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Urban wildlife use of existing highway crossings and access points

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ABSTRACT

Roads and traffic are a significant source of mortality for many wildlife species and compromise habitat integrity. Despite widespread recognition that maintaining or restoring wildlife population connectivity is the single most effective mitigation measure for species conservation, roads and highways are rarely designed or modified to facilitate safe wildlife crossing.

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Understanding wildlife reactions to roads and existing crossing structures is critical for the development of effective conservation programs, minimizing property damage, and reducing human casualties caused by vehicle collisions. Here, we used camera arrays to quantify the extent to which six common mid- to large-bodied mammals associated with near urban environments used safe (i.e., underpasses and culverts) and risky (i.e., gaps in fencing which allow wildlife direct highway access) passages to cross a high volume, 8-lane Interstate highway in a major metro area. We then analyzed spatial and temporal variation in species-specific detection or risky movements. Our results suggest preferences that vary by species and crossing type, and though raccoons, gray foxes and coyotes were more likely to be detected at safe crossings than unsafe crossings, nearly all study species were frequently detected at unsafe crossings near the highway. Our research illustrates the diversity and frequency of wildlife using the land on the highway edge, helping explain why this section of highway has some of the highest incidence of wildlife-vehicle collisions in California. To make the highway safer for both wildlife and drivers, we suggest sturdy and well-maintained exclusionary fencing in conjunction with modification of already-available crossing structures (culverts and underpasses) for use by wildlife.

KEY WORDS bobcat, connectivity, coyote, deer, fragmentation, gray fox, puma, raccoon, roads, underpass, urban wildlife, wildlife-vehicle collision.

Habitat loss and fragmentation are the primary threats to biological diversity worldwide (McDonald et al. 2008). Roads represent a conservation concern at all scales, acting as a source of direct mortality of individual animals, and by severing demographic connectivity of otherwise large and intact populations (Bateman and Fleming 2012). And the threat from roads continues to grow: the global road network length has increased by more than 12 million kilometers since the beginning of the 21st century (Dulac 2013), with a projected 25+ million kilometers of new paved roads to be added by 2050 (Laurance et al. 2014). Although roadways can be used as movement corridors and can offer refuge and food resources to some species (Seiler 2001), roads and automobile traffic largely exert negative effects on wildlife populations (Underhill and Angold 2000; Van Der Ree et al. 2011) such as loss of habitat connectivity and subsequent reductions in genetic diversity.

In addition to indirect effects, roads represent a direct source of mortality for many species via wildlife-vehicle collisions (Foster and Humphrey 1995; Forman and Alexander 1998; Seiler 2001; Ng et al. 2004; Shepard et al. 2008). It has been estimated that deer alone are involved in 1. 2 million vehicle collisions each year in the United States, causing numerous injuries, over 200 human fatalities, and costing over $1.6 billion in vehicle and other property damage (Conover et al. 1995, Gilbert et al. 2016). Although roadkill can be reduced by a combination of exclusionary fencing and appropriate crossing structures (Clevenger et al. 2001*a*; Sawyer et al. 2012; Shilling et al. 2013; Rytwinski et al. 2016), building such infrastructure is expensive and time-consuming and sometimes not feasible. Furthermore, fencing and crossing structures often need to be tailored to specific species (Mata et al. 2008). For example, weasels (*Mustela erminea* and *M. frenata*) prefer culverts with high clearance and low openness, whereas American martens (*Martes americana*), which cohabitate with weasels in many areas in North America, prefer the opposite – culverts with low clearance and high openness (Clevenger et al. 2001*b*). Therefore, it is important to parameterize species preferences for various structures before building or modifying any potential wildlife crossing structures because investing in one structure to facilitate the movement of one species may be at the expense of other wildlife species (Mata et al. 2008).

Here we have studied wildlife detections and movement behaviors near a highly trafficked Interstate highway in a major metropolitan area – the San Francisco Bay Area in California. In particular, this highway, I-280, has among the highest reported frequencies of wildlife-vehicle collisions state-wide (Shilling et al. 2018). In fact, the interstate logs a wildlife-vehicle collision at least once every three days (Shilling et al. 2013, 2018) even though I-280 includes several potential safe-crossing structures for wildlife such as underpasses, overpasses and drainage culverts (Rodriguez et al. 1996; Mata et al. 2008), though these structures have not been specifically retrofitted for wildlife passage. Here we specifically comparing the extent to which gray fox (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), coyotes (*Canis lupis*), mule deer (*Odocoileus hemionus*), and pumas (*Puma concolor*) use these structures versus fence gaps which permit direct access to the highway in an effort to make recommendations to increase traffic and wildlife safety. Our objectives were to: (1) identify and quantify species accessing the highway and various crossing structures and describe patterns regarding preferences for each potential crossing; (2) evaluate species-specific detection frequencies as a function of time of day, crossing dimensions, vegetative cover or distance from the highway; and (3) determine if crossing characteristics could predict frequency of risky behavior by each species.

We expected that, across taxa, wildlife would generally use culverts and underpasses disproportionately (Mata et al. 2008), but because these structures were few and far between we did expect to detect wildlife at fence gaps that permitted direct crossing of the highway. Regarding the fence gaps, we predicted that responses would vary as a function of species-specific preferences, e.g., gap size (Ordenana et al. 2010). Given that vegetation cover is preferred by most wildlife, we predicted that well vegetated fence gaps would be used at greater frequencies than those where vegetation was low or absent (Anderson 1990, Beier 1995, Dickson et al. 2005, Grilo et al. 2008). Most of our focal species are nocturnal or crepuscular but wildlife near urban areas have been documented to shift to a more nocturnal activity pattern to avoid additional contact with humans; for this reason we expected wildlife detections would be highest at night when roads were less busy (Riley et al. 2003; Baker et al. 2007; Murray and St. Clair 2015; Wang et al. 2015; Gaynor et al. 2018).

STUDY AREA

Our study area is along Interstate 280 (I-280), a busy 92 km stretch of highway that connects San Francisco in the north and Silicon Valley in the south, passing through both undeveloped and urban areas. The San Francisco International Airport is located nearby, and the region is home to nearly 800,000 people (United States Census Bureau 2018). As such, the roads are extremely busy, accommodating about 150,000 vehicles daily (CalTrans 2016). However, despite the anthropogenic disturbance, the area is still a part of the California Floristic Province – a biodiversity hotspot (Myers 1990).

