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Urban development can have multiple effects on mammalian carnivore communities. We conducted a meta-analysis of 7,929 photographs from 217 localities in 11 camera-trap studies across coastal southern California to describe habitat use and determine the effects of urban proximity (distance to urban edge) and intensity (percentage of area urbanized) on carnivore occurrence and species richness in natural habitats close to the urban boundary. Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) were distributed widely across the region. Domestic dogs (*Canis lupus familiaris*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), mountain lions (*Puma concolor*), and Virginia opossums (*Didelphis virginiana*) were detected less frequently, and long-tailed weasels (*Mustela frenata*), American badgers (*Taxidea taxus*), western spotted skunks (*Spilogale gracilis*), and domestic cats (*Felis catus*) were detected rarely. Habitat use generally reflected availability for most species. Coyote and raccoon occurrence increased with both proximity to and intensity of urbanization, whereas bobcat, gray fox, and mountain lion occurrence decreased with urban proximity and intensity. Domestic dogs and Virginia opossums exhibited positive and weak negative relationships, respectively, with urban intensity but were unaffected by urban proximity. Striped skunk occurrence increased with urban proximity but decreased with urban intensity. Native species richness was negatively associated with urban intensity but not urban proximity, probably because of the stronger negative response of individual species to urban intensity. DOI: 10.1644/09-MAMM-A-312.1.

Key words: camera trap, mammalian carnivores, richness, southern California, species distribution, urbanization

Habitat loss and fragmentation due to urbanization are among the primary threats to global biodiversity (Mcdonald et al. 2008; McKinney 2002). Mammalian carnivores tend toward large home ranges, low population densities, and slow population growth rates, making them especially vulnerable to extinction brought on by habitat loss or human persecution (Gittleman et al. 2001; Noss et al. 1996). Carnivores have been considered prophetic indicators of the overall fate of ecosystems due to their top-level trophic position (Crooks et al. 2010; Estes et al. 2001; Faeth et al. 2005; Noss et al. 1996). Therefore, carnivores can be useful study species when attempting to measure the relative health of ecosystems undergoing urbanization, such as those in southern California.

In coastal southern California human population growth and urban sprawl have created the largest metropolitan area in the United States (Beier et al. 2006) and one of the world's primary regions of endangerment and extinction (Dobson et al. 1997; Myers 1990). Urban development in the region can

Table 1.—Sources of information on occurrence of carnivores in southern California based on camera traps.

Study area	Time period	County	No. camera traps	No. sampling nights	Source
Puente-Chino Hills	1997–1998	San Bernardino, Riverside, Los Angeles	6	248	Haas (2000)
State Highway 71	1997–2001	San Bernardino, Riverside	18	3,345	Lyren (2001)
Tenaja Corridor	1999–2000	Riverside	15	4,729	Fisher and Crooks (2001)
Nature Reserve of Orange County	1999–2001	Orange	50	4,112	George and Crooks (2006)
East Orange/Central Irvine Ranch	2002	Orange	22	2,138	Haas et al. (2002)
North/Central Irvine Ranch	2002–2003	Orange	14	4,299	Lyren et al. (2006)
San Joaquin Hills	2006–2007	Orange	38	9,536	Lyren et al. (2008b)
El Toro	2007	Orange	22	3,445	Lyren et al. (2008a)
San Diego Regional Corridor	2000–2002	San Diego	18	1,747	Hayden (2002)
Rancho Jamul Ecological Reserve	2001–2002	San Diego	5	681	Hathaway et al. (2002)
Santa Ysabel Ecological Reserve	2002–2003	San Diego	9	1,872	Hathaway et al. (2004)

affect carnivores in multiple ways, such as habitat fragmentation, barriers to gene flow, mortality due to vehicular collision, increased human activity and persecution, and increased disease exposure. Habitat fragmentation due to urbanization can cause the decline or local extinction of fragmentation-sensitive carnivores (Crooks 2002). The loss of large carnivores can facilitate the ecological release of smaller mesopredators that readily adapt to urban environments, potentially contributing to increased predation on smaller prey such as birds (Crooks and Soulé 1999). In addition, roads and urban development can act as physical and social barriers for gene flow and direct causes of mortality due to collision (Dickson et al. 2005; Riley et al. 2006; Tigas et al. 2002). Increased human activity and recreation associated with urbanization can lead to the behavioral displacement of carnivores (George and Crooks 2006; Mathewson et al. 2008; Riley et al. 2003; Tigas et al. 2002). Exposure of carnivores to wildlife diseases and poisons also is common in urban areas (Riley et al. 2003, 2004, 2007). Landscape connectivity via corridors, coupled with the preservation of large habitat areas, can lessen the numerous impacts of urbanization and are considered important for the persistence of carnivores in urban areas (Crooks and Sanjayan 2006).

