



## Research Article

# Wildlife Interactions within Highway Underpasses

MOLLY R. CALDWELL <sup>1</sup>, California Department of Fish and Wildlife, 1701 Nimbus Road, Gold River, CA 95670, USA  
 J. MARIO K. KLIP, California Department of Fish and Wildlife, 1701 Nimbus Road, Gold River, CA 95670, USA

**ABSTRACT** Highway underpasses are a common management tool used to lessen wildlife-vehicle collisions on roadways. Despite their widespread use, the effects of predator-prey interactions and human disturbances on wildlife within underpasses have not been well studied. To understand the effect of species interactions and human disturbances on wildlife traveling through underpasses, we analyzed camera data from 3 underpasses in Hallelujah Junction Wildlife Area, Sierra County, California, USA, from June 2017 to December 2018. We recorded 3,589 detections, which were predominately mule deer (*Odocoileus hemionus*), rodents, lagomorphs, California quail (*Callipepla californica*), bobcats (*Lynx rufus*), mountain lions (*Puma concolor*), and coyotes (*Canis latrans*). We used occupancy modeling and daily activity estimates to analyze species' spatial and temporal activity within the underpasses. Predator-prey interactions and human disturbances were among the most important factors that influenced wildlife travel through the underpasses. Mule deer avoided underpasses highly used by mountain lions, and mountain lions followed mule deer daily temporal activity patterns and seasonal activity patterns. These results indicate that predator-prey interactions influenced deer and mountain lion use of the underpasses. Coyotes favored underpasses and seasons with higher rodent and lagomorph presence, suggesting that the presence of prey was also important to coyote use of the underpasses. Coyotes, mountain lions, and bobcats all exhibited either temporal or spatial avoidance of human activity within the underpasses. California quail avoided predators within the underpasses and favored underpasses and times with high human activity. Our study suggests that underpass managers need to closely monitor the effect of predator-prey interactions and human activity on wildlife within underpasses to ensure these interactions do not discourage wildlife from using them. © 2019 The Wildlife Society.

**KEY WORDS** bobcat, California, California quail, coyote, highway underpasses, human disturbance, mountain lion, mule deer, predator-prey interactions, species interactions.

Wildlife-vehicle collisions on roads and highways are one of the foremost causes of wildlife mortalities and negatively affect many wildlife species (Trombulak and Frissell 2000, Huijser et al. 2008, Fahrig and Rytwinski 2009, Brunton et al. 2018). There were an estimated 300,000 to 2,000,000 wildlife-vehicle collisions (WVCs) in the United States annually as of 2008, and the economic costs of WVCs in the United States were estimated to be 8.4 billion dollars annually (Huijser et al. 2008). Roads also negatively affect many wildlife communities because of their contribution to the fragmentation of landscapes and destruction and degradation of habitat (Jackson 2000, Trombulak and Frissell 2000). The movement of many wildlife species, from small mammals to large carnivores, is often restricted by roads (Brody and Pelton 1989, Jackson 2000, Riley et al. 2006, Rico et al. 2007). As barriers to wildlife movement, roads can reduce gene flow between populations of species and affect migration and dispersal routes (Mansergh and

Scotts 1989, Riley et al. 2006, Shepard et al. 2008, Coe et al. 2015, Haddad et al. 2015, Seidler et al. 2015). Further, the survival of many endangered and threatened species is negatively affected by roadways (Maehr et al. 1991, Huijser et al. 2008, Brunton et al. 2018, Lepczyk et al. 2019).

Wildlife crossing structures (WCS) such as overpasses and underpasses are increasingly used to provide wildlife with a safe passage across roadways (Smith et al. 2015). They decrease the risk of WVCs and increase the permeability of roadways for many wildlife communities (Smith et al. 2015). Researchers have reported that different variables such as structural features, anthropogenic activity, and species interactions influence the usage of WCSs by wildlife (Clevenger 1998, Clevenger and Waltho 2005, Gagnon et al. 2011, Alonso et al. 2014, Barrueto et al. 2014). Human usage and vehicle traffic volume of WCSs can influence the use of WCSs by many ungulates and large carnivores, with most species being highly affected by human foot traffic through WCSs (Clevenger 1998, Grilo et al. 2008, Barrueto et al. 2014). Although less studied, predator-prey interactions also affect wildlife movement through WCSs (Mata et al. 2015). As enclosed travel

Received: 11 July 2019; Accepted: 1 November 2019

<sup>1</sup>E-mail: Molly.Caldwell@Wildlife.ca.gov

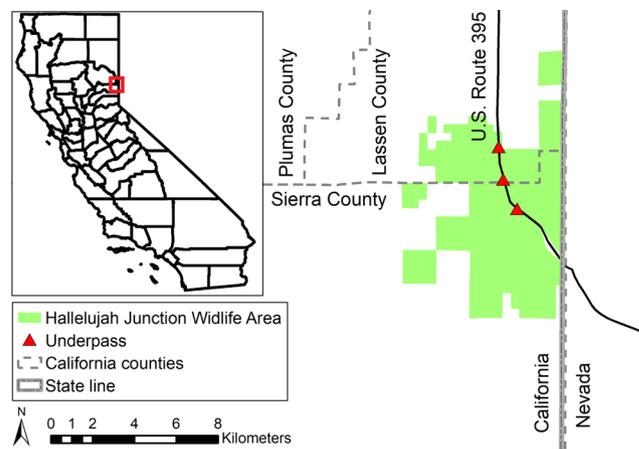
corridors, WCSs have been predicted to be used by predators to ambush prey, which could result in WCS avoidance by prey species and altered behaviors and population dynamics of predator and prey species living near roads (Foster and Humphrey 1995, Little et al. 2002, Mata et al. 2015). Contrasting evidence supports this theory, with some researchers reporting that predators use WCSs frequented by prey more often than expected by chance and others reporting no evidence that prey movements affect predator behavior at WCSs (Ford and Clevenger 2010, Mata et al. 2015). A limited number of studies have also concluded that prey such as deer (*Odocoileus* spp.), elk (*Cervus canadensis*), and small mammals avoid using WCSs that are also used by predators (Foster and Humphrey 1995, Clevenger and Waltho 2000). There is also limited information on intraguild species interactions within WCSs, such as carnivore avoidance of WCSs used by other carnivore species. Increased monitoring of wildlife interactions within WCSs is needed to determine how predator-prey interactions and intraguild species interactions affect wildlife movement through these corridors.