We specifically monitored the west side of the northern-most 15 km of I-280 between Whitman Way (37.617662, -122.425017) in the north and the Highway 92 interchange (37.509189, -122.334175) in the south (Figure 1). This section of the highway has 8 lanes of traffic and is lined by several types of fencing. The most common fencing types were steel mesh fencing (1.2-1.4 m high) and 4-stranded barbed wire, but concrete walls (0.6 m) and guardrails were also present. In this area, there is typically undeveloped land to the west (owned by the local public utilities) and dense residential development to the east (Figure 1B).

METHODS

Camera Trapping

Possible wildlife passages were identified by walking along the west side of I-280 where there is easier access for both humans and wildlife. In total we monitored 30 potential crossings with 31 cameras (Bushnell Trophy Cam HD): 21 gaps in the fencing that permitted direct contact between wildlife and vehicles as well as 9 permanent structures that wildlife could potentially use to safely cross I-280 – 7 underpasses and 2 culverts (Figure 1). All cameras were active between 19 October 2017 and 29 June 2018. Cameras were set to take a series of 3 photographs after each trigger and were angled in order to determine whether an animal was going towards or away from the highway. Cameras were serviced every 3 - 4 weeks.

All photographs were catalogued by co-author AJ using the Colorado Parks and Wildlife photo database v.4.0 (Ivan and Newkirk 2016). For each picture, we identified (1) the species detected, including humans, (2) the number of individuals, and (3) the direction and type (risky, non-risky, or neither) of animal movement. Specific behaviors were defined as:

- Animal is moving *away from* the highway (non-risky)
- Animal is moving *towards* the highway (risky)
- Animal is walking along the fence on the *non-highway* side (non-risky)
- Animal is walking along the fence on the *highway* side (risky)
- Animal is foraging near the crossing (other)
- Animal is doing something not defined above; unsure if the movement was towards or away from highway (other)

Photographs with no identifiable animal or human were discarded. Unless photos contained 2+ individuals simultaneously, each species captured in a 30 min period were considered a single event in order to reduce potential for double-counts (Reilly et al. 2017).

Predictor Variables

Variables used as predictors included passage type and time of day. Crossing type was identified as an underpass, culvert, or fence gap (Figure 1A). Time of day was categorized as: night (20:00-06:00), dawn (06:00-08:00), day (08:00-18:00), or dusk (18:00-20:00).

We hypothesized that variables associated with the dimensions and surroundings of the crossing structure would predict animal detection frequency at that structure, but the number of available culverts and underpasses (2 and 7, respectively) were too low for separate statistical analyses. For this reason, we recorded the following environmental measurements only at fence gaps: width and height of the gap in meters; percent canopy and ground cover; and distance to the highway in meters (Figure 1A). Total gap size was calculated by multiplying gap width by gap height (m^2).

Vegetation cover at each camera location remained the same throughout the study. So, to estimate canopy cover, we used a GRS densitometer (Forestry Suppliers®) in January 2018. Measures were taken by walking the distance of a half-diagonal (10 m) from the center of the gap in the four cardinal directions (Limpert et al. 2007). We were only interested in percent canopy cover in the immediate vicinity of the fence gaps and chose a maximum distance of 10 m from the center point (fence gap) due to proximity to the interstate. Horizontal ground cover was measured in February 2018 using the staff ball method (Collins and Becker 2001) along the same half-diagonals and with the sampling points used for measuring canopy cover. We measured fence gap size on-site with measuring tape (Figure 1a) and used Google Earth to estimate gap distance to the highway, both in meters.

Data Analyses

For our first goal, to detect preferences in regards to crossing type, we created a contingency table using our complete data set that totaled the number of detections of each species at the 3 types of crossing structures we monitored. The table was then used for Chi-squared analyses to compare observed proportions to expected proportions (culverts: n = 2 of 31 = 6.5%; fence gaps: 21/31 = 67.7%; underpasses: 8/31 = 25.8%).

For our second objective, to examine species-specific detection frequencies as a function of time of day, crossing dimensions, vegetative cover or distance from the highway, we used two analytical methods. To determine overall and species-specific patterns in detections by time of day we built a contingency table, as above, with the full data set. We then used a Chi-squared analyses to compare observed proportions to expected proportions (night and day: 10 hrs periods = 41.7% each; dawn and dusk: 2 hrs periods: 8.3% each). For the remaining variables, we subset our full data set to only include detections at fence gaps because these are the only locations where percent ground cover; percent canopy cover; gap width, height and total size; and distance to the highway were measured. With this data set, we ran multinomial regression analyses using the multinom() function in the *nnet* package of R, with species as our dependent variable and the above continuous variables as our independent variables. P-values were determined by calculating a Wald statistic.

For our final objective, to determine if variation in crossing characteristics could predict risky behaviors by each species, we further subset our fence gap data to only include risky and non-risky movements. Then to determine whether overall proportions of risky versus non-risky behavior as well as for comparing time of day to expected proportions, we created contingency tables and ran chi-squared tests. For our continuous variables, we used logistic regression, again using the multinom() function with binary data about whether a movement was risky or non-risky as the dependent variable, and with ground cover; canopy cover; distance to the highway;

gap width, height or total size; or median width as the independent variable. Logistic regression analyses were completed for each species.

All analyses were run using R V. 1.1.463 (R Development Core Team 2008).

RESULTS

In total we collected 75,143 images of animals and humans over 5,034 trap nights. After binning the data into independent detections (number of each species photographed within a 30-minute period), we had a total of 16,098 detections of which 9,872 were wildlife including more than 17 species (Appendix A). Regarding our focal species, we detected gray fox a total of 415 times, raccoons 966 times, bobcats 111 times, coyotes 255 times, mule deer 639 times, and pumas 26 times, on our cameras during the study period. Detection of species was spatially variable (Figure 2).

Overall structure preferences

We first analyzed whether each of our focal species plus pumas were more or less likely to use certain types of crossing structures. All 6 species – raccoons, bobcats, coyotes, deer, gray foxes and pumas – used crossing structures in proportions significantly different from what was expected (Figure 3a; Appendix B, table B1a). Specifically, raccoons, gray foxes and coyotes were all significantly less likely to be detected at fence gaps and more likely to be detected at underpasses. Bobcats and deer, on the other hand, were significantly more likely to be detected at fence gaps and less likely to be detected at underpasses. Additionally, deer and coyotes were also significantly less likely to be detected at culverts. Pumas were almost exclusively detected at underpasses and avoided gaps.

Characteristics of detection probability

As with crossing structure usage, all 6 species were detected at times of day significantly different than what was expected (Figure 3b; Appendix B, table B1b). All 6 species were significantly more likely to be detected at night and significantly less likely to be detected during the day than expected. Additionally, raccoons and foxes were also significantly more likely to be detected at dusk and less likely to be detected at dawn. Whereas coyotes were less likely to be detected at dusk and deer were more likely to be detected at dawn than expected.

