	0.92	0.65
#2	4	37	55	12	108	#2	0.13	0.76	1.00	0.45	0.59
#3	13	41	63	98	215	#3	0.75	0.37	0.97	0.93	0.76
Total	17	101	157	253	528	Mean	0.29	0.60	0.99	0.77	0.66

* Thirty-three bighorn sheep excluded because of unknown sex.

verts generally increased over time, they only represent a very small subset of total sheep crossing at all of the structures combined. Crossings at the two monitored underpasses gradually increased from 53 crossings in one year in 2011 to 171 crossings in the final year (2014). Although use of the culverts was minimal overall, culvert use increased from only one crossing in year 1 (0.03 crossings/approach) to 67 crossings (0.43 crossings/approach) in year 2 and continued to increase in year 3 to 110 crossings (0.50 crossings/approach) before dropping back down to only 17 crossings (0.07 crossings/approach) in year 4 (Figure 10). Rams, ewes, and young appeared to adapt to the overpasses at a relatively similar rate (Table 4; Figure 11).

Passage rates and the odds of a successful crossing in year 1 were greater for the 30-m-wide overpass #3 (0.44 crossings/approach) compared to overpass #1 and #2, which were only 15 m wide (0.24 and 0.16 crossings/approach, respectively; OR = 2.87; 95% CI = 2.07 – 3.97, $P < 0.01$). This was followed by a reversal in year 2 with the chance of a successful crossing at the 15-m-wide overpasses exceeded that of the 30-m-wide overpass (OR = 2.29; 95% CI = 1.75 – 2.99, $P < 0.01$). However, years 3 (OR = 0.77; 95% CI = 0.49 – 1.23, $P = 0.27$) and 4 (OR = 1.48; 95% CI = 0.92 – 2.39, $P = 0.10$) showed no preference of overpass width, and by the end of the study, all 3 structures had passage rates within 5% of each other (Table 4; Figure 10).

Changes in vehicular collisions

Following completion of the wildlife crossings and fencing, we documented 8 sheep–vehicle collisions (2 rams and 6 ewes) from the beginning of 2011 through 2020, or 0.8 sheep–vehicle collisions/year. This is an overall 93.3% reduction from the average of 12 sheep–vehicle collisions per year documented by Cunningham and Hanna (1992). Seven of the 8 collisions occurred in years 1 (2011) and 2 (2012) with 1 collision documented from 2013 through 2020 (Figure 11). Additional reduction in sheep–vehicle collisions after the first year were likely because of the adaptive mitigation measures undertaken throughout the study.

Use of adaptive mitigation to improve mitigation success

We documented 5 sheep–vehicle collisions in the year immediately following the completion of the US 93 project. Additionally, the agencies we worked with to collect sheep–vehicle collision data documented regular occasions of sheep in the right-of-way during the first year. After visual inspection of these areas, we identified 4 probable locations where sheep may have been breaching the exclusionary fencing. These potential breach locations consisted of sections of cut fence, areas where sheep could get under the fence, a fence terminus at a cliff, the escape ramps (i.e., jump-outs), and 4 cattle guards.

Once identified, these breach points were repaired to prevent sheep from accessing the roadway. We also placed cameras at 2 single cattle guards and 6 of 30 escape ramps to monitor breaches at these locations. Our cameras documented 15 sheep entering the right-of-way at the ramps while 135 others used them in the proper direction to escape the right-of-way. Because we were only monitoring 20% (6/30) of the ramps in the study area, we assumed that ramp breaches were more common than we documented.

To address the right-of-way access points at the escape ramps, we added polyvinyl chloride pipe crossbars at varying heights and continued to monitor and adjust crossbars to determine the most effective height for reducing sheep access to the right-of-way while still allowing egress. Based on this monitoring, all 30 escape ramps were permanently modified in the first year post-construction by adding a horizontal metal bar approximately 50 cm above the ramp platform. We continued our camera monitoring at the escape ramps into 2019 and documented only 3 escape ramp breaches while 99 sheep successfully escaped at these locations.