The objectives of our study were to document wildlife use of 3 underpasses located on United States Route 395 in Hallelujah Junction Wildlife Area (HJWA), Sierra County, California, USA, and evaluate the effect of location, season, year, time of day, human usage, and interspecies interactions on the spatial and temporal use of underpasses by species. The interspecies interactions we focused on in this study included predator-prey interactions and intraguild interactions between carnivores. Based on previous research by Clevenger and Waltho (2000), Barreto et al. (2014), and Mata et al. (2015), we predicted that human usage of underpasses and interspecies interactions would affect the spatial and temporal usage of underpasses by species. The predators documented in the study included mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) and the prey species included were mule deer (*Odocoileus hemionus*), California quail (*Callipepla californica*), rodents, and lagomorphs.

## STUDY AREA

We monitored underpasses in HJWA Sierra County, California (39°41'N 120°01'W) from June 2017 to December 2018. The California Department of Fish and Wildlife (CDFW) owns HJWA, which is a 53.4-km<sup>2</sup> property (Fig. 1). The CDFW first acquired part of the HJWA in 1989 and later purchased 6 subsequent acquisitions of surrounding areas up to 2005 and 1 recent acquisition in 2019. The Fish and Game Commission declared HJWA a wildlife area in 1991. Before becoming a wildlife area, there were several historical wildfires and extensive livestock grazing on the land. In 2007, a large wildfire occurred in the area and destroyed many areas of bitterbrush (*Purshia* spp.); cheatgrass (*Bromus tectorum*) grew in these areas and reduced the habitat suitability of the burned areas for migrating deer.

The area was 1,585 m above sea level with gentle slopes. Vegetation in the area was dominated by bitterbrush,



**Figure 1.** Overview of study site in Hallelujah Junction Wildlife Area, California, USA, and its location in relation to California counties and the California-Nevada state line. United States Route 395 is depicted with the locations of 3 underpasses. We placed 2 cameras within each underpass, for 6 camera sites, and collected data June 2017 through December 2018. The location of the study area in relation to all California counties is in red in the upper left corner.

big sagebrush (*Artemisia tridentata*), juniper woodlands (western juniper [*Juniperus occidentalis*] and Utah juniper [*Juniperus osteosperma*]), wet meadows, and wetlands. Long Valley Creek ran through the wildlife area from north to south and 3 other major creeks (Evans Canyon, Balls Canyon, and Purdy creeks) branched off Long Valley Creek on the west side. The study area had an arid climate with seasonal variations in temperature and precipitation. The mean summer (20 Jun–22 Sep) temperature during the study period was 23.6°C with total summer precipitation of 7.67 cm for 2017–2018. The mean winter (21 Dec–19 Mar) temperature was 5.2°C with winter snowfall of 74.6 cm for 2017–2018 (National Oceanic and Atmospheric Administration 2019).

Part of the Loyalton-Truckee mule deer herd migrated through the area each spring (19 Mar–20 Jun) and fall (23 Sep–21 Dec). Many other species used the area including mountain lion, bobcat, black bear (*Ursus americanus*), coyote, American badger (*Taxidea taxus*), pronghorn (*Antilocapra americana*), California quail, various rodents and lagomorphs, and birds. The area was surrounded by 1-m fencing and was closed to public entry from 1 February through 30 June. Hunting, hiking, and wildlife viewing were permitted in the area during the rest of the year. Cattle were also herded through the area each year and grazed on cheatgrass in designated, fenced areas from the beginning of May to the end of October. United States Route 395 ran through the center of the property from north to south. Three highway underpasses were constructed underneath United States Route 395 in the mid-1970s and about 6 km of deer-proof fencing were added to each side of the highway above the underpasses. The underpasses were concrete passageways underneath the highway with openings on the east and west sides of the highway (Fig. 2). Fencing (2.4 m high) on the sides of the underpasses helped funnel wildlife through them, but degradation of the fences allowed wildlife



**Figure 2.** One of 3 highway underpasses on United States Route 395 in Hallelujah Junction Wildlife Area, California, USA, February 2019. The underpasses all had a similar structure, with an open atria in the center and fencing on the sides. The underpasses were approximately 120 m in length, 5 m high, and 6 m wide.

to access the highway in some areas. The underpasses were each approximately 120 m in length, 5 m high, and 6 m wide and were about 1.5 km apart from each other. They included open atria in the highway median and vegetation grew in these openings. These atria contributed to a greater degree of perceived openness of the underpasses by wildlife species than completely enclosed underpasses.

## METHODS

### Camera Trapping

We sampled species moving through the 3 underpasses using remote infrared cameras (model HC500; RECONYX, Holmen, WI, USA). We deployed 4 of the cameras on 15 June 2017 in the northern and middle underpasses, and we deployed 2 cameras on 16 August 2017 in the southern underpass. The data collected ended 13 December 2018 for all cameras. We set 6 cameras in the underpasses, 1 within each entrance. We set them on wooden posts on the sides of the underpasses, approximately 50 cm above the ground. We checked each camera to ensure that they detected movement on the far side of the underpasses. We removed vegetation that would trigger the cameras or blocked the cameras' views. We checked camera batteries and replaced memory cards monthly. We set cameras to high sensitivity and to trigger every time movement was detected. At night, the cameras had an infrared flash when triggered. Additionally, we set the cameras to take 3 pictures/trigger with a 1-second interval between pictures. All procedures involving wildlife species were approved by the CDFW.

### Analysis

To prevent the double-counting of individuals triggering both cameras within the underpasses, we created a data set with the second detection of individuals of the same species (i.e., unduplicated data set) traveling in same underpass and within 30 minutes of the first detection removed (Ridout and Linkie 2009). Also, for all analyses we created 2 groups of similar species: rodents and lagomorphs (squirrels [*Otospermophilus* spp. and *Sciurus* spp.], chipmunks [*Tamias* spp.], cottontail rabbits [*Sylvilagus* spp.], and black-tailed jack rabbits [*Lepus californicus*]) and birds (all birds detected other than California quail, which included birds in the orders Passeriformes and Strigiformes).

