Effects of Urbanization and Habitat Fragmentation on Bobcats and Coyotes in Southern California

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Abstract: *Urbanization and habitat fragmentation are major threats to wildlife populations, especially mammalian carnivores. We studied the ecology and behavior of bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) relative to development in a fragmented landscape in southern California from 1996 to 2000. We captured and radiocollared 50 bobcats and 86 coyotes, determined home ranges for 35 bobcats and 40 coyotes, and measured their exposure to development ("urban association") as the percentage of each home range composed of developed or modified areas. Both species occupied predominantly natural home ranges. Adult female bobcats had low levels of urban association, significantly lower than coyotes, adult male bobcats, and young female bobcats. Home-range size was positively correlated with urban association for coyotes and adult male and young female bobcats, suggesting that human-dominated areas were less suitable than natural areas in some important way. Animals more associated with non-natural areas had higher levels of night activity, and both bobcats and coyotes were more likely to be in developed areas at night than during the day. Survival rates were relatively high and were not related to urban association, at least for animals >6–9 months of age. Mortality rates from human-related causes such as vehicle collisions and incidental poisoning were also independent of urban association. In this region, even the few animals that had almost no human development within their home range were vulnerable to human-related mortality. Carnivore conservation in urban landscapes must account for these mortality sources that influence the entire landscape, including reserves. For bobcats, preserving open space of sufficient quantity and quality for adult females is necessary for population viability. Educating local residents about carnivores is also critical for conserving populations in urban areas.*

Efectos de la Urbanización y la Fragmentación del Hábitat sobre Gatos Silvestres (*Lynx rufus*) y Coyotes en el Sur de California

Resumen: *La urbanización y la fragmentación del hábitat son las amenazas más grandes para las poblaciones de animales silvestres, especialmente de mamíferos carnívoros. Estudiamos la ecología y conducta de gatos silvestres (*Lynx rufus*) y coyotes (*Canis latrans*) en relación al desarrollo en un paisaje fragmentado del sur de California entre 1996 y 2000. Capturamos y colocamos collares de radiotelemetría en 50 gatos silvestres y 86 coyotes, y determinamos los rangos de hogar para 35 gatos y 40 coyotes y medimos su exposición al desarrollo urbano ("asociación urbana") como el porcentaje de cada rango de hogar compuesto por áreas desarrolladas o modificadas. Ambas especies ocuparon rangos de hogar naturales en su mayoría. Las hembras adultas de gatos silvestres mostraron niveles bajos de asociación urbana, significativamente menores que los coyotes, los machos adultos y las hembras jóvenes de gatos silvestres, lo cual sugiere que estas áreas dominadas por humanos fueron notablemente menos adecuadas que las áreas naturales. Los animales más estrechamente asociados con áreas no naturales, gatos adultos machos y coyotes, tienen niveles más altos de actividad nocturna y mayor probabilidad de ocupar áreas urbanizadas durante la noche que durante el día.*

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Las tasas de supervivencia fueron relativamente altas y no se relacionaban con la asociación urbana, al menos para animales >6–9 meses de edad. Las tasas de mortalidad por causas relacionadas con la población humana, tales como el atropellamiento por vehículos y el envenenamiento accidental también fueron independientes del desarrollo urbano. En esta región, los pocos animales que casi no incluían áreas urbanizadas en sus rangos de hogar, eran vulnerables a la mortalidad causada por humanos. La conservación de carnívoros en paisajes urbanos debe tomar en cuenta estas fuentes de mortalidad que afectan a todo el paisaje, incluyendo las reservas. Para la preservación de la viabilidad poblacional de gatos silvestres, hace falta conservar suficiente espacio abierto de calidad para hembras adultas. Es también de importancia crucial educar a los residentes locales sobre los carnívoros para conservar poblaciones en áreas urbanas.

Introduction

Conversion of natural habitat to human uses, including urban development, agriculture, and extractive industries such as mining and intensive forestry reduces the amount of intact natural habitat and fragments what remains (Saunders et al. 1991). Wide-ranging and low-density species such as mammalian carnivores are particularly vulnerable to the processes of habitat loss and fragmentation (Noss et al. 1996; Gittleman et al. 2001).

