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*Research Article*

# Roadkill Distribution at the Wildland-Urban Interface

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**ABSTRACT** The growing wildland-urban interface is a frontier of human-wildlife conflict worldwide. Where natural and developed areas meet, there is potential for negative interactions between humans and wild animals, including wildlife-vehicle collisions. Understanding the environmental and anthropogenic factors leading to these collisions can inform transportation and habitat planning, with an objective of reducing animal mortality and human costs. We investigated spatial, temporal, and species-specific patterns of roadkill on Interstate-280 (I-280) in California, USA, and examined the effects of land cover, fencing, lighting, and traffic. The highway is situated just south of San Francisco, dividing a large wildlife refuge to the west from dense residential areas to the east, and therefore presents a major barrier to wildlife movement. Areas with a higher percentage of developed land east of I-280 and areas with more open space on the west side of I-280 were associated with an increase in overall roadkill, suggesting that hard boundaries at the wildland-urban interface may be zones of high risk for dispersing animals. This pattern was especially strong for raccoons (*Procyon lotor*) and black-tailed deer (*Odocoileus hemionus*). The presence of lighting correlated with increased roadkill with the exception of coyote (*Canis latrans*). Contrary to our expectations, we found weak evidence that fencing increases roadkill, perhaps because animals become trapped on roadways or because fencing is not sufficient to block access to the road by wildlife. Finally, we found strong evidence for roadkill seasonality, correlated with differences in movement and dispersal across life-history stages. We highlight the value of citizen-science datasets for monitoring human-wildlife conflict and suggest potential mitigation measures to reduce the negative effects of wildlife-vehicle collisions for people and wildlife. © 2019 The Wildlife Society.

**KEY WORDS** human-wildlife conflict, mammals, road ecology, roadkill, wildland-urban interface, wildlife-vehicle collisions.

As the global human population grows, the wildland-urban interface rapidly expands (Venter et al. 2016, United Nations Department of Economics and Social Affairs 2018). At these borderlands between densely populated urban areas and open spaces with natural vegetation, people are coming into contact with wild animals. The wildland-urban interface is frequently discussed in the context of wildfire risk, but it is also an important frontier of human-wildlife conflict (Stewart et al. 2009). Negative interactions between humans and wildlife at this interface can compromise wildlife conservation efforts and affect human safety and welfare. Thus, mitigating conflict at the wildland-urban interface can promote coexistence between humans and wildlife (Treves et al. 2006, Dickman 2010).

Roads are a prominent feature in the wildland-urban interface, and often create a barrier between natural areas or between natural areas and developed areas. Wildlife-vehicle collisions on these roads are a frequent form of human-wildlife conflict, posing risk to animals and people. In the United States alone, over a million vertebrates are killed per day as a result of vehicle collisions (Forman and Alexander 1998). In addition to directly reducing wildlife populations and compromising habitat connectivity by limiting animal movement (Hanski 1999, Coffin 2007, Crooks et al. 2011), wildlife-vehicle collisions also present a high cost to society (Gilbert et al. 2016). Across the state of California, USA, collisions with wildlife result in nearly 300 injuries to people and >5 human deaths/year and >$130 million in property damage (Shilling 2016, Shilling et al. 2017). Furthermore, each county in the United States typically spends up to $90,000 annually to remove roadkill from roadways (Huijser et al. 2008).

Knowledge of roadkill patterns can inform strategies to reduce the frequency of wildlife-vehicle collisions and

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mitigate effects on humans and wildlife. Roadkill is frequently used as a proxy for wildlife-vehicle collisions, given that many (though not all) animals that are struck by vehicles die alongside the road. At the wildland-urban interface, features of urban landscapes and ecological cues can influence roadkill distribution. Spatial and temporal hotspots for roadkill often emerge in areas of high wildlife dispersal, density, and movement (Shilling et al. 2017, Tejera et al. 2018) or in areas with moderate traffic volume or low driver visibility (Romin and Bissonette 1996, Brockie 2007, Main and Allen 2002, Hobday and Minstrell 2008). Patterns of wildlife movement and driver detection of wildlife are influenced by aspects of the natural and built environment; thus, ecological and anthropogenic factors interact to determine spatial and temporal patterns of wildlife-vehicle collisions at the wildland-urban interface.

Given that wildlands provide habitat for wildlife populations, it is likely that wildlife-vehicle collisions occur most often in areas adjacent to large patches of wildlands (Seo et al. 2015, Bartonička et al. 2018, Jakubas et al. 2018). Indeed, roadkill occurs more frequently in areas with high vegetative cover, large wildland patch size, and greater quantities of food sources (Smith 1999, Clevenger et al. 2003, Langen et al. 2009, Wilson 2012, Jakubas et al. 2018). Animals that are adapted to human presence may even be attracted from wildland to urbanized areas in search of anthropogenic food sources and predator refuge, making a road that separates wildlands and urban areas an even more likely site for wildlife-vehicle collisions (Nielsen et al. 2003).

Some features of transportation infrastructure, such as fencing and lighting, are designed to maximize human safety but may also alter wildlife road crossing patterns and thus wildlife-vehicle collisions. For instance, fences can limit movement of larger mammals, in turn limiting habitat connectivity but also reducing wildlife-vehicle collisions (Roof and Wooding 1996, Rytwinski et al. 2016). Breaks in continuous fencing, however, may funnel animals toward specific spots in roadways and make it difficult for wildlife to find areas to escape the road (van der Ree et al. 2015).

