The Effects of Urbanization on Carnivore Species Distribution and Richness in Southern California

By

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ABSTRACT

Urban development results in habitat loss and fragmentation, and may have multiple effects on native carnivores. We conducted a meta-analysis of data from 217 localities in 11 camera trap studies to address questions about the effects of urbanization on carnivores at a regional scale across southern California. We described habitat use and determined the effects of urban proximity (distance to urban edge) and intensity of urbanization (percentage of area urbanized) on carnivore occurrence and species richness in natural habitats close to the urban boundary. Camera traps detected 8 native and 3 nonnative species. Coyotes and bobcats were widely distributed across the region; domestic dogs, striped skunks, raccoons, gray foxes, mountain lions, and Virginia opossums were relatively common; and long-tailed weasels, American badgers, and domestic cats were rare. Habitat use generally reflected habitat availability, especially for coyotes and bobcats, although there was some evidence of preference for oak woodlands by mountain lions, gray foxes, striped skunks, and Virginia opossums. The occurrence of coyotes and raccoons increased with both proximity to urbanization and with intensity of urbanization, indicating that both species responded positively to urbanization at a regional scale. In contrast, the occurrence of bobcats, gray foxes, and mountain lions decreased with both proximity to and intensity of urbanization, indicating these three species responded negatively to urbanization. Domestic dogs and Virginia opossums indicated positive and weak negative relationships, respectively, with the intensity of urbanization, and both were unaffected by proximity to urbanization. Striped skunks exhibited a negative ($p<0.05$) relationship with both proximity to urbanization and intensity of urbanization, indicating that striped skunks had a mixed relationship with urbanization at a regional scale. Almost all camera traps detected a native carnivore and 80% detected multiple species. Urban intensity had a negative effect on native species richness but urban proximity did not, probably because of the stronger negative response of individual species to urban intensity. Our results indicate that a remarkable variety of carnivores is persisting close to the urban boundary in southern California, but that the response of individual species to urbanization varies greatly.

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INTRODUCTION

Habitat loss and fragmentation due to urbanization are among the primary threats to global biodiversity (Wilcove et al., 1998; Czech et al., 2000; 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 (Noss et al., 1996; Woodroffe and Ginsberg, 1998). Carnivores have been considered prophetic indicators of the overall fate of ecosystems, due to their top-level trophic position (Noss et al., 1996; Crooks, 2002; Estes et al., 2001; Crooks et al., in press). 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 USA (Beier et al., 2006) and one of the world's primary "hot-spots" of endangerment and extinction (Myers, 1990; Dobson et al., 1997). Urban development in the region may affect carnivores in multiple ways, such as habitat fragmentation, barriers to gene flow, increased human activity, poisoning, wildlife diseases, and mortality due to vehicular collision. Habitat fragmentation due to urbanization can cause the decline or local extinction of fragmentation-sensitive carnivores (Crooks, 2002). The loss of large carnivores can lead to the ecological release of smaller "mesopredators" that readily adapt to urban environments and urban edges, leading to increased predation on birds (Crooks and Soulé, 1999). In addition, roads and urban development may act as physical and social barriers for gene flow, as well as direct causes of mortality due to collision (Dickson and Beier, 2002; Tigas et al., 2002; Dickson et al., 2005; Riley et al., 2006). Increased human activity and recreation associated with urbanization can lead to the behavioral displacement of carnivores (Tigas et al., 2002; Riley et al., 2003; George and Crooks, 2006; Mathewson et al., 2008). Exposure of carnivores to wildlife diseases and poisons is also common in urban areas (Riley et al., 2003; Riley et al., 2004; Riley et al., 2007). Landscape connectivity via corridors coupled with the preservation of large habitat areas may lessen the numerous impacts of urbanization and are considered important for the persistence of mammalian carnivores in urban areas (Crooks and Sanjayan, 2006).

Camera traps are a useful tool for recording the activity of various wildlife species (Mace et al., 1994; Karanth, 1995; Jacobson et al., 1997; Heilbrun et al., 2006), and they are especially useful for studying mammalian carnivores, which often have secretive behavior, nocturnal activity, low densities, and wariness of humans (Long et al., 2008). 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 determine the effects of urban proximity and intensity on carnivore occurrence and species richness in natural habitats close to the urban boundary.