At the 2 cattle guards we monitored with cameras, we confirmed that sheep were entering the right-of-way at single-wide cattle guards by either jumping over them or walking along the edge. From 2011 to 2015, our cameras recorded 124 instances where sheep accessed the right-of-way at the 2 single-wide cattle guards. Because we monitored only 2 of 4 cattle guards in the study area, these breaches likely occurred more often than we recorded. We installed single-wide cattle guards adjacent to each of the 4 existing single-wide guards to increase the width needed to jump over the guards. Additionally, we added a fence that excluded access to the edge of the cattle guards.

During our continued monitoring of the cattle guards from 2015 to 2019, when we removed the camera, we documented zero crossings of the cattle guards. The last documented sheep–vehicle collision in our study was in 2014. The repairs and improvements implemented through the adaptive mitigation approach incrementally decreased collisions along US 93 from MP 0–17 to zero collisions in the last 6 years of collision monitoring (2015–2019; Figure 11).

Discussion

Through the use of GPS collar data, camera trap monitoring, and sheep–vehicle collision tracking, we were able to document the success of mitigation efforts to reduce sheep–vehicle collisions and habitat fragmentation along US 93 in northwestern Arizona. Although initially successful, long-term monitoring of these mitigation efforts identified the need for additional modifications to maximize their efficacy.

Sheep used overpasses more than underpasses and culverts at the sizes of structures we monitored. This finding is consistent with earlier data in this area where only 32 ram crossings were documented at 3 underpasses in a 2-year period leading to the recommendation of overpasses (Bristow and Crabb 2008). Although initially the 30-m-wide overpass was used more than 15-m-wide overpasses, that difference did not hold over time, indicating a 15-m-wide overpass is adequate for desert bighorn sheep over a 4-lane divided highway at the width we evaluated.

Bristow and Crabb (2008) studied sheep crossings through underpasses along State Route 68 in the same area, and they reported higher use for 1 structure (Union Pass) located in what could be considered relatively high-quality habitat. Union Pass was built specifically for sheep rather than drainage purposes, compared to the other 2 underpasses to the west, which were designed more for hydrology than wildlife. Of the remaining 2 lesser-used structures, the one nearest to Union Pass (The Hole), although still in good sheep habitat, did not have a clear view all the way through the structure, which presumably led to lack of use.

The Arabian Mine underpass, the remaining structure monitored by Bristow and Crabb (2008), was simply a bridge over a large dry drainage in less optimal habitat. However, the minimal number of ram only crossings (32 total) at the underpasses documented by Bristow and Crabb (2008) appears disproportional in relation to the movements of GPS-collared sheep (12 rams and 13 ewes) captured during their study. Although both sexes traveled in close proximity to SR 68, only 12% of collared animals crossed the highway in the study area, and all of those animals were rams, accounting for 27% of the rams collared in that study (Bristow and Crabb 2008). This overrepresentation of rams is not a surprise given the higher propensity of rams to cross roads than ewes (Bleich et al. 2016). In contrast, our documentation of 5,861 (89.3%) bighorn sheep crossings at the 3 overpasses versus only 702 (10.7%) crossings at the other 5 structures supports the effectiveness of overpasses in facilitating bighorn sheep crossings. Our camera data combined with the GPS data documenting 68% of collared rams and 68% of collared ewes crossing US 93 throughout the study points to the effectiveness of overpasses in facilitating permeability of both sexes.