Camera traps are a useful noninvasive survey tool, especially for mammalian carnivores, which often have secretive behavior, nocturnal activity, low densities, and wariness of humans (Carbone et al. 2001; Kauffman et al. 2007; Moruzzi et al. 2002). Several camera-trap studies have been conducted to assess carnivore activity in southern California, primarily because of the conservation value of these species relative to the multiple impacts of rapid urbanization. Although these studies all used camera traps as the method for data collection, objectives varied and geographic scopes were relatively local. We conducted a meta-analysis of these data sets to address questions about the effects of urbanization on carnivores at a regional scale. Our objectives were to describe habitat use by carnivores and to determine the effects of urban proximity and intensity on carnivore occurrence and species richness in natural habitats close to the urban boundary.

Materials and Methods

Study area.—The south coast ecoregion, with a human population of more than 19 million, is the most populated ecoregion in California (Beier et al. 2006). Our study area included several native habitats with various levels of urbanization in Riverside, San Bernardino, Orange, San Diego, and Los Angeles counties in southern California. The dominant native vegetation types consisted of California sage scrub, annual grassland, chaparral, and oak woodland (Barbour et al. 2007).

Camera analyses.—We performed a meta-analysis based on 11 camera-trap studies conducted in southern California from 1997 through 2007 (Table 1). These studies were conducted either for baseline biodiversity surveys or to determine site-specific relationships between carnivore communities, human activity, and urbanization. In total, the 11 studies represented 217 camera traps (Fig. 1) totaling 36,152 sampling nights. Sampling effort among camera traps ranged from 25 to 542 nights. Each record of a carnivore included the species, time, and date of photograph, number of individuals per photograph, and the global positioning system location of the camera trap. Film cameras (Camtrakker, Watkinsville, Georgia) were used in all studies, except for El Toro, where digital cameras (Cuddeback, Park Falls, Wisconsin) were employed. All cameras were operated continuously over 24 h. Cameras were set to 1- to 3-min time delays between successive photographs.

We assessed the occurrence of each carnivore species by searching the photographic record for each camera trap and assigning a score of 1 (present), if a given species was detected at least once, or 0 (absent) if it was never detected. Because we could not identify individual animals in photographs, these analyses represent occurrence and not abundance at a camera station. Species scored as present were summed for each camera trap to calculate native, nonnative, and total species richness. We measured the responses of species occurrence and species richness to 2 measures of urbanization, distance from the camera trap to urban edge (urban proximity), and the proportion of the area surrounding the camera trap that was urbanized (urban intensity).

Geographic information system analyses.—We used geographic information system analysis (ArcGIS 9.2; ESRI,

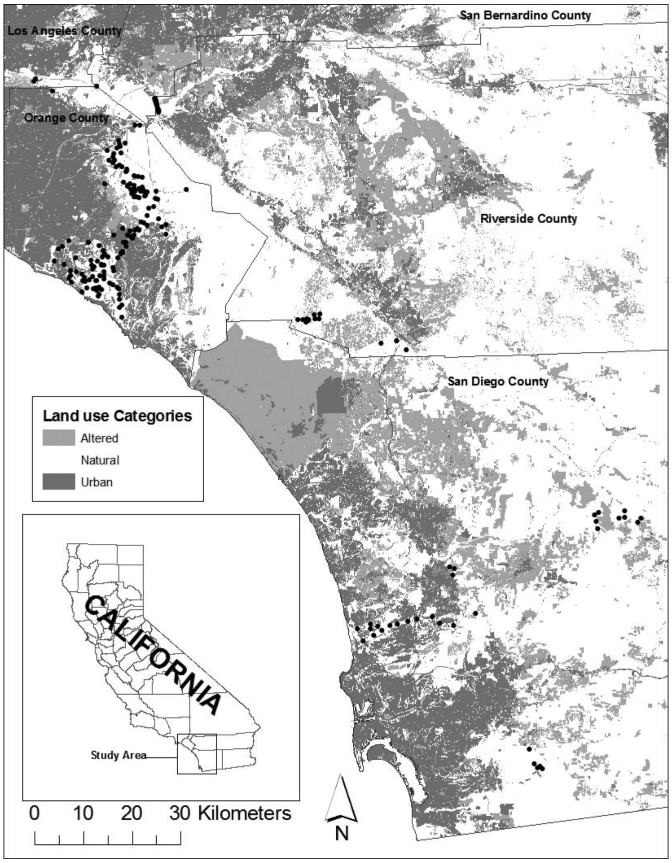

FIG. 1.—Locations of 217 camera traps from 11 studies in southern California conducted from 1997 through 2007.

