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Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape

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ABSTRACT

Roads in urbanized areas can impact carnivore populations by constraining their movements and increasing mortality. Bobcats (*Lynx rufus*) are felids capable of living in urban environments, but are sensitive to habitat fragmentation and, thus, useful indicators of landscape connectivity; in particular, bobcat habitat selection, movement, and mortality may be affected by roads. We analyzed movement patterns of 52 bobcats in southern California in three study sites and investigated: (1) how bobcats responded to two types of roads within their home ranges; (2) how they placed their home ranges with respect to roads within the study area; and (3) whether male and female bobcats differed in their behavioral responses to roads. Within home ranges, primary and secondary roads did not influence movements, but bobcats more frequently crossed secondary roads when road densities were higher within their home ranges, thus increasing mortality risk. However, road densities within each study site were several times higher than road densities within home ranges, suggesting bobcats selected against roaded areas in home-range placement. Male home ranges bordering roads were smaller than home ranges for other males, but male home ranges containing roads were larger than those without roads. Male bobcats also were more likely to cross roads than females, potentially reflecting larger male home range sizes. Our results suggest roads have important impacts on urban bobcats, with stronger effects on males than females, and continued efforts to mitigate the effects of roads on carnivores and other fragmentation-sensitive species would help promote connectivity conservation in urban systems.

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1. Introduction

Roads have strong impacts on the structure, function, and species composition of ecosystems (Coffin, 2007; Forman and Alexander, 1998). Road impacts are pervasive given the ubiquitous presence of road networks in the modern world. Most of the conterminous United States is no more than 35 km from a road (Watts et al., 2007), and approximately 15–20% of the country's land area is ecologically affected by roads (Forman and Alexander, 1998). Roads increase habitat fragmentation and decrease landscape connectivity for many wildlife species, which can result from either simple avoidance of roads or higher mortality risk when crossing roads (Reed et al., 1996). The more subtle effects of roads on animal behavior, such as how animals structure their movements relative to road networks, are often poorly understood (Roedenbeck et al., 2007). This limitation may reduce our ability to design transportation networks to mitigate the negative effects of roads on wildlife, although properly located and designed crossing structures often receive frequent use (Dodd et al., 2004; Foster and Humphrey, 1995; Ng et al., 2004).

Roads affect the movement and distribution of wide-ranging carnivores, including felids, particularly those living in fragmented habitats near urbanized areas. Mountain lions (*Puma concolor*) in southern California displayed an aversion to paved roads when establishing their home ranges (Dickson and Beier, 2002) and constrained their movements to avoid such roads (Dickson et al., 2005). Florida panthers (*P. c. coryi*) tended to avoid crossing roads and contracted their home ranges in the presence of roads, with females more road-averse than males (Cramer and Portier, 2001;

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Maehr et al., 1991). Mortality from vehicle collisions can be high when individuals do cross roads; in Florida panthers, 35% of deaths over a 21-year period were due to roadkill, the greatest cause of mortality (Taylor et al., 2002). Collectively, roads and urbanization often reduce habitat suitability and increase mortality risk in felids (Burdett et al., 2010; Dickson and Beier, 2002).

Bobcats (*Lynx rufus*) are widespread, medium-sized carnivores and may be the most urban-adaptable wild felid species (Riley et al., 2010a). Collisions with vehicles in urban-fragmented areas can be an important source of mortality in bobcats (Tigas et al., 2002); mortalities from vehicle collisions in Ventura and Los Angeles Counties in southern California were highest in areas where roads were common and crossed open space (Riley et al., 2003). Home ranges of bobcats in Wisconsin contained low densities of highways, and individuals crossed paved roads less than expected, suggesting that roads can impact habitat selection and movements of bobcats (Lovallo and Anderson, 1996). Bobcats in Ventura and Los Angeles Counties had larger home ranges when they contained high proportions of non-natural areas, suggesting that such areas provide less suitable habitat (Riley et al., 2003). Additionally, bobcat home-range perimeters often bordered major roads, and these home ranges were smaller than those that did not border roads, suggesting that roads affect both home-range size and boundaries and represent barriers to bobcat movements (Riley et al., 2006). Further, adult female bobcats in Marin County, California, were less likely to be located near urban development than male bobcats, indicating that behavioral responses to roads and urbanization may differ between males and females (Riley, 2006).

Understanding movement behavior in response to landscape features is a critical question in ecology and conservation biology (Morales et al., 2010; Tracey et al., 2013), and the ability of animals to move through fragmented systems is a fundamental determinant of functional landscape connectivity (Crooks and Sanjayan, 2006; Taylor et al., 1993). We studied bobcat movement patterns relative to roads in an urbanized landscape in coastal southern California. Bobcats are moderately sensitive to urban fragmentation and thus useful indicators of landscape connectivity in this system (Crooks, 2002). The objectives of our study were to determine: (1) how bobcats responded to two different types of roads within their home ranges; (2) how they placed their home ranges with respect to roads within the study area; and (3) whether male and female bobcats differed in their behavioral responses to roads, including the placement and size of their home ranges. Our use of Global Positioning System (GPS) telemetry to address these objectives enabled us to document fine-scale, high-resolution movement paths of bobcats and, thus, to evaluate their road crossings and other movement characteristics near roads.

2. Methods

2.1. Study area

Our study area in southern California included parts of three counties, Orange, Riverside, and San Bernardino, in urbanized landscapes south of Los Angeles. We conducted our study in three sites: (1) the Santa Ana Mountains and adjacent foothills and the former Marine Corps Air Station El Toro, in Orange County; (2) the San Joaquin Hills, in coastal Orange County between the cities of Costa Mesa and Laguna Niguel; and (3) the Chino Hills, in the area around State Routes 71 and 91, including Chino Hills State Park and Prado Flood Control Basin, encompassing parts of all three counties (Fig. 1). The climate was Mediterranean, with warm, dry summers and a mean annual precipitation of 29.7 mm, primarily occurring during the wet season (November–April; World Climate Data, 2011a). Monthly temperatures ranged from a mean low of 7.4° C in December to a mean high of 28.8° C in August (World Climate Data, 2011b). The most common vegetation communities in the study area were coastal sage scrub, chaparral, riparian, coastal oak woodlands, and annual grasslands.