We fitted single-species occupancy models in the methods of MacKenzie et al. (2002) to the unduplicated data set using the unmarked package (Fiske and Chandler 2011) in the program R (version 3.5.1, [www.r-project.org](http://www.r-project.org), accessed 20 Sep 2018) to estimate detection probabilities of the most abundant species at the camera sites. We used single-species occupancy models rather than multi-season or multi-species models because we had only 3 study sites. We did not use the occupancy estimates from the models because the sites were too close together to assume spatial independence (Legendre 1993, MacKenzie et al. 2002, Lazenby and Dickman 2013). Although species' population sizes near camera sites can affect their detection probabilities, we did not document population sizes or include them in our occupancy models because the underpasses were close together (within 1.5 km), within the same land cover type, and sampled at the same time (Royle and Nichols 2003). Therefore, we assumed that the population dynamics of species were the same at each camera site and would not bias the results because the species using each underpass were likely from the same populations in the vicinity of HJWA.

The detection covariates we used were ordinal day, season, year, species detection rates, human disturbances, location of the camera site, and underpass side of the camera site (Table 1). The species detection rates were the number of occurrences of a species at a camera site divided by the number of camera days at that site. We used the data without duplicates removed to calculate the species detection rates to correctly estimate the use of each site by the species. We used only species detection rates with known predator-prey interactions and possible carnivore competition interactions in the models. We included the location and underpass side of the sites in the models to account for any small-scale differences in habitat characteristics, appearance, or distance to resources of the underpasses at each site that might affect species detection probabilities. Prior to fitting models, we calculated Spearman's correlation coefficients for all the covariates to ensure collinearity was not an issue (Spearman's  $\rho > 0.70$ ,  $P < 0.05$ ). Mountain lion and California quail detection rates were correlated ( $\rho = 0.83$ ,  $P < 0.05$ ), and we removed California quail detection rates from the analysis. Additionally, we did not use

**Table 1.** Summary of the detection covariates included in single-species occupancy models as potential variables affecting detection probabilities for California quail, rodents and lagomorphs, coyotes, bobcats, mountain lions, and mule deer. We collected data from 6 camera sites within 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018.

Variable	$\bar{x}$	SE	Description
Bobcat detection rate	0.043	0.053	Number of bobcats detected at each camera divided by the number of camera days.
California quail detection rate	0.041	0.051	Number of quails detected at each camera divided by the number of camera days.
Coyote detection rate	0.049	0.043	Number of coyotes detected at each camera divided by the number of camera days.
Human disturbance detection rate	0.060	0.019	Sum of number of humans, all-terrain vehicles, and domestic dogs detected at each camera divided by the number of camera days.
Mountain lion detection rate	0.014	0.012	Number of mountain lions detected at each camera divided by the number of camera days.
Mule deer detection rate	1.420	0.780	Number of deer detected at each camera divided by the number of camera days.
Rodent and lagomorph detection rate	0.190	0.120	Number of rodents and lagomorphs detected at each camera divided by the number of camera days.
Location			Defined by location of underpass as middle, south, or north.
Side			Defined by location of camera within the underpass as east or west.
Ordinal day			Ordinal date of each camera day. Range of 1–365.
Season			Season of each camera day (summer, fall, winter, spring).
Year			Yr of each camera day (2017 or 2018).

mountain lion detection rates in the California quail occupancy models. We identified collinearity issues between mountain lion detection rates and location and between rodent and lagomorph detection rates and location during the fitting of the models, and we removed location from the analyses including both rodent and lagomorph or mountain lion detection rates and location.

We compared the models using a second-order Akaike's Information Criterion ( $AIC_c$ ), using the R package *AICcmodavg*, to correct for biases of models in the candidate sets (Burnham and Anderson 2002, Mazerolle 2019). We considered models with differences in  $AIC_c < 4.0$  ( $\Delta AIC_c < 4.0$ ) as the best approximations for the data (Anderson 2008). For each of the models considered, we calculated the predicted detection probabilities, regression coefficients ( $\beta$ ), standard error, and  $P$ -values for the covariates using the *unmarked* package in R (Fiske and Chandler 2011). The models we used to predict detection probabilities were in the form of the following equation:

$$\text{logit}(p_{ij}) = \beta_0 + \beta_1(\text{covariate } 1)_j + \beta_1(\text{covariate } 2)_j + \dots + \beta_n(\text{covariate } n)_j,$$

where *logit* is the logarithm of the odds,  $p_{ij}$  is the detection probability of species  $i$  at site  $j$  and covariates 1 through  $n$  are the values of each covariate used in the model at site  $j$ .

To estimate the temporal use of underpasses, we fitted kernel density functions to the detection times from the unduplicated data for the most abundant species (detections >25) in the methods of Ridout and Linkie (2009) with the *overlap* package in R. We calculated the overlap between 2 kernel density daily activity estimations with the  $\hat{\Delta}_4$  method for sample sizes >50 and the  $\hat{\Delta}_1$  method for sample sizes <50 using the *overlap* package in R (Ridout and Linkie 2009). We computed the 95% confidence intervals of the overlap (i.e., coefficient of overlap) between kernel density estimations using the bootstrap method of Ridout and Linkie (2009) with 1,000 bootstrap samples. We considered

coefficients of overlap without overlapping confidence intervals as significantly different.

## RESULTS

We collected an average of  $526 \pm 31$  (SD) days of camera data per site. We captured 3,589 unduplicated species detections, which were predominately mule deer, rodents and lagomorphs, and coyotes (Table 2).

We used single-species occupancy models to analyze detection probabilities of California quail, rodents and lagomorphs, mule deer, coyote, bobcat, and mountain lion. We compared 15 models for California quails. Their predicted detection probabilities for each camera site from the supported model (Table 3) ranged from 0.002–0.126. Their detection probabilities increased in summer ( $p = 0.013$ – $0.126$ ;  $\beta = 0.738$ ,  $P < 0.01$ ) and decreased in winter ( $p = 0.002$ – $0.026$ ;  $\beta = -0.958$ ,  $P < 0.05$ ) compared to fall ( $p = 0.006$ – $0.064$ ). California quail detection probabilities were positively correlated to human disturbance

**Table 2.** Summary of species detected at 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018.

Common name	Number detected
Birds <sup>a</sup>	18
California quail	105
Snake	1
Rodents and lagomorphs	409
Human	116
American badger	3
Raccoon ( <i>Procyon lotor</i> )	7
Striped skunk ( <i>Mephitis mephitis</i> )	1
Black bear	3
Coyote	123
Domestic dog	11
Bobcat	83
Mountain lion	29
Mule deer	2,661
Domestic cattle	5
Pronghorn	3
All-terrain vehicle	11
Total	3,588

<sup>a</sup> Bird species in the orders Passeriformes and Strigiformes.