Some carnivores have adapted well to the presence of humans. Raccoons (*Procyon lotor;* Riley et al. 1998), skunks (*Mephitis mephitis*, Rosatte et al. 1990), and red foxes (*Vulpes vulpes;* Harris 1981) reach their highest densities in urban areas, and Crooks (2002) found that the relative abundance of gray foxes (*Urocyon cinereoargenteus*) and opossums (*Didelphis virginianus*) is highest in the smallest habitat fragments. Other species, however, are less able to coexist with humans. Large carnivores come into conflict with humans and their domestic animals, and more-specialized species may not benefit from human-associated foods such as ornamental fruit or garbage. Mammalian carnivores, although often controversial (Kellert et al. 1996), generate public interest and are often the focus of conservation. As top predators in many terrestrial ecosystems, carnivores may also affect other carnivores (Palomares & Caro 1999) and populations in lower trophic levels (Sovada et al. 1995; Crooks & Soulé 1999).

Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) are common predators throughout North America, yet little is known about how they respond to urban development and habitat fragmentation. A few studies have examined urban or suburban coyotes in southern California (Gill & Bonnett 1973), around Seattle, Washington, (Quinn 1997*a*; 1997*b*), in Tucson, Arizona (McClure et al. 1995; Bounds & Shaw 1997; Grinder & Krausman 2001*a*, 2001*b*), and in British Columbia (Atkinson & Shackleton 1991). Although interesting results have been obtained, particularly for urban coyote diets, the radiotracking components of these studies have all included <10 animals and have been of short duration, except for the study by Grinder and Krausman (2001*a*) which addressed largely younger animals (13 of 16). Harrison (1998) interviewed residents in a rural residential area about bobcat sightings, and Riley (1999) studied bobcats and gray foxes in unfragmented habitats adjacent to urban areas in northern California. Studying bobcats and coyotes in an urban area allows an evaluation of how two relatively adaptable but also quite different carnivores are affected by urbanization. Although both bobcats and coyotes range across the entire continent and utilize a variety of habitats, coyotes are larger, more social, and more omnivorous than bobcats.

We studied the use of a fragmented urban landscape by bobcats and coyotes to better understand the conservation of carnivores in the face of urbanization. We estimated the level of exposure to development of these two carnivores by measuring the percentage of developed and altered area within their home range, or their "urban association." Our goals were to determine whether exposure to urban areas was related to species, age and sex class, homerange size, degree of nocturnal or diurnal activity, survival rates, and causes of mortality.

Methods

Study Area

Our study area was in the central Santa Monica Mountains and Simi Hills of southern California, west of the city of Los Angeles (Fig. 1). Natural vegetation varied and included mixed chaparral, coastal sage scrub, oak woodland and savanna, riparian areas, and introduced annual grasslands. Human land uses included commercial development, low- to high-density residential development, golf courses, landscaped areas in parks and adjacent to office buildings, agricultural land, and a 120-ha landfill. An 8- to 10-lane freeway (U.S. Route 101) and numerous secondary roads intersected the study area (Fig. 1).

Animal Capture and Radiotelemetry

Bobcats and coyotes were captured with padded foothold traps and necksnares. Captured animals were fitted with radiocollars with activity/mortality sensors that indicated whether animals were active, inactive, or dead