2.2. Bobcat trapping and GPS telemetry

We captured bobcats using wire-cage traps from December 2002 to January 2008 in the Santa Ana Mountains study site, January 2006 to February 2007 in the San Joaquin Hills, and December 2008 to March 2009 in the Chino Hills. We identified trap locations based upon sign (e.g., bobcat scat and tracks) and placed the traps along potential movement paths, including drainages, wildlife trails, or roadways through natural areas. In the Santa Ana Mountains and San Joaquin Hills study sites, we conducted trapping throughout open space areas, whereas in the Chino Hills study site, we placed traps within a 1-km buffer of State Highways 71 and 91 to sample animals that were most likely to cross these roads, because evaluating the efficacy of recent road mitigation was the primary goal of that study. We injected each captured bobcat with a combination of ketamine (10 mg/kg) and xylazine HCl (1 mg/kg), and then sexed, weighed, measured, and ear-tagged them. We then attached a GPS collar to all adult (>12 months) bobcats >5.0 kg.

We used one of four types of GPS collars: (1) Televilt Tellus Basic (Telemetry Solutions, Walnut Creek, California, USA); (2) Televilt GPS-Posrec™ (Telemetry Solutions, Walnut Creek, California, USA); (3) HABIT Research (H.A.B.I.T. Research/Locator Systems Corp., Victoria, British Columbia, Canada); or (4) Sirtrack Satellite GPS (Sirtrack Ltd., North Liberty, Iowa, USA). We used the first three collar types in the Santa Ana Mountains and San Joaquin Hills study sites, whereas we used only Sirtrack collars in the Chino Hills site. We programmed collars to collect GPS locations every 15–30 min, but time schedules varied by collar. Televilt and HABIT Research collars collected data in 2–3.5 h bouts several times per week. Sirtrack collars collected data every 15 min for a 24-h period either 2 times or 4 times per week. Most collars also recorded the number of satellites used in calculating a GPS fix, with more satellites providing more accurate locations. All collars were either equipped with automatic drop-off mechanisms or contained fabric that allowed the collars to eventually drop off with wear. We attempted to retrieve collars that did not drop off by re-trapping bobcats. We downloaded data from collars either remotely from a receiver when the collars were still deployed (HABIT Research collars) or after collars were retrieved (all other collars). The capture and handling protocol used in this study followed guidelines of the U.S. Geological Survey, Western Ecological Research Center, Animal Care and Use Committee and was approved by the Colorado State University and University of California Davis Animal Care and Use Committees.

2.3. Bobcat movement paths

We derived movement paths from GPS data to analyze behavioral responses of bobcats to both primary and secondary roads in the three study sites. Primary roads were major interstate and state highways, and secondary roads were high-capacity roads intended to deliver traffic to primary roads and between urban centers. We did not examine traffic volume or evaluate how bobcats responded to low- to medium-capacity roads and local streets. Some primary and secondary roads in our study sites had structures under roads, such as culverts, and habitat under span bridges suitable for wildlife crossing. Although we did not quantify such structures or bobcat use of them in this study, they likely influenced roadway permeability and, hence, differences in crossing frequencies among study sites (see Section 4).

Because we were interested in evaluating bobcat movements relative to roads, rather than using the point-based locations, we