Redlands, California) to calculate distance to urban edge and to classify habitat and urban percentage surrounding each camera trap. We used land-use layers from the Southern California Association of Governments (2005) and the San Diego Association of Governments (2008) and combined them into 1 layer using the ArcGIS merge tool. Land-use types were classified into 4 land-use categories, natural, altered, urban, and water, based on criteria developed by the National Park Service, Santa Monica Mountains National Recreation Area (Riley et al. 2003). Altered land-cover types included golf course, flood waterway, military training area, and agriculture (e.g., irrigated cropland and improved pastureland, orchards and vineyards, and nonirrigated cropland). Distance to urban edge was calculated by using the ArcGIS spatial join tool to measure the distance of each camera-trap location to the edge of the nearest polygon classified as urban. Urban percentage was calculated by measuring the proportion of urban polygon area within a radius of 3 km surrounding each camera-trap location. This radius size was chosen to avoid a high correlation between distance to urban edge and urban percentage that was evident at shorter radii, and to best represent the relatively large scale at which urbanization occurs in southern California.

Habitat use by carnivores was assessed by calculating the predominant land-cover types within a 150-m radius of each camera trap, using a land-cover layer from the Fire and Resource Assessment Program (2002) of southern California. Native habitats identified were California sage scrub, annual grassland, oak woodland, chaparral, riparian, mixed conifer, and emergent wetland. We used a 150-m radius because it was an area small enough to identify habitat types that sometimes occurred at small scales, such as riparian vegetation, thereby reflecting the habitat type within the immediate vicinity of a camera trap. For urban and other human-altered land-cover types we required 100% coverage of the 150-m radius for classification as the habitat type. We did this to avoid overlooking small fragments of native vegetation in highly urbanized areas that might be important for carnivore persistence (Crooks 2002; Dickson et al. 2005; Ng et al. 2004; Riley 2006; Riley et al. 2003). For habitat classified as <100% human-altered we used the predominant native vegetation fragment within the radius to assign a habitat type. Habitat availability was calculated as the proportional distribution of camera traps among habitat types.

Statistical analyses.—To analyze habitat selection we used chi-square analysis to test for significant difference between the expected (based on availability) and observed detections of each species among habitat types. We assumed that observations among and within camera traps were independent. Minimum expected frequencies satisfied guidelines as described by Zar (1999). If the null hypothesis of random selection in proportion to availability was rejected, we determined which habitat types were selected more or less often than expected by constructing simultaneous Bonferroni confidence intervals ($\alpha = 0.05$; $k = 6$; $Z_{\alpha/2k} = Z_{0.0083} = 2.638$) around the proportion of habitat use and comparing these with the available proportions (Byers et al. 1984; Manly et al. 2002; Neu et al. 1974).

We used bivariate logistic regression models to identify relationships between the probability of occurrence of carnivore species and the 2 urbanization variables, distance to urban edge and urban percentage. For these logistic regression models we excluded those carnivore species detected at <10% of camera traps. We also used Spearman's rank correlation (r_s) to evaluate the relationships between species richness (native, nonnative, and total) and the 2 urbanization variables. False discovery rate corrections were used to control for type I errors that were associated with simultaneous multiple testing (Benjamini and Hochberg 1995).

RESULTS

Species distribution.—Twelve carnivore species were identified from a total of 7,929 carnivore images among 217 camera traps (Table 2), including 9 native carnivores: coyote (*Canis latrans*), bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), mountain lion (*Puma concolor*), long-tailed weasel (*Mustela frenata*), western spotted skunk (*Spilogale gracilis*), and American badger (*Taxidea taxus*). The 3 nonnative species detected by camera traps were

Table 2.—Camera-trap visitation by carnivore species in southern California during 36,152 camera-trap sampling nights across 217 camera traps, 1997–2007.