Although fencing tends to affect wildlife in more predictable ways, artificial lighting may have complex and interacting effects on different species; wildlife may be attracted to or repelled from areas with artificial light depending on their sensory modes and tolerance of human disturbance (Longcore and Rich 2001). For example, some predators may be attracted to well-lit areas in search of vulnerable nocturnal prey that are blinded by artificial lighting (Rich and Longcore 2006), though other predators may be wary of human activity and avoid anthropogenic light (Darrow and Shivik 2008). Light can also increase driver visibility, allowing people to detect and avoid animals on the road (Reed et al. 1982). Overall, current research remains ambiguous regarding the effects of artificial lighting on the frequency of wildlife-vehicle collisions.

In addition to understanding the ways in which the physical landscape alters wildlife-vehicle collisions, it is important to assess the temporal dynamics of collisions. Ecological dynamics affect temporal patterns of wildlife movement that likely influence crossing and collision rates. Previous researchers have reported that peak roadkill coincides with mating seasons and times of juvenile dispersal (Romin and Bissonette 1996, Boitet and Mead 2014, Garriga et al. 2017). Collision rates may also vary with lunar cycles; moonlight has been linked to increased mammalian and avian movement (Mizuta 2014). On finer time scales, wildlife-vehicle collisions may vary according to the diel activity patterns of wildlife species and local patterns of vehicle traffic (Waller et al. 2005). Collisions may also increase between dusk and dawn because driver visibility is reduced (Magnus et al. 2004).

Although many studies of wildlife-vehicle collisions and roadkill have been conducted in rural areas, fewer have considered the wildland-urban interface, where such collisions are particularly common, costly, and have a unique set of ecological and anthropogenic influences. In many areas of California, some wildlife populations are adapting or even thriving at wildland-urban interfaces like those in the San Francisco Bay Area (California Department of Fish and Game, unpublished data). In this region, Interstate-280 (I-280) is situated directly along a wildland-urban interface, creating a hazardous 8-lane barrier between wildland areas to the west and dense urban areas to the east (Fig. 1). As such, I-280 has one of the highest levels of roadkill in the state (Shilling et al. 2017), and it is therefore critical to understand dynamics of wildlife-vehicle collisions, which may inform local management and reveal general patterns of collisions at the wildland-urban interface.

We conducted a study of spatial and temporal patterns of roadkill along I-280 in the San Francisco Bay Area where the human population and associated development are growing rapidly (Walker and Schafran 2015). Our hypothesis was that animals are dispersing from the source habitat of wildland areas and potentially attracted to anthropogenic subsidies and refuge in urban areas. We predicted that roadkill observations would be concentrated in areas of the highway adjacent to open natural areas to the west, and developed land to the east. We also hypothesized that fencing would act as a barrier to animal movement and that lighting would increase movement, and therefore predicted that roadkill observations would be greatest in areas of the highway with more continuous fencing and artificial lighting, and that roadkill would be highest during lighter moon phases. We predicted that roadkill would be highest in areas of the highway with intermediate traffic given our hypothesis that vehicle traffic increases collision rates except at high levels, when animals are less likely to cross roads. We hypothesized that animal movement would vary seasonally, and predicted peak periods during juvenile dispersal and breeding seasons (autumn).

## STUDY AREA

Our study area included a 50-km stretch of I-280 in the San Francisco Bay Area metropolitan region of northern California. Specifically, we focused on the area from Highway 280 in San Bruno in the north to North Foothill