Inherently, prey species may prefer overpasses to underpasses because of the confined nature of most underpasses; however, some species that rely on eyesight to identify predators would be even more inclined to avoid crossing at places where vision is impaired. Clevenger and Barrueto (2014) documented a preference for more open structures or overpasses for deer, elk, and moose during their 17 years of research. Simpson et al. (2016) also noted a preference for overpasses compared to underpasses by mule deer (*Odocoileus hemionus*) when given the choice. Pronghorn, who use eyesight to identify predators, also appear to prefer overpasses to underpasses. Sawyer et al. (2012) evaluated use of overpasses and underpasses by mule deer and pronghorn and found that 93% of 19,290 pronghorn highway crossings occurred at overpasses versus 7% at adjacent underpasses.

Sheep live in relatively open treeless habitat and are able to stay elevated with an unobstructed field of view to stay vigilant for approaching predators. It is unclear if the same preference for overpasses would be consistent for the closely related Rocky Mountain bighorn sheep, which tends to reside in areas adjacent to more heavily treed habitat than the desert sub-species we studied. Although Clevenger and Barrueto (2014) were not able to confirm enough bighorn sheep crossings to recommend a wildlife crossing design for Rocky Mountain bighorn sheep, they did not document bighorn sheep using overpasses but regularly saw bighorn sheep use underpasses to descend to the highway to lick salt and return to escape terrain. Their findings highlight the need for additional research on species preference of wildlife crossings and species-specific considerations when designing wildlife crossings.

Sheep and potentially other prey species' preference for overpasses rather than underpasses may not be as disparate when the size of underpasses and underpasses increase to create a larger visual opening. McKinney and Smith (2007) noted sheep regularly used and could be observed sleeping in the shade of the 275-m-wide Sugarloaf Mesa Bridge less than a kilometer from our study area. Preferences for large underpasses 100 m wide over a 15-m overpass has been documented in preliminary data collected in Nevada about 6 km west of our study area (Arizona Game and Fish Department and Nevada Department of Transportation, unpublished data). In this particular case, their preference was likely due to the area beneath the large underpasses maintaining larger expanses of natural habitat than the underpasses evaluated in our study or Bristow and Crabb (2008).

Our study illustrated the value of using GPS collar data to both identify locations of wildlife crossings and fencing and to evaluate the effectiveness of roadway mitigation measures. In part, the overpasses we evaluated were successful because their placement was based on movements of GPS-collared sheep (McKinney and Smith 2007). If underpasses were to be placed in the same manner to take advantage of existing high use corridors, they may have seen more use but likely not to the level of the overpasses. Ultimately, GPS collar data showed that sheep movements across the newly constructed 4-lane divided highway increased substantially over the pre-construction 2-lane highway and these crossings were focused at the overpasses.

Long-term monitoring was crucial in our study to evaluate the efficacy, acclimation, and adoption of new overpasses. Other studies have documented adoption rates of new structures over time for deer (Sawyer et al. 2012, Sawyer et al. 2016, Cramer and Hamlin 2019), elk (Gagnon et al. 2011), pronghorn (Sawyer et al. 2016), and a variety of other species (Clevenger and Barrueto 2014). However, the length of time needed for animals to adapt to these structures can be dependent on whether the animals are resident or migratory (Dodd et al. 2007*b*, Simpson et al. 2016). Understanding the rate of learning helps in planning to maximize cost-effectiveness and design requirements for wildlife crossings. Our long-term monitoring effort provided an opportunity to work with ADOT to improve upon the mitigation measures initially constructed along US 93. Although sheep–vehicle collisions were reduced by 54.6% in year 1 compared to prior estimates, using this adaptive mitigation approach ultimately allowed for a complete elimination of collisions over the last 6 years of monitoring (McKinney and Smith 2007).

Ideally, the effectiveness of wildlife crossings would be evaluated with a Before-After-Control-Impact experimental design (Beier and Noss 1998, Clevenger and Sawaya 2010, Simmons et al. 2010, van der Grift et al. 2013). Additionally, long-term genetic monitoring may allow the detection of barriers to, or re-establishment of, gene flow. However, because transportation infrastructure is planned by other entities for other reasons, it is not always possible to achieve optimal study design in terms of replication, pre-construction monitoring, and identical treatments (i.e., crossing structure locations).