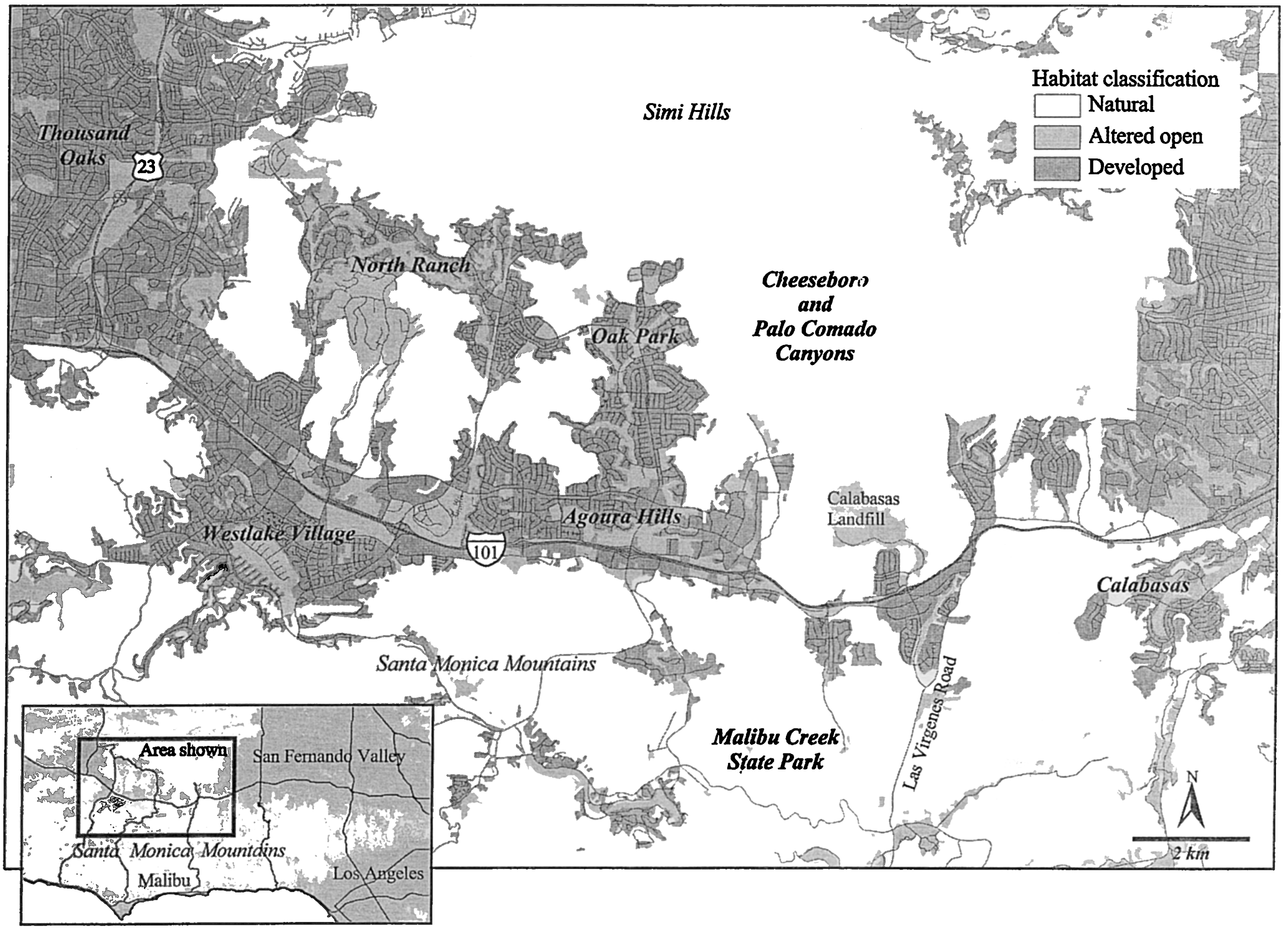

Figure 1. Land-use classification of bobcat and coyote study area in Los Angeles and Ventura Counties, California. The landscape within the study area was classified according to three land-use types: developed areas, altered open areas, and natural areas.

by variation in signal frequency (Advanced Telemetry Systems, Isanti, Minnesota, and Telemetry Solutions, Concord, California). We recorded sex, weight, morphological measurements, and age (juvenile, yearling, adult) for each animal. Juvenile animals were equipped with radiocollars with compressible polyurethane foam inserts to accommodate growth. "Young" animals included juveniles (0–1 year) and yearlings (1–2 years). To locate radiocollared animals by ground triangulation, observers recorded azimuths and their own location. We measured the accuracy of the radiotelemetry with test collars by comparing geographic positioning system locations of the collars to triangulated locations. Mean error distance was 42.4 m (SD = 50.2). This measure may underestimate the error of some locations, because test collars were generally close to the observers. However, we minimized the distance between observers and collared animals to acquire accurate locations, especially near land-use edges. We rechecked locations in or near the urban edge before conducting analyses, and we discarded those locations for which the observer was not positioned along the urban edge because we could not know with certainty on which side of the edge the animal was located.