For the multinomial regression analyses, we rotated through all 5 species as reference variables in our multinomial regression models to compare differences between focal species detection at fence gaps with certain environmental characteristics (Figure 4; model output with bobcat as the reference species in Appendix B, table B2). Regarding percent canopy cover, raccoons preferred the most cover, followed by foxes, coyotes, deer and then bobcats, which preferred gaps with small amounts of canopy cover (Figure 4a). Likewise, raccoons preferred fence gaps with high amounts of ground cover, followed again by foxes and then coyotes; deer and bobcats were more likely to be detected at fence gaps with low levels of ground coverage (Figure 4b). Raccoons were more likely to be detected at fence gaps that were further from I-280 whereas bobcats and deer were more likely to be detected at fence gaps that were closer to I-280 (Figure 4c). Bobcats were more likely to be detected at gaps that were wider whereas raccoons were more likely at gaps that were narrower, on average (Figure 4d). Bobcats and raccoons were both more likely to be detected at gaps that were taller (i.e., gap height) and overall larger (i.e., gap size) than other species; coyotes and foxes preferred shorter gaps that were smaller overall (Figures 4e, f).

Characteristics of risky behavior

In considering whether and how variables predicted risky movement behavior, we found that bobcats, coyotes, and raccoons were all significantly more likely to be detected committing a risky behavior as compared to a non-risky behavior (Appendix B, table B3). Risky behavior was more common at night than expected for bobcats and coyotes and less common at night than expected for deer and raccoons (Appendix B, table B4). Similarly, bobcats were significantly less likely to engage in risky behavior during the day.

With respect to predictors of behavioral risk-taking, bobcats performed more risky behaviors with higher levels of ground or canopy cover while deer were the opposite, they were more likely to engage in risky behavior when ground or canopy cover was low (Appendix B, table B5). Like deer, foxes were also more likely to engage in risky behavior when canopy cover was low (Appendix B, table B5). Foxes, deer and raccoons were also more likely to engage in risky behavior at fence gaps that were further from the highway (Appendix B, table B5). Bobcats were more likely to engage in risky behaviors when gaps were narrow, short or generally small whereas foxes were more likely to engage in risky behavior when gaps were small but wide (Appendix B, table B5). Both coyotes and deer engaged in risky behaviors at fence gaps that tended to be taller (Appendix B, table B5).

DISCUSSION

All monitored crossing structures, including fence gaps, underpasses, and culverts were used repeatedly by our six focal species. Many of our focal species exhibited clear and predictable spatial and temporal patterns in crossing behavior, but these preferences varied by species and movement type.

Wildlife crossing structure preferences

Crossing frequency and behavior were spatial clustered by species which is likely due to environmental preferences and habitat context. Focal species generally fell into two groups when it came to overall crossing structure usage. Bobcats and deer were more likely to be detected at fence gaps (near highway shoulders), especially those with vegetation, and were rarely detected at underpasses. Conversely, raccoons, foxes and coyotes avoided fence gaps and use underpasses instead. When these mesocarnivores were detected at fence gaps, the sites tended to be further from the highway, smaller and have more vegetative cover.

Wildlife underutilized vehicle underpasses, using only 3 of 7 monitored sites, and only 1 of the 3, site 22/23, was used by larger animals. Habitat context and the level of human disturbance may help explain this pattern. Of the 3 underpasses that were used (sites 1, 2, and 22/23), all three had some or even dense vegetation on one or both sides and sites 2 and 22/23 did not have sidewalks and were therefore rarely used by humans. That is compared to the 4 underpasses that were not frequently used by wildlife (sites 5, 7, 9, and 14) which had little cover, lots of concrete, and human foot traffic on both sides of the underpass. Of the used underpasses, sites 1 and 2, though vegetated, had nearby urbanization, and was used preferentially by foxes and raccoons - the two most synanthropic species in our sample. In contrast, site 22/23 was approximately 10 times larger than any other monitored underpasses (45.1 x 12.8 x 50 m), was quieter and darker, and surrounded by wildlands. Conditions more amenable to larger species and species sensitive to human activity (Davies et al. 2013; Francis and Barber 2013).

Despite their reputation as a safe highway crossing structure culverts were rarely used by wildlife in our study. Of the 2,412 species detections we analyzed, only 93 (3.9%) were at culverts, even though these structures represented 6.5% of our monitored sites. Culvert use has been documented for all of our focal species (Clevenger et al. 2001*b*; Sparks and Gates 2012), but, consistent with previous findings (Ng et al. 2004; Sparks and Gates 2012) raccoons and gray foxes were the primary species to use culverts in our sample. Although deer were detected at culverts on occasion, none actually passed through them. This is most likely explained by the small size of our culverts. Though Krawchuk *et al.* (2005) observed mule deer using drainage culverts as small as 2.1 m wide by 1.5 m tall, Reed *et al.* (1975) suggested a 'minimum' diameter of 4.27 m for deer, substantially larger than the 0.9 m diameter of the culverts monitored here.

Consistent with previous work (Riley et al. 2003; Baker et al. 2007; Murray and St. Clair 2015; Wang et al. 2015;), all species in this study were more likely to be detected at night and avoided the highway during the day. This is probably an important survival mechanism for urban-dwelling wildlife. Indeed, nocturnal coyotes seem to display higher survival rates than their crepuscular counterparts when crossing roads (Murray and St. Clair 2015), and many species amplify their nocturnal tendencies in the presence of human activity (Gaynor et al. 2018).

Bobcats, raccoons and coyotes engaged in risky behaviors more than half of the time they were detected, whereas gray foxes and deer showed no pattern. Risky behaviors were more common at night for bobcats and coyotes but less so for raccoons and deer. Bobcats also tended to engage in risky behaviors at fence gaps with more cover. This is the opposite pattern to what we found with respect to overall detections for this species; that is, bobcats were more likely to be detected at sites with less cover. This may suggest that bobcats are more likely to engage in risky behaviors when they are moving through unsuitable habitats. Similarly, foxes were also more likely engaged in risky behaviors at sites with less cover despite being more likely to be detected at sites with more cover in general. This is in contrast to deer which engaged in risky behaviors at gaps with less cover – consistent with overall detection of this species.