METHODS

Study Area

The study area included several habitats with varying levels of urbanization in San Bernardino, Riverside, Orange, San Diego, and Los Angeles counties. Over 19 million people reside in the south coast ecoregion, and from 1990 to 2000, the human population of San Bernardino County increased by 20%, Riverside County by 32%, Orange County by 18%, San Diego County by 13%, and Los Angeles Counties by 7-8% (U. S. Census Bureau, 2000). The dominant vegetation types consisted of coastal sage scrub, annual grassland, chaparral, and oak woodland.

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 (e.g., George and Crooks, 2006). In total, the 11 studies represented 217 camera traps (Figure 1) totaling 36,152 sampling nights. Sampling effort among camera traps ranged 25-542 nights. Each record of a carnivore included the species, time, and date of photograph, number of images per photograph, and the GPS location of the camera trap. Film cameras Camtrakker, Watkinsville, GA) were used in all studies, except for El Toro, where digital cameras were employed (Cuddeback, Park Falls, WI). All cameras were operated continuously over 24 hours. Cameras were set to 1 to 3 minute time delays between successive photographs, which provided minimal variation between time delays across all camera traps.

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. 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 and the proportion of the area surrounding the camera trap that was urbanized.

GIS Analyses

We used GIS (Geographic Information System) analysis (ArcGIS 9.2, ESRI, Redlands, CA) 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 (SCAG, 2005) and the San Diego Association of Governments (SANDAG, 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). 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 buffer radius of 3 km surrounding each camera trap location. This buffer 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 use layer from the Fire and Resource Assessment Program (FRAP, 2002) of southern California. Native habitats identified were coastal sage scrub, grassland, oak woodland, chaparral, riparian, mixed conifer, and emergent wetland. We used a 150-m radius because it was a small enough area 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 human-altered land cover types, urban, golf course, flood waterway, and agriculture (e.g., irrigated cropland and improved pastureland, orchards and vineyards, non-irrigated cropland), we required a 100% coverage of the 150-m buffer for classification as the habitat type. We did this to avoid overlooking small fragments of native vegetation in highly urbanized areas that may be important for carnivore persistence (Crooks, 2002; Riley et al., 2003; Ng et al., 2004; Dickson et al., 2005; Riley, 2006). For buffers classified as <100% human-altered, we used the predominant native vegetation fragment within the buffer to assign a habitat type.

Statistical Analyses

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. We excluded those carnivore species detected at

<10% of camera traps. We used Spearman's rank correlation (ρ) 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). Statistical analyses were performed using the program JMP 7.0 (SAS, Cary, NC).

RESULTS

Species Distribution

Eleven carnivore species were identified from a total of 7,929 carnivore images among 217 camera traps (Table 2), including 8 native carnivores: coyote (*Canis latrans*), bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), mountain lion (*Puma concolor*), long-tailed weasel (*Mustela frenata*), and American badger (*Taxidea taxus*). The 3 nonnative species were domestic dog (*Canis familiaris*), Virginia opossum (*Didelphis virginiana*), and domestic cat (*Felis catus*). Coyotes and bobcats were detected at ≥74% of camera traps, indicating they were widely distributed across the region (Table 2). Domestic dogs, striped skunks, raccoons, gray foxes, mountain lions, and Virginia opossums were less widely distributed but still relatively common, being detected at 13-32% of camera traps. Long-tailed weasels, American badgers, and domestic cats were rarely detected (≤3% of camera traps), and thus excluded from further analyses.

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, coastal sage scrub, grassland, oak woodland, and chaparral, characterized the locations of 88% of camera traps, and human-altered habitat characterized 8% of camera traps (Table 3). For coyotes and bobcats, habitat use closely matched habitat availability (Table 3). For other species, habitat use corresponded generally to availability, although there was some evidence of a preference for oak woodlands by striped skunks, gray foxes, mountain lions, and Virginia opossums (Table 3), possibly because of the cover provided by the vertical structuring in woodlands. Further, gray foxes used grasslands less frequently than available, and human-altered habitat was used rarely by gray foxes and not at all by mountain lions.

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, and Virginia opossums showed a negative relationship that approached statistical significance (Table 4, Figure 2). In contrast, logistic regression revealed significant positive relationships between urban percentage and the occurrence for coyotes, domestic dogs, and raccoons (Table 4, Figure 2).