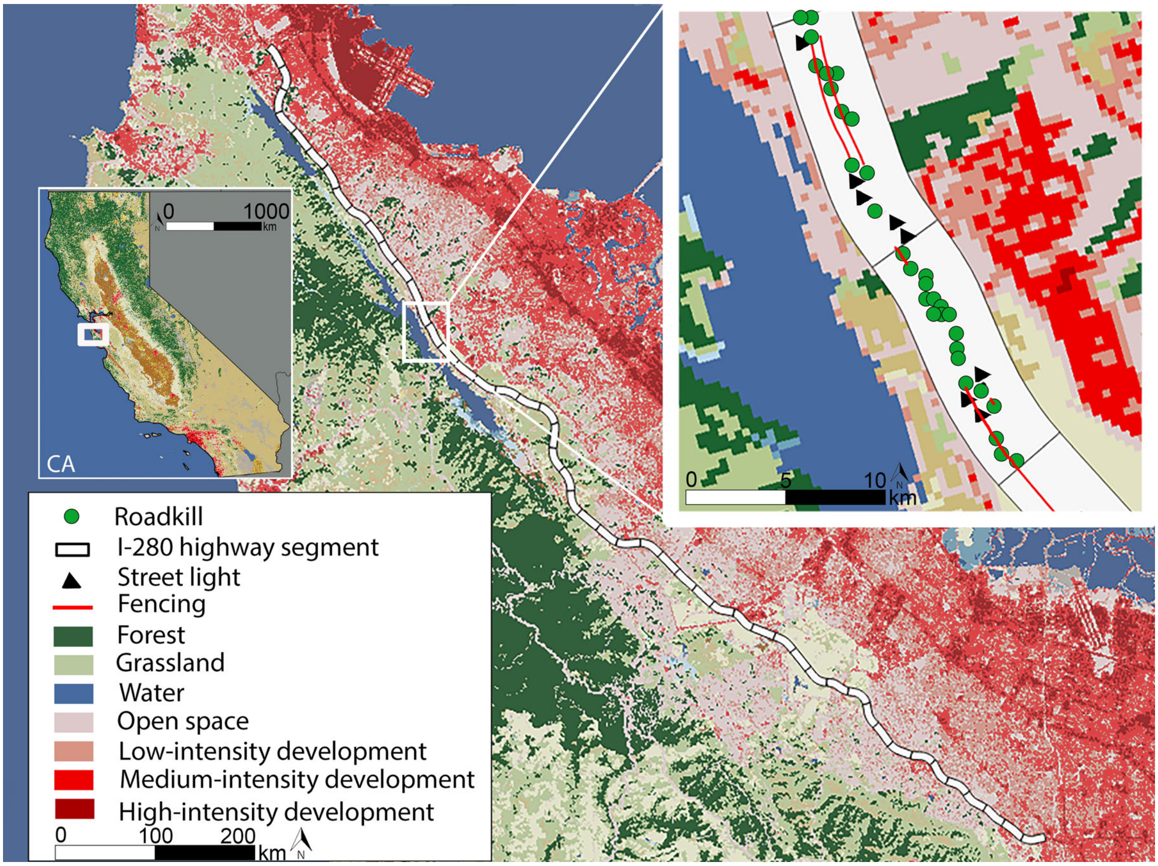

**Figure 1.** Study area and land cover type, including the 50-km stretch of California, USA, Interstate-280 segmented into discrete segments for analysis between Los Altos and San Bruno. In the inset, 2 of the 50 1-km bins are highlighted to display roadkill in 2006–2017 with predicting factors, including land cover, artificial lighting, and fencing.

Boulevard in Los Altos in the south (37.630 N, 122.434 W to 37.334 N, 122.059 W), and associated areas within 1.25 km of the highway. This major highway has wide lanes and fast-moving vehicles, and experiences heavy traffic due to the high density of nearby residential development and proximity to San Francisco and the Silicon Valley (Fig. 1). This route is used by thousands of commuters daily, with average traffic reaching 125,000 cars/day in certain sections (Caltrans 2016).

The area is characterized by undeveloped wildland to the west, dominated by mixed evergreen and deciduous forests and grassland vegetation, and urban areas to the east, and as such represents a major demarcation of the wildland-urban interface (Stewart et al. 2009). The area east of I-280 is heavily developed for residential and commercial use, including 3 cities with populations >70,000 each: San Mateo, Redwood City, and Mountain View (Bay Area Census 2010). The area to the west of the highway is comparatively undeveloped and includes several parks, protected areas, and reservoirs. These wildland areas are important habitat for many species, including black-tailed deer (*Odocoileus hemionus*), coyote (*Canis latrans*), mountain lion (*Puma concolor*), and raccoon (*Procyon lotor*; Felidae Conservation Fund, unpublished data). This area experiences a Mediterranean climate with 4 distinct, though mild, seasons with summer droughts and winter rains and is located in relatively flat terrain, just above sea level.

## METHODS

We assessed the anthropogenic and environmental correlates of spatial patterns of roadkill for medium (>3 kg) to large mammal species (>15 kg) on I-280, and examined patterns over lunar and seasonal cycles. To understand overall patterns of wildlife-vehicle collisions in the study area, we quantified various environmental features, such as fencing, land cover, and traffic volume, and amounts of roadkill in the study area. To further evaluate species-specific patterns, we conducted separate analyses for each of the 3 most common roadkill species with large sample sizes: black-tailed deer, coyote, and raccoon.

### Roadkill Data

We obtained roadkill data from the Road Ecology Center's California Roadkill Observation System (CROS, http://www.wildlifecrossing.net/california/, accessed 12 Oct 2017). Observations occurred between September 2006 and April 2017, with 21% of observations from the last 3 years (2014–2017). This database relies on observations from citizen scientist volunteers. When observations are recorded in the public online database, volunteers enter the species killed, their level of confidence in the species identification, and global positioning system (GPS) coordinates of the carcass. Data reviewers at the Road Ecology Center at University of California Davis rejected any obviously inaccurate reports. A recent study compared observer-recorded coordinates for observations with the GPS coordinates that are embedded in digital photographs for the same observations and found location and taxonomic identification to be accurate (Waetjen and Shilling 2017). For our analysis of overall roadkill patterns, we used data of all species including those labeled as unknown. These unknown observations are also likely common roadkill species, and we did not want to introduce bias by excluding species that were more difficult to identify. For the species-specific analyses on deer, coyote, and raccoon, we used only observations where the observer marked species with 100% confidence.

For spatial analyses, we binned highway I-280 into 50 1-km segments. We chose a 1-km segment length to ensure that roadkill locations were appropriately paired with surrounding environmental and anthropogenic features while avoiding oversampling and providing an intuitive and accessible unit to the public and policymakers. To capture all roadkill points associated with I-280, we created a 160-m buffer around the highway (corresponding to the max. width of the highway in our study area) and removed data points that were outside of this buffer.