Ungulates, particularly deer, are among the most common roadkill species in the US and in our study area (Kreling et al. in review, Conover 1995, Shilling and Waetjen 2015). Our study reflected this general pattern. Although our results indicate that risk behavior in deer is negatively correlated with distance to roads, we frequently detected deer near the highway, often foraging only a few meters from fast-moving traffic. This is in contrast to Rost and Bailey (1979) where they found mule deer keep a distance of 200 m from heavily trafficked areas in more rural settings, but consistent with our previous work in which we found a positive correlation between deer occupancy and road density (Coon et al. in review). The increased roadkill frequency is therefore likely due, at least in part, to the sheer number of deer in our study area and their preference for disturbed and early successional plant comminutes commonly found along roads (DeStefano and DeGraaf 2003).

Pumas are a common member of the faunal communities throughout coastal California, and are present in wildland habitats adjacent to this study area (cameras set up for: Coon et al. in review) and given the frequency of depredation, complaints in neighboring communities, and roadkill on I-280, we expected greater puma detection frequencies at crossing structures. However, we only detected this species twice at fence gaps over the 9-month survey period, and in one of those cases the puma was photographed minutes later retreating from the highway (Appendix C). Instead, nearly all puma detections were at site 22/23, the largest and least anthropogenically disturbed underpass we monitored. As noted, site 22/23 is less affected by noise disturbance and light pollution, stimuli to which pumas are sensitive (Beier 1995, Smith et al. 2017). That said, our findings are consistent with Gustafson *et al.* (2018), who reported only 7 of 146 pumas sampled (all male) crossed a similarly large (10-lane) freeway in southern California during a 15-year study.

Management Implications

It has been estimated that 1 to 2 million large vertebrate-vehicle collisions occur each year in the United States, causing over 200 human fatalities and costing over $1.1 billion in vehicle and other property damage (Conover et al. 1995). In California, it is estimated that wildlife were involved in more than 19,800 vehicle collisions between 2015 and 2017 alone (Shilling et al. 2018). The best way to preclude wildlife access to roads will be with adequate and well-maintained fencing. Fencing can be effective in reducing wildlife-vehicle collisions without wildlife crossing structures (Rytwinski et al. 2016) but effectiveness reaches over 80% when combined with safe crossing structures (Clevenger et al. 2001*a*; Huijser et al. 2008; Sawyer et al. 2012; Rytwinski et al. 2016). For example, a fence built along a 9.65 km stretch along Highway 241 in southern California reduced puma, bobcat, and deer mortality by 100% and coyote mortality by 93% over a one-year period (Feremenga et al. 2018). That fencing was 3 - 3.6 m high, buried 60 cm, and provided escape ramps in case any wildlife had managed to move around the fence. Though expensive, the benefits of fencing tend to exceed costs over time (Huijser et al. 2008).

Given the costs and widespread need for crossing structures, our goal was to provide clear guidelines on the types of structures that facilitate or impede wildlife movement with respect to driver safety and wildlife conservation efforts. To reduce wildlife-vehicle collisions while increasing wildlife population connectivity, protocols should be developed that minimize direct highway access but also permit safe crossing for the most species possible. Unfortunately, site and structure preferences varied among species, and because of this, we suggest that managers integrate species-specific data related to crossing behavior, collision frequency, and property damage cost estimates to create a spatially-explicit, cost-benefit model for prioritizing development or retrofitting crossing structures. This will necessarily involve trade-offs with respect to species conservation and minimizing property damage and threats to public safety. For example, Kreling *et al.* (*in review*) reported raccoons, coyotes and deer are the most common roadkill in our study system, yet vehicle damage and associated costs likely vary inversely with animal body mass. As such, managers may want to focus efforts on keeping larger species such as deer and coyotes off the highway because of the greater costs associated with accidents involving these species as compared to smaller ones like foxes, raccoons or bobcats. Likewise, accidents with pumas are costly and dangerous because of their size, but these animals are also numerically rare, making safe crossing of individuals a greater conservation concern than with more abundant species. Taken together crossing structures for deer and pumas should be given higher priority than those for small or common species in order to retain genetic continuity and facilitate seasonal migrations, while also making highways safer for human drivers. Luckily these two species most frequently used the same passage to cross I-280 – site 22/23 – an large underpass infrequently used by humans with ample vegetative cover which is consistent with studies of other wildlife road crossings (Gloyne and Clevenger 2001, Ng et al. 2004).

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Figure Captions

Figure 1**.** Study area and camera locations in San Mateo County, California, USA. (A) Camera location information corresponding to locations on map. Under "type" U denotes Underpass, G denotes Gap, and C denotes Culvert, and the subscripts in that column count the number of each type. length (L), width (W), height (H) and distance to road were all measured in meters. (B) Map shows the location of camera traps along Interstate 280, which runs north to south on the San Francisco Peninsula.

Figure 2. Detections hotspots (a) and detections (b) of focal species and pumas along the I-280 study area. Species were typically spatially segregated with raccoon and bobcat detections dominating the northern part of the study area and coyotes and foxes dominated the southern part of the study area. Pumas were almost exclusively detected at one location whereas deer were detected at nearly every camera trapping location. Cameras are numbered from north to south the type of passage is indicated in (b) where U refers to underpass, G to fence gap, and C to culvert. Note the broken x-axis on the main (b) graph; the inset graph shows the full extent of detections at camera location 1.

Figure 3. Comparison of observed structure usage (a) and time of detection (b) to expected. Significance is based on chi-squared tests with P-values indicated: $P = 0.001\text{-}0.01^{**}$; $P < 0.001^{***}$.

Figure 4. Figures show species preferences for fence gap characteristics: Percent canopy cover, percent ground cover, distance to road, gap width, gap height and gap size. Box plots indicate the

average with the center line, first and third quartile with the lower and upper limits of the box, respectively, and minimum and maximum measurement with the lower and upper whiskers, respectively, of the characteristic at which the species was detected. Letters indicate significant differences between species. For example, in the 'gap size' graph the average sized gap that coyotes (AB) were detected at was significantly different (smaller) than bobcats (C) but not different than fox (A), deer (B), or raccoons (B).

APPENDIX A. Species detections.

A – List and number of detections of each species during the course of the study. To minimize recounting the same individuals, an animal (including humans) can only be "detected" once every 30-minutes.