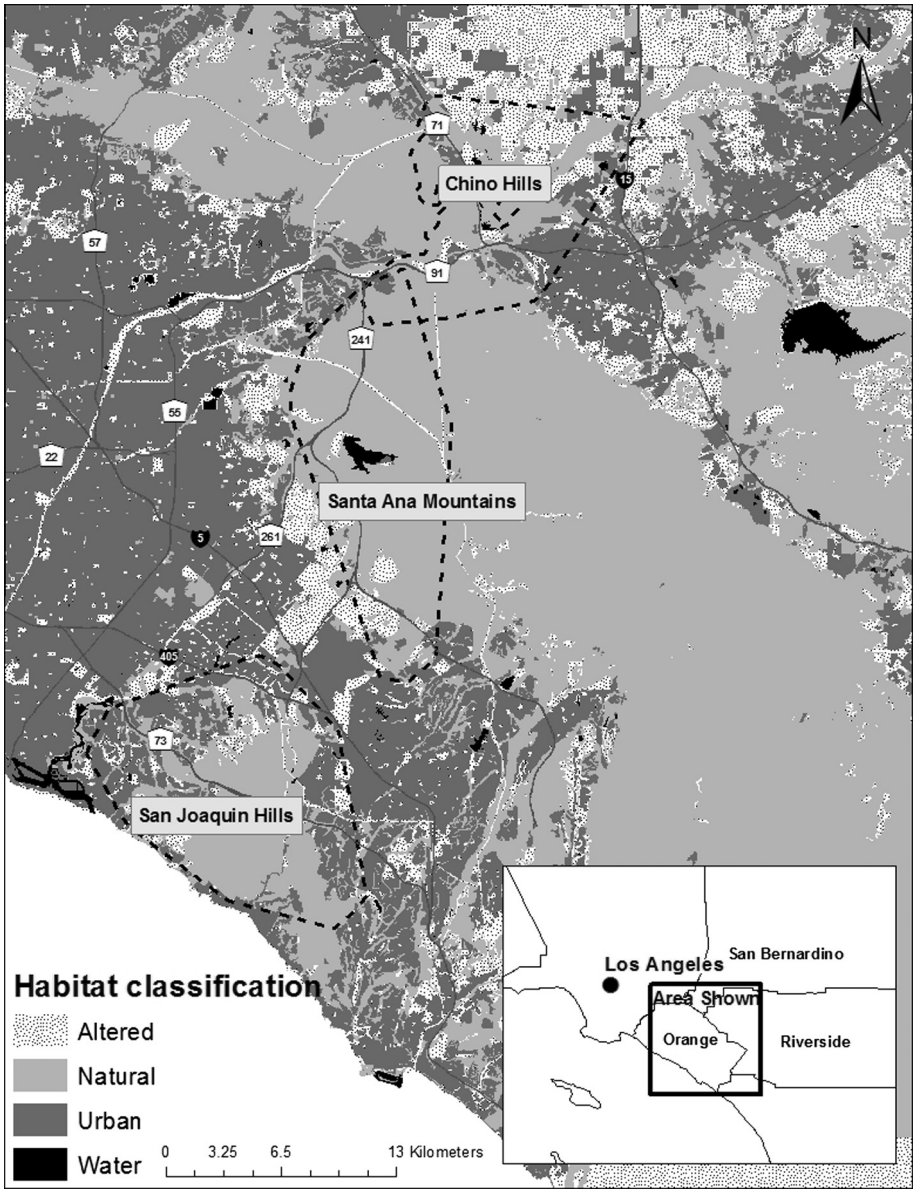

Fig. 1. Land-use classification of study area in southern California, 2002–2009, delineating the three study sites (indicated by dashed lines) and primary roads. Study sites are 95% minimum convex polygons using the locations of all resident bobcats within each site.

created movement paths of bobcats using the XTools Pro Extension (Data East, 2007) for ArcGIS v.9.2 (ESRI, Redlands, California, USA) to draw straight lines between each bobcat's consecutive GPS locations. We excluded GPS locations based on fewer than three satellites because these locations were less accurate. To define a movement path, we specified that the path had at least two locations, connected GPS locations were separated by 35 min or less, and the path was at least 100 m in length (i.e., the sum of the length of segments within the movement path was $\geqslant$100 m). Upon examination of our data, we determined that longer time periods between locations may not accurately reflect direct movements of bobcats and that shorter paths would be unsuitable to address our study objectives.

We then created random movement paths by randomly relocating each actual movement path within a bobcat's home range. To do so, we first calculated a 95% minimum convex polygon (MCP) for each individual bobcat using the Hawth's Tools extension for ArcGIS (Beyer, 2004). We used MCPs in our analyses rather than kernel home-range estimators because they better characterized the space use of bobcats in our highly-fragmented urban landscape by including the areas between separate polygons often created by kernel estimators, which could be important habitat for bobcats, and MCPs also minimize the extent to which home ranges cross hard boundaries, such as roads (Riley et al., 2003, 2010b). In the Chino Hills study site, we removed from each individual's MCP, when necessary, a recently (i.e., November 2008) burned area in the western part of the study area (the Freeway Complex Fire) and a frequently inundated water basin in the central part of the study area (Prado Flood Control Basin). The wildfire, which occurred immediately before our bobcat trapping efforts, was severe and resulted in a barren landscape with little to no suitable bobcat habitat, and the water basin was inundated to an elevation of 152 m from September 2008 to March 2009; hence, we considered both of these areas to be unavailable to bobcats. We included only those actual movement paths, or segments thereof, for an individual that were contained within that individual's MCP. We then used the Alternate Animal Movement Routes Extension (Jenness, 2004) for ArcView 3.3 (ESRI, Redlands, California, USA)

to create an equal number of matching random paths. We placed these random paths within each MCP but modified the origin and orientation of each path to represent an alternate path the bobcat could have used instead of its actual path.

2.4. Home-range scale analyses

We conducted two analyses at the home-range scale to evaluate bobcat responses to roads (3rd order selection; Johnson, 1980). First, we assessed distances to primary roads, secondary roads, and primary and secondary roads combined with a use-availability sampling design. The use data were the actual bobcat movement paths, and the availability data were the random paths. We calculated the average distance from each actual and random path to the nearest road of each type. To do so, we first created three Euclidean distance rasters (i.e., grids of equally-sized cells, with each cell containing one attribute value) of 30-m resolution over the study area; we created one raster for primary roads, one for secondary roads, and one for both types of roads combined. Each raster calculated, for each cell in the raster, the distance from the center of that cell to the nearest road. Next, we used Hawth's Tools (Beyer, 2004) to calculate an average nearest distance for each actual and random path by averaging the distance values of those cells in each raster that intersected with the path. We then averaged these path distances per individual bobcat by road and path type. Finally, we used paired *t*-tests to determine whether nearest distances to roads differed between movement paths and random paths among individual bobcats within each of the three study sites. We log-transformed the response variables for the test comparing distances to primary roads for Chino Hills and the test comparing distances to both primary and secondary roads combined for San Joaquin Hills; for all other tests, the response variables met distributional assumptions and were not transformed.

Second, we modeled the number of road crossings of bobcat movement paths for both primary and secondary roads. These road crossings represented both surface crossings as well as crossings through structures under roads, such as culverts, or through habitat found under span bridges. Because most bobcats never crossed a road (see Section 3), resulting in many zero counts in the road crossings response variable, we analyzed our data using a two-part generalized linear model that first used a logistic regression to model the probability that bobcat paths crossed a road or not (accounting for excessive zeroes) and then used a negative binomial regression to model the zero-truncated count-based process for the number of times bobcat paths crossed a road (Welsh et al., 1996). We found this two-part approach had fewer estimation issues than alternative statistical models, such as a zero-inflated negative binomial model (Hilbe, 2011). Our primary explanatory variable of interest was the density of primary and secondary roads within a bobcat's home range. However, in addition to investigating the biological process among bobcats, road crossings, and road densities, we also included two additional covariates investigating the sampling process in this two-part model: (1) the sum of time elapsed for all paths for an individual bobcat (i.e., monitoring time); and (2) study site, which we implemented as a dummy variable using the Santa Ana Mountains as the baseline site to determine differences among sites. We chose the Santa Ana Mountains as the baseline because it had the lowest number of primary and secondary road crossings (see Section 3). The sample size for the two-part model was the number of collared bobcats in each study site. We ran separate two-part models for primary and secondary roads. In addition to the models, we also calculated bobcat crossing rates for each study site by first computing a rate for each individual bobcat by dividing the number of crossings by the monitoring time, and then averaging these rates across all bobcats within a study site.