Given an estimated error of ±100 m in recorded GPS locations (Shilling 2016), we created a 100-m buffer around the reported location of each roadkill observation. We then calculated the number of roadkill observations in each highway segment. When buffered points fell into 2 segments (66 of 473 observations), we calculated the fraction of the buffer that overlapped each respective highway segment and counted this fraction towards the number of roadkill observations in each respective highway segment. In addition to determining the number of roadkill observations in each segment, we also assessed roadkill distribution for 3 focal species. For raccoon and black-tailed deer, we quantified the number of roadkill in each segment (continuous variable). For coyotes, which had a smaller sample size, we determined whether coyote roadkill had been recorded in a given highway segment. Thus, we treated coyote roadkill incidents as a binary response variable.

### Lighting, Fencing, and Traffic Flow

Given the high resolution of freely available data and high traffic speeds of the highway in the study area, which would have impeded field data collection, we gathered information on fencing and lighting using remotely sensed imagery. To map lighting and fencing along I-280, we used Google Earth satellite images, Google Maps, and Google Street View imagery (Google, Mountain View, CA, USA) from 2016 through 2018. Using 2006 and 2008 historical imagery, we detected no changes that occurred in fencing and lighting during the roadkill data collection period. We assigned each highway segment a value of 0 or 1 for lighting within 50 m of the highway, where zero indicates no lights present and 1 indicates ≥1 light was present.

We mapped the 6 most common fencing types located within 50 m of I-280: noise abatement walls, bridge walls, chain link fence, small chain link fence, small concrete walls, and guardrails. Within each 1-km segment of highway, we quantified fencing by measuring the length of fencing within highway segments.

To quantify traffic in each highway segment, we used 2016 average annual daily traffic (AADT), which is a vehicle count for each section of highway between exits. For highway segments that fell entirely within 2 adjacent exits, we assigned them the AADT value that corresponded to the previous exit. For highway segments that included an exit, we determined the percentage of the segment that corresponded to each area between exits and calculated a weighted average for AADT within the highway segment. Because traffic volume has a negative quadratic relationship to roadkill, we incorporated AADT as a second-order term in our final linear regression models (Clarke et al. 1998, Seiler 2005, Farmer and Brooks 2012). Although total daily traffic volume increased slightly from 102,900 vehicles in 2011 to 112,150 vehicles in 2016, the distribution of vehicle traffic throughout the study area remained the same (Caltrans 2016). And though some studies of roadkill have found shortcomings of AADT data quality (Bissonette et al. 2008), the spatial scale of the AADT data used in this study corresponded to the scale of the roadkill and environmental data, and therefore provide a suitable proxy for relative traffic volume in the study period. Seasonal traffic volume was not available for our study period, and we therefore only examined the effects of spatial variation in traffic volume on spatial distribution of roadkill and could not use traffic as a covariate in temporal analyses.

### Land Cover

We used the United States Geological Survey National Land Cover Database (NLCD 2016) to determine land cover alongside each highway segment. We first created buffers of 2 different fixed widths (0.625 km and 1.25 km) alongside the highway segments. We chose these values based on approximate home range sizes of medium-sized predators and large herbivores (Riley et al. 2003, National Resource Convention Service 2005). These buffer widths resulted in 2 sets of polygons near or equal to 1.25 $km^2$ and 2.5 $km^2$ on either side of the highway because areas were not consistent across segments, given the road curvature. Because of extreme differences in land cover type to the west (typically undeveloped wildland) and east (typically developed urban areas) of the highway, we chose to treat aspects of each side of the highway as independent variables rather than combine them, recognizing that differences in land cover on either side of the road could influence roadkill.

We took 2 different approaches to assessing land cover effects because species differ in their tolerance of human disturbance and use of developed areas. We first made a developed land category that included the following NLCD classes: open developed space, low-intensity development, medium-intensity development, and high-intensity development. This grouped category allowed us to distinguish the importance of anthropogenic development as a whole, in comparison to undeveloped classes and cropland. Second, we looked at the percentage of deciduous forest, coniferous forest, mixed forest, grassland, and herbaceous scrub or shrub to discern if certain land cover types were more predictive of roadkill presence at a finer scale.

We used the extract function from the raster package in R (R version 2.8-19, www.cran.r-project/package=raster, accessed 10 Dec 2017) to determine the percentage of land cover in the undeveloped categories alongside I-280. In initial exploratory modeling, we first compared Akaike's Information Criterion (AIC) values of models of roadkill with each of the 2 different polygon sizes for the different land cover categories. In all cases, 1 set of polygon sizes minimized AIC values across all land cover categories. We then used this polygon size in the final linear regression models. For the overall, coyote, and raccoon models, we used 1.25-km$^2$ polygons, and for the deer models, we used 2.5-km$^2$ polygons. During modeling, we considered only 1 land cover classification at a time to avoid collinearity. We selected a land cover type or category in a similar way to polygon size selection, using the land cover type that minimized AIC values in exploratory models in the final model generation process. For the coyote, raccoon, and overall roadkill models, we used the percentage of developed land, and for the deer models, we used the percentage of coniferous forest.

### Moon Phase, Month, and Season

To assess the effect of moonlight on patterns of roadkill, we assigned all roadkill observations a category corresponding to the moon phase on the date of the observation. Low denoted a new moon and the 3 days before or after; intermediate denoted a moon in first or last quarter and the 3 days before or after; and high denoted a full moon (which provides the most amount of natural light) and the 3 days before or after.

We also quantified the number of roadkill reported in each month across all species to explore seasonal patterns. Additionally, we determined the monthly distribution of black-tailed deer and raccoon roadkill, the only 2 species that had large enough sample sizes for species-specific analyses of temporal factors. We then subset these 2 species and overall roadkill by season: winter (21 Dec–19 Mar), spring (20 Mar–20 Jun), summer (21 Jun–21 Sep), and autumn (22 Sep–20 Dec). We used chi-square tests to compare roadkill events across moon phases, seasons, and months.