**Table 3.** Top-ranked single-species occupancy models tested to estimate the detection probabilities ( $p$ ) of California quail, rodents and lagomorphs, coyotes, bobcats, mountain lions, and mule deer at 6 camera sites within 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018. We ranked models by the second-order Akaike's Information Criterion (AIC<sub>c</sub>) and considered models with a difference in AIC<sub>c</sub> ( $\Delta$ AIC<sub>c</sub>) < 4 to be supported. We evaluated covariate effects only on the detection probabilities and not the occupancy ( $\Psi$ ) of the sites by species. We also provide the models with no covariates (.) as comparison, the number of model parameters ( $K$ ), and the model weights ( $w_i$ ).

Models by species <sup>a</sup>	$K$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
California quail				
$\Psi(.) p(\text{season} + \text{human disturbance DR} + \text{side})$	8	693.36	0.00	1.00
$\Psi(.) p(.)$	2	754.37	115.01	0.00
Rodents and lagomorphs				
$\Psi(.) p(\text{season} + \text{year} + \text{mountain lion DR})$	7	1,809.59	0.00	0.86
$\Psi(.) p(\text{season} + \text{year} + \text{coyote DR})$	7	1,813.22	3.63	0.14
$\Psi(.) p(.)$	2	2,001.11	191.52	0.00
Coyote				
$\Psi(.) p(\text{season} + \text{year} + \text{rod-lag DR})$	7	722.44	0.00	0.77
$\Psi(.) p(\text{season} + \text{year} + \text{rod-lag DR} + \text{human disturbance DR})$	8	725.21	2.77	0.19
$\Psi(.) p(.)$	2	816.78	94.34	0.00
Bobcat				
$\Psi(.) p(\text{season} + \text{year} + \text{mountain lion DR})$	7	460.96	0.00	0.88
$\Psi(.) p(.)$	2	DNC <sup>b</sup>		
Mountain lion				
$\Psi(.) p(\text{season} + \text{year} + \text{bobcat DR})$	7	252.57	0.00	0.45
$\Psi(.) p(\text{season} + \text{year} + \text{mule deer DR})$	7	252.89	0.32	0.38
$\Psi(.) p(\text{season} + \text{year} + \text{human disturbance DR})$	7	256.01	3.44	0.08
$\Psi(.) p(.)$	2	DNC		
Mule deer				
$\Psi(.) p(\text{season} + \text{year} + \text{mountain lion DR})$	7	3,388.21	0.00	0.94
$\Psi(.) p(.)$	2	3,590.44	202.23	0.00

<sup>a</sup> DR = detection rate (defined as number of species detections at each camera divided by the number of total camera days), rod-lag = species in the orders Rodentia and Lagomorpha, human disturbance = the combined detections of humans, domestic dogs, cattle, and all-terrain vehicles.

<sup>b</sup> The model did not converge.

detection rates ( $\beta = 37.620$ ,  $P < 0.001$ ; Fig. 3A). Their detection rates were also positively correlated with the west side of the underpasses ( $p = 0.005$ – $0.126$ ;  $\beta = 1.559$ ,  $P < 0.001$ ) compared to the east side ( $p = 0.002$ – $0.041$ ).

Predicted detection probabilities for rodents and lagomorphs from the supported models (Table 3) ranged from 0.020–0.478 (17 models compared). Their detection probabilities decreased in 2018 ( $p = 0.030$ – $0.196$ ;  $\beta = -0.762$ ,  $P < 0.001$ ) compared to 2017 ( $p = 0.062$ – $0.344$ ). Detection probabilities of rodents and lagomorphs increased in spring ( $p = 0.145$ – $0.344$ ;  $\beta = 1.134$ ,  $P < 0.001$ ) and decreased in winter ( $p = 0.030$ – $0.087$ ;  $\beta = -0.569$ ,  $P < 0.01$ ) compared to fall ( $p = 0.052$ – $0.144$ ). Their detection probabilities were positively correlated with mountain lion detection rates ( $p = 0.030$ – $0.344$ ;  $\beta = 11.800$ ,  $P < 0.05$ ) and coyote detection rates ( $p = 0.020$ – $0.478$ ;  $\beta = 10.890$ ,  $P < 0.001$ ). Detections of rodents and lagomorphs were similar between the duplicated and unduplicated data sets (only 35% of the unduplicated

detections were duplicated), showing that they were not detected on the other end of the underpass in most detection events.

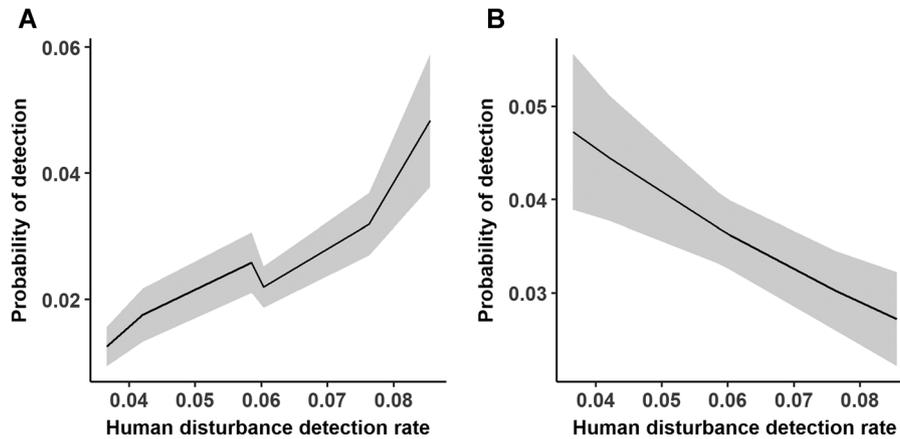
Predicted mule deer detection probabilities from the supported occupancy models (Table 3; 19 models compared) ranged from 0.096–0.498. There were no significant changes in mule deer detection probabilities by year ( $P = 0.666$ ). Mule deer detection probabilities increased in the spring ( $p = 0.300$ – $0.502$ ;  $\beta = 0.690$ ,  $P < 0.001$ ) and decreased in winter ( $p = 0.096$ – $0.199$ ;  $\beta = -0.698$ ,  $P < 0.001$ ) compared to fall ( $p = 0.175$ – $0.333$ ). Deer detection probabilities were negatively correlated with mountain lion detection rates ( $\beta = -25.860$ ,  $P < 0.001$ ; Fig. 4A).