2.5. Study-area scale analysis

To analyze the response of bobcats to roads at the study-area scale (2nd order selection; Johnson, 1980), we calculated densities (m/km^2) of primary and secondary roads within each of the three study sites and within each bobcat's MCP home range. We defined the boundaries of each study site by calculating a 95% MCP around the GPS locations of all resident bobcats within each site. For the Chino Hills site, we removed from the MCP the burned area and the water basin. We then averaged densities of roads within home ranges for all bobcats for each study site and compared them to road densities within each study site. Because many bobcat home ranges contained no roads and, thus, had zero road densities, the response variables could not meet distributional assumptions. Hence, we used nonparametric Wilcoxon signed-rank tests to compare road densities.

2.6. Analysis of sex differences in response to roads

We examined bobcat behavioral responses to roads by sex. We first identified home ranges that bordered primary roads as those ranges that contained no primary roads within their boundaries but had a border located less than the average path length of all bobcats (825 m, SD = 592) from a primary road. Similarly, we identified home ranges that bordered secondary roads as those ranges that contained no secondary roads within their boundaries but had a border less than the average path length from a secondary road. Lastly, we identified home ranges that bordered either type of road as those ranges that contained no primary or secondary roads within their boundaries but had a border less than the average path length from either type of road. We then used *t*-tests to compare, for both male and female bobcats and for primary roads, secondary roads, and either type of road, the sizes of home ranges that bordered these road types to those that did not but may or may not have contained such roads within their boundaries. Further, we used *t*-tests to compare, for both males and females and for primary roads, secondary roads, and either type of road, the sizes of home ranges that contained these road types within their boundaries to those that had no such roads. We used a log transformation on the response variables for all tests comparing male home ranges and a negative inverse transformation for all tests comparing female home ranges. We considered all statistical tests, which were two-tailed, with $P < 0.05$ to be significant and $0.05 < P < 0.1$ to be marginally significant. We conducted all analyses within SAS (SAS Institute Inc., 2011) and Stata 12 (StataCorp, 2011).

3. Results

3.1. Collared bobcats

We captured 71 bobcats and deployed 57 GPS collars (36 males; 21 females) from the three study sites. Of these, we were able to retrieve data from the collars of 52 bobcats (32 males; 20 females) with 69,554 GPS locations (Table 1). The collars collected locations from December 2002 to May 2004 for 16 bobcats and from February 2007 to April 2008 for four bobcats in the Santa Ana Mountains, from January 2006 to June 2007 in the San Joaquin Hills, and from December 2008 to July 2009 in the Chino Hills.

3.2. Home-range scale analyses

3.2.1. Distances to roads

Average distances of bobcat movement paths from primary roads ranged from 395 m (Chino Hills females) to 2766 m (San Joaquin Hills females), and average distances of bobcat movement paths from secondary roads ranged from 1033 m (San Joaquin Hills

Table 1
Summary of mean (SD) number of GPS locations, home range size, number of movement paths, and average distances of bobcat movement paths to primary and secondary roads of all, male, and female bobcats captured and collared in the three study sites in southern California, USA, 2002–2009.

Study site	GPS locations	95% MCP[a] home range size (km^2)	Movement paths within home ranges	Average distances to primary roads (m)[b]	Average distances to secondary roads (m)[b]
Santa Ana Mountains					
All (n = 20 bobcats)	651 (1041)	4.93 (5.38)	63 (82)	1847 (1005)	1712 (1093)
Males (n = 12 bobcats)	904 (1302)	6.78 (6.34)	81 (104)	1836 (773)	1412 (966)
Females (n = 8 bobcats)	271 (52)	2.15 (0.81)	36 (5)	1862 (1342)	2163 (1178)
San Joaquin Hills					
All (n = 17 bobcats)	738 (1275)	8.04 (6.40)	72 (108)	2414 (1452)	1121 (884)
Males (n = 9 bobcats)	1051 (1717)	8.41 (5.96)	99 (145)	2100 (1332)	1199 (889)
Females (n = 8 bobcats)	385 (274)	7.62 (7.25)	41 (26)	2766 (1588)	1033 (930)
Chino Hills					
All (n = 15 bobcats)	2933 (1864)	15.17 (15.18)	83 (53)	1250 (1522)	1465 (710)
Males (n = 11 bobcats)	3028 (2194)	19.62 (15.49)	89 (61)	1561 (1683)	1381 (766)
Females (n = 4 bobcats)	2672 (237)	2.93 (1.75)	69 (12)	395 (181)	1698 (542)

[a] Minimum convex polygon.
[b] Average distances calculated as the average of the distances to roads for all movement paths for an individual bobcat.

females) to 2163 m (Santa Ana Mountains females; Table 1). Distances of bobcat movement paths to both primary and secondary roads combined were no different than expected in each site (Santa Ana Mountains: paired $t_{19} = 0.03$, $P = 0.975$; San Joaquin Hills: paired $t_{16} = 0.08$, $P = 0.941$; Chino Hills: paired $t_{14} = -1.50$, $P = 0.155$; Fig. 2). Bobcat movement paths were farther from primary roads than expected in the Santa Ana Mountains (paired $t_{19} = 2.56$, $P = 0.019$), but not in the San Joaquin Hills (paired $t_{16} = 0.91$, $P = 0.374$) or the Chino Hills (paired $t_{14} = -1.60$, $P = 0.131$). Distances of bobcat movement paths to secondary roads were no different than expected in the Santa Ana Mountains (paired $t_{19} = -1.17$, $P = 0.256$) or the San Joaquin Hills (paired $t_{16} = -1.20$, $P = 0.248$) and only marginally different in the Chino Hills (paired $t_{14} = -1.77$, $P = 0.098$), with movement paths tending to be closer to secondary roads than expected.