Species	Count of detections
Barn owl (*Tyto alba*)	4
Bobcat (*Lynx rufus*)	111
Brush rabbit (*Sylvilagus bachmani*)	1,760
Coyote (*Canis latrans*)	245
Falcon (Family: Falconidae)	7
Grey fox (*Urocyon cinereoargenteus*)	411
Long-tailed weasel (*Mustela frenata*)	1
Mouse (Genus: Mus)	1,314
Mule deer (*Odocoileus hemionus*)	579
Puma (*Puma concolor*)	26
Raccoon (*Procyon lotor*)	833
Rat (Genus: Rattus)	3,015
Squirrel (Family: Sciuridae)	490
Striped skunk (*Mephitis mephitis*)	313
Turkey (*Meleagris gallopavo*)	3
Virginia opossum (*Didelphis virginiana*)	143
Other bird (class: Aves)	617
SUBTOTAL – *wildlife detections*	**9,872**
Human (*Homo sapiens*)	5,453
Domestic cat (*Felis catus*)	44
Domestic dog (*Canis lupus familiaris*)	729
GRAND TOTAL – *all detections*	**16,098**

APPENDIX B. Statistical results tables.

B1 – Contingency tables and chi-squared analyses results for each focal species and pumas by (a) type of crossing structure and (b) time of day. Overall analyses determined whether there were differences between variable usage by species, and because each was significant we continued to test observed proportions to expected proportions. Raw counts of detection are listed in the “Observed Counts” row with percent of total in parentheses. P-values have undergone Bonferroni correction.

		gray fox	raccoons	bobcats	coyotes	deer	pumas
a) GAP TYPE Overall	**χ^2**	54.477	831.730	36.878	103.990	97.222	60.073
	P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Observed Counts (% total)	**culvert – 2 (6.5)**	32 (8)	53 (5)	0 (0)	1 (0)	7 (1)	0 (0)
	gap – 21 (67.7)	213 (51)	274 (28)	105 (95)	119 (47)	547 (86)	2 (8)
	underpass – 8 (25.8)	170 (41)	639 (66)	6 (5)	135 (53)	85 (13)	24 (92)
χ^2 statistics	**culvert**	1.090	1.491	7.655	15.510	30.370	1.793
	gap	51.180	685.454	36.627	51.830	93.280	42.904
	underpass	49.800	821.128	24.129	98.060	52.180	60.054
P-values	**culvert**	0.889	0.666	0.170	<0.001	<0.001	0.542
	gap	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	underpass	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
b) TIME OF DAY Overall	**χ^2**	292.770	760.350	73.714	228.740	42.904	21.077
	P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Observed Counts (% total)	**night – 10 (41.7)**	315 (76)	715 (74)	87 (78)	224 (88)	304 (48)	22 (85)
	dawn – 2 (8.3)	14 (3)	35 (4)	4 (4)	14 (5)	87 (14)	2 (8)
	day – 2 (41.7)	20 (5)	28 (3)	7 (6)	14 (5)	204 (32)	1 (4)
	dusk – 2 (8.3)	66 (16)	188 (19)	13 (12)	3 (1)	44 (7)	1 (4)
χ^2 statistics	**night**	200.140	415.930	61.550	223.705	9.175	19.732
	dawn	13.360	28.060	3.251	2.698	23.335	0.014
	day	231.820	597.340	57.102	137.305	24.950	15.301
	dusk	31.130	156.610	1.658	17.098	1.753	0.685
P-values	**night**	<0.001	<0.001	<0.001	<0.001	0.010	<0.001
	dawn	0.001	<0.001	0.286	0.402	<0.001	1.000
	day	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	dusk	<0.001	<0.001	0.791	<0.001	0.742	1.000

B2 – Results from multinomial regression models built to test whether species were more likely to use fence gaps with specific environmental characteristics. Bobcats are the reference category. P = 0.01-0.05*; P = 0.001-0.01**; P < 0.001***.

	Intercept Coef.s	Variable Coef.s	Intercept Std Err	Variable Std Err	Intercept P-value	Variable P-value
% Ground Cover						
fox	-1.058	0.040	0.269	0.006	<0.001	<0.001***
raccoon	-2.035	0.060	0.313	0.006	<0.001	<0.001***
coyote	-0.647	0.018	0.268	0.006	0.016	0.003**
deer	1.536	0.001	0.187	0.005	<0.001	0.891
% Canopy Cover						
fox	-1.339	0.046	0.223	0.004	<0.001	<0.001***
raccoon	-2.980	0.069	0.332	0.005	<0.001	<0.001***
coyote	-1.098	0.031	0.220	0.005	<0.001	<0.001***
deer	1.175	0.014	0.139	0.004	<0.001	<0.001***
Distance to Roads (m)						
fox	0.294	0.020	0.227	0.010	0.194	0.037*
raccoon	-1.599	0.086	0.261	0.009	<0.001	<0.001***
coyote	-0.668	0.032	0.265	0.010	0.012	0.002**
deer	1.610	-0.003	0.202	0.009	<0.001	0.752
Gap Width (m)						
fox	2.182	-0.326	0.236	0.043	<0.001	<0.001***
raccoon	2.589	-0.412	0.236	0.046	<0.001	<0.001***
coyote	1.253	-0.255	0.263	0.048	<0.001	<0.001***
deer	2.733	-0.242	0.212	0.033	<0.001	<0.001***
Gap Height (m)						
fox	4.133	-3.205	0.741	0.663	<0.001	<0.001***
raccoon	-5.500	5.411	1.330	1.125	<0.001	<0.001***
coyote	3.615	-3.368	0.791	0.718	<0.001	<0.001***
deer	3.948	-2.191	0.714	0.630	<0.001	0.001**
Total Gap Size (m^2)						
fox	2.140	-0.290	0.220	0.036	<0.001	<0.001***
raccoon	2.200	-0.268	0.215	0.034	<0.001	<0.001***
coyote	1.326	-0.252	0.246	0.042	<0.001	<0.001***
deer	2.702	-0.212	0.197	0.026	<0.001	<0.001***

B3 – Chi-squared tests indicate that bobcats, coyotes and raccoons were significantly more likely to engage in risky behaviors at fence gaps as compared to non-risky behaviors. P = 0.01-0.05*; P = 0.001-0.01**; P < 0.001***.

	# detected risky behaviors	**# detected non-risky behaviors**	χ^2	**P-value**
gray fox	102	89	0.885	0.347
raccoon	135	93	7.737	0.005**
bobcat	67	23	21.511	<0.001***
coyote	84	21	37.800	<0.001***
deer	190	219	0.056	0.152

B4 – Chi-squared tests indicate that, in most instances, risky behaviors occur in expected proportions with the exception being at night. P = 0.05-0.1• ; P = 0.01-0.05*; P = 0.001-0.01**; P < 0.001***.

