The Journal of Wildlife Management 1–7; 2021; DOI: 10.1002/jwmg.22043

*Research Article*

# Mule Deer Migrations and Highway Underpass Usage in California, USA

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**ABSTRACT** Roadways may pose barriers to long-distance migrators such as some ungulates. Highway underpasses mitigate wildlife-vehicle collisions and can be an important management tool for protecting migration corridors. In northern California, 3 underpasses were built on United States Route 395 (Route 395) in Hallelujah Junction Wildlife Area (HJWA) in the 1970s for a migratory mule deer (*Odocoileus hemionus*) herd that had been negatively affected by highway traffic. To determine whether these underpasses were still reducing mule deer mortalities >40 years after construction, we investigated deer use of the underpasses from 2006–2019 using cameras, global positioning system (GPS) collars, and roadkill records. We used occupancy models, approximations of GPS-collared mule deer movement paths, and roadkill locations to estimate the highway crossing patterns of deer. From camera data, there was higher use of the underpasses by deer during migration (spring [Mar–Jun], fall [Oct–Dec]) than in summer (Jul–Sep), when only resident deer were present. Higher underpass usage occurred in the spring compared to fall migrations. Eleven of 21 GPS-collared migrating mule deer crossed Route 395. We estimated 30% of the crossings (by 7 of the 11 deer) occurred south of the underpasses where deer could easily access the highway because of short (1-m high) and deteriorating highway fencing. Roadkill data confirmed that deer-vehicle collisions were occurring south of the underpasses and at the underpasses. This was likely due to deteriorating infrastructure at the underpasses that allows wildlife access to the highway. Overall, our study indicated that although underpasses can provide safe passage for migratory deer decades (>40 yr) after their construction, deteriorating infrastructure such as fencing and gates can lead to wildlife mortalities on highways near underpasses. 

**KEY WORDS** highway, mule deer, *Odocoileus hemionus*, roadkill, underpass, wildlife-vehicle collisions.

Roadways affect wildlife via mortalities, fragmentation of movement corridors, and degradation of habitat (Jackson 2000, Trombulak and Frissell 2000, Huijser et al. 2008, Fahrig and Rytwinski 2009, Brunton et al. 2018). For migratory wildlife, roadways may impede annual migrations, particularly for large terrestrial species, such as ungulates (Lendrum et al. 2012, Sawyer et al. 2012, Seidler et al. 2015). Wildlife-vehicle collisions (WVCs) are also costly for humans, resulting in human fatalities and injuries, and an estimated economic cost of 8.4 billion dollars annually in the United States (Conover et al. 1995, Huijser et al. 2008).

To reduce WVCs and improve migration corridors across roadways, crossing structures (i.e., underpasses and overpasses) are an effective solution in many countries (Clevenger and Waltho 2000, Olsson et al. 2008, Smith et al. 2015, Sawyer et al. 2016*b*, Caldwell and Klip 2020). Researchers have reported that wildlife crossing structures are effective at reducing mortalities and improving permeability along wildlife corridors, particularly for large migratory species, such as mule deer (*Odocoileus hemionus*; Mata et al. 2008, Sawyer et al. 2012, Stewart 2015, Simpson et al. 2016). Mule deer migrations can range 15–200 km, and migration paths often cross developed areas and roadways (Sawyer and Kauffman 2011, Lendrum et al. 2012, Sawyer et al. 2016*a*). Mule deer exhibit fidelity to traditional migration routes (Monteith et al. 2011, Lendrum et al. 2013). Roadways that bisect traditional migration routes often have higher levels of deer-vehicle collisions during migration (Coe et al. 2015). Areas with high levels of WVCs are logical candidates for crossing structures (Sawyer et al. 2012, Simpson et al. 2016). Crossing structures, such as overpasses and underpasses, are successful at decreasing deer-vehicle collisions at migration corridors, and the combination of wildlife highway fencing and crossing structures is considered one of the most effective strategies to promote connectivity and reduce WVCs (Huijser et al. 2009, Sawyer et al. 2012). Highway fencing with insufficient height or length, however, can reduce the effectiveness of crossing structures (Huijser et al. 2016). Other factors that can affect crossing structure effectiveness include traffic volume, human use of crossing structures, predator-prey interactions, and crossing type and location (Clevenger and Waltho 2005, Gagnon et al. 2011,

Received: 1 October 2020; Accepted: 31 January 2021

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Sawyer et al. 2012, Barrueto et al. 2014, Caldwell and Klip 2020). Most existing research that assessed the effectiveness of crossing structures focused on the first 15 years of post-construction, with the majority focusing on the first 5 years (Clevenger and Waltho 2005, Gagnon et al. 2011, Sawyer et al. 2012, Barrueto et al. 2014). Research is lacking on the long-term effectiveness of crossing structures along migratory corridors, particularly identifying factors that may reduce effectiveness decades after construction.