### Spatial Analyses

Using R, we created multiple linear regression models with 4 different roadkill dependent variables (coyotes, raccoons, deer, all roadkill). Our roadkill dependent variables were continuous variables (number of roadkill observations), except for coyote roadkill, which was binary (presence or absence), and the highway segment was our unit of analysis ($n = 50$). Independent variables were artificial lighting features (0 or 1), fencing length, vehicle traffic volume (second-order), and land cover east and west of I-280. We standardized (z-score) all continuous variables prior to analysis. Models only incorporated 1 land cover variable to avoid collinearity, with the polygon size and land cover type determined in exploratory modeling as described above. We used the dredge function of the MuMin package in R for model selection and ranking (R version 1.42.1, www.cran.r-project.org/package=MuMin, accessed 20 Dec 2017).

For each species and for overall roadkill, we ranked models from lowest to highest AIC value. We calculated Akaike weights for each model with an AIC <2 from that of the best model to explore different possible explanations for roadkill density and distribution (Wagenmakers and Farrell 2004). These weights correspond to the relative likelihood that the model best describes the data. We then used a full model average of the coefficients of the selected top models using the model.avg function from MuMin. We presented these averaged models to acknowledge that more than just the best model can explain these results, thus reducing uncertainty from model choice (Hodges 1987, Draper 1995).

## RESULTS

The CROS database included 473 roadkill observations over the 10.5-year study period in our study area. All 50 highway sections contained ≥1 roadkill observation. There was an average of 9.7 ± 8.54 (SD) roadkill observations/highway section, ranging from 1 to 34.19. Observers reported an average of 39.42 ± 45.56 roadkill annually, ranging between 1 (2006) and 150 (2010). Observers identified the species with 100% certainty for 288 observations, including 143 raccoons, 94 black-tailed deer, 18 striped skunks, 16 coyotes, 6 mountain lions, and 17 various other large and medium omnivores and herbivore observations. Of the 50 highway sections, 31 contained ≥1 streetlight. Most lighting was located near highway exit and entrance ramps. Highway volume in 2016 ranged from 102,000 cars/day to 126,000 cars/day, with average of 113,787 cars/day/segment.

Roadkill was present throughout the study area but more common in the north. This pattern was likely influenced by the high number of raccoon roadkill observations concentrated in the northern portion of the study area. Deer roadkill was more uniformly distributed throughout the study area. Though there was a limited sample size of 16 observations, coyote roadkill was clustered in 2 areas (stretches of highway 6 km and 5 km each). Thirteen of 16 coyote roadkill were found within these 11 km (Fig. S1, available online in Supporting Information).

There were 4 top models for spatial patterns of overall roadkill, and 5 top models each for coyote, deer, and raccoon. The amount of developed land on both the east and west sides of the highway within 1.25 km$^2$ were the most important predictors of overall roadkill (Table 1; Fig. S2, available online in Supporting Information). Overall roadkill was negatively correlated with the amount of developed land west of the highway (estimate = −3.486, relative importance = 1.00) and positively correlated with developed land east of the highway (estimate = 1.640,

**Table 1.** Results of MuMIn full model averaging of the top models within 2 Akaike's Information Criterion of the best model for individual species (black-tailed deer, coyote, and raccoon) and all roadkill in 2006–2017 on California Interstate-280, California, USA. We report model estimates from averaged and best models, along with importance values of each covariate derived from model averaging. East land cover and west land cover correspond to the amount of developed land within 1.25-km$^2$ polygons, with the exception of the deer models, which instead included the amount of coniferous forest within 2.5-km$^2$ polygons. The area to the west of the highway consisted largely of wildlands, whereas the area to the east was largely urban.

| | East land cover | West land cover | Lighting | Traffic | Fencing |
|---|---|---|---|---|---|
| All roadkill | | | | | |
| Averaged model | 1.640 | −3.486 | 0.887 | −0.012 | 0.081 |
| Best model | 1.642 | −3.572 | 1.232 | | |
| Importance | 1.00 | 1.00 | 0.73 | 0.15 | 0.18 |
| Coyote | | | | | |
| Averaged model | −1.182 | 0.002 | −0.013 | 0.028 | 0.098 |
| Best model | −1.16 | | | | |
| Importance | 1.00 | 0.13 | 0.14 | 0.14 | 0.22 |
| Deer | | | | | |
| Averaged model | 0.017 | 0.540 | 0.430 | −0.141 | −0.010 |
| Best model | | 0.596 | 0.504 | | |
| Importance | 0.13 | 1.00 | 0.87 | 0.41 | 0.13 |
| Raccoon | | | | | |
| Averaged model | 0.972 | −1.253 | 0.150 | −0.005 | 0.334 |
| Best model | 0.951 | −1.158 | | | 0.567 |
| Importance | 1.00 | 1.00 | 0.37 | 0.11 | 0.60 |

relative importance = 1.00). The land cover adjacent to the highway was also an important predictor of deer, raccoon, and coyote roadkill. For raccoons, roadkill was also positively correlated with developed land on the east and negatively correlated with developed land on the west. Deer roadkill was positively correlated with the amount of coniferous forest west of I-280. An increase in coniferous forest from the lowest observed value (0%) to the highest observed value (9.9%) corresponded to an increase in roadkill by a factor of 1.3. Contrary to overall patterns, coyote roadkill was lower in areas with more developed land on the eastern, more urban side of the highway. An increase in east developed land from the lowest observed value (8.3%) to the highest observed standardized value (100%) corresponded to an increase in total roadkill by a factor of 1.2, a decrease in coyote roadkill by a factor of 2.0, and an increase in racoon roadkill by a factor of 10.1. An increase in west developed land from the lowest observed value (6.8%) to the highest observed value (97.9%) corresponded to a decrease in total roadkill by a factor of 0.85 and a decrease in raccoon roadkill by a factor of 0.92.