	Observed counts (risky / non-risky)				**χ2 statistics**				**P-values**			
TIME OF DAY	**night**	**dawn**	**day**	**dusk**	**night**	**dawn**	**day**	**dusk**	**night**	**dawn**	**day**	**dusk**
Fox	69/78	1/4	4/2	15/18	0.551	1.800	0.667	0.273	0.458	0.180	0.414	0.602
Raccoon	74/114	6/9	1/1	12/11	8.511	0.600	0.000	0.043	0.004**	0.439	1.000	0.835
Bobcat	18/54	1/2	0/5	4/6	18.000	0.333	5.000	0.400	<0.001***	0.564	0.025*	0.527
Coyote	17/74	3/5	1/3	0/2	35.703	0.500	1.000	2.000	<0.001***	0.480	0.317	0.157
Deer	123/78	27/30	58/63	11/19	10.075	0.158	0.207	2.133	0.002**	0.691	0.649	0.144

B5 – Results from logistic regression models built to test whether environmental variables predicted each species' use of fence gaps.

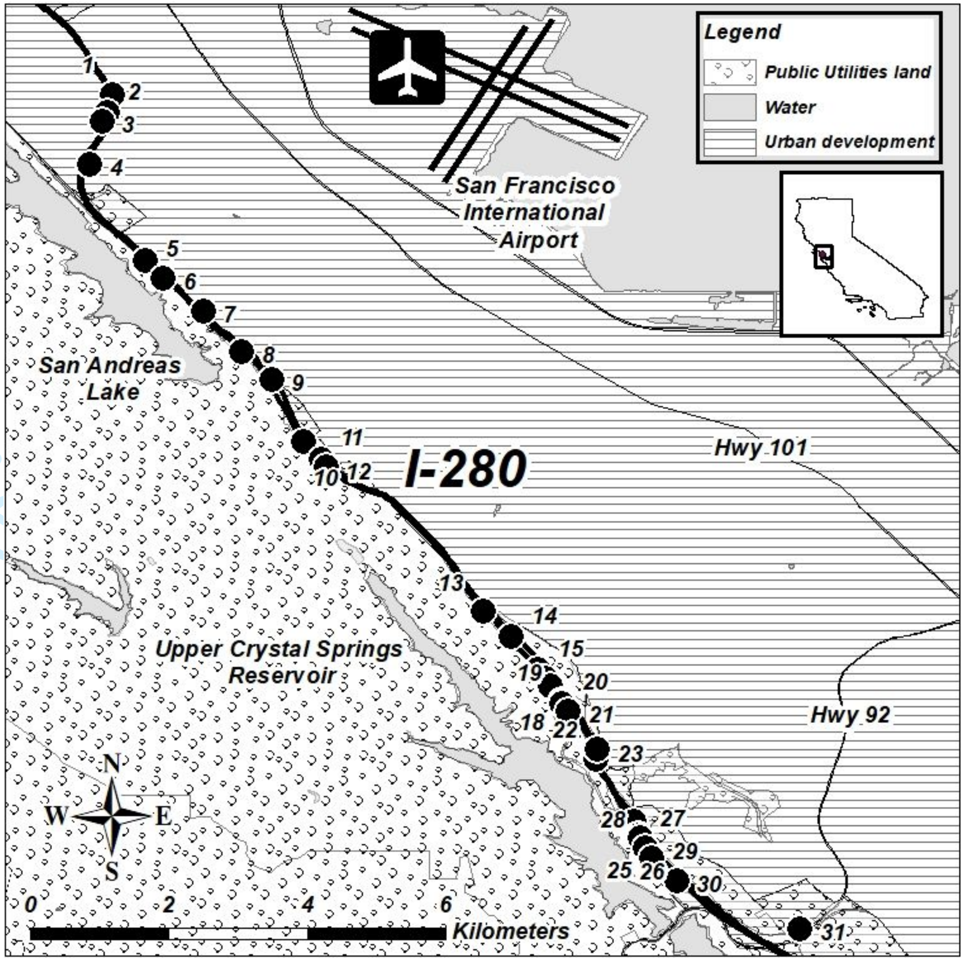
	Coefficient	Std Err	Z-value	P-value
Percent Ground Cover				
foxes	0.003	0.007	0.435	0.663
raccoon	0.004	0.011	0.415	0.678
bobcat	0.050	0.012	4.085	<0.001
coyote	-0.025	0.015	-1.601	0.109
deer	-0.018	0.004	-4.014	<0.001
Percent Canopy Cover				
foxes	-0.021	0.008	-2.850	0.004
raccoon	-0.002	0.005	-0.435	0.664
bobcat	0.043	0.010	4.054	<0.001
coyote	-0.013	0.007	-1.704	0.088
deer	-0.009	0.003	-2.943	0.003
Distance to Roads (m)				
foxes	-0.078	0.019	-4.176	<0.001
raccoon	-0.030	0.010	-2.863	0.004
bobcat	0.001	0.015	0.046	0.963
coyote	-0.010	0.016	-0.629	0.529
deer	-0.047	0.010	-4.873	<0.001
Gap Width (m)				
foxes	0.133	0.067	1.983	0.047
raccoon	0.050	0.098	0.509	0.611
bobcat	-0.464	0.145	-3.212	0.001
coyote	0.090	0.086	1.042	0.297
deer	-0.017	0.049	-0.336	0.737
Gap Height (m)				
foxes	0.084	0.654	0.129	0.897
raccoon	0.061	1.488	0.041	0.968
bobcat	-4.414	1.733	-2.546	0.011
coyote	4.354	1.459	2.984	0.003
deer	1.380	0.488	2.830	0.005
Total Gap Size (m^2)				
foxes	0.124	0.056	2.197	0.028
raccoon	0.036	0.084	0.425	0.671
bobcat	-0.371	0.115	-3.220	0.001
coyote	0.127	0.067	1.906	0.057
deer	0.035	0.042	0.839	0.402

APPENDIX C. Puma detection at fence gap.