In northern California, part of the Loyalton-Truckee mule deer herd migrates across United States Route 395 (Route 395) every spring (Mar–Jun) and fall (Oct–Dec). The Loyalton-Truckee herd is an interstate population with summer ranges in California and winter ranges in Nevada and California. The herd experienced high levels of highway mortality when crossing Route 395, and in the early 1970s the California Department of Transportation (CalTrans) and the California Department of Fish and Wildlife (CDFW, previously California Department of Fish and Game) identified the herd's migration route and areas of high deer mortality along the highway (Kahre 1980). In 1976, CalTrans widened the highway to a 4-lane divided highway and completed construction of 3 highway underpasses and highway fencing in what is now the Hallelujah Junction Wildlife Area (HJWA). Fencing was 2.4-m-tall metal mesh fencing that was roughly 6 km in length on both sides of the highway with 1-way exits for wildlife to leave the highway near underpasses, human and vehicle access gates near the underpasses, and 1-m-tall barbed wire fencing approximately 1.5 km south of the underpasses. The 1-way exits consisted of angled, horizontal metal bars that allowed deer and other mid-sized wildlife to exit, but not enter, the highway. In the few years following the completion of the underpasses, CDFW conducted track counts of migrating deer using the underpasses and assessed highway mortalities in the area (Kahre 1980). Kahre (1980) reported that about 500–1,500 deer were successfully migrating through the underpasses and reported an almost total elimination of highway deer mortalities (with known mortalities attributed to access gates being left open).

Our study documented mule deer migrations through the HJWA underpasses on Route 395 during 2006–2019, >40 years after the crossing structures were completed. Our objectives were to determine seasonal mule deer use of the underpasses, whether the underpasses were still effective in reducing deer-vehicle collisions, and whether they still promoted successful migrations of the Loyalton-Truckee herd. Based on field observations and previous research, we predicted that although the underpasses were still effective corridors for migrating mule deer, factors such as deteriorating fencing and 1-way exits around the underpasses may contribute to higher deer-vehicle collisions during migratory periods (Sawyer et al. 2012, Huijser et al. 2016).

## STUDY AREA

The HJWA (39°41′N 120°01′W) was a CDFW-owned 53.4-km$^2$ property in Sierra and Lassen counties, California (Fig. 1). The property was at 1,585 m in elevation and the terrain consisted of gentle slopes. We monitored collared deer in the area in 2006–2015 and monitored underpass use on Route 395 in HJWA in 2017–2019. The property was acquired by CDFW in 1989 for the benefit of migratory Loyalton-Truckee deer and became the HJWA in 1991. The CDFW purchased 7 additional parcels of surrounding areas up to 2019. Much of HJWA is bordered by federal lands owned by the United States Forest Service and Bureau of Land Management. Prior to 1991 and during the study period, portions of the area was grazed by livestock; it also sustained several wildfires. Extensive wildfires occurred at HWJA in 2007 and in 2020 that destroyed much of the area's natural vegetation, including bitterbrush (*Purshia* spp.). After the 2007 fire, cheatgrass (*Bromus tectorum*) invaded the burned areas and reduced suitable habitat for migratory deer as seen in many other western states (Clements and Young 1997).