Species	No. observed sites	% observed sites
Coyote	187	86
Bobcat	161	74
Domestic dog[a]	70	32
Striped skunk	64	29
Raccoon	60	28
Gray fox	43	20
Mountain lion	39	18
Virginia opossum[a]	29	13
Long-tailed weasel	6	3
American badger	2	0.9
Domestic cat[a]	2	0.9
Western spotted skunk	2	0.9

[a] Nonnative species.

domestic dog (*Canis lupus familiaris*), domestic cat (*Felis catus*), and Virginia opossum (*Didelphis virginiana*), a marsupial introduced to California around 1910 but that we include here along with the order Carnivora species given its similar ecological niche (Jameson and Peters 1988). We did not detect black bears (*Ursus americanus*) or ringtails (*Bassariscus astutus*), native carnivores known to generally occur in southern California (Jameson and Peters 1988) but not common in our specific study sites. We also did not detect red foxes (*Vulpes vulpes*), a nonnative species in southern California that has experienced multiple introductions and subsequent range expansion in California, including into coastal areas in Los Angeles, Orange, and San Diego counties (Lewis et al. 1999).

Coyotes and bobcats were detected at $\geq$74% of camera traps, indicating they were distributed widely across the region (Table 2). Domestic dogs, striped skunks, raccoons, gray foxes, mountain lions, and opossums were distributed less widely but still relatively common, being detected at 13–32% of camera traps. Long-tailed weasels, American badgers, western spotted skunks, and domestic cats were rarely detected ($\leq$3% of camera traps) and thus were excluded from species-specific analyses of habitat use and response to urbanization.

Table 4.—Logistic regression models of the effects of urban percentage on distribution of carnivore species across 217 camera traps in southern California, 1997–2007.

Species	χ^2_1	Coefficient	*SE*	*P*
Coyote	6.677	3.022	1.325	0.010
Bobcat	7.516	−2.005	0.729	0.006
Domestic dog[a]	8.849	2.075	0.702	0.003
Striped skunk	4.875	−1.723	0.816	0.027
Raccoon	4.980	1.608	0.716	0.026
Gray fox	25.049	−6.195	1.631	<0.0001
Mountain lion	27.103	−7.266	1.941	<0.0001
Virginia opossum[a]	2.864	−1.849	1.170	0.091

[a] Nonnative species.

Species habitat use.—Camera traps were located in 11 different habitats, including 7 classified by vegetation cover and 4 by human activities. Four habitat types, California sage scrub, annual grassland, oak woodland, or chaparral, characterized the locations of 88% of camera traps, and human-altered habitat characterized 8% of camera traps (Table 3). Visitations among habitat types differed significantly from that expected based on availability for gray foxes and mountain lions. Simultaneous Bonferroni confidence intervals indicated significant selection for oak woodlands and selection against grasslands for gray foxes. Mountain lions were detected more frequently in oak woodlands than expected, with only slight overlap of the Bonferroni confidence interval with the available proportion; notably, mountain lions were never detected in the human-altered habitat category. Detections did not differ significantly from expected based on availability for coyotes, bobcats, domestic dogs, or opossums. A marginally nonsignificant ($0.05 < P < 0.10$) trend for disproportional habitat selection was evident for striped skunks and raccoons.

Response of carnivore occurrence to urbanization.—Logistic regression models indicated significant negative relationships between urban percentage and the probability of occurrence at camera traps for bobcats, striped skunks, gray foxes, and mountain lions; opossums showed a marginally nonsignificant negative relationship (Table 4; Fig. 2a). In contrast, logistic regression revealed significant positive

Table 3.—Distribution of camera-trap locations and carnivore visitations among habitat types in southern California, 1997–2007. Numbers in parentheses are percentages of total column.

	California sage scrub	Annual grassland	Oak woodland	Chaparral	Other native	Human-altered[a]	Total	χ^2_5 (*P*)
Total camera traps	85 (39%)	65 (30%)	24 (11%)	17 (8%)	8 (4%)	18 (8%)	217	
Coyote	75 (40%)	57 (30%)	18 (10%)	15 (8%)	5 (3%)	17 (9%)	187	1.079 (0.956)
Bobcat	67 (42%)	47 (30%)	19 (12%)	13 (8%)	7 (4%)	8 (5%)	161	2.707 (0.745)
Domestic dog[b]	36 (51%)	18 (26%)	3 (4%)	7 (10%)	3 (4%)	3 (4%)	70	7.853 (0.165)
Striped skunk	16 (25%)	24 (38%)	13 (20%)	4 (6%)	3 (5%)	4 (6%)	64	10.153 (0.071)
Raccoon	22 (37%)	14 (23%)	4 (7%)	7 (12%)	6 (10%)	7 (12%)	60	10.455 (0.063)
Gray fox	18 (42%)	5 (12%)	13 (30%)	6 (14%)	0 (0%)	1 (2%)	43	24.680 (<0.001)
Mountain lion	18 (46%)	9 (23%)	10 (26%)	1 (3%)	1 (3%)	0 (0%)	39	13.350 (0.020)
Virginia opossum[b]	7 (24%)	10 (34%)	7 (24%)	1 (3%)	1 (3%)	3 (10%)	29	7.220 (0.205)

[a] Includes both urban and other altered land-cover types.
[b] Nonnative species.