For all roadkill, the other variables in the top models included lighting (relative importance = 0.73), fencing (relative importance = 0.18), and traffic (relative importance = 0.15). Artificial lighting had positive correlations with overall roadkill and all species except coyote. The difference in lighting between absence and presence correlated to an increase in overall roadkill by a factor of 0.34 and an increase in deer roadkill by a factor of 1.3. Fencing had positive correlations with all species and overall roadkill except deer roadkill, with which it had a slight negative correlation. For all roadkill and all individual species except for coyote, traffic had a negative correlation with roadkill.

We did not observe a relationship between moonlight and overall roadkill ($\chi_2^2 = 0.021$, $P = 0.99$), or for any of the focal species. Roadkill observations varied across seasons ($\chi_3^2 = 90.29$, $P < 0.001$). Autumn had the greatest number of observations of overall roadkill (200 of 473 observation). More specifically, roadkill peaked in October (111 of 473 observations), followed by November (69 of 473 observations; Fig. 2). Roadkill was observed least in the winter. These patterns were consistent with

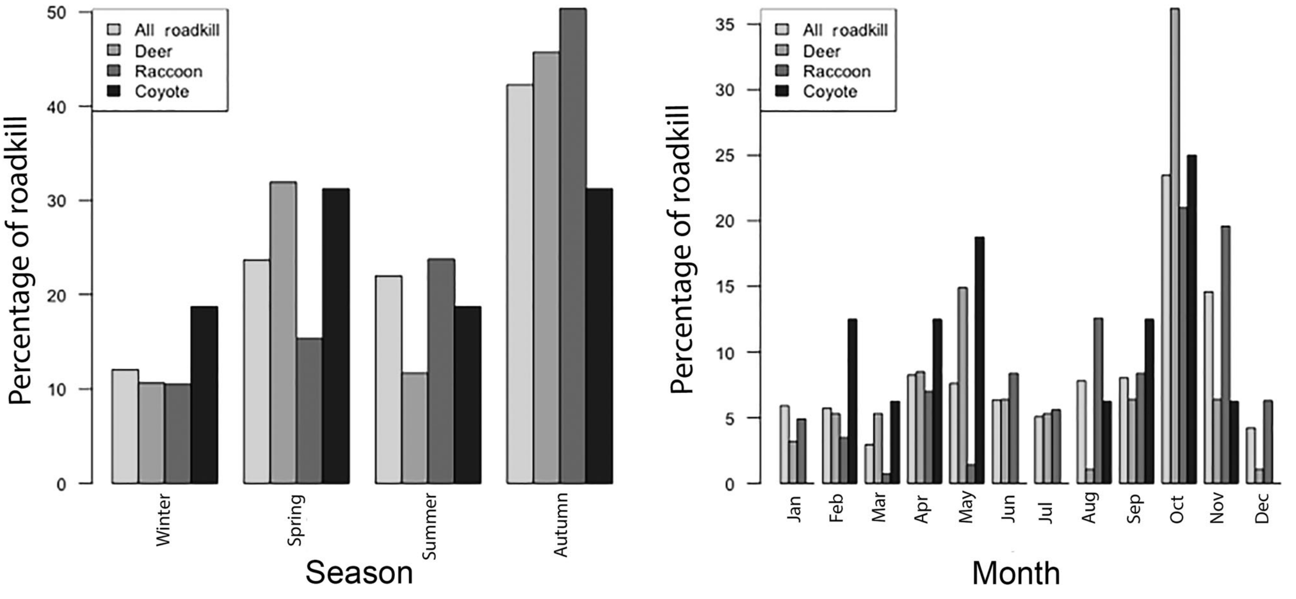

**Figure 2.** Percentage of roadkill occurring per season (left) and month (right) for different species and total roadkill on California Interstate-280, USA. Graph uses observation data from 2006–2017 from the University of California Davis California Roadkill Observation System database.

**Table 2.** Results of chi-square tests for month and season of individual species and all roadkill on California Interstate-280, USA, 2006–2017. There were statistically significant differences ($P < 0.05$) in roadkill across seasons and months for all roadkill, raccoons, and black-tailed deer (but not coyote). We defined seasons as winter (21 Dec–19 Mar), spring (20 Mar–20 Jun), summer (21 Jun–21 Sep), and autumn (22 Sep–20 Dec).

| Variable | Species | DF | $\chi^2$ | $P$ |
|---|---|---|---|---|
| Season | | | | |
| | Black-tailed deer | 3 | 54.17 | <0.001 |
| | Raccoon | 3 | 32.38 | <0.001 |
| | Coyote | 3 | 1.00 | 0.801 |
| | All roadkill | 3 | 90.29 | <0.001 |
| Month | | | | |
| | Black-tailed deer | 11 | 111.53 | <0.001 |
| | Raccoon | 11 | 78.86 | <0.001 |
| | Coyote | 11 | 14.00 | 0.233 |
| | All roadkill | 11 | 194.15 | <0.001 |

deer and raccoons. Coyotes, however, showed no temporal trend (Table 2).