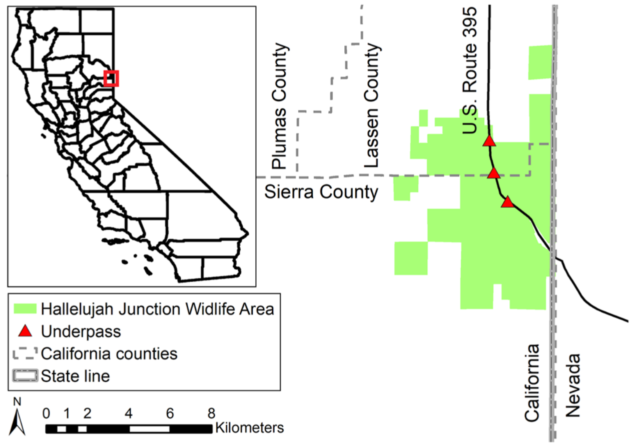


**Figure 1.** The location of 3 underpasses on United States Route 395 in Hallelujah Junction Wildlife Area, California, USA, during study period (2006–2019). The location of Hallelujah Junction Wildlife Area in relation to California counties is shown in the upper left corner.

Four creeks, some ephemeral and fed by snowmelt and natural springs, were the main natural sources of water on the HJWA: Long Valley, Evans Canyon, Balls Canyon, and Purdy creeks. The vegetation of the area was mostly sagebrush scrub (*Artemisia* spp.), cheatgrass, bitterbrush, juniper woodlands (western juniper [*Juniperus occidentalis*], Utah juniper [*J. osteosperma*]), wet meadows, and wetlands. The climate of HJWA was arid with a mean summer (20 Jun–22 Sep) temperature of 22.1°C and a mean winter temperature (21 Dec–19 Mar) of 3.8°C during 2017–2019. The average monthly summer precipitation during the study period was 2.5 cm and the average monthly winter precipitation was 4.4 cm (National Oceanic and Atmospheric Administration 2020). Spring was defined as 20 March–19 June and fall was defined as 23 September–20 December.

Wildlife present in the area included mule deer, pronghorn (*Antilocapra americana*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), black bear (*Ursus americanus*), coyote (*Canis latrans*), and California quail (*Callipepla californica*). The HJWA was seasonally open to the public for recreation (hunting, hiking, wildlife viewing) during July–February.

In May–October, cattle grazed in designated areas. Route 395 bisected the property from north to south; in the 1970s, 3 underpasses (~1.5 km apart) were built underneath the highway within HJWA. All the underpasses were about 120 m long, 5 m high, and 6 m wide. In the center of the underpasses, open atria allowed sunlight to pass through, resulting in vegetation growth. About 6 km of fencing was built on either side of the highway at the underpasses, with deer-proof (2.4-m high) fencing at the underpasses and lower (1-m high) fencing approximately 1.5 km south of the underpasses. Because of degrading fencing, wildlife could access the highway in several places. One-way exits near the underpasses also degraded, allowing wildlife to access the highway.

## METHODS

### Field Methods

Using 6 remote infrared cameras (model HC500; RECONYX, Holmen, WI, USA), we photographed deer moving through the 3 underpasses at HJWA. We deployed 4 of the cameras in June 2017 and 2 cameras in August 2017. The data used in this study ended June 2019, but data collection is ongoing. We set cameras within each entrance of the underpasses on posts about 50 cm above the ground. We checked camera batteries and replaced memory cards monthly. We set cameras to high sensitivity and to take 3 pictures (1 photo/second) every time movement was detected. The cameras had an infrared flash during low-light periods.

We used global positioning system (GPS) data from 26 adult female mule deer from the Loyalton-Truckee herd during 2006–2013; 5 of the GPS-collared deer were non-migratory, and we removed them from the analyses. We captured the mule deer via darting on their summer or winter ranges and fitted them with GPS collars (Iridium VHF collars models G2000, G2110B and D; Advanced Telemetry Systems, MN, USA) set to take fixes once every hour during spring (May–Jul) and fall (Nov–Dec) migrations and 1–2 times a day at other times for 1–2 years. All procedures involving wildlife species were approved by the CDFW and followed guidelines from the California Fish and Game Wildlife Restraint Handbook (Jessup et al. 2001).

We obtained Route 395 roadkill data from CalTrans for years 2015–2019, the California Roadkill Observation System (CROS) for years 2011–2019 (Waetjen and Shilling 2017), and the California Highway Patrol (CHP) wildlife-vehicle collision data for years 2015–2017. The data from CalTrans and CHP included highway mile or GPS coordinates during road checks. The CROS data were reported by the general public via the CROS smart phone application and were opportunistic sightings along the highway (Waetjen and Shilling 2017). All roadkill data included the date the roadkill was recorded and the species killed.