Logistic regression indicated significant negative relationships between distance to urban edge and the occurrence of coyotes, striped skunks, and raccoons (Table 5, Figure 3). In contrast, significant positive relationships between distance to urban edge and occurrence were shown for bobcats, gray foxes, and mountain lions (Table 5, Figure

3). Occurrence of domestic dogs and Virginia opossums showed no significant relationship with distance to urban edge (Table 5, Figure 3).

Response of Species Richness to Urbanization

The number of native species detected at a given camera trap ranged from 0 to 6, with a mean of 2.6 (Figure 4). The number of nonnative species detected at a given camera trap ranged from 1 to 3, with a mean of 0.5. The number of total species detected at a given camera trap ranged from 1 to 8, with a mean of 3.0 (Figure 5). We found a significant negative correlation between native species richness and urban percentage (ρ=-0.207, p=0.017), a significant positive correlation between nonnative species richness and urban percentage (ρ=0.163, p=0.002), and a trend toward a significant negative correlation between total species richness and urban percentage (ρ=-0.118; p=0.084). We found no significant correlations between distance to urban edge and native (ρ=0.048, p=0.478), nonnative (ρ=-0.090, p=0.188), or total species richness (ρ=0.010, p=0.887).

DISCUSSION

Coyotes and bobcats were notable in their widespread distribution across the region, perhaps a reflection of their behavioral plasticity and adaptability in comparison to other large carnivore species in southern California (Crooks, 2002). The relative commonness of striped skunks, raccoons, and Virginia opossums is not surprising, since these species are often found in association with humans (Prange et al, 2004; Meckstroth and Miles, 2005; Markovchik-Nicholls et al., 2008). 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. Mountain lions are a species with large space requirements and often associated with wildlands, yet they were recorded at almost 1 in 5 camera traps; importantly, however, mountain lions typically occurred in larger patches of habitat (unpublished data) and none were detected in human-altered land cover types such as urban and agricultural development. The persistence of such a diverse carnivore community across a region characterized by rapid urbanization may result from the relatively generalized habitat requirements of these species, in combination with the relatively large wildland areas that still persist in the south coast ecoregion, particularly in rugged and higher elevation habitats (Beier et al., 2006). Preservation of native habitat likely is important for the persistence of carnivores in southern California (Dickson and Beier, 2002; Ng et al., 2004).

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

Coyote occurrence increased with both proximity to urbanization and with intensity of urbanization, indicating that coyotes responded positively to urbanization at a regional scale. Similarly, previous studies in southern California suggested that coyotes are relatively tolerant of urbanization due to their highly adaptable behavior and omnivorous diet, especially in areas with human-subsidized foods such as garbage, cultivated fruit, pet food, and domestic animals (Fedriani et al., 2001; Crooks, 2002; Riley et al., 2003). Coyotes associated with urban areas may benefit from the availability of human-subsidized foods, but they are also more vulnerable to mortality from vehicle collision and poisoning (Tigas et al., 2002; Riley et al., 2003; George and Crooks, 2006). Other studies in southern California found positive relationships between coyotes and corridor width, natural habitat, and fragment area (Crooks and Soulé, 1999; Tigas, 2002; Crooks, 2002), suggesting an overall preference by coyotes for natural habitat. Additionally, coyotes in southern California displayed a positive relationship with human activity but a negative relationship with urban development (Ng et al., 2004), suggesting a tolerance threshold for urbanization. Therefore, coyotes may prefer urban habitat but require access to a certain amount of natural habitat with sufficient connectivity in order to persist (Crooks and Soulé, 1999, Crooks, 2002; Tigas et al., 2002). Coyote persistence may indirectly benefit native birds by preventing the ecological release of mesopredators that prey on birds (Crooks and Soulé, 1999).

Although bobcats and coyotes were the most widely distributed species, they had consistent and opposite responses to urbanization. Unlike coyotes, bobcat occurrence declined with both increasing proximity and increasing intensity of urbanization. Other studies in southern California found that bobcats are more sensitive to urbanization than coyotes (Tigas et al., 2002, Riley et al., 2003, George and Crooks, 2006). Further, bobcats require larger and less isolated fragments within urban matrices (Crooks, 2002; Tigas et al., 2003), and are less willing than coyotes to move through urban development and across roads (Tigas et al., 2002). Bobcats are strictly carnivorous and solitary, making them more prone to local extinction and displacement from urban areas than carnivores with flexible diets and social structures (Nowak, 1999; Crooks, 2002; Riley et al., 2006).