# DISCUSSION

Roadkill was most common in areas with more developed land to the east, and peaked during periods of seasonal dispersal and movement of wildlife. Notably, roadkill was also more common in areas with less developed land (and therefore more undeveloped land) to the west, which could represent either attraction to development, retreat to the wildlands, or a combination thereof. This finding suggests that the wildland-urban interface is an important area for wildlife-vehicle collisions. Roadkill was also positively associated with the presence of artificial lighting and with more fencing.

Raccoons were the most commonly identified roadkill species. The high prevalence of raccoon roadkill may be attributed to their high population density, ecology, or physiology. For example, their size, speed, and nocturnality may make them more difficult for drivers to see and avoid (Crawford and Andrews 2016). With comparatively low maximum movement speeds of 24 km/hour, it is likely that raccoons cannot quickly move out of the way of traffic as effectively as larger mammals such as deer or coyotes (Garland 1983). Raccoons are also easily recognizable, and perhaps more likely to be reported by citizen scientists than other species.

The second most commonly reported roadkill species was black-tailed deer. Although black-tailed deer that cross the highway are more likely to be spotted by drivers because of their size and may be better equipped to evade fast-moving cars relative to other species (can move ~30 km/hr and leap ≥2 m), deer tend to freeze in the presence of the bright lights of oncoming vehicles (Wallmo 1981, Davis and Schmidly 1994). This response makes deer especially unpredictable and difficult for drivers to avoid. There are no other mammal species in the area that can be easily confused with black-tailed deer, which likely leads to a higher confidence in deer roadkill identification by citizen scientists.

Unlike raccoons and deer, coyotes are seemingly well physiologically adapted to avoid traffic (can move ~70 km/hr and leap >1.5 m). However, coyotes are scavengers and may be attracted to carrion at the sides of roads, leading to increased roadway presence and thus a higher likelihood of collisions with vehicles (Zimmerman 1943, Thompson 1979, Schwartz et al. 2018).

### Spatial Patterns

In accordance with our hypothesis, we found that less developed wildland areas to the west were associated with higher amounts of roadkill for all species except for coyote. Animals may leave western wildland areas when seeking out new territory, food resources, or mates (Trewhella et al. 1998). Given that roadkill numbers peak in autumn, when many species' juveniles are dispersing, it is likely that many animals cross the highway in search of new territories (Harrison 1992, Ghert and Fritzell 1998).

The association between roadkill and developed land to the east of the highway is perhaps less intuitive but still in accordance with our hypothesis. Animals may be attempting to leave areas of high human development to avoid disturbance or may turn back after crossing the highway from the wildlands and finding no suitable areas. Alternatively, areas of higher human development may actually be an attractant to some species that find some benefit from living close to human dwellings. Many species in this analysis, including raccoon and black-tailed deer, are well-adapted to urban lifestyles and can exploit anthropogenic resources such as refuse, gardens, and artificial water sources (Fedriani et al. 2001, Tigas et al. 2002, Larson et al. 2015, Rowand 2016). This is true of species across the wildland-urban interface, suggesting these findings may be relevant in many other systems. Additionally, urban settings generally host a smaller number of large predators and may serve as a relative refuge or human shield from predation (Ritchie and Johnson 2009).

Our models revealed a negative relationship between the amount of developed land east and west of the highway and coyote roadkill suggesting that coyotes are not often crossing between 2 urban environments. Instead, coyotes are more likely to be using the less developed lands because they are ideal hunting grounds for coyotes; they contain more small rodents, the primary prey source of coyotes (Fedriani et al. 2001). The 2 regions of the study area where coyote roadkill was abundant were far more open on both sides of the highway in terms of vegetative cover. The presence of annual grasses was also far more common than in adjacent areas (S. E. S. Kreling, University of California Berkeley, personal observation).

Reports of roadkill, except for coyote, were higher on highway segments where artificial lighting was present. Lights might serve as an attractant for animals, or animals might be more likely to cross at night when there is more visibility (Haikonen and Summala 2001). Alternatively, the placement of lights may be confounded by other variables. For example, along this stretch of I-280, street lights were concentrated at exit on and off ramps, bridges, and overpasses. These are areas where there are higher rates of merging and congestion, and drivers may be paying less attention to animals on the road or have less ability to alter course (Sen et al. 2003). Higher congestion, increased lighting, and slower vehicle speeds at exits may also have aided citizen science observers in sighting, remembering, and recording roadkill, leading to a higher number of observations reported around these areas (Daganzo 2002).

Contrary to our prediction that fencing would prevent roadkill by keeping animals off the road, fencing length was positively correlated with roadkill for all models in which it was present except deer. Animals are likely finding ways onto the highway (Felidae Conservation Fund, unpublished data) and possibly having trouble making it to safety beyond the fence line on the opposite side of the highway. Larger species, such as coyotes and deer, may have more trouble finding fence breaks large enough to fit through after crossing the highway. Although our study design and sample size did not allow for a comparison of the effect of fence design on roadkill, it is likely that different styles of fencing have different implications for animal movement and should be explored in future studies.