In 2019, we surveyed the highway and underpasses on foot. We focused on areas within 3 km of the underpasses and areas with high reported levels of roadkill. We recorded locations of deer tracks, established wildlife trails, and wildlife remains to document where wildlife crossed the highway.

### Analysis

We used single-species occupancy models (MacKenzie et al. 2002) to assess mule deer use of the underpasses using the unmarked package (Fiske and Chandler 2011) in Program R (version 3.5.1; R Core Team 2020). We used a subset of the camera data that excluded consecutive detections of the same individuals traveling in the same underpass within 30 minutes of first detection (Lazenby and Dickman 2013). We used only the detection probabilities, not the occupancy estimates, from the models because the cameras were too close together to meet the assumption of spatial independence (MacKenzie et al. 2002, Lazenby and Dickman 2013). We did not include population dynamics in our modeling because the underpasses were within the same geographic area (<1.5 km apart) and sampled at the same time (Royle and Nichols 2003); we assumed the population of mule deer using each underpass was the same.

To determine whether there were temporal or spatial patterns of mule deer underpass use, we modeled detections with the following covariates: ordinal day, season, migration season, year, underpass location (north, middle, or south), and camera side (east or west [i.e., side of the underpass the camera was in]). We defined migration seasons as the periods in spring or fall when the daily number of mule deer detections exceeded the maximum daily number of detections during the summer, when only resident mule deer were present in HJWA. These estimates of migratory seasons corresponded with peaks of high mule deer activity within the underpasses. We used Spearman's correlation coefficients for the detection covariates to confirm there was no collinearity (Spearman's $\rho > 0.70$, $P < 0.05$). We used second-order Akaike's Information Criterion ($AIC_c$) to compare models using the R package AICcmodavg (Burnham and Anderson 2002, Mazerolle 2019). We selected models with differences in $AIC_c$ ($\Delta AIC_c$) <4.0 as the best approximations for the data and calculated the predicted detection probabilities, regression coefficients ($\beta$), standard error, and *P*-values for the covariates using the unmarked package in R (Anderson 2008, Fiske and Chandler 2011).

We determined approximate movement patterns for the 21 collared migratory deer by plotting straight-line distances between starting GPS points and subsequent points using ArcMap (version 10.5; Esri, Redlands, CA, USA). We determined the approximate migration dates and paths from straight-line distances by visually inspecting the GPS data and plotting when collared deer departed from or arrived at their winter or summer ranges. We estimated where collared deer crossed Route 395 by determining where their straight-line distances between consecutive GPS points intersected the highway. Although straight-line distances did not represent exactly where deer crossed the highway, we considered it a reliable estimate because most of the highway crossings occurred during the migration when

GPS points were taken every hour. We then visually inspected the approximate locations of highway crossings and grouped crossings into 2 categories: crossings that were likely at the underpasses (<0.75 km from underpass) and crossings that were likely at the short fencing south of the underpasses (<0.75 km from shorter, 1-m highway fence). These distances corresponded with clusters of crossings around the underpasses and at the lower fencing south of the underpasses.

To further investigate where mule deer crossed Route 395, we also analyzed roadkill data from the area. We removed roadkill data from different sources at similar locations recorded within 7-day spans to ensure that duplicated reports were not included in the analysis. We visually inspected the locations of roadkills and grouped the locations into the same categories as the GPS-collar crossings (i.e., roadkill <0.75 km from the underpasses, and roadkill <0.75 km from the short fence).

## RESULTS

### Underpass Cameras

During 2017–2019 we detected 6,112 mule deer within underpasses at HJWA, with means of $682.83 \pm 35.16$ (SD) days of camera data per site (Table 1). We determined the approximate migration dates of mule deer: fall migrations occurred 27 October 2017–25 December 2017 and 24 October 2018–18 December 2018, and spring migrations occurred 22 March 2018–2 June 2018 and 16 March 2019–21 May 2019.