Like bobcats, occurrence of mountain lions declined with both proximity and intensity of urbanization. Similarly, other studies in southern California found that mountain lions show a negative relationship with roads, artificial lighting, and housing density, and prefer native vegetation that provides vertical cover (Beier, 1995; Dickson and Beier, 2002; Dickson and Beier, 2005; Markovchik-Nicholls et al., 2008). Mountain lions, like bobcats, are solitary (Crooks, 2002) and strictly carnivorous (Nowak, 1999), causing them to be less adaptable to urban areas than carnivores with more flexible diets and social structures. Mountain lions are also large animals with large area requirements, hence they require larger intact blocks of land than other carnivores (Beier, 1993; Crooks, 2002).

Gray fox occurrence declined with both proximity to urbanization and with intensity of urbanization, a somewhat surprising result for a species considered adaptable due to its omnivorous diet and behavioral plasticity (Riley et al., 2003; Riley et al., 2006). Gray foxes in southern California were found to be tolerant of urban areas (Riley, 2006) and were considered "fragmentation-enhanced" due to the fact that they were more abundant in smaller fragments and near urban edges (Crooks, 2002). However, other studies in California found that gray foxes prefer natural vegetation, park interiors, and highly vegetated and wide corridors over human altered landscapes (Hilty and Merenlender, 2004; Riley, 2006; Borchert, 2008; Markovchik-Nicholls et al., 2008). Gray foxes may face intraguild predation and behavioral displacement by coyotes, and thus might find refugia in urbanizing landscapes in sites with fewer coyotes (Crooks and

Soulé, 1999; Crooks et al., in press; Farias, et al., 2005; Fedriani et al., 2000; Riley, 2006; Gosselink et al. 2003, 2007). Fox refugia from coyotes might include highly vegetated areas away from the urban edge where coyotes are less active, as well as within small habitat patches immersed within the urban matrix where coyotes decline or disappear (Crooks, 2002). Interestingly, 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/km^2. Although this might suggest that gray foxes show 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 (Crooks and Soulé 1999; Farias et al., 2005).

Raccoons responded positively to urbanization, with occurrence increasing with both urban intensity and urban proximity. Similarly, other studies in California identified raccoons as a species that is tolerant of or enhanced by urban development (Crooks and Soulé, 1999; Crooks, 2002; Ng et al., 2004), and a study in Illinois indicated that raccoons thrive in edge habitat, especially in areas with human subsidized resources (Prange et al., 2004).

The response of striped skunks to urbanization was mixed; occurrence increased with urban proximity, which is in agreement with results from previous studies (Bixler and Gittleman, 1999; Prange and Gehrt, 2004; Meckstroth and Miles, 2005), but decreased with urban intensity. Striped skunks in California displayed a preference for habitat distant from the urban edge (Crooks, 2002), as well as wide, natively vegetated corridors (Hilty and Merenlender, 2004), which are uncommon in more highly urbanized areas. Striped skunks are an omnivorous species that can capitalize on human-subsidized food. Our results suggest that skunks are more likely to occur along the urban-wildland interface, in close proximity to urbanization, perhaps because of access to food, but also within natural habitat, perhaps because of a preference for access to natural areas with vertical cover or suitable den sites.

Occurrence of Virginia opossums, a non-native species in California, showed a marginally significant decrease with increasing urban intensity and were unaffected by urban proximity. These results are inconsistent with other studies conducted in southern California, which revealed that opossums preferred developed habitat (Markovchik-Nicholls et al., 2008) and habitat near urban edges (Crooks, 2002). Although opossums certainly will frequent urban development, similar to striped skunks, they may also prefer natural areas with access to vegetative cover and den sites. Further, opossums are inferior intraguild competitors to both raccoons (Ginger et al., 2003; Kasparian et al., 2004) and coyotes (Crooks and Soulé, 1999), which frequent urban areas, potentially explaining the negative relationship between opossum occurrence and urban intensity.