3.2.2. Road crossings

Across our three study sites, only 248 (7%) of the 3727 movement paths within bobcat home ranges crossed primary roads. Six of 20 (30%) bobcats in the Santa Ana Mountains, four of 17 (24%) bobcats in the San Joaquin Hills, and 11 of 15 (73%) bobcats in the Chino Hills had movement paths crossing primary roads. For those bobcats, only 10% of 2549 movement paths crossed primary roads, and crossings occurred, on average, 3.7 times (SD = 3.3; range = 1–10) during 14.72 days (SD = 15.49; range = 2.64–38.21) of monitoring time per individual in the Santa Ana Mountains, 12.5 times (SD = 15.2; range = 2–35) during 18.09 (SD = 23.67; range = 3.79–53.43) monitoring days in the San Joaquin Hills, and 33.9 times (SD = 42.2; range = 1–132) during 33.21 (SD = 21.32; range = 16.06–76.93) monitoring days in the Chino Hills. Thus, for each bobcat that crossed a primary road, crossings occurred,

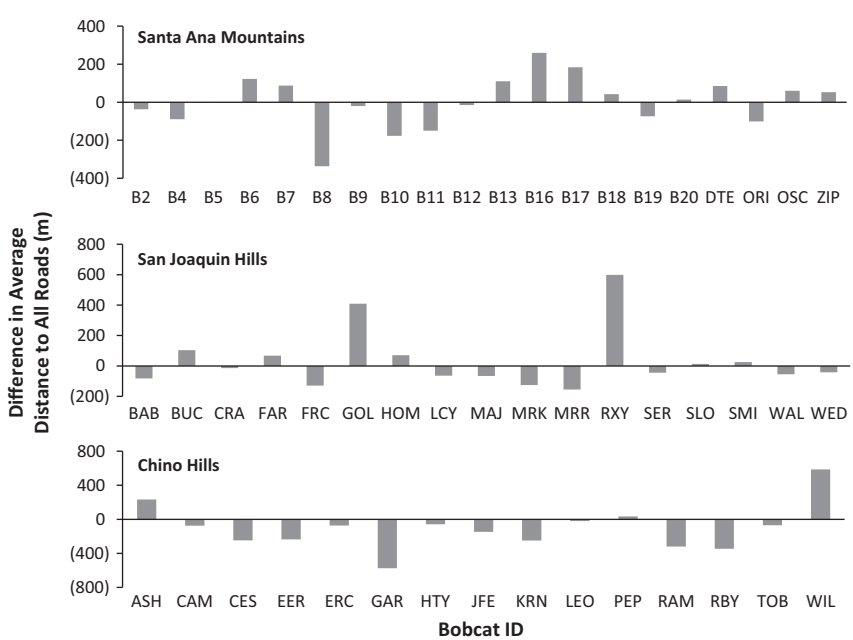

Fig. 2. Differences in average distances to primary and secondary roads combined between actual bobcat movement paths and matching random paths within bobcat home ranges in each study site in southern California, 2002–2009. Bars above the zero line indicate bobcat movement paths farther from roads than random paths, and bars below the zero line indicate bobcat movement paths closer to roads than random paths.

on average, 0.49 times (SD = 0.43; range = 0.07–1.04) per day of monitoring time in the Santa Ana Mountains, 1.64 times (SD = 1.52; range = 0.04–3.69) per monitoring day in the San Joaquin Hills, and 0.95 times (SD = 1.03; range = 0.06–3.68) per monitoring day in the Chino Hills. Primary road density within home ranges was positively related to the binomial probability of bobcat paths crossing a primary road ($n = 52$, $z = 2.47$, $P = 0.014$; Fig. 3a), whereas monitoring time ($z = 1.37$, $P = 0.170$) and study site (San Joaquin Hills: $z = -1.48$, $P = 0.140$; Chino Hills: $z = -0.35$, $P = 0.727$) were not. In contrast, monitoring time was positively associated with the number of primary road crossings ($n = 21$, $z = 2.13$, $P = 0.033$), whereas primary road density was not ($z = 1.12$, $P = 0.262$). The number of primary road crossings was higher in the San Joaquin Hills ($z = 2.50$, $P = 0.012$) and the Chino Hills ($z = 2.20$, $P = 0.028$) than in the Santa Ana Mountains.

Across our three study sites, 158 (4%) of the movement paths crossed secondary roads. Six of 20 (30%) bobcats in the Santa Ana Mountains, nine of 17 (53%) bobcats in the San Joaquin Hills, and five of 15 (33%) bobcats in the Chino Hills had movement paths crossing secondary roads. For those bobcats, 8% of 1992 movement paths crossed secondary roads, and crossings occurred, on average, 6.0 times (SD = 4.0; range = 1–13) during 14.26 days (SD = 15.91; range = 1.63–38.21) of monitoring time per individual in the Santa Ana Mountains, 8.0 times (SD = 8.7; range = 1–29) during 8.56 (SD = 16.88; range = 0.97–53.43) monitoring days in the San Joaquin Hills, and 24.4 times (SD = 32.1; range = 5–81) during 23.22 (SD = 6.47; range = 16.06–29.51) monitoring days in the Chino Hills. Thus, for each bobcat that crossed a secondary road, crossings occurred, on average, 0.98 times (SD = 0.94; range = 0.23–2.45) per monitoring day in the Santa Ana Mountains, 1.62 times (SD = 1.06; range = 0.54–4.10) per monitoring day in the San Joaquin Hills, and 1.01 times (SD = 1.10; range = 0.20–2.85) per monitoring day in the Chino Hills. Secondary road density within home ranges was marginally and positively related to the binomial probability of bobcat paths crossing a secondary road ($n = 52$, $z = 1.93$, $P = 0.053$; Fig. 3b), whereas monitoring time ($z = -0.33$, $P = 0.742$) and study site (San Joaquin Hills: $z = -0.25$, $P = 0.804$; Chino Hills: $z = -0.36$, $P = 0.717$) were not. Secondary road density ($n = 20$, $z = 1.85$, $P = 0.064$) was marginally and positively associated and monitoring time ($z = 3.51$, $P < 0.001$) was positively associated with the number of secondary road crossings. The number of secondary road crossings did not differ between the Santa Ana Mountains and the San Joaquin Hills ($z = -0.52$, $P = 0.603$), but crossings were higher in the Chino Hills than in the Santa Ana Mountains ($z = 2.25$, $P = 0.024$).