We compared 16 occupancy models to determine whether seasonal or location variables affected detection probabilities at camera sites; migration season, underpass location, and underpass side of the camera were among the most important predictive variables (Table 2). Predicted detection probabilities ranged 0.089–0.577 in the best supported model. Detection probabilities ($p$) were positively correlated with both spring migrations compared to fall 2017 (spring 2018: $p = 0.409-0.535$, $\beta = 0.476$, $P < 0.01$; spring 2019: $p = 0.450-0.577$, $\beta = 0.645$, $P < 0.001$; Fig. 2) and the southern underpass compared to the middle ($p = 0.139-0.577$, $\beta = 0.508$, $P < 0.001$). Detections were negatively correlated with summer seasons compared to fall 2017 (summer 2017: $p = 0.170-0.254$, $\beta = -0.742$, $P < 0.001$; summer 2018: $p = 0.167-0.250$, $\beta = -0.764$, $P < 0.001$) and both winter seasons compared to fall 2017 (winter 2017: $p = 0.089-0.139$, $\beta = -1.485$, $P < 0.01$; winter 2018: $p = 0.244-0.349$, $\beta = -0.286$, $P = 0.054$; Fig. 2). Detection probabilities had no significant correlation with underpass side of the camera ($p = 0.088-0.579$, $\beta = 0.022$, $P = 0.758$).

**Table 2.** Mule deer top-ranked (difference in second-order Akaike's Information Criterion, $\Delta AIC_c < 4$) single-species occupancy models at 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017–June 2019. We tested only the covariate effects on the detection probabilities ($p$) and not the occupancy ($\Psi$) of mule deer at camera sites. We also provide the model with no covariates (.), the number of model parameters ($K$), and the model weights ($w_i$).

| Models | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| $\Psi$(.) $p$(migration season + underpass location[a]) | 11 | 4,475.11 | 0.00 | 0.66 |
| $\Psi$(.) $p$(migration season + underpass location + underpass side[b]) | 12 | 4,476.40 | 1.33 | 0.34 |
| $\Psi$(.) $p$(.) | 2 | 4,858.80 | 383.69 | 0.00 |

[a] Underpass location = which underpass the camera sites were located in (middle, north, or south).

[b] Underpass side = the side of the underpasses where the camera sites were located (east or west).

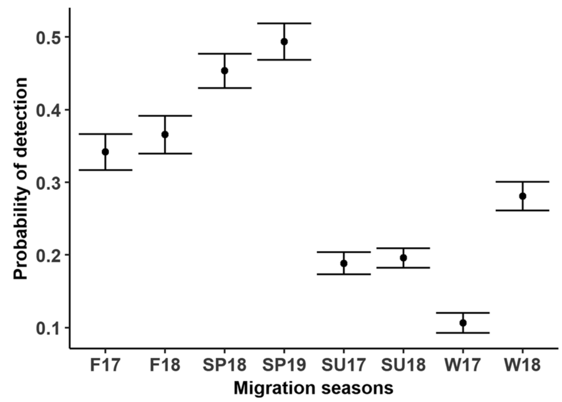


**Figure 2.** The probability of detection of mule deer during migratory and non-migratory seasons (fall 2017 = F17, fall 2018 = F18, spring 2018 = SP18, spring 2019 = SP19, summer 2017 = SU2017, summer 2018 = SU18, winter 2017–2018 = W17, winter 2018–2019 = W18) based on the occupancy model including the effects of migration seasons and underpass location. We collected data at 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017–June 2019. The error bars represent 95% confidence intervals.

**Table 1.** Detection rates (number of individuals detected divided by number of days camera was deployed) and number of detections of mule deer by migratory season at 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, 2017–2019.

| Migratory season | Dates | Detection rate | Number of detections[a] |
|---|---|---|---|
| Summer 2017 | 15 Jun 2017–26 Oct 2017 | 1.602 | 157 |
| Fall 2017 | 27 Oct 2017–25 Dec 2017 | 5.538 | 327 |
| Winter 2017 | 26 Dec 2017–21 Mar 2018 | 3.458 | 273 |
| Spring 2018 | 22 Mar 2018–02 Jun 2018 | 17.311 | 1,281 |
| Summer 2018 | 03 Jun 2018–23 Oct 2018 | 2.831 | 306 |
| Fall 2018 | 24 Oct 2018–18 Dec 2018 | 7.031 | 387 |
| Winter 2018 | 19 Dec 2018–15 Mar 2019 | 17.118 | 1,403 |
| Spring 2019 | 16 Mar 2019–21 May 2019 | 26.853 | 1,824 |

[a] Total detections excluded consecutive detections of the same individuals. Individuals were not uniquely identifiable; counts are a measure of the overall level of deer underpass usage, not number of unique individuals.