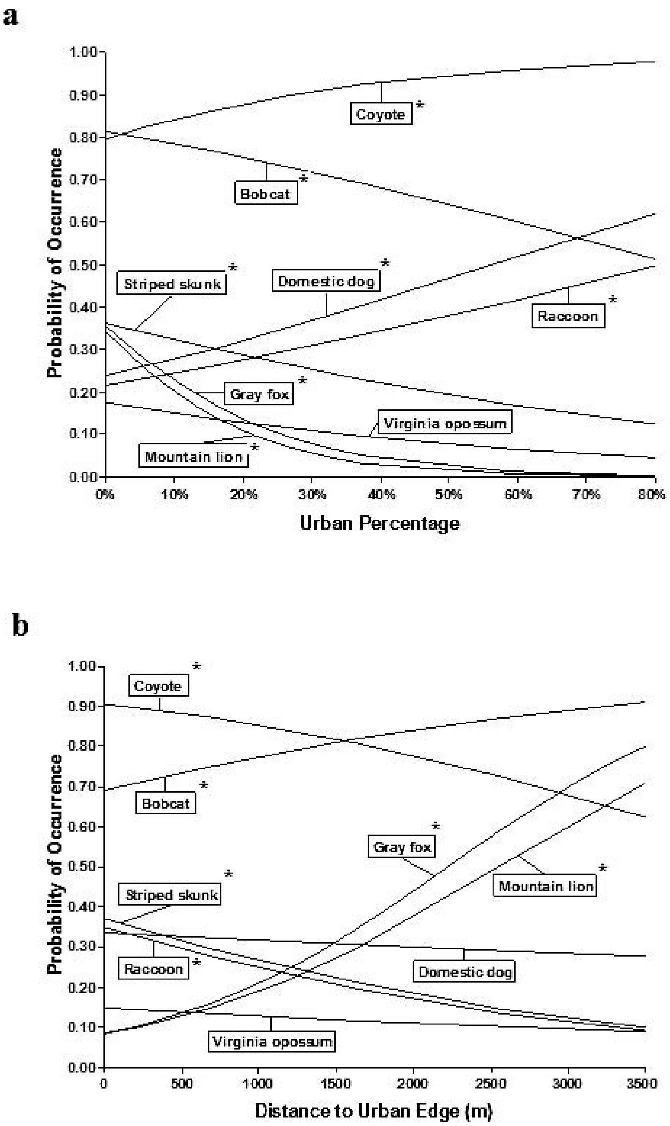

FIG. 2.—Logistic regression models of the probability of occurrence of native and nonnative carnivores as a function of a) urban percentage and b) distance to urban edge in southern California. Asterisks (*) indicate statistically significant ($P < 0.05$) relationships (see Tables 4 and 5).

relationships between urban percentage and the occurrence of coyotes, domestic dogs, and raccoons.

Logistic regression indicated significant negative relationships between distance to urban edge and the occurrence of coyotes, striped skunks, and raccoons (Table 5; Fig. 2b). In contrast, significant positive relationships between distance to urban edge and occurrence were indicated for bobcats, gray foxes, and mountain lions. Occurrence of domestic dogs and Virginia opossums showed no relationship with distance to urban edge.

Response of species richness to urbanization.—The number of native and nonnative species detected at a given camera trap ranged from 0 to 6 ($\bar{X} = 2.6$) and from 0 to 3 ($\bar{X} = 0.5$), respectively. The number of total species detected at a given camera trap ranged from 1 to 8, with a mean of 3.0. We found a significant negative correlation between native species richness and urban percentage ($r_s = -0.197$, $P = 0.003$, $n = 217$) and a significant positive correlation between nonnative species richness and urban percentage ($r_s = 0.163$, $P = 0.002$, $n = 217$) but no significant correlation between total species richness and urban percentage ($r_s = -0.116$, $P = 0.106$, $n = 217$). Distance to urban edge was not significantly related to native ($r_s = 0.040$, $P = 0.555$, $n = 217$), nonnative ($r_s = -0.090$, $P = 0.188$, $n = 217$), or total species richness ($r_s = 0.007$, $P = 0.918$, $n = 217$).

TABLE 5.—Logistic regression models of the effects of distance to urban edge on carnivore species distribution across 217 camera traps in southern California, 1997–2007.