Estimates of Home Range

We used minimum convex polygon (MCP) home ranges (Hayne 1949) for our analyses because they more accurately characterized the landscape used by radiocollared animals in our study area. The highly fragmented nature of the landscape produced clumps of locations in disjunct areas, and kernel home ranges for these animals often included separate polygons with no utilized area in between, but these areas were potentially important. Our study area also had many linear boundaries, such as roads and freeways, across which many animals rarely or never moved, and kernel home ranges included areas on the far side of such boundaries, whereas MCPs did not. Home-range area-observation curves reached asymptotes around 20 locations, so we determined home ranges for each animal with ≥20 radiolocations. Over our 4-year study, some animals made home-range shifts. If an animal completely shifted its area of use, we computed the home range based on the area that was used for the longest period. We estimated two different home ranges for one male bobcat that spent substantial time in two distant areas. We compared home-range size between species and age and sex groups with Mann-Whitney *U* tests.

Urban Association

To classify land use in the study area, we generalized a digital land-use map (Southern California Association of Governments 1993) into three types of land use: natural areas, developed areas, and altered open areas (Fig. 1). "Natural areas" consisted of large, contiguous areas of natural vegetation. "Developed areas" included commercial and residential areas with at least one house per 0.40 ha (1 acre). "Altered open" areas included golf courses; the Calabasas Landfill; graded areas (e.g., future construction sites); landscaped lawns such as office parks, playing fields, and city parks; low-density residential areas (one house per 2 ha), and small patches or strips of natural vegetation within high-density residential development (e.g., stream corridors). These altered open areas were potentially more attractive to carnivores than developed areas.

We measured urban association as the percentage of each animal's home range consisting of these non-natural types of land use. Land-use association can also be measured by calculating the percentage of locations that occurred in the different types of land use (e.g., Mannan & Boal 2000), and contrasting the percentage of locations with the home range or the percentage of the home range with the study area could illuminate habitat selection (sensu Johnson 1980). However, we focused on the extent to which animals were exposed to urban areas, regardless of whether they "selected" them or not. We believe that the percentage of the home range is the best measure of this exposure.

With Arc-Info (Environmental Systems Research Institute, Redlands, California), we overlaid the 95% MCP home ranges for each animal onto the land-use classification map and measured the percentage of its home range consisting of development, altered open areas, or both. We refer to the combined developed and altered open areas as "non-natural areas." We also counted the number of animals that had no non-natural area within their home range as animals with no urban association. For logistic reasons there was probably some bias against developed areas in our trap locations, but we believe it unlikely that we missed any strictly urban bobcats or coyotes, or that this bias compromised our results.

We used Mann-Whitney *U* and Kruskall-Wallis tests to evaluate differences in degree of urban association between species and sexes, and Fisher exact tests to test for differences in the number of animals with no urban association. We used Spearman rank correlations with two-sided tests of significance to determine the relationship between urban association and home-range size.

Survival and Cause-Specific Mortality Rates

We monitored radiocollared animals at least weekly to assess survival. When a mortality signal was discovered, we attempted to determine cause of death in the field. If this was not possible, carcasses were sent to the California Department of Fish and Game Wildlife Investigations Laboratory. We used the program MICROMORT (Heisey & Fuller 1985) to calculate survival rates. For both sexes of each species we calculated survival and cause-specific mortality rates annually, during wet (November–April) and dry (May–October) seasons and over relevant life-history periods. If radio contact was lost and the animal's fate was unknown, the animal was excluded from the analysis.

We tested for differences in survival rates and cause-specific mortality rates with the chi-square methods of Sauer and Williams (1989) and the program CONTRAST (Hines & Sauer 1989). We examined the relationship between survival rate and urban association by classifying bobcats and coyotes into three groups based on breaks in the histogram of the percentage range non-natural. We then computed survival rates for the animals in those categories and tested for differences between groups with multiple comparisons and Bonferroni corrections. Because we computed urban association by using home ranges and we only computed home ranges for animals with >20 locations, many radiocollared animals were not included. Animals with few locations may have died sooner, potentially producing a bias toward high survival rates. To detect this bias, we used the percentage of locations in non-natural areas (because we did not compute home ranges for these animals) to determine urban association for the 26 coyotes and five bobcats with 5–19 locations. We tested survival rates based on these 66 coyotes and 40 bobcats for a relationship between urban association and survival rate and compared the results with those from the animals with ≥ 20 locations. We also used this larger group of animals to look for a relationship between cause-specific mortality rates and urban association, this time using the histogram of percentage points non-natural to split bobcats into three groups and coyotes into four groups for computing mortality rates based on urban association.