Occurrence of domestic dogs increased with urban intensity but showed no relationship with urban proximity. Since our detections of domestic dogs were likely of pet dogs accompanied by humans, these patterns may be more a reflection of human density and activity. Dogs displayed positive relationships with human activity in studies conducted in California (Ng et al., 2004; George and Crooks, 2006; Reed and Merenlender, 2008), most likely because they were companion animals. Domestic dogs were relatively common in our study, and their presence may have influenced that of native carnivores, since domestic dogs may temporally displace native carnivores such as urban-sensitive bobcats and even urban-tolerant coyotes (George and Crooks, 2006; Mathewson et al., 2008).

Almost all (99%) camera traps recorded a native carnivore and 80% recorded multiple species, demonstrating that on a regional scale native carnivores are persisting 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, hence it is no surprise that we found no relationship between urban proximity and native species richness. Nonnative species showed no relationship with urban proximity, hence they had little influence on the relationship between total species richness and urban proximity. Crooks (2002) found a somewhat similar relationship for carnivores in habitat fragments in San Diego County. Like our study, native species richness showed no relationship with proximity to the urban edge, while total species richness increased with proximity to the urban edge, suggesting that nonnative species were driving the relationship for total species (Crooks, 2002).

In our study a majority of native species responded negatively to urban intensity, which is reflected in a negative relationship between native species richness and urban intensity. Nonnative species showed a mixed relationship to urban intensity, so they had little influence on the relationship for total species richness. The response of native carnivores to urban intensity might reflect the loss and fragmentation of native habitat with increasing urbanization within the 3-km buffer. Similarly, other studies in California found that native carnivore richness increased with increasing fragment size (Crooks, 2002, Tigas et al., 2003, Hilty and Merenlender, 2004). However, carnivores may also 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 is persisting 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 may even benefit from 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. Regardless of their response, most species we studied may require the availability of native habitat for their persistence in the face of urbanization in southern California.

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Table 1: Sources of information on carnivore occurrence in southern California based on camera traps.

Study Area	Time Period	County	Number of Camera Traps	Number of Sampling Nights	Source
State Highway 71	1997-2000	San Bernardino, Riverside	18	3345	(Lyren, 2001)
Puente-Chino Hills	1997-1998	San Bernardino, Riverside, Los Angeles	6	248	(Haas, 2000)
North/Central Irvine Ranch	2002-2003	Orange	14	4299	(Lyren et al., 2006)
East Orange /Central Irvine Ranch	2002	Orange	22	2138	(Haas et al., 2002)
Nature Reserve of Orange County	1999-2001	Orange	50	4112	(George and Crooks, 2006)
Rancho Jamul Ecological Reserve	2001-2002	San Diego	5	681	(Hathaway et al., 2002)
Santa Ysabel Ecological Reserve	2002-2003	San Diego	9	1872	(Hathaway et al., 2004)
San Diego Regional Corridor	2000-2002	San Diego	18	1747	(Hayden, 2002)
San Joaquin Hills	2006-2007	Orange	38	9536	(Lyren et al., 2008)
El Toro	2007	Orange	22	3445	(Lyren et al., 2008)
Tenaja Corridor	1999-2000	Riverside	15	4729	(Fisher and Crooks, 2001)

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	Number of Observed Sites	% Observed Sites
Coyote	187	86%
Bobcat	161	74%
Domestic dog[n]	70	32%
Striped skunk	64	29%
Gray fox	43	20%
Raccoon	60	28%
Mountain lion	39	18%
Virginia opossum[n]	29	13%
Long-tailed weasel	6	3%
American badger	2	.92%
Domestic cat[n]	2	.92%

n=Nonnative Species

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.

	Coastal Sage Scrub	Grassland	Oak Woodland	Chaparral	Other Native	Human-Altered	Total
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
Bobcat	67 (42%)	47 (30%)	19 (12%)	13 (8%)	7 (4%)	8 (5%)	161
Domestic dog[n]	36 (51%)	18 (26%)	3 (4%)	7 (10%)	3 (4%)	3 (4%)	70
Striped skunk	16 (25%)	24 (37%)	13 (20%)	4 (6%)	3 (5%)	4 (6%)	64
Gray fox	18 (42%)	5 (12%)	13 (30%)	6 (14%)	0 (0%)	1 (2%)	43
Raccoon	22 (37%)	14 (23%)	4 (7%)	7 (12%)	6 (10%)	7 (12%)	60
Mountain lion	18 (46%)	9 (23%)	10 (26%)	1 (3%)	1 (3%)	0 (0%)	39
Virginia opossum[n]	7 (24%)	10 (34%)	7 (24%)	1 (3%)	1 (3%)	3 (10%)	29