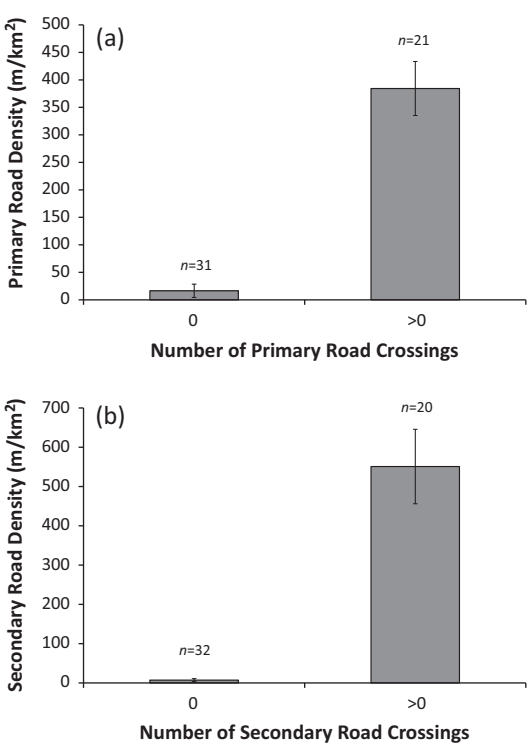

Fig. 3. Mean densities (±SE) of primary (a) and secondary (b) roads within bobcat home ranges for bobcats that did and did not cross roads in southern California, 2002–2009. Sample sizes (n) represent numbers of individual bobcats.

3.3. Study-area scale analysis

Twenty-three of the 52 bobcats (44%) had primary roads within their MCP home ranges, 24 bobcat home ranges (46%) had secondary roads, and 31 home ranges (60%) had either primary or secondary roads. Bobcat home ranges contained 88.5 m/km^2 (SD = 161.7; range = 0–619) of primary roads in the Santa Ana Mountains, 110.9 m/km^2 (SD = 182.7; range = 0–574) of primary roads in the San Joaquin Hills, and 328.4 m/km^2 (SD = 298.3; range = 0–1084) of primary roads in the Chino Hills. Densities of primary roads were higher in the study site than in bobcat home ranges for the Santa Ana Mountains (2.2 times higher) and the San Joaquin Hills (1.4 times higher; Fig. 4a), although this difference was significant only for the Santa Ana Mountains (Santa Ana Mountains: $S = 70.0$, $P = 0.005$; San Joaquin Hills: $S = 24.5$, $P = 0.238$). Only six of 20 (30%) bobcat home ranges in the Santa Ana Mountains and six of 17 (35%) home ranges in the San Joaquin Hills contained primary roads. In contrast, densities of primary roads within the Chino Hills site were 37% lower than average densities of primary roads within bobcat home ranges for Chino Hills (Fig. 4a), although this difference was not significant ($S = -23.0$, $P = 0.202$). Eleven of 15 (73%) bobcat home ranges in the Chino Hills contained primary roads.

Bobcat home ranges contained 81.3 m/km^2 (SD = 152.0; range = 0–466) of secondary roads in the Santa Ana Mountains, 446.6 m/km^2 (SD = 539.3; range = 0–1385) of secondary roads in the San Joaquin Hills, and 135.1 m/km^2 (SD = 209.0; range = 0–650) of secondary roads in the Chino Hills. Densities of secondary roads were higher in the study site than in bobcat home ranges for the Santa Ana Mountains (1.7 times higher), the San Joaquin Hills (1.5 times higher), and the Chino Hills (2.5 times higher; Fig. 4b); this difference was significant for the Chino Hills ($S = 49.0$, $P = 0.003$) and marginally significant for the Santa Ana Mountains ($S = 44.0$, $P = 0.083$) and the San Joaquin Hills ($S = 37.5$, $P = 0.076$). Six of 20 (30%) bobcat home ranges in the Santa Ana Mountains, 11 of 17 (65%) home ranges in the San Joaquin Hills, and seven of 15 (47%) home ranges in the Chino Hills contained secondary roads.

3.4. Analysis of sex differences in response to roads

Across the three study sites, 16 male (50%) and five female (25%) bobcats had movement paths crossing primary roads, and 16 male (50%) and four female (20%) bobcats had movement paths crossing secondary roads. For male bobcats, home ranges that bordered roads were almost 2.5 times smaller than those that did not for primary roads ($t_{14} = -2.22$, $P = 0.044$; Fig. 5a), almost 3.5 times smaller than those that did not for secondary roads ($t_8 = -3.35$, $P = 0.010$; Fig. 5a), and almost 3 times smaller than those that did not for either type of road ($t_{24} = -3.42$, $P = 0.002$; Fig. 5a). However, male home ranges containing primary roads were almost 3 times larger than those without such roads ($t_{30} = 3.90$, $P < 0.001$; Fig. 6a), those containing secondary roads were more than 3 times

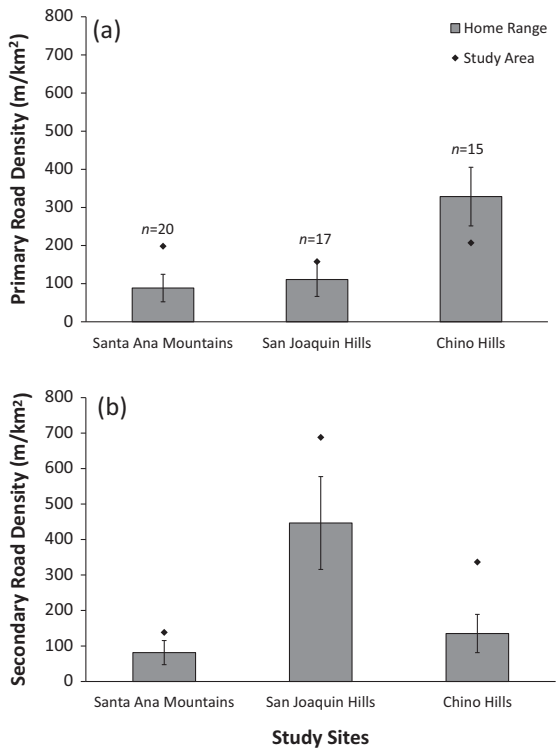

Fig. 4. Mean densities (±SE) of primary (a) and secondary (b) roads within bobcat home ranges and within each study area (total densities) in southern California, 2002–2009. Sample sizes (n) represent numbers of individual bobcats for home range road densities.