Activity

When an animal was located, its activity level was recorded as active or inactive and time of day was classified as night (between 2200 and 0500 hours, the period during which human activity was significantly decreased) or day (other hours). On the level of the individual animal, we used Spearman rank correlation to determine the relationship between urban association and the percentage of nocturnal locations that were active. To summarize the relationship between urban association, time of day, and activity across animals, for each animal we computed (separately for both active and inactive locations) the percentage of locations in the different types of land use that occurred at night or during the day. We then took the mean of these percentages across bobcats and coyotes, a procedure that uses individual animals as independent sampling units and avoids pseudoreplication.

We used an α of 0.10 as the level of significance for all statistical tests because of our small sample sizes and the need to use nonparametric tests, both of which reduced statistical power. Statistical analyses were performed with the program SYSTAT.

Results

We captured and radiocollared 50 bobcats (23 males; 27 females) and 86 coyotes (49 males; 37 females). We computed 95% MCP home ranges for 35 bobcats and 40 coyotes (Table 1) with ≥20 radiolocations (coyotes: mean = 48 locations, SD = 22, range = 20–177; bobcats: mean = 49 locations, SD = 30, range = 23–147). Males had significantly larger home ranges than females for both bobcats ($U = 66.5, p = 0.005$) and coyotes ($U = 119, p = 0.054$). These sex differences were also significant within age class for bobcats (adults: $U = 40, p = 0.068$; young: $U = 2, p = 0.041$) but not for coyotes (adults: $U = 67, p = 0.262$; young: $U = 8, p = 0.123$). Adult and young home ranges were not different for bobcats ($U = 141.5, p = 0.736$) or coyotes ($U = 160, p = 0.951$).

Urban Association

Male bobcats were significantly more urban-associated than female bobcats (Table 1; Fig. 2; range developed: $U = 86, p = 0.027$; range non-natural: $U = 68.5, p = 0.006$). This difference was most striking for adult males and females (range developed: $U = 16, p = 0.001$; range non-natural: $U = 17.5, p = 0.002$). Young females were not significantly more urban-associated than young males (range developed: $U = 19, p = 0.149$; range non-natural: $U = 12, p = 1.00$). However, adult males were more urban-associated than young males (range developed: $U = 35, p = 0.036$; range non-natural: $U = 34.5, p = 0.043$), and adult females were less urban-associated than young females (range developed: $U = 15, p = 0.014$; range non-natural: $U = 24, p = 0.098$). Only two bobcats, one adult female and one young male, had no urban association, so we did not test for sex or age differences in this measure. More adult females than adult males had no developed area in their home range (adult females, 6 of 11; adult males, 1 of 13; Fisher's test, $p = 0.023$). However, the proportion of young females with no urban association did not differ from the proportion of adult females (Fisher's test, $p = 0.147$) or the proportion of adult males (Fisher's test, $p = 1.00$).

Male coyotes were more urban-associated than females by percentage range developed ($U = 135, p = 0.085$), although not for percentage range non-natural ($U = 142, p = 0.128$). Young animals were not significantly more urban-associated than adults (range developed: $U = 115, p = 0.116$; range non-natural: $U = 124, p = 0.194$).

Table 1. Home range size and urban association[a] of bobcats and coyotes in the Santa Monica Mountains and Simi Hills.

						Number of animals with	
Species	n	*95% MCP[b] home range size (km^2) mean ± SD*	*Developed area in home range (%)*	*Altered open area in home range (%)*	*Natural area in home range (%)*	*no developed area in home range*	*no non-natural[c] area in home range*
Bobcats	35		7.6	11.5	80.9	10	2
males	16	3.21 ± 2.55	10.8	14.6	74.6	3	0
females	19	1.55 ± 1.44	4.8	8.9	86.3	7	0
adult males	13	3.03 ± 2.57	12.9	15.9	71.2	1	1
adult females	11	1.72 ± 1.80	1.4	9.5	89.2	6	0
young males	3	3.99 ± 2.83	2.0	8.9	89.1	2	1
young females	8	1.30 ± 0.76	9.6	8.1	82.3	1	0
Coyotes	40		17.6	9.1	73.3	9	4
males	22	6.17 ± 7.44	22.3	8.5	69.2	4	2
females	18	2.84 ± 2.81	11.8	9.8	78.4	5	2
adults	28	4.96 ± 6.91	15.6	7.9	76.6	9	4
young animals	12	4.18 ± 3.66	22.3	11.9	65.8	0	0