Coyote predicted detection probabilities from the supported occupancy models (Table 3) ranged from 0.005–0.151 (20 models compared). Coyote detection probabilities decreased in 2018 ( $p = 0.005$ – $0.063$ ;  $\beta = -0.880$ ,  $P < 0.001$ ) compared to 2017 ( $p = 0.012$ – $0.139$ ). Their detection probabilities increased in spring ( $p = 0.011$ – $0.139$ ;  $\beta = 0.839$ ,  $P < 0.050$ ) and summer ( $p = 0.011$ – $0.136$ ;  $\beta = 0.815$ ,  $P < 0.010$ ) compared to fall ( $p = 0.005$ – $0.065$ ). Coyote detections were positively correlated with rodent and lagomorph detection rates ( $\beta = 5.172$ ,  $P < 0.001$ ; Fig. 4B) and negatively correlated with human disturbance detection rates ( $\beta = -21.120$ ,  $P < 0.01$ ; Fig. 3B).

Bobcat detection probabilities ranged from 0.001–0.067 in the supported model (Table 3; 19 models compared). Bobcat detection probabilities decreased in year 2018 ( $p = 0.001$ – $0.027$ ;  $\beta = -0.944$ ,  $P < 0.01$ ) compared to year 2017 ( $p = 0.002$ – $0.067$ ). Their detection probabilities were positively correlated with mountain lion detection rates ( $p = 0.001$ – $0.067$ ;  $\beta = 39.180$ ,  $P < 0.01$ ).

Mountain lion predicted detection probabilities from the supported models (Table 3) ranged from 0–0.036 (26 models compared). Their detection probabilities increased in 2018 ( $p = 0.001$ – $0.036$ ;  $\beta = 1.258$ ,  $P < 0.05$ ) compared to 2017 ( $p = 0$ – $0.010$ ). Mountain lion detection probabilities decreased in winter ( $p = 0$ – $0.004$ ;  $\beta = -2.295$ ,  $P < 0.05$ ) compared to fall ( $p = 0.004$ – $0.036$ ). Their detection probabilities were positively correlated with bobcat detection rates ( $p = 0$ – $0.036$ ;  $\beta = 8.170$ ,  $P < 0.05$ ) and negatively correlated with mule deer detection rates ( $p = 0$ – $0.027$ ;  $\beta = -0.664$ ,  $P < 0.05$ ). Mountain lion detection probabilities were not significantly correlated with human disturbance detection rates ( $P = 0.170$ ).

The coefficients of overlap ( $\Delta$ ) for species' kernel density daily activity patterns showed a large variance (0.076–0.861) in the daily temporal activity overlap of different species (Fig. 5). Bobcat coefficients of overlap with coyotes ( $\Delta = 0.585 \pm 0.114$ ) and mountain lions ( $\Delta = 0.642 \pm 0.127$ ) were higher than their coefficients of overlap with humans ( $\Delta = 0.241 \pm 0.055$ ), rodents and lagomorphs ( $\Delta = 0.259 \pm 0.053$ ), and California quail ( $\Delta = 0.076 \pm 0.100$ ; Fig. 5). The coyote coefficient of overlap with mountain lions ( $\Delta = 0.642 \pm 0.127$ ) was higher than their coefficients of overlap with humans ( $\Delta = 0.444 \pm 0.094$ ) and California quail ( $\Delta = 0.092 \pm 0.066$ ). Coyote coefficients of overlap with bobcats ( $\Delta = 0.585 \pm 0.114$ ), humans ( $\Delta = 0.444 \pm 0.094$ ), and rodents and lagomorphs



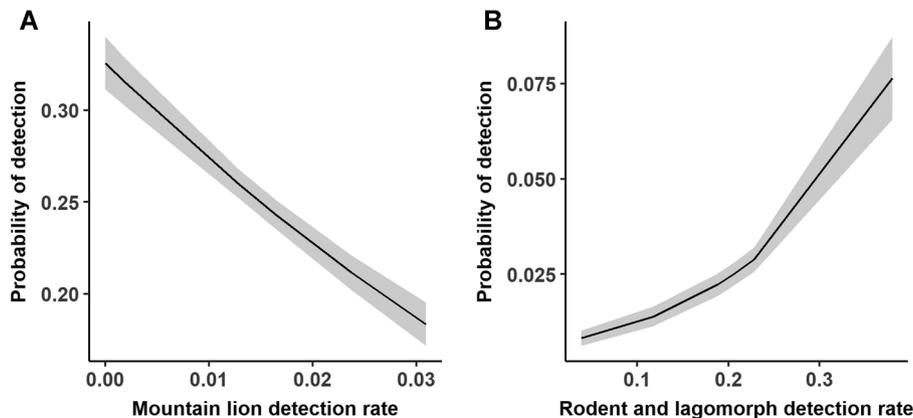
**Figure 3.** The effects of human disturbance detection rates (number of humans, all-terrain vehicles, and cattle detected at a camera site divided by number of camera days) on predicted probabilities of detection for A) California quail and B) coyote at 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018. Frame A displays the predicted effects of human disturbance on California quail detection probabilities based on the occupancy model including the effects of season, human disturbance detection rate, and underpass side on detection probability. Frame B displays the predicted effects of human disturbance on coyote detection probabilities based on the occupancy model including the effects of season, year, rodent and lagomorph detection rate, and human disturbance detection rate on detection probability. The 95% confidence intervals are in gray. California quail exhibited preference of camera sites with higher human disturbance, whereas coyotes exhibited avoidance of camera sites with higher human disturbance.