Though some studies have reported a clear quadratic relationship between traffic volume and roadkill location, because there is a threshold over which higher traffic volumes do not correlate to increased roadkill, our results varied (Clarke et al. 1998, Seiler 2005, Farmer and Brooks 2012). The effect of traffic volume on roadkill may be greater than the results suggest if there is a reporting bias towards areas of lower traffic volume. High traffic volume may deter observers from being able to make observations in these areas, where driving may take more vigilance or parts of the road and shoulder are more likely to be obstructed from view by other vehicles (Collinson 2013). Additionally, some species may be deterred from attempting to cross roadways that have high traffic flow and vehicle speed (Jacobson et al. 2016). Overall, we found that the effect of traffic was the least important variable in predicting roadkill presence.

### Temporal Patterns

Consistent with findings from other studies of wildlife-vehicle collisions, roadkill varied seasonally and peaked in autumn especially for deer and raccoon. The temporal trends we observed correspond to known periods of dispersal and times of increased movement (e.g., breeding; Romin and Bissonette 1996, Garriga et al. 2017). Seasonal differences in the number of drivers on the road could also influence both seasonal roadkill patterns and observer reports. Observed patterns of roadkill seasonality, however, did not match up with seasonal patterns of traffic (Memmott and Young 2008), suggesting that species biology is the major factor influencing observed seasonal roadkill patterns.

The lower number of deer roadkill observations in the spring may reflect the reduced movement that occurs during the spring months, when forage is generally green, dense, and nutrient-rich and when fawning occurs (Sommer et al. 2007). Autumn peaks in deer roadkill have been recorded throughout the United States and are mainly attributed to the onset of mating season when individual activity is high (Romin and Bissonette 1996, Haikonen and Summala 2001). Additional male deer movement during the rut while searching for receptive females, in addition to non-receptive females evading aggressive males, influences a seasonal increase in movement, which may lead to more frequent highway crossings and increased probability of collision (Romin and Bissonette 1996).

The high occurrence of raccoon roadkill in the autumn likely results from seasonal patterns of juvenile male dispersal. The average dispersal distance of raccoons ranges between 2.3 km and 13 km, and animals living along the periphery of highway I-280 may cross the highway to disperse (Urban 1970, Ghert and Fritzell 1998). Though not statistically significant, a peak in coyote roadkill also occurred in the autumn. And, like racoons, juvenile coyote dispersal also peaks between October and November (Harrison 1992) and averages 5–6 km from the birth site, making freeway crossing especially plausible for those coyotes born where habitat or resources may be less available (Tesky 1995).

We found no relationship between moon phase and roadkill patterns, in accordance with some other studies and it may be species specific (Collinson 2013). Although drivers may be better able to see animals in the roadway during periods of moonlight, the additional lighting is likely to coincide with higher animal movement, which may correspond to higher crossing incidence (Biebouw and Blumstein 2003, Mizuta 2014). The effects of moonlight on driver visibility and animal movement may therefore counteract each other, leading to no net effect on wildlife-vehicle collisions. Alternatively, there may be no effect of moon phase on wildlife movement, perhaps as a result of high amounts of artificial lighting in the area.

Every year, hundreds of roadkill carcasses are observed throughout California and reported to the University of California Davis CROS database. However, these reported observations are likely to only be a fraction of the number of wildlife killed in wildlife-vehicle collisions (Shilling et al. 2017). An expansion in this citizen science data collection effort would simultaneously promote education and community involvement and generate large amounts of data (Dickinson et al. 2016).

Although citizen science can provide a valuable tool for monitoring roadkill patterns at the wildland-urban interface, it has some limitations (Olson et al. 2014). Data accuracy is often unknown, which leads to concerns on how to account for sampling error in statistical analyses (Dickinson et al. 2010, Wiggins and Crowston 2011). In our case, sampling errors are most likely in the form of misidentified species, inaccurate geographic coordinates, and lack of systemized collection. Furthermore, observations of roadkill are likely biased by travel speed, traffic conditions, weather, lighting, and other environmental factors. Observers are not generally experts in the field of wildlife identification, resulting in a bias toward more recognizable species. Even though there may be errors present in the data, these are estimated to be rather small, ±14–100 m error in location and 97% species identification (Shilling 2016, Waetjen and Shilling 2017). Ideally, citizen science would be used in conjunction with more systematically collected data from regional animal services and wildlife rehabilitation centers, which may have access to data on roadkill. A centralized and standard system would enhance data sharing across organizations, citizen scientists, and agencies.

As a caveat to our study, we did find evidence of spatial autocorrelation between roadkill segments and dependent variables and covariates, which may have caused us to overestimate the magnitude of effects of some of the covariates. We therefore recommend future studies across multiple road systems at wildland urban interfaces to better understand factors influencing roadkill at broader spatial scales.

## MANAGEMENT IMPLICATIONS

Our study can inform management efforts to reduce wildlife-vehicle collisions, enhance connectivity, and maintain gene flow between populations in urban areas. Our study found that fencing is not correlated with reduced roadkill abundance and may not be the most effective mitigation strategy. Mitigation techniques should be installed and applied in areas where there are highest amounts of natural land cover available to the west of the highway and developed areas to the east, where the most roadkill was predicted. Additionally, as we found signs of temporality in roadkill abundance, we suggest placing higher emphasis on mitigations strategies employed during times of high seasonal movement.

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Additional supporting information may be found online in the Supporting Information section at the end of the article.