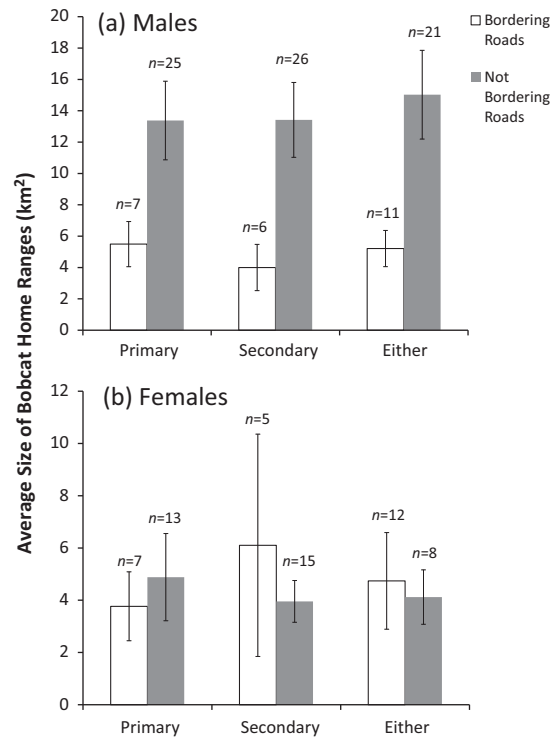

Fig. 5. Bobcat home range sizes (mean ± SE) bordering and not bordering primary roads, secondary roads, and either type of road for males (a) and females (b) in southern California, 2002–2009. Home ranges bordering roads did not contain roads, and home ranges not bordering roads may or may not have contained roads. Sample sizes (n) represent numbers of individual bobcats for home range sizes.

larger than those without such roads ($t_{26} = 4.48$, $P < 0.001$; Fig. 6a), and those containing either type of road were more than 3 times larger than those without such roads ($t_{21} = 4.55$, $P < 0.001$; Fig. 6a). In contrast, the sizes of female home ranges that bordered roads were not significantly different from those that did not, for primary roads ($t_{15} = -0.11$, $P = 0.916$; Fig. 5b), secondary roads ($t_5 = -0.93$, $P = 0.397$; Fig. 5b), or either type of road ($t_{18} = -1.29$, $P = 0.212$; Fig. 5b). Likewise, the sizes of female home ranges containing roads were not different from those without roads, for primary roads ($t_6 = 0.44$, $P = 0.673$; Fig. 6b), secondary roads ($t_6 = 1.02$, $P = 0.344$; Fig. 6b), or either type of road ($t_{14} = 0.80$, $P = 0.434$; Fig. 6b).

4. Discussion

Our findings suggest that the distribution of primary and secondary roads influenced the establishment of bobcat home ranges in an urbanized landscape. With the exception of primary roads in the Chino Hills, primary and secondary road densities tended to be higher within each study site than within home ranges. Additionally, 40% of the bobcats in our study had no primary or secondary roads within their home ranges, and most (90%) of the movement paths we defined did not cross such roads. Similarly, Dickson et al. (2005) determined that cougars avoided 2-lane paved roads in an overlapping study area in southern California, and Riley (2006) found that roads represented home range boundaries for bobcats in Marin County, California, suggesting a general aversion to high-traffic roads by felids. Although bobcats may be evading primary and secondary roads, we emphasize that they were nonetheless more likely to cross both types of roads when road densities

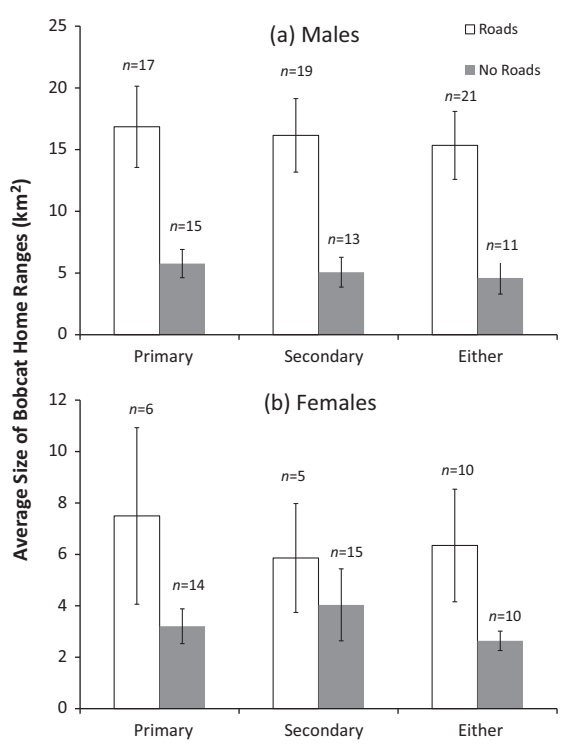

Fig. 6. Bobcat home range sizes (mean ± SE) with and without primary roads, secondary roads, and either type of road for males (a) and females (b) in southern California, 2002–2009. Sample sizes (n) represent numbers of individual bobcats for home range sizes.

were higher, thus increasing mortality risk (Riley et al., 2003). We also note that the higher prevalence of primary roads, and primary road crossings, within bobcat home ranges in the Chino Hills was likely due to our targeted trapping near two State Highways (71 and 91) to evaluate road mitigation efforts, as well as the recently burned area and water basin that might have constrained bobcat movement to available habitat near these roads (see Section 2). These two highways also had multiple underpasses, likely increasing their permeability and, hence, the likelihood of road crossings in this study site.