n=Nonnative Species

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

Species	Chi-square	Coefficient	Standard error	P-value
Coyote	6.677	3.022	1.325	0.010**
Bobcat	7.5164	-2.005	0.729	0.006**
Domestic Dog[n]	8.849	2.075	0.702	0.003**
Striped Skunk	4.875	-1.723	0.816	0.027**
Gray fox	25.049	-6.195	1.631	<0.0001***
Raccoon	4.980	1.608	0.716	0.026**
Mountain Lion	27.103	-7.266	1.941	<0.0001***
Virginia opossum[n]	2.864	-1.849	1.170	0.091*

n=Nonnative species, *=p<0.10, **=p<0.05, ***=p<0.0001

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	Chi-square	Coefficient	Standard error	P-value
Coyote	4.598	-0.0005	0.0002	0.032**
Bobcat	5.123	0.0005	0.0002	0.024**
Domestic Dog[n]	0.185	-8.045×10^{-5}	0.0002	0.667
Striped Skunk	5.471	-0.0005	0.0002	0.019**
Gray fox	26.262	0.001	0.0002	<0.0001***
Raccoon	5.216	-0.0005	0.0002	0.022**
Mountain Lion	19.077	0.001	0.0002	<0.0001***
Virginia opossum[n]	0.414	-0.0002	0.0003	0.520