## GPS Collars and Roadkill Data

We recorded 25 fall and spring migrations during 2006–2010 and 2013–2015 for GPS-collared migratory mule deer. For fall migrations, the mean departure from summer range was 3 November ±22 days (SE) and mean arrival to winter range was 9 November ±23 days (SE). For spring migrations, the mean departure from winter range was 29 April ±14 days (SE) and the average arrival on summer range was 4 May ±15 days (SE).

Eleven of the collared deer crossed Route 395 a total of 70 times. More highway crossings occurred during fall and spring migrations (45 spring and 14 fall) compared to other times (11 winter and 0 summer; exact binomial test, $P < 0.001$). Twenty-one estimated crossing points intersected the highway at the shorter fence south of the underpasses, and the remaining crossing points were clustered around the underpasses (Fig. 3).

Thirty-two deer roadkills were reported near HJWA on Route 395 during 2011–2019. More roadkills were recorded during migrations (13 spring and 9 fall) than other times (6 winter and 4 summer; exact binomial test, $P = 0.05$). Roadkills were grouped near the underpasses and at the shorter fencing (Fig. 3).

From our field observations of the highway and underpasses during 2019, we observed mule deer tracks and remains at the highway side of fencing at the underpasses, where deer were likely getting through holes in the fencing and were subsequently unable to access the underpasses. We also observed deer tracks and trails leading to the highway at the shorter fencing south of the underpasses. Additionally, our cameras photographed deer on the highway side of the fence within the underpasses multiple times.

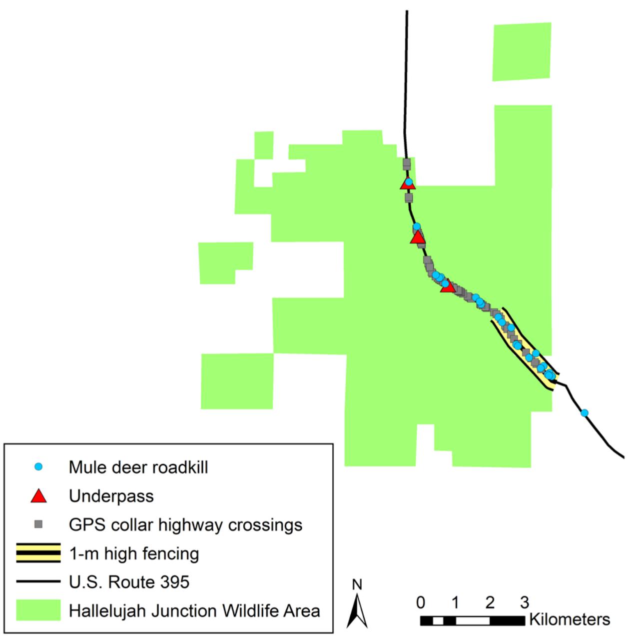


**Figure 3.** Locations of mule deer roadkills and estimated highway crossing points from 21 global positioning system (GPS)-collared mule deer on United States Route 395 near Hallelujah Junction Wildlife Area, Sierra County, California, USA. We collected roadkill data in 2011–2019 and the GPS-collar data is from 2006–2015.

# DISCUSSION

The underpasses at HJWA were still important crossing points for mule deer migrating across Route 395 over 40 years after they were constructed. But roadkill along the highway and non-underpass crossing routes were common near and within HJWA, supporting our hypothesis that deteriorating highway crossing infrastructure due to age and deferred maintenance led to an increase of deer-vehicle collisions near underpasses. During field visits, we observed deer tracks going towards the highway at several holes in the deer-proof highway fencing and lower (1-m high) highway fencing approximately 1 km south of the underpasses. Additionally, 1-way exits built near the underpasses were not functional for all wildlife species in the area, including mule deer. Future designs planned by CalTrans for Route 395 highway infrastructure at HJWA will focus on wildlife permeability in general, not just mule deer, and will include jump-out ramps, which effectively reduce highway mortalities for a variety of species (Siemers et al. 2015, Jensen 2018).