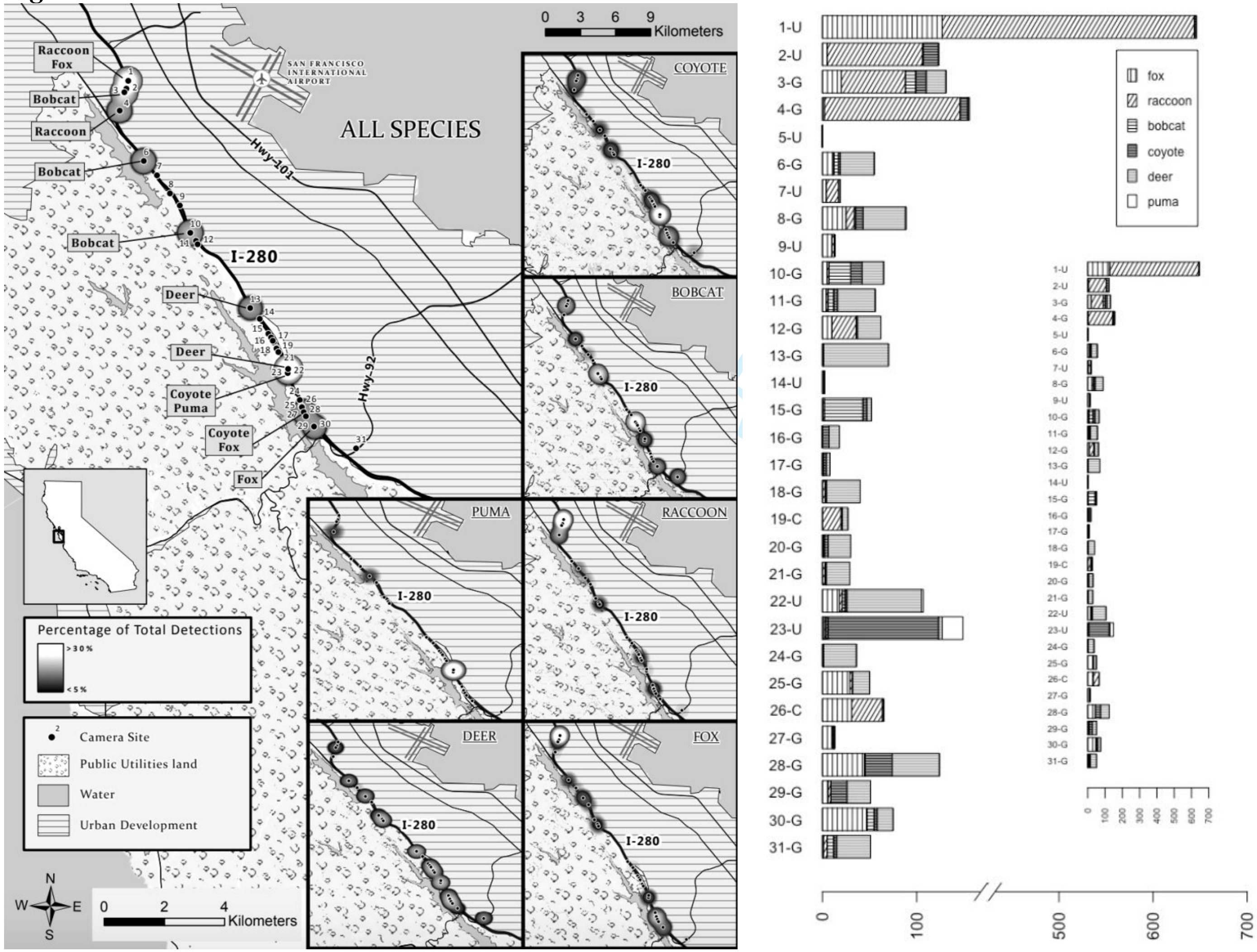
C – Puma detected at location 8 (Figure 1) moving toward I-280 at 03:10:11 and then away from I-280 at 03:12:06 indicating the animal did not cross the highway. Note the change in ear position. The visible black spot ~10 cm below the base of the tail and thin stature suggests the puma is likely a young dispersing male.

TABLES AND FIGURES

ID	Type	L	W	H	Distance to road	%Canopy cover	%Ground cover
1	U_1	81.7	12.7	10.5	-	-	-
2	U_2	81.0	9.4	5.0	-	-	-
3	G_1	-	1.9	1.2	61.4	76.9	63.9
4	G_2	-	3.0	1.2	40.0	100.0	61.1
5	U_3	46.9	13.7	4.7	-	-	-
6	G_3	-	4.5	1.2	7.0	38.5	58.3
7	U_4	46.9	13.7	4.7	-	-	-
8	G_4	-	0.6	1.2	12.0	84.6	47.2
9	U_5	81.4	19.5	4.7	-	-	-
10	G_5	-	1.2	1.1	5.3	23.1	33.3
11	G_6	-	3.3	1.2	32.0	0.0	22.2
12	G_7	-	3.6	1.2	33.3	46.2	75.0
13	G_8	-	5.0	1.1	11.0	0.0	0.0
14	U_6	75.3	12.6	4.6	-	-	-
15	G_9	-	12.1	1.2	15.7	0.0	11.1
16	G_{10}	-	9.7	1.2	8.0	0.0	8.3
17	G_{11}	-	3.0	1.1	7.6	0.0	30.6
18	G_{12}	-	2.8	1.2	8.9	0.0	0.0
19	C_1	-	0.9	0.9	-	-	-
20	G_{13}	-	1.3	0.7	13.7	15.4	41.7
21	G_{14}	-	4.0	1.2	7.2	23.1	16.7
22	U_7	45.1	12.8	50.0	-	-	-
23	U_7						
24	G_{15}	-	4.4	0.7	11.7	0.0	0.0
25	G_{16}	-	7.6	1.2	14.4	84.6	19.4
26	C_2	-	0.9	0.9	-	-	-
27	G_{17}	-	6.4	0.8	12.4	92.3	38.9
28	G_{18}	-	3.6	0.9	24.5	84.6	47.2
29	G_{19}	-	4.8	0.5	32.2	61.5	36.1
30	G_{20}	-	1.4	0.8	18.1	53.9	80.6
31	G_{21}	-	6.9	1.0	24.0	15.4	55.6