n=Nonnative species, *=p<0.10, **=p<0.05, ***=p<0.0001

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

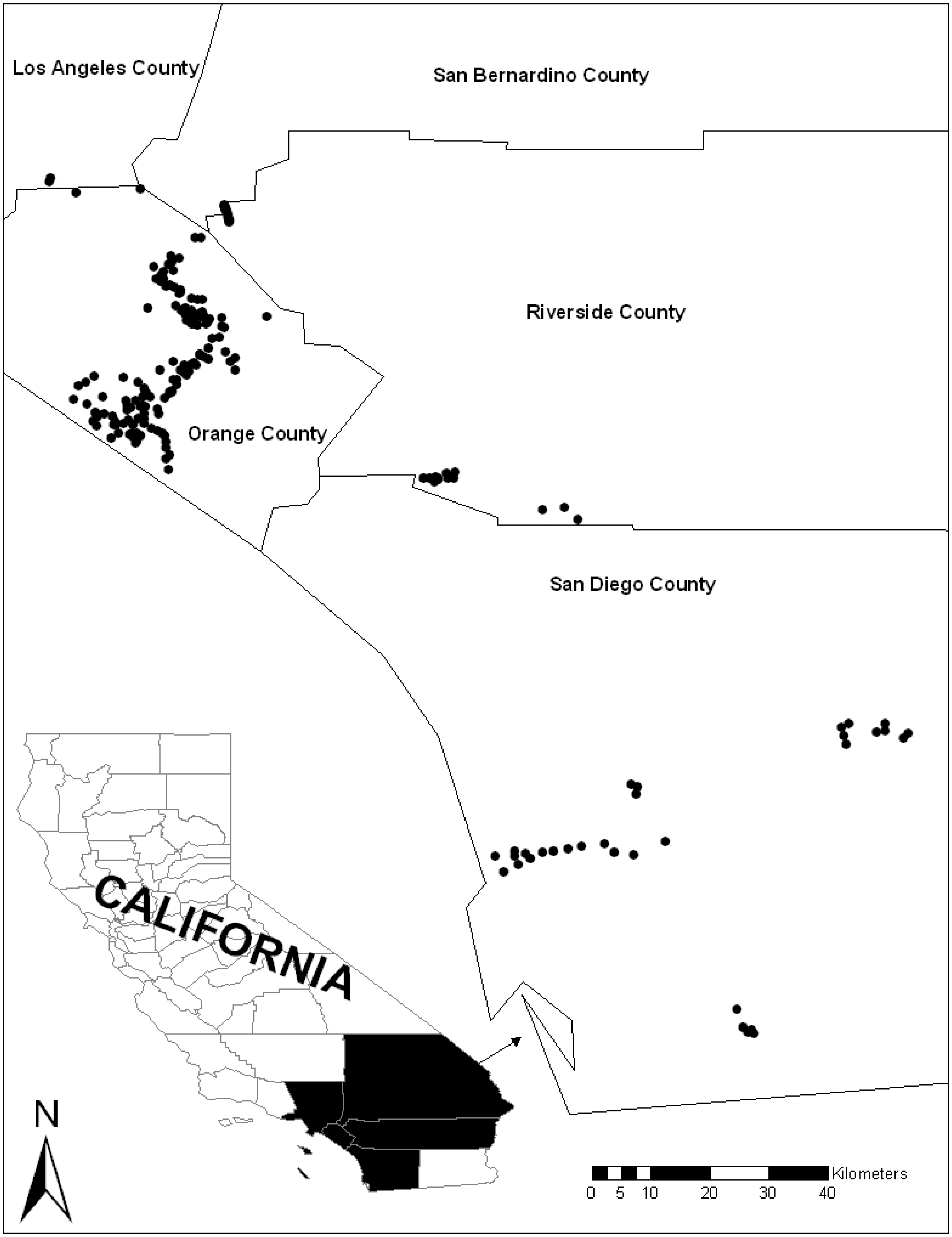

Figure 2: Logistic-regression models of the probability of occurrence of native and nonnative carnivores as a function of urban percentage in southern California. Asterisks (*) indicate statistically significant relationships (see Table 4).

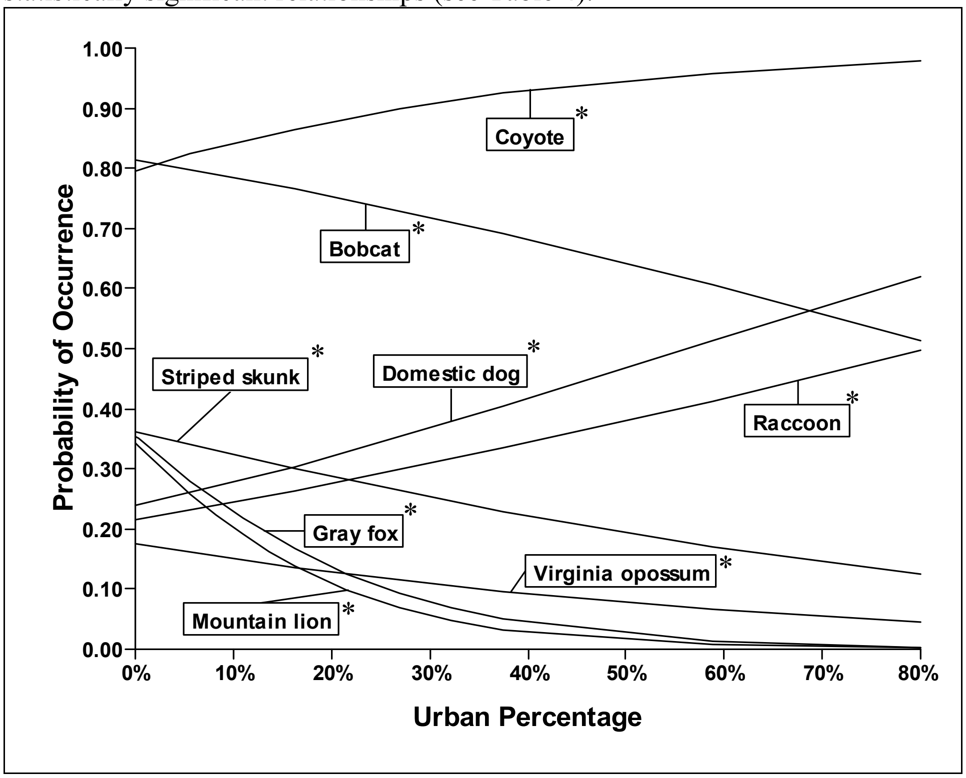

Figure 3: Logistic-regression models of the probability of occurrence of native and nonnative carnivores as a function of distance to urban edge in southern California. Asterisks (*) indicate statistically significant relationships (see Table 5).