Underpass cameras and deer GPS data confirmed that there was higher use of the underpasses and increased Route 395 crossings during migrations compared to summer when only resident deer were present. Although 70% of estimated highway crossing points from GPS data were clustered near the underpasses, approximately 30% of the crossings were clustered at the shorter fence south of the underpasses, indicating this was a highly used highway crossing point. Additionally, during 2011–2019, 32 deer roadkills were recorded with most occurring during migrations (69%), at the underpasses, and at the southern lower fencing; the actual roadkill volume was likely 10–30 times higher because factors such as scavengers, injured deer moving off the highway, and sampling frequency decrease tallied roadkills (Slater 2002, Bager and da Rosa 2011, Zimmermann et al. 2013). Underpass cameras captured deer traveling through the underpasses on the highway side of the fencing, where they were unable to access the underpass and were subsequently trapped on the highway. Clusters of roadkill at the underpasses illustrated how deteriorating underpass structures contributed to WVCs. Because the shorter fence south of the underpasses was a well-used corridor in our study but was not reported as an area of WVCs by Kahre's (1980) study of the same underpasses, deer and other wildlife may have learned to penetrate the lower fencing and become accustomed to using this area as a crossing point over time (Kinsey 1976, Beringer et al. 2003). Habituation of mule deer to crossing structures and highway fencing can take several years; patterns of mule deer use of lower highway fencing may have increased years after construction (Sawyer et al. 2012). The differences in our roadkill results from Kahre's (1980) report may have been due to differences in methods and our ability to use modern sampling tools such as roadkill reporting smart phone applications.

Detection probabilities for deer within the underpasses during spring migrations were higher than during fall migrations. Our GPS-collar data confirmed that mule deer followed roughly the same migration routes in the spring and fall, as with other mule deer (Monteith et al. 2011, Sawyer and Kauffman 2011). We had expected that lower use of underpasses in the fall by deer may have been because nearby routes did not pass through the underpasses. Both GPS-collar data and roadkill data indicated that most of the non-underpass highway crossings during migration occurred during spring. This suggests that other factors may be contributing to less underpass use during fall migration, but incomplete roadkill data and few collared deer may have influenced our results. Lower fall migration underpass use could result if migrating mule deer used HJWA as a spring stopover where they would use both sides of Route 395 and thus exploit the underpasses more, or if fall hunting pressure discouraged deer from using the underpasses (Garrott et al. 1987, Kufeld et al. 1988, Kucera 1992, Kamei et al. 2010).

Our results indicated that although underpasses along migratory routes can effectively serve as highway crossing points for many decades and reduce WVCs, several factors can reduce their effectiveness. Deferred maintenance of crossing structures decades after construction can lead to higher WVCs around crossing structures because of deterioration of highway fencing, 1-way exits, and unfinished infrastructure. Highway fencing that is <2 m in height and <5 km long around crossing structures can contribute to WVCs (Huijser et al. 2016). There are plans by CalTrans to repair and update the highway infrastructure at HJWA to help reduce highway collisions for all species in the area, including mule deer. Continued monitoring in the area will allow us to determine whether these measures are successful in reducing WVCs and support additional use of the underpasses. Our study surveyed a small number of similarly constructed underpasses in a limited geographical area; therefore, further research is needed to determine whether these results apply to different types of crossing structures in a wider variety of settings.

## MANAGEMENT IMPLICATIONS

The underpasses in our study were used by mule deer during migrations immediately after construction and >40 years later, with similar numbers of spring deer detections (between 1,000–2,000), suggesting long-term effectiveness of the crossing structures. More roadkills and higher use of non-underpass crossings were facilitated by deterioration of underpass and fencing infrastructure and lower (1-m tall) highway fencing 1.5 km south of the underpasses. Therefore, we recommend managers ensure long-term maintenance of crossing structures and highway fencing to promote connectivity and reduce WVCs. Installing taller (>2 m) deer-proof highway fencing >2 km from crossing structures may also make the structures more effective.

## ACKNOWLEDGMENTS

For their contributions to the maintenance of cameras and tagging of photos, we thank C. S. McDonald Ryan, A. J. Meyer, L. E. Pilatti, and S. A. Thomas. We thank S. M. Holm for providing the GPS-collar data used. We also thank K. Kawsuniak and F. M. Shilling for providing roadkill data. This study was funded by the CDFW.

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