( $\Delta = 0.606 \pm 0.094$ ) were higher than their overlap with California quail ( $\Delta = 0.092 \pm 0.066$ ). Mountain lion coefficients of overlap with mule deer ( $\Delta = 0.703 \pm 0.072$ ), coyotes ( $\Delta = 0.750 \pm 0.142$ ), and bobcats ( $\Delta = 0.642 \pm 0.127$ ) were higher than their coefficients of overlap with humans ( $\Delta = 0.392 \pm 0.078$ ), rodents and lagomorphs ( $\Delta = 0.319 \pm 0.081$ ), and California quail ( $\Delta = 0.288 \pm 0.091$ ). Despite the high coefficient of overlap between mountain lions and deer, the periods exhibiting the highest densities of mule deer coincided with periods with the lowest densities of mountain lions (Fig. 6). The California quail coefficient of overlap with humans ( $\Delta = 0.861 \pm 0.094$ ) was higher than their coefficients of overlap with mountain lions ( $\Delta = 0.288 \pm 0.091$ ), bobcats ( $\Delta = 0.076 \pm 0.100$ ), and coyotes ( $\Delta = 0.092 \pm 0.066$ ). The rodent and lagomorph coefficient of overlap with coyotes ( $\Delta = 0.606 \pm 0.094$ ) was higher than their overlap with

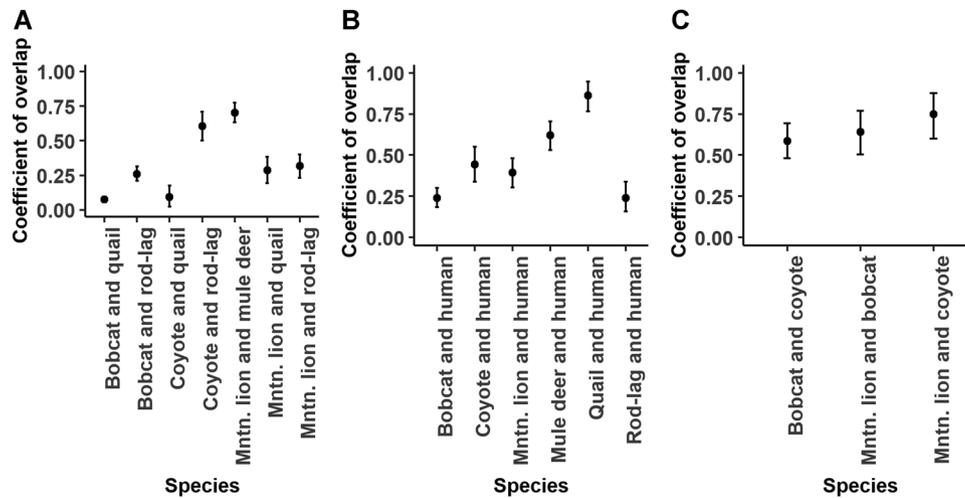
bobcats ( $\Delta = 0.259 \pm 0.053$ ), mountain lions ( $\Delta = 0.319 \pm 0.081$ ), and humans ( $\Delta = 0.241 \pm 0.084$ ).

## DISCUSSION

Our results confirmed our original hypothesis that interspecies interactions, particularly predator-prey interactions and human disturbances, would be important in the spatial and temporal usage of highway underpasses by wildlife in this study. The HJWA underpasses had been in place for about 40 years; therefore, this study offers insight into species activity patterns in underpasses after they have become accustomed to using these structures. In addition, although pronghorn were abundant in HJWA, we recorded only 3 occurrences of pronghorn using underpasses (Table 2). Therefore, pronghorn likely avoided using the underpasses, which is supported by other studies showing



**Figure 4.** The effects of predator and prey detection rates (number of detections at a camera site divided by number of camera days) on predicted probabilities of detection for A) mule deer and B) coyote at 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018. Frame A displays the predicted effects of mountain lion detection rates on the detection probabilities of mule deer based on the occupancy model including the effects of season, year, and mountain lion detection rate on detection probability. Frame B displays the predicted effects of rodent and lagomorph detection rates on the detection probabilities of coyotes based on the occupancy model including the effects of season, year, and rodent and lagomorph detection rate on detection probability. The 95% confidence intervals are in gray. Mule deer exhibited avoidance of camera sites with higher predator detections, and coyotes exhibited preference of camera sites with higher prey detections.



**Figure 5.** The coefficients of overlap of species' daily activity patterns as estimated by kernel density functions for 3 groups of species: predators and prey (A), humans and wildlife (B), and carnivore competitors (C). We collected data from 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018. The species included were California quail (quail), rodents and lagomorphs (rod-lag), mule deer, coyotes, bobcats, and mountain lions (mntn. lion). The error bars represent the 95% confidence intervals.

that pronghorns used overpasses more commonly than underpasses (Forman et al. 2003, Sawyer et al. 2016).

### Seasonal Use of Underpasses

Most species that traveled through the underpasses displayed seasonal patterns of use. Mule deer and rodents and lagomorphs used the underpasses more in the spring and less in the winter compared to fall. California quails used the underpasses more in the summer and less in the winter compared to fall. These variations in seasonal usage could be due to migratory patterns of deer, the dispersal patterns of quail, and the availability of resources for deer, rodents, lagomorphs, and quail in the area at different times of the year. The seasonal patterns of migratory deer traveling through the area were also likely affected by wildfires in the surrounding areas in 2017 and 2018, which decreased habitat suitability for the migrating herds. Coyotes used the

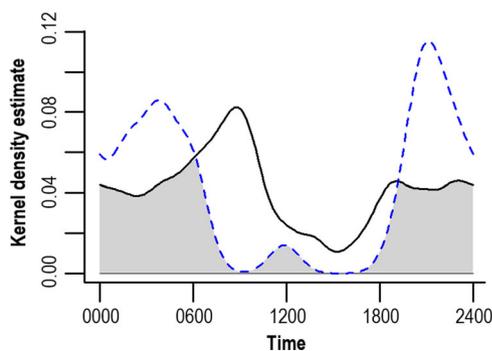
underpasses more in spring and summer compared to fall and this corresponded to high use of the underpasses by common prey of coyotes (rodents, lagomorphs, and California quails). Mountain lions used the underpasses the least in winter, which corresponded to the season of least usage by their prey, mule deer. Therefore, predators such as coyotes and mountain lions may have been influenced by seasonal use of the underpasses by their prey; further research is needed to confirm this.

### Location Effects on Underpass Use

Underpass location was not an important factor in the activity of most species within the underpasses. This may have been due to the underpasses being relatively close together in our study compared to most other underpass studies (Foster and Humphrey 1995, Clevenger and Waltho 2000, Gagnon et al. 2011). Additionally, there were no visually discernable structural or vegetation differences between the underpasses; however, the cameras detected California quail more on the west side of the underpasses compared to the east. Therefore, California quail were likely traveling east more often than traveling west. This could be due to their annual dispersal routes and illustrates that the underpasses may have been an important corridor for their dispersal. California quail detected in the underpasses were often traveling in large groups (>5 quails), further suggesting the underpasses may have been a part of quail coveys' dispersal routes (Calkins et al. 2014).