At the home-range scale, we did not detect a notable effect of primary or secondary roads on where bobcats moved within their home ranges, suggesting that bobcats do not necessarily avoid movements near roads. However, if bobcats locate their home ranges to minimize or avoid crossing busy roads, this pattern of home-range placement could lessen the impact of such roads on movement patterns within home ranges. Our path-based analysis was conducted at a scale that measured fine-grained behavioral responses to roads. Since many home ranges lacked any primary or secondary roads, the principal behavioral response of bobcats to roads possibly may emerge at a higher order of selection, such as when they established home ranges within the broader landscape. Further, bobcat movement is undoubtedly a complex process (Tracey et al., 2013), and our focus on roads does not explicitly consider other factors that would influence bobcat movement, such as distribution of prey, topography, vegetative cover, mating opportunities, or other types of development.

We determined that increased density of roads in bobcat home ranges increased the probability of bobcat crossings for both primary and secondary roads. Further, the density of roads in home ranges affected the number of secondary road crossings but not the number of primary road crossings. This finding suggests that bobcats may increase their crossings of secondary roads as the density of these roads increases within their home ranges, but they do not similarly increase their crossings of major highways when the density of these roads increases in their home ranges. Hence, although bobcats rarely crossed either type of road, primary roads may be a more effective barrier to bobcat movement than secondary roads. However, we also found that length of monitoring time increased the number of bobcat road crossings for both types of roads. This result was an unsurprising outcome of the sampling process and confirms that bobcats can and do cross primary and secondary roads, but the chances of studying these processes will increase when bobcats are monitored for longer time periods.

Sex of bobcats was important in determining movement near primary and secondary roads, with males exhibiting a stronger response to roads than females. Notably, male home ranges containing either primary or secondary roads within their boundaries were substantially larger than male home ranges without such roads. This result is consistent with the findings of Riley et al. (2003), who found that home ranges of adult male bobcats were larger in non-natural areas. We also found that sizes of male home ranges bordering either primary or secondary roads (that did not contain such roads) were considerably smaller than home ranges for other males (that may or may not have contained such roads). This finding might suggest that both types of roads impeded movements, and hence functional connectivity, across the landscape for some animals and may have functioned as territorial boundaries. Such was the case for Riley et al. (2006), who determined that the Ventura Freeway near Los Angeles, California, was a significant barrier to movements of both male and female bobcats and that home range perimeters tended to follow but not cross major roadways. However, we note that in our study, smaller male home ranges bordering roads were likely driven in part by the demonstrated effect of larger male home ranges containing roads.

In contrast to males, female home-range sizes did not differ based on proximity to roads or on whether or not home ranges contained roads. One reason simply might be that the smaller home ranges of females were less likely to cross major roads than the larger home ranges of males, even though a higher proportion of female home ranges bordered roads than the proportion of male home ranges. Indeed, 50% of the male bobcats in our study crossed both primary and secondary roads, suggesting elevated mortality risk for males, whereas only 25% of female bobcats crossed primary roads and 20% of females crossed secondary roads. Bobcats display a typical felid social structure where the smaller home ranges of females are located in high-quality habitat with abundant resources for raising young, whereas males maintain larger home ranges to access multiple breeding females (Conner et al., 1999; Riley et al., 2003; Sandell, 1989). Female bobcat home ranges near primary roads in the Santa Ana Mountains and near secondary roads in the San Joaquin Hills tended to overlap each other (see also Riley et al., 2006); such a female distribution might allow males to more readily access several females, contributing to smaller male home-range sizes near roads.

5. Conclusions

Bobcats in southern California generally placed their home ranges in areas of relatively low road density compared to the surrounding landscape, but bobcats had little opportunity to avoid roads entirely. Roads affected the size of bobcat home ranges and were infrequently incorporated into their ranges, suggesting that they can represent barriers to movement and, hence, functional landscape connectivity. Our results also demonstrate that male and female bobcats exhibit varying behavioral responses to roads, revealing important differences between sexes in movement patterns, mortality risk, and connectivity in urban areas. The fragmentation effects of roads were particularly evident for male bobcats due to their larger home ranges, and males were also more likely to cross roads, increasing mortality risk. Although our findings are specific to bobcats, we emphasize that these wide-ranging, area-dependent carnivores are a valuable indicator of the degree of landscape connectivity in coastal southern California (Crooks, 2002; Riley et al., 2010a; Tracey et al., 2013), the largest metropolitan area in the United States (Beier et al., 2006) and a global hotspot of biodiversity and species endangerment (Dobson et al., 1997).

Because of the continued expansion of the road network in this highly-developed region, functional connectivity for bobcats, and likely other fragmentation-sensitive species, will become increasingly compromised. Major roads, such as multi-lane freeways, are particularly significant barriers to animal movement and can lead to genetic isolation between populations, as has been demonstrated for urban bobcats in southern California (Lee et al., 2012; Riley et al., 2006; Ruell et al., 2012). A promising method of maintaining connectivity in roaded areas is the use of wildlife crossing structures along new and existing roads (Clevenger and Wierzchowski, 2006). Bobcats are known to use underpasses (Cain et al., 2003; Foster and Humphrey, 1995; Ng et al., 2004) including in this study area (Alonso et al., in press), and such structures may help reduce vehicle-bobcat collisions, a leading cause of bobcat mortalities in California (Riley et al., 2003; Tigas et al., 2002). Indeed, recently constructed crossing structures along State Route 71 in the Chino Hills site in our study area have facilitated successful road crossings of bobcats despite concurrent road construction that widened the roadway and increased traffic volume (Alonso et al., in press). The continued implementation of such strategies should benefit the conservation of bobcats and other species by increasing survival, movement, gene flow, and landscape connectivity in fragmented urban systems.

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U.S. Geological Survey co-authors (EEB, LML, and RSA) participated in all aspects of the project. Otherwise, the funding sources had only an advisory role in study design and in the collection, analysis, and interpretation of data, and had no role in the writing of the manuscript or the decision to submit it for publication.

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