Species	χ^2_1	Coefficient	*SE*	*P*
Coyote	4.598	−0.0005	0.0002	0.032
Bobcat	5.123	0.0005	0.0002	0.024
Domestic dog[a]	0.185	-8.045×10^{-5}	0.0002	0.667
Striped skunk	5.471	−0.0005	0.0002	0.019
Raccoon	5.216	−0.0005	0.0002	0.022
Gray fox	26.262	0.001	0.0002	<0.0001
Mountain lion	19.077	0.001	0.0002	<0.0001
Virginia opossum[a]	0.414	−0.0002	0.0003	0.520

[a] Nonnative species.

DISCUSSION

Coyotes and bobcats were distributed widely across southern California, suggesting their behavioral plasticity and adaptability relative to other large carnivore species (Crooks 2002). The commonness of striped skunks, raccoons, and Virginia opossums was not surprising because they often are associated with humans (Hadidian et al. 2010; Markovchik-Nicholls et al. 2008; Rosatte et al. 2010), as are domestic dogs, which were frequently detected in our study. In contrast, mountain lions often are associated with wildlands, yet they were recorded at almost 1 in 5 camera traps. However, mountain lions were not detected in human-altered land-cover types such as urban and agricultural development, and they exist primarily in larger patches of habitat in southern California (Crooks 2002). All of the common carnivore species (>10% of camera traps) were detected in all 4 of the common habitat types, and habitat use generally reflected availability for most species. Domestic cats were rarely detected, probably in part because they tend to avoid or be killed by coyotes (Crooks and Soulé 1999), which were present at most sampling stations. Domestic cats elsewhere typically did not venture far (<100 m) from the urban edge (Crooks 2002; Kays and DeWan 2004). American badgers, western spotted skunks, and long-tailed weasels also were rarely detected, perhaps because of their patchy distribution and restricted habitat preferences (Crooks 2002). In all, the persistence of such a diverse carnivore community across a region characterized by rapid urbanization likely results from the generalized habitat requirements of these species in combination with the relatively large wildland areas that still persist in the south coast ecoregion (Beier et al. 2006).

Although almost all camera traps (92%) were located in native habitat, 64% were within 1 km of urbanization, and all were within 3.5 km of urbanization. Hence, our study assessed carnivore distribution within or close to the urban boundary. Distance to urban edge might represent the linear proximity of human development, and urban percentage could represent the spatial intensity of human disturbance that animals encounter in their home range. Both measures of urbanization revealed consistent responses to urbanization by most carnivores.

Both bobcats and coyotes were distributed widely but had consistent yet opposite responses to urbanization. Coyote occurrence increased with both proximity and intensity of urbanization, indicating a positive response to urbanization at a regional scale. Previous studies in southern California have demonstrated that coyotes can exploit urban areas due to their highly adaptable behavior and omnivorous diet, especially in areas where garbage, cultivated fruit, pet food, and domestic animals are available as food subsidies (Crooks 2002; Fedriani et al. 2001; Riley et al. 2003). Urban coyotes can benefit from the availability of these anthropogenic foods, but they are also more vulnerable to mortality from vehicle collision and poisoning (Riley et al. 2003; Tigas et al. 2002). Previous southern California studies found positive relationships between coyotes and corridor width, natural habitat, and fragment area (Crooks 2002; Crooks and Soulé 1999; Tigas et al. 2002), suggesting an overall preference by coyotes for natural habitat. Additionally, coyotes in southern California related positively with human activity but negatively with urban development (Ng et al. 2004) and declined in urban habitat fragments that were too small or isolated (Crooks 2002), suggesting a tolerance threshold for urbanization. Therefore, coyotes might frequent urban habitat but likely require access to sufficient natural areas to persist (Crooks 2002; Crooks and Soulé 1999; Tigas et al. 2002).

Unlike coyotes, bobcat occurrence declined with both increasing proximity and intensity of urbanization. Similarly, other studies in southern California have found that bobcats were more sensitive to urbanization and human activity than were coyotes (George and Crooks 2006; Riley et al. 2003; Tigas et al. 2002) and were less willing to move through urban development and across roads (Tigas et al. 2002). Bobcats are strictly carnivorous and solitary, likely making them less adaptable to urban areas than carnivores with flexible diets and social structures (Crooks 2002; Riley et al. 2006).