### Interspecies Effects on Underpass Use

California quail, mule deer, coyotes, rodents, lagomorphs, bobcats, and mountain lions were likely affected by other species using the underpasses. Mule deer avoided underpasses with high mountain lion activity, indicating that predation pressures within the underpasses influenced mule deer travel through the underpasses (Fig. 4A). Other researchers have also reported that deer may avoid underpasses used by their



**Figure 6.** The overlap of daily temporal activity patterns of mule deer (solid black line) and mountain lion (blue dashed line) from 6 camera sites in 3 underpasses at Hallelujah Junction Wildlife Area, Sierra County, California, USA, June 2017 to December 2018. The highest densities of deer activity correspond with the lowest densities of mountain lion activity, suggesting some temporal avoidance of mule deer to mountain lions.

predators (Foster and Humphrey 1995, Clevenger and Waltho 2000). These activity patterns could be influenced by the predator-prey landscape of fear model that postulates prey can learn and respond to differing levels of predation risk across the landscape by avoiding areas of high predator usage (Laundré et al. 2010). In addition, the highest density of temporal mule deer activity corresponded with the lowest density of mountain lion activity, indicating that mule deer may have been using the underpasses most during times of lowest mountain lion activity (Fig. 6). The overall high overlap between mule deer and mountain lion temporal activity showed that the majority of mountain lion and mule deer occurrences within the underpasses occurred within similar time periods and suggests that mountain lions followed deer temporal activity (Fig. 5). Another study on mountain lion usage of underpasses also reported that mountain lions followed deer activity within underpasses (Gloyne and Clevenger 2001).

Coyotes favored underpasses with high rodent and lagomorph activity, suggesting that coyote preference of underpasses was determined by the presence of their prey (Fig. 4B). Researchers of medium carnivores and small mammals also reported that carnivores were more likely to use underpasses frequented by prey (Mata et al. 2015). These results could be the outcome of a behavioral response between coyotes and their prey, where coyotes used areas with higher abundances of their prey to increase their chances of predation success (Sih 2005). In our study, we observed that rodents and lagomorphs foraged in the underpasses daily and did not travel all the way through the underpasses; this suggests that they were using the underpasses as habitat. Therefore, coyotes may have been hunting within the vicinity of the underpasses for rodents and lagomorphs; however, more evidence is needed for support. Coyotes also had a large overlap with rodent and lagomorph daily temporal patterns within the underpasses, indicating that coyotes followed the temporal activity of rodents and lagomorphs within underpasses (Fig. 5). Further, the cameras captured several occurrences of bobcats carrying killed rodents and lagomorphs within the underpasses, which provides supporting evidence that rodents and lagomorphs were being hunted by predators within the vicinity of the underpasses.

Rodents and lagomorphs had little temporal activity overlap with bobcats and mountain lions, which may have been due to differences in species biology or avoidance of rodents and lagomorphs to these felids (Fig. 5). California quail also avoided bobcats, mountain lions, and coyotes temporally, indicating that they preferred to use the underpasses at times of low carnivore activity (Fig. 5).

We found that intraguild carnivore interactions did not have a significant effect on most carnivore species studied within the underpasses. Both mountain lions and bobcats favored the same underpasses, suggesting that there may have been factors about certain underpasses that were favorable to these 2 felid carnivores such as differences in vegetative cover or topography. In addition, mountain lions, coyotes, and bobcats had similar temporal daily activity patterns, which indicates that temporal avoidance

between carnivores did not affect their activity within the underpasses (Fig. 5).

### **Human Disturbance Effects on Underpass Use**

We found that human disturbances, measured by the detections of humans, dogs, all-terrain vehicles, and cattle within the underpasses, were an important factor in usage of the underpasses. Coyotes avoided underpasses with higher human disturbances, indicating that human disturbance deterred some carnivores from using underpasses (Fig. 3B). This is supported by other researchers that have also reported that carnivores avoided underpasses used by humans (Gloyne and Clevenger 2001, Grilo et al. 2008, Barreto et al. 2014). Temporally, bobcats and mountain lions avoided using the underpasses during times that humans did (Fig. 5).

California quail favored underpasses with higher human disturbance (Fig. 3A). California quail also had a high amount of overlap with human activity temporally within the underpasses, indicating that they preferred to use the underpasses during times that humans used them (Fig. 5). Because the underpasses and times with the highest human disturbances were avoided by carnivores, California quail may have favored those underpasses and times because of lower occurrences of carnivores. This is supported by previous researchers that reported that prey may use areas and times of high human activity to avoid predators (Berger 2007, Rogala et al. 2011).

Our results on the spatial and temporal usage of the underpasses by wildlife showed the large effect predator-prey interactions and human disturbances had on which underpasses species traveled through and what times they used these corridors. Given our results, we recommend studies to research the effects of predator-prey interactions on the use of underpasses by wildlife communities. Specifically, we recommend future studies to focus on predation rates in the vicinity of underpasses and whether prey species take alternative routes across roadways to avoid predators within underpasses. Additionally, further research on the effects of human disturbances on wildlife within underpasses is needed to determine whether species are negatively affected by human disturbances within underpasses.

## **MANAGEMENT IMPLICATIONS**

Our results indicate the importance of monitoring wildlife using underpasses for the effects of predator-prey interactions and human disturbances. Underpasses that target specific species should be closely monitored to ensure that target species are not deterred from using underpasses by their predators or human disturbances. This is particularly important in areas like HJWA, where the underpasses provide safe passage for mule deer under the highway along a migratory corridor. In addition, we suggest managers should limit human foot traffic within underpasses to encourage usage of underpasses by larger carnivores. Further, because of the low use of the underpasses by pronghorn at HJWA, we encourage managers to consider factors that may influence different species' use of crossing

structures when planning for and constructing crossing structures.

## ACKNOWLEDGMENTS

We thank C. S. McDonald-Ryan, A. J. Meyer, L. E. Pilatti, and S. A. Thomas for their contributions to the maintenance of cameras and tagging of photos. We thank 2 anonymous reviewers for their valuable insight. This study was funded by the CDFW.