[a] *Urban association is measured by the percentage of the home range that is made up of developed and altered open habitats.*
[b] *Minimum convex polygon (Hayne 1949).*
[c] *Non-natural area = developed area + altered open area.*

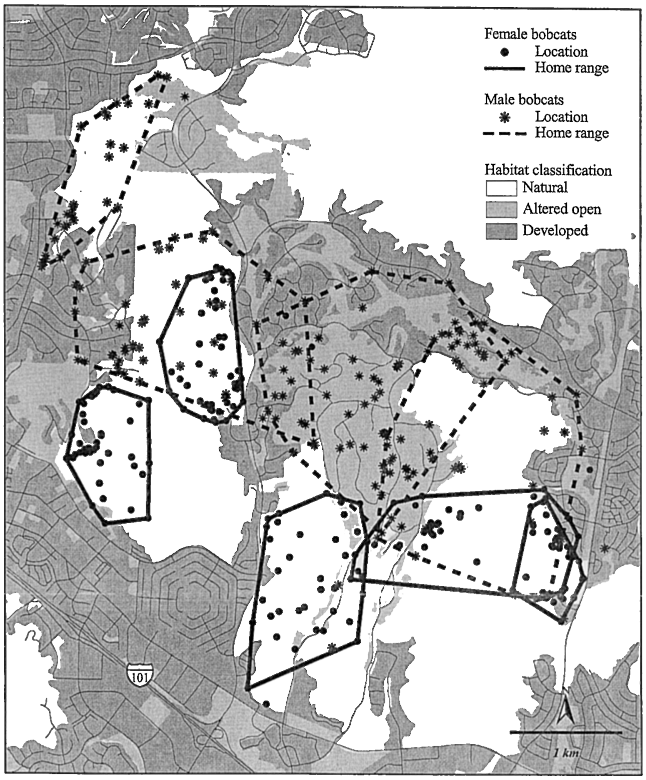

Figure 2. Home ranges (95% minimum convex polygons) of male and female bobcats relative to land use in the Simi Hills region, Ventura County, California. Altered open areas include low-density residential areas, golf courses, and small vegetated patches or strips.

Sexes were not different within ages, and ages were not different within sexes.

Only 4 of 40 coyotes, all adults, had no non-natural area within their home range. There was no difference between males and females (Fisher's test, $p = 0.705$) in the proportion of coyotes with no developed area in their home ranges.

To compare urban association among species, we separated adult male, adult female, and young female bobcats, excluded young male bobcats because of small sample size ($n = 3$), and considered coyotes as one group. Kruskall-Wallis tests showed a significant effect of species-age-sex group on urban association (range developed: $H = 11.415$, $p = 0.010$; range non-natural: $H = 8.105$, $p = 0.044$). To specifically compare each bobcat group with coyotes, we carried out three contrasts with an overall α of 0.075. Adult female bobcats were significantly less urban-associated than coyotes (at $\alpha = 0.025$, critical difference = 13.97, range developed difference = 23.24, range non-natural difference = 17.66), but adult male bobcats (critical difference = 13.10, range developed difference = 0.12; range non-natural difference = 4.26) and young female bobcats (critical difference = 15.88, range developed difference = 5.99, range non-natural difference = 7.36) were not.

More adult female bobcats than coyotes had no developed area in their home range (adult female bobcats: 6 of 11, coyotes: 9 of 40; Fisher's test, $p = 0.061$), but neither adult male bobcats (Fisher's test, $p = 0.419$) nor young female bobcats (Fisher's test, $p = 1.00$) were different from coyotes in this measure.