Like bobcats, occurrence of mountain lions declined with both proximity and intensity of urbanization. Similarly, previous studies in the region found that mountain lions showed a negative relationship with roads, artificial lighting, and housing density, and preferred native vegetation that provides vertical cover (Beier 1995; Dickson et al. 2005; Markovchik-Nicholls et al. 2008). This is consistent with our finding that mountain lions selected for oak woodlands, perhaps because of the cover provided by the vertical structuring of woodlands. Similar to bobcats, mountain lions are solitary and strictly carnivorous, likely increasing their sensitivity to urbanization (Crooks 2002).

Occurrence of gray foxes declined with both proximity and intensity of urbanization, a somewhat surprising result for a species considered adaptable due to an omnivorous diet and behavioral plasticity (Riley et al. 2003, 2006). In previous studies gray foxes in southern California were found to be tolerant of urban areas (Riley 2006) and were considered ''fragmentation-enhanced'' because they were more abundant in smaller urban fragments (Crooks 2002). However, gray foxes typically prefer natural vegetation, park interiors, and highly vegetated and wide corridors over human-altered landscapes (Borchert et al. 2008; Hilty and Merenlender 2004; Markovchik-Nicholls et al. 2008; Riley 2006). Gray foxes also might face intraguild predation by coyotes and thus avoid sites in urban areas where coyotes are more active (Crooks and Soulé 1999; Crooks et al. 2010; Farias et al. 2005; Fedriani et al. 2000). In the Santa Monica Mountains north of Los Angeles, Fedriani et al. (2000) reported that gray foxes were restricted largely to brushy habitat and suggested that they might avoid grasslands where coyotes were particularly abundant, consistent with our results that gray foxes select for oak woodlands and against grasslands. Harrison (1997) found that although gray foxes in New Mexico were tolerant of and even benefited from urban areas, they avoided urban areas with a dwelling density exceeding 125 dwellings/km^2. Although this might suggest that gray foxes have a threshold of tolerance for urban intensity, they can still persist even in small habitat fragments in southern California that are surrounded by high-density urban development, particularly those with reduced coyote activity (Crooks and Soulé 1999; Farias et al. 2005).

Raccoons responded positively to urbanization; occurrence increased with both urban intensity and proximity. Other studies in California identified raccoons as a species that is tolerant of or enhanced by urban development (Crooks 2002; Crooks and Soulé 1999; Ng et al. 2004). Raccoons are resource generalists that are highly efficient at exploiting human structures and food sources (Hadidian et al. 2010), probably more so than opossums or skunks (Prange and Gehrt 2004). Raccoons also might be somewhat tolerant of the presence of coyotes in urban areas (Crooks et al. 2010); raccoons seemed less impacted by coyote activity in urban San Diego than other mesopredators such as gray foxes (Crooks and Soulé 1999), and they did not avoid coyotes or experience coyote-related mortality in urban Illinois (Gehrt and Prange 2007).

In contrast to raccoons, the response of striped skunks and opossums to urbanization in southern California was mixed. Striped skunk occurrence increased with urban proximity but decreased with urban intensity. This suggests that skunks are more likely to occur along the urban–wildland interface, in proximity to urbanization that may provide food sources, but also within natural habitat that may provide cover or den sites. In previous studies striped skunks were more common in the interior of small habitat fragments within urban development in southern California (Crooks 2002), in wide, natively vegetated corridors through vineyards in northern California (Hilty and Merenlender 2004), and in field habitats close to urban development in Toronto (Rosatte et al. 2010), further suggesting a preference for vegetative cover adjacent to human-altered landscapes. Although striped skunks are generalized omnivores that certainly reside within urban areas, they do not seem to respond as positively to urbanization as do other generalist carnivores such as raccoons (Prange and Gehrt 2004; Rosatte et al. 2010).

Virginia opossum occurrence tended to decrease with urban intensity, similar to the pattern observed for striped skunks, but was unaffected by urban proximity. These results at a regional scale are somewhat inconsistent with studies conducted at a more local scale in and around San Diego, which detected opossums more frequently in habitat surrounded by intensive development (Markovchik-Nicholls et al. 2008) and near edges of habitat fragments within the urban matrix (Crooks 2002). Similarly, opossums were found more in and near urban areas than in woodland habitat in central Massachusetts (Kanda et al. 2006). Like striped skunks, opossums might not be as effective as raccoons in exploiting urban environments (Prange and Gehrt 2004); opossums frequent urban development, but they also might prefer natural areas with access to vegetative cover and den sites. Further, opossums might be inferior intraguild competitors to both raccoons (Ginger et al. 2003; Kasparian et al. 2004) and coyotes (Crooks and Soulé 1999), both of which frequent urban areas.