Despite the somewhat opportunistic nature of our study, we showed a substantial improvement in motorist safety and the ability to facilitate movement of sheep across a 4-lane highway with properly designed wildlife crossings and exclusionary fencing. The ability of sheep along US Highway 93 to safely access their entire range and resources on both sides of the roadway can help reduce the potential for detrimental effects caused by roads, including mortality and habitat fragmentation.

Management implications

Long-term monitoring of mitigation measures and wildlife–vehicle collision rates can provide valuable insight for species-specific design and inform adaptive mitigation opportunities to further increase effectiveness of mitigation. We documented the importance of the combination of ungulate exclusionary fencing and wildlife crossings, particularly overpasses, in reducing road mortality and maintaining habitat connectivity for desert bighorn sheep. We recommend: (1) using movement data gathered with GPS collars to facilitate identification of proper locations of wildlife crossings, particularly for species with minimal available road mortality data, (2) constructing 15–30-m-wide overpasses over 4-lane roads for sheep versus the smaller underpasses and culverts of the size we monitored, (3) using long-term monitoring to document effectiveness of new mitigation, and (4) addressing areas of concern identified through monitoring and document the outcome of those adaptive mitigation efforts.

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Associate Editor: S. Nicole Frey

Jeffrey W. Gagnon has worked for Arizona Game and Fish Department (AZGFD) for >25 years. He received his B.S. and M.S. degrees from Northern Arizona University, focusing on the effects of traffic volumes on ungulates. He is currently a statewide research biologist and the lead for AZGFD's Highways and Wildlife Connectivity program specializing on wildlife–highway interactions and habitat connectivity related projects. He specializes in implementation and evaluation of innovative solutions to mitigate wildlife–vehicle collisions and habitat fragmentation throughout Arizona and other neighboring states.

Scott C. Sprague is a wildlife specialist statewide supervisor for the Arizona Game and Fish Department (AZGFD), where he has worked since 2002. He got his B.A. degree from Colgate University and M.S. degree from Northern Arizona University, where he studied the effects of roads on the genetic population structure of northern Arizona pronghorn. He has been a core member of AZGFD's Highways and Wildlife Connectivity program since 2006 and has contributed to numerous projects across the southwest that focus on the relationships between anthropogenic infrastructure and wildlife movements.

Chad D. Loberger has been an Arizona Game and Fish research biologist for 17 years. During that time, he has had the opportunity to serve on multi-agency, inter-disciplinary teams that coordinate wildlife crossing structure implementation and monitoring activities on roadways in Arizona, Nevada, and New Mexico.

Susan R. Boe is a senior GIS analyst for the Arizona Game and Fish Department, where she worked for >30 years, retiring in 2023. She worked on a wide variety of projects, both terrestrial and aquatic, including numerous wildlife-highway interaction projects. She received her B.S. and M.S. degrees from the University of Minnesota – Duluth, with a focus on wetland ecology.

Kari S. Ogren is the warehouse supervisor for the Arizona Game and Fish Department (AZGFD). She worked in Contracts Branch as the image analysis specialist for the Highways and Wildlife Connectivity program. She received a B.S. degree in environmental biology from Grand Canyon University in December 1999 and has worked for AZGFD since 2002. She managed all still and video surveillance image data from numerous projects that assess wildlife permeability of roadways and functionality of mitigation components. She analyzed the image data from these and various other AZGFD wildlife projects for presence and behavior of detected wildlife.

Raymond E. Schweinsburg was a research program supervisor with Arizona Game and Fish Department (AZGFD) for >20 years before retiring in 2016. He received his Ph.D. degree from the University of Arizona. He conducted extensive wildlife research in the Canadian arctic, including studies on polar bears. During his time with AZGFD, he focused on enhancing wildlife habitat connectivity throughout Arizona.