## LITERATURE CITED

- Alonso, R. S., L. M. Lyren, E. E. Boydston, C. D. Haas, and K. R. Crooks. 2014. Evaluation of road expansion and connectivity mitigation for wildlife in southern California. *Southwestern Naturalist* 59:181–187.
- Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, New York, USA.
- Barrueto, M., A. T. Ford, and A. P. Clevenger. 2014. Anthropogenic effects on activity patterns of wildlife at crossing structures. *Ecosphere* 5:1–19.
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* 3:620–623.
- Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17:5–10.
- Brunton, E. A., S. K. Srivastava, and S. Burnett. 2018. Spatial ecology of an urban eastern grey kangaroo (*Macropus giganteus*) population: local decline driven by kangaroo-vehicle collisions. *Wildlife Research* 45:685–695.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Calkins, J. D., J. Gee, J. C. Hagelin, and D. F. Lott. 2014. California quail (*Callipepla californica*). Account 473 in A. F. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Clevenger, A. P. 1998. Permeability of the Trans-Canada Highway to wildlife in Banff National Park: importance of crossing structures and factors influencing their effectiveness. Pages 109–119 in G. L. Evink, editor. Proceedings of the International Conference on Wildlife Ecology and Transportation (ICOWET). Florida Department of Transportation, Tallahassee, USA.
- Clevenger, A. P., and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology* 14:47–56.
- Clevenger, A. P., and N. Waltho. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation* 121:453–464.
- Coe, P. K., R. M. Nielson, D. H. Jackson, J. B. Cupples, N. E. Seidel, B. K. Johnson, S. C. Gregory, G. A. Bjornstrom, A. N. Larkins, and D. A. Speten. 2015. Identifying migration corridors of mule deer threatened by highway development. *Wildlife Society Bulletin* 39:256–267.
- Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14:21.
- Fiske, I., and R. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1–23.
- Ford, A. T., and A. P. Clevenger. 2010. Validity of the prey-trap hypothesis for carnivore-ungulate interactions at wildlife-crossing structures. *Conservation Biology* 24:1679–1685.
- Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, et al. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.
- Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. *Wildlife Society Bulletin* 23:95–100.
- Gagnon, J. W., N. L. Dodd, K. S. Ogren, and R. E. Schweinsburg. 2011. Factors associated with use of wildlife underpasses and importance of long-term monitoring. *Journal of Wildlife Management* 75:1477–1487.
- Gloyne, C. C., and A. P. Clevenger. 2001. Cougar (*Puma concolor*) use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. *Wildlife Biology* 7:117–124.
- Grilo, C., J. A. Bissonette, and M. Santos-Reis. 2008. Response of carnivores to existing highway culverts and underpasses: implications for road planning and mitigation. *Biodiversity and Conservation* 17: 1685–1699.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1:1–9.
- Huijser, M. P., P. McGowen, J. Fuller, A. Hardy, A. Kociolek, A. P. Clevenger, D. Smith, and R. Ament. 2008. Wildlife-vehicle collision reduction study: report to congress. Federal Highway Administration, McLean, Virginia, USA.
- Jackson, S. D. 2000. Overview of transportation impacts on wildlife movement and populations. Pages 7–20 in T. A. Messmer and B. West, editors. *Wildlife and highways: seeking solutions to an ecological and socio-economic dilemma*, 7th Annual Meeting of the Wildlife Society. The Wildlife Society, Bethesda, Maryland, USA.
- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1–7.
- Lazenby, B. T., and C. R. Dickman. 2013. Patterns of detection and capture are associated with cohabiting predators and prey. *PLoS ONE* 8:1–16.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Lepczyk, C. A., J. E. Fantle-Lepczyk, K. Misajon, D. Hu, and D. C. Duffy. 2019. Long-term history of vehicle collisions on the endangered Nēnē (*Branta sandvicensis*). *PLoS ONE* 14:1–11.
- Little, S. J., R. G. Harcourt, and A. P. Clevenger. 2002. Do wildlife passages act as prey-traps? *Biological Conservation* 107:135–145.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- Maehr, D. S., E. D. Land, and M. E. Roelke. 1991. Mortality patterns of panthers in southwest Florida. *Proceedings of the Annual Conference of Southeast Fish and Wildlife Agencies* 45:201–207.
- Mansergh, I. M., and D. J. Scotts. 1989. Habitat continuity and social organization of the mountain pygmy-possum restored by tunnel. *Journal of Wildlife Management* 53:701–707.
- Mata, C., R. Bencini, B. K. Chambers, and J. E. Malo. 2015. Predator-prey interactions at wildlife crossing structures: between myth and reality. Pages 190–197 in R. Van Der Ree, D. J. Smith, and C. Grilo, editors. *Handbook of road ecology*. John Wiley and Sons, Chichester, West Sussex, United Kingdom.
- Mazerolle, M. J. 2019. AICcmovavg: model selection and multimodel inference based on (Q)AIC(c). <<https://cran.r-project.org/package=AICcmovavg>>. Accessed 01 Apr 2019.
- National Oceanic and Atmospheric Administration. 2019. National weather service forecast office. <<https://w2.weather.gov/climate/index.php?wfo=rev>>. Accessed 20 Oct 2019.
- Rico, A., P. Kindlmann, and F. Sedlacek. 2007. Barrier effects of roads on movements of small mammals. *Folia Zoologica* 56:1–12.
- Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* 14:322–337.
- Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology* 15:1733–1741.
- Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecology and Society* 16:1–16.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790.
- Sawyer, H., P. A. Rodgers, and T. Hart. 2016. Pronghorn and mule deer use of underpasses and overpasses along U.S. Highway 191. *Wildlife Society Bulletin* 40:211–216.
- Seidler, R. G., R. A. Long, J. Berger, S. Bergen, and J. P. Beckmann. 2015. Identifying impediments to long-distance mammal migrations. *Conservation Biology* 29:99–109.
- Shepard, D. B., A. R. Kuhns, M. J. Dreslik, and C. A. Phillips. 2008. Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation* 11:288–296.

Sih, A. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. Pages 240–250 in P. Barbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, New York, New York, USA.

Smith, D. J., R. Van Der Ree, and C. Rosell. 2015. Wildlife crossing structures: an effective strategy to restore or maintain wildlife connectivity across roads. Pages 172–182 in R. Van Der Ree, D. J. Smith, and

C. Grilo, editors. Handbook of road ecology. John Wiley and Sons, Chichester, West Sussex, United Kingdom.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

*Associate Editor: David Euler.*