Occurrence of domestic dogs increased with urban intensity but showed no relationship to urban proximity. Our detections of domestic dogs were probably those of pets accompanied by humans, and therefore these patterns could be more reflective of human activity. Similarly, dogs displayed positive relationships with human activity in studies conducted in California (George and Crooks 2006; Ng et al. 2004; Reed and Merenlender 2008). Domestic dogs were relatively common in our study, and their presence could have influenced native carnivores by temporally displacing species such as urban-sensitive bobcats and even urban-tolerant coyotes (George and Crooks 2006; Mathewson et al. 2008).

Almost all (99%) camera traps recorded 1 native carnivore and 80% recorded multiple species, demonstrating that on a regional scale a suite of native carnivores persists in the face of urbanization in southern California. Effects of urbanization on species richness reflect the collective responses of individual species to urban intensity and urban proximity. Among the native carnivores we detected, half responded negatively to urban proximity and half positively, and we found no relationship between urban proximity and nonnative species richness. Hence it is no surprise that we found no relationship between urban proximity and total species richness. Crooks (2002) also found no relationship with proximity to the urban edge for native carnivores in habitat fragments in San Diego County.

In our study a majority of native species responded negatively to urban intensity, which is reflected in a significant negative relationship between native species richness and urban intensity. In contrast, nonnative species showed a positive relationship to urban intensity, likely because 2 of the 3 nonnative species were domestic animals typically found in close association with humans. The response of native carnivores to urban intensity might reflect the loss and fragmentation of native habitat with increasing urbanization within the 3-km radius we used. Similarly, other studies in California found that native carnivore richness increased with fragment size (Crooks 2002; Hilty and Merenlender 2004; Tigas et al. 2003). However, carnivores also could be reacting to humans and their activities. Studies elsewhere in California reported that total species richness of carnivores in an urban park declined in areas most frequently used by hikers and dogs (Mathewson et al. 2008), and that native species richness was lower in parks and reserves that allowed human recreation, contributing to a shift in community composition from native to nonnative species (Reed and Merenlender 2008).

Our results indicate that a remarkable variety of carnivores persists close to the urban boundary in southern California but that the response of individual species to urbanization varies greatly. Some, like coyotes and raccoons, are tolerant of and even benefit from some degree of urbanization. Others, like bobcats and mountain lions, are negatively affected by urbanization. Responses to urbanization seem to be influenced by a variety of factors such as dietary breadth, behavioral adaptability, habitat requirements, and interspecific interactions among carnivores and with humans. Regardless of their response, most species we studied seem to require the availability of some natural areas for their persistence in the face of urbanization in southern California.

Resumen

El desarrollo urbano puede tener múltiples efectos en las comunidades de mamíferos carnívoros. Se realizó un meta-análisis de 7,929 fotografías obtenidas en 217 localidades a través de 11 estudios de trampas cámara distribuidas en la región costera del sur de California, para describir el uso del hábitat y determinar los efectos de la proximidad urbana (distancia del borde urbano) y la intensidad de urbanización (porcentaje del área urbanizada), sobre la presencia de carnívoros y la riqueza de especies en hábitat naturales cerca de los limites urbanos. Los coyotes (*Canis latrans*) y linces rojos (*Lynx rufus*) se distribuyeron ampliamente en toda la región; perros domésticos (*Canis lupus familiaris*), zorrillos rayados (*Mephitis mephitis*), mapaches (*Procyon lotor*), zorros grises (*Urocyon cinereoargenteus*), pumas (*Puma concolor*), y zarigüeyas de la Virginia (*Didelphis virginiana*) se detectaron con menor frecuencia, en tanto las comadrejas de cola larga (*Mustela frenata*), tejones Americanos (*Taxidea taxus*), zorrillos pintos (*Spilogale gracilis*), y gatos domésticos (*Felis catus*) fueron detectados en raras ocasiones. El uso del hábitat en general, refleja disponibilidad para la mayoría de las especies. La presencia del coyote y el mapache aumentó tanto con la proximidad como con la intensidad de la urbanización, mientras que la presencia del lince rojo, el zorro gris, y el puma disminuyó con ambos, la proximidad urbana y la intensidad de urbanización. Los perros domésticos y las zarigüeyas exhibieron relaciones positivas y negativas débiles, respectivamente, con la intensidad urbana, pero no se vieron afectados por la proximidad urbana. La presencia de zorrillos rayados aumentó con la proximidad urbana, pero disminuyó con la intensidad de urbanización. La riqueza de especies nativas se asoció negativamente con la intensidad de urbanización, pero no con la proximidad urbana, probablemente debido a la más fuerte respuesta negativa de especies individuales con la intensidad urbana.

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