3 ***Figure 2***


ALL SPECIES
COYOTE
BOBCAT
PUMA
RACCOON
DEER
FOX
I-280
Hwy-101
Hwy-92
SAN FRANCISCO INTERNATIONAL AIRPORT
Raccoon Fox
Bobcat
Raccoon
Bobcat
Bobcat
Deer
Deer
Coyote Puma
Coyote Fox
Fox
0 3 6 9 Kilometers
0 2 4 Kilometers
Percentage of Total Detections
>30%
<5%
Camera Site
Public Utilities land
Water
Urban Development
fox
raccoon
bobcat
coyote
deer
puma
1-U
2-U
3-G
4-G
5-U
6-G
7-U
8-G
9-U
10-G
11-G
12-G
13-G
14-U
15-G
16-G
17-G
18-G
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20-G
21-G
22-U
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24-G
25-G
26-C
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29-G
30-G
31-G
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100
500
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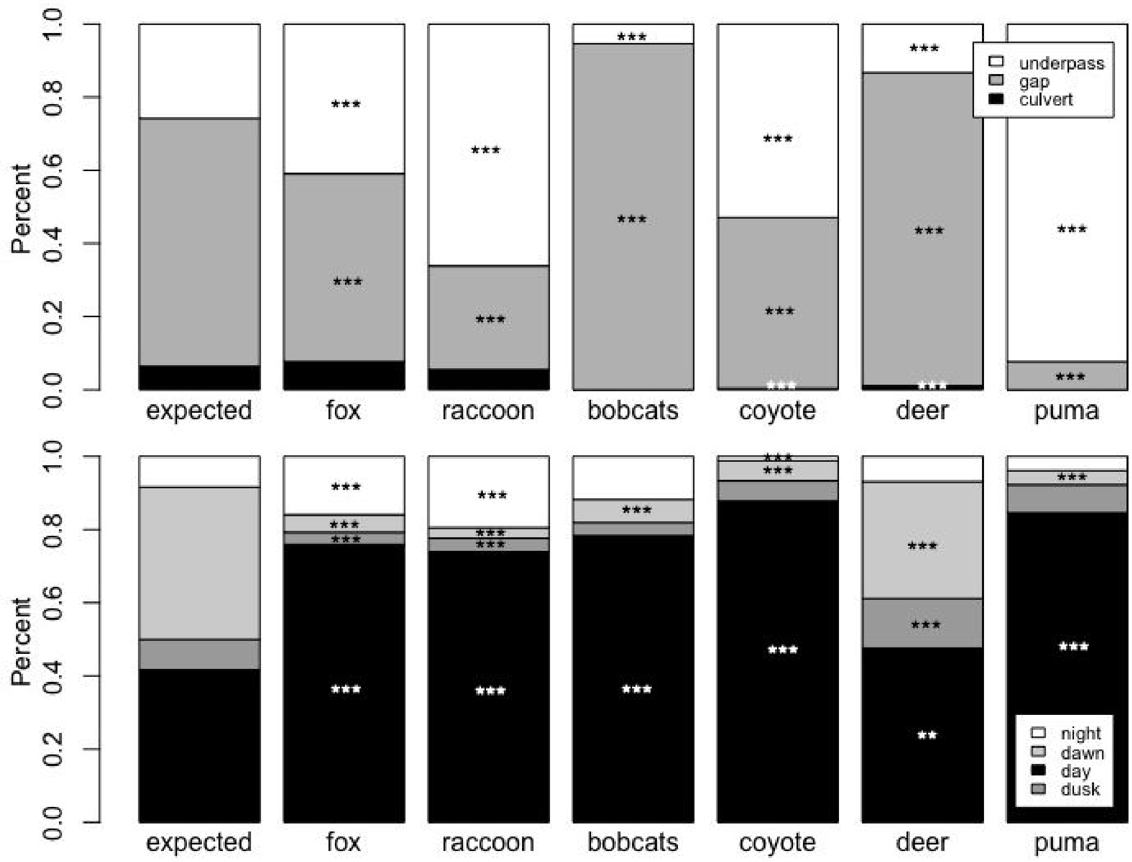
4

Figure 3


Percent
1.0
0.8
0.6
0.4
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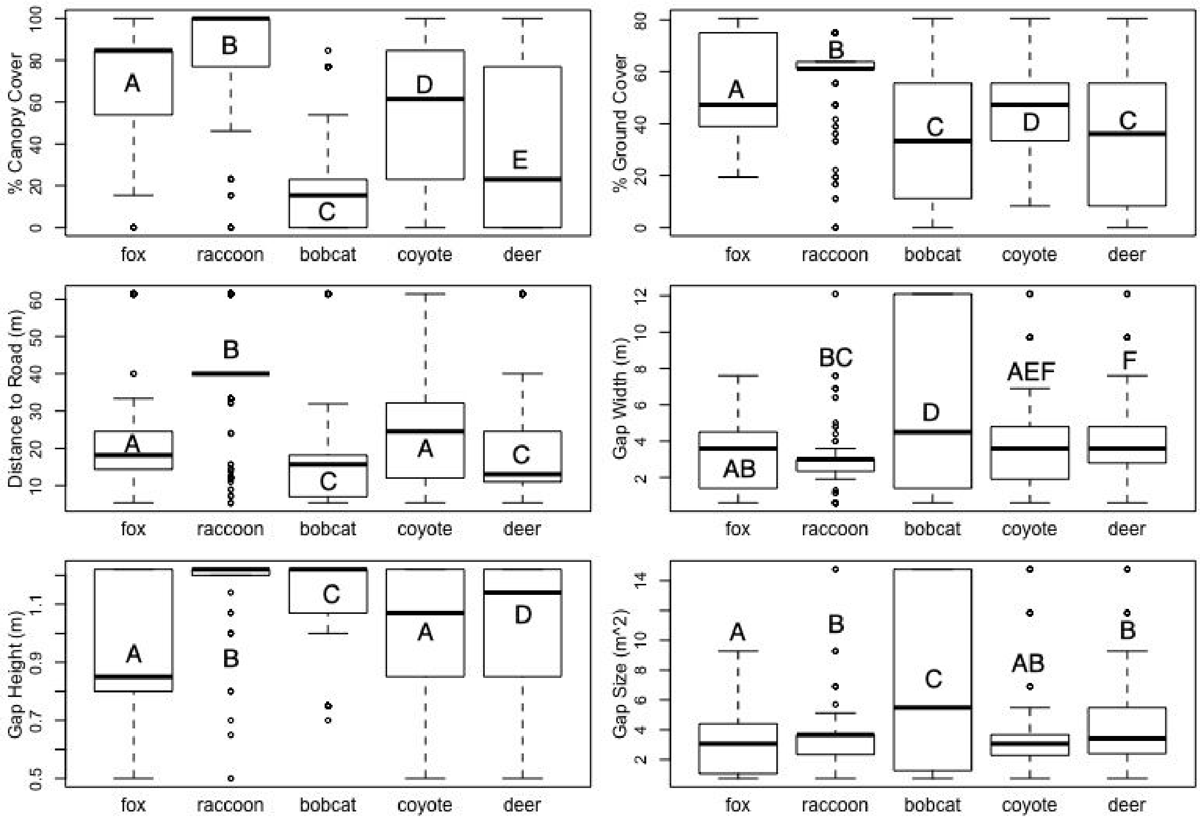
expected
fox
raccoon
bobcats
coyote
deer
puma
underpass
gap
culvert
***
**
night
dawn
day
dusk

Figure 4


% Canopy Cover
A
B
C
D
E
% Ground Cover
A
B
C
D
C
Distance to Road (m)
A
B
C
A
C
Gap Width (m)
AB
BC
D
AEF
F
Gap Height (m)
A
B
C
A
D
Gap Size (m^2)
A
B
C
AB
B
fox
raccoon
bobcat
coyote
deer