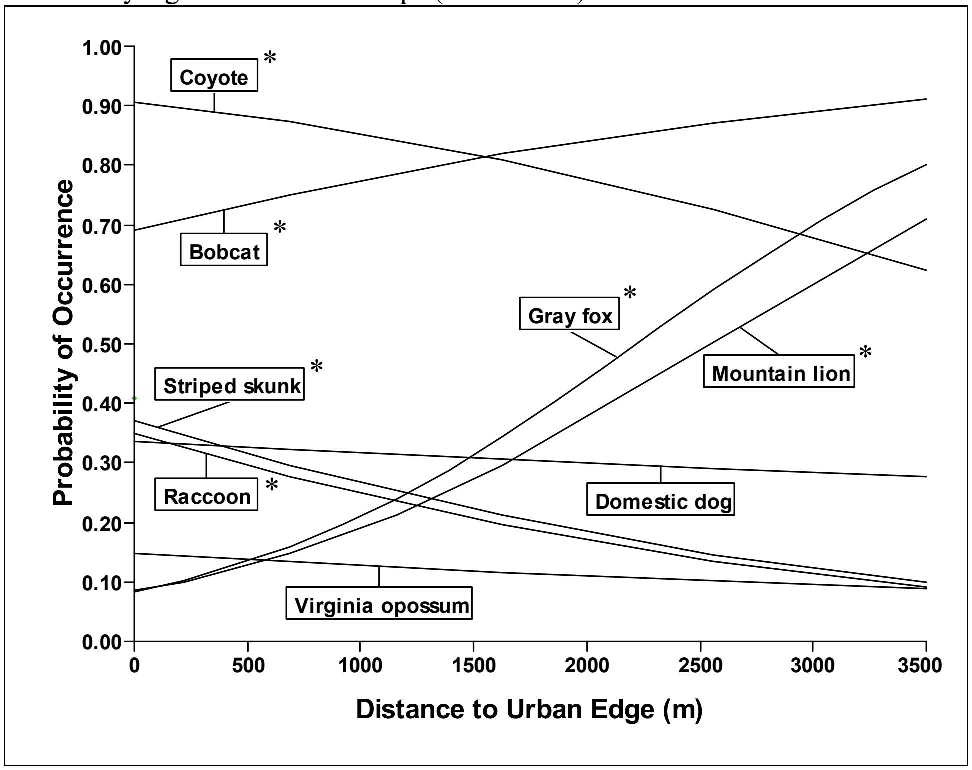

Figure 4: Distribution of native species richness of carnivores among 217 camera traps in southern California. Number of camera traps displayed above bars, 1997-2007.

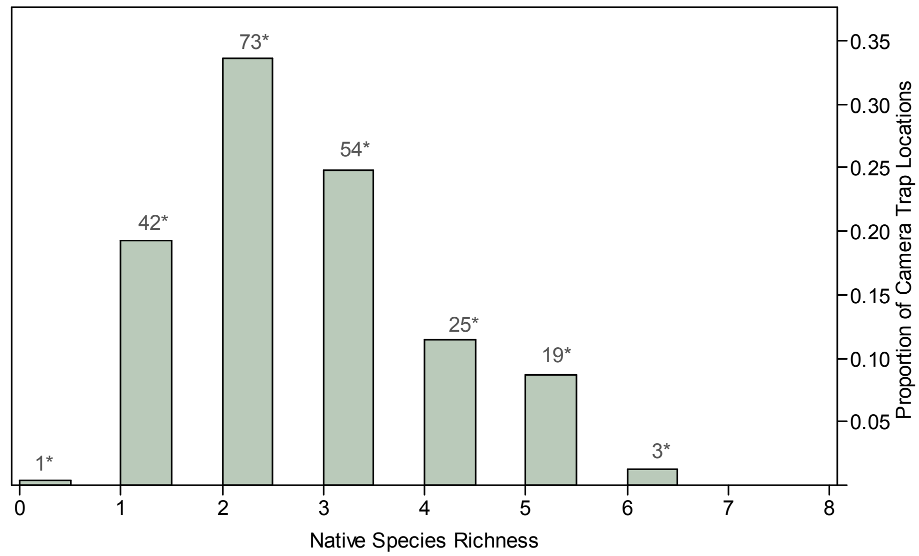

Figure 5: Distribution of total species richness of carnivores among 217 camera traps in southern California. Number of camera traps displayed above bars, 1997-2007.