Urban Association and Home Range Size

For all bobcats, home range size was larger for animals with higher urban association, particularly for percent range non-natural ($n = 35$, range developed: $r_s = 0.319$, $0.10 > p > 0.05$; range non-natural: $r_s = 0.681$, $p < 0.001$). This positive relationship was significant for adult males ($n = 13$; $r_s = 0.484$, $p = 0.10$, for percent developed; $r_s = 0.302$, $0.50 > p > 0.20$, for percent non-natural) and young females ($n = 8$; $r_s = 0.548$, $0.20 > p > 0.10$, for percent developed; $r_s = 0.643$, $p = 0.10$, for percent non-natural). The relationship was not significantly negative for adult females ($n = 11$; $r_s = -0.484$, $0.20 > p > 0.10$, for percent developed; $r_s = -0.368$, $0.50 > p > 0.20$, for percent non-natural). We could not compute a relationship for young males ($n = 3$).

For all coyotes ($n = 39$), home range size increased with percent range non-natural ($r_s = 0.275$, $0.10 > p > 0.05$) but not with percent range developed ($r_s = 0.210$, $p = 0.20$). For adult male coyotes ($n = 15$; range developed: $r_s = 0.481$, $0.10 > p > 0.05$; range non-natural: $r_s = 0.593$, $0.05 > p > 0.02$) the relationship was stronger.

Survival and Mortality Causes Relative to Urban Association

Average annual survival rates were similar between species (bobcats, $n = 50$, survival rate = 0.761, vs. coyotes, $n = 86$, survival rate = 0.742: $\chi^2_1 = 0.093$, $p = 0.760$) and between sexes within species (male bobcats, $n = 21$, survival rate = 0.822, vs. female bobcats, $n = 29$, survival rate = 0.745: $\chi^2_1 = 0.910$, $p = 0.340$; male coyotes, $n = 49$, survival rate = 0.770, vs. female coyotes, $n = 37$, survival rate = 0.730: $\chi^2_1 = 0.392$, $p = 0.531$). Survival rates were higher in the sample of animals for which we computed home ranges (those with >20 locations; Table 2).

With the expanded sample of 66 coyotes and 40 bobcats with >5 locations, survival rates did not vary with urban association (Table 3; bobcats: $\chi^2_2 = 4.46$, $p = 0.107$; coyotes: $\chi^2_3 = 1.38$, $p = 0.709$). Similarly, for those animals with > 20 locations (Table 2), average annual survival rates were not related to urban association for bobcats ($\chi^2_2 = 3.91$, $p = 0.142$) or coyotes ($\chi^2_2 = 0.362$, $p = 0.830$). Vehicles, other carnivores, and toxins—specifically anticoagulant rodenticides—were the principal causes of death for bobcats and coyotes (Table 3). For bobcats, the average annual vehicle mortality rate was related to urban association ($\chi^2_2 = 6.20$, $p = 0.045$), but

Table 2. Average annual survival rates of bobcats and coyotes in urban Southern California, 1996–2000, relative to urban associaton.[a]

	Urban association (%)	n	*Average annual survival rate[b]*	*Total no. radio days*	*No. deaths*
Bobcats					
group 1	0–9	13	0.825	8,874	6
group 2	10–21	14	0.829	8,755	3
group 3	>36	7	0.943	6,189	2
Coyotes					
group 1	0–14	16	0.873	12,952	6
group 2	22–40	14	0.828	9,842	6
group 3	>45	10	0.856	8,368	5

[a] *Urban association is measured by the percentage of the home range that consists of developed and altered open areas.*
[b] *Survival rates based on the 34 bobcats and 40 coyotes with ≥20 locations.*

Bonferroni-corrected pairwise comparisons were not significant, even between the groups with the most and least urban association (0.141 vs. 0.00; $\chi^2_1 = 3.91, p = 0.048$). The mortality rate from predation was not related to urban-association group ($\chi^2_2 = 1.41, p = 0.494$).

For coyotes, the vehicle mortality rate was not related to urban association ($\chi^2_3 = 0.837, p = 0.841$), but both the predation mortality rate ($\chi^2_3 = 11.43, p = 0.0096$) and the toxin mortality rate ($\chi^2_3 = 11.39, p = 0.010$) were. Although the group with the highest urban association had the highest average annual mortality rate from toxins (Table 3), there was no consistent relationship between urban association and toxin mortality, and corrected pairwise comparisons were not significant. The predation mortality rate in the animals with no urban association was higher than that in animals with some non-natural area in their home range ($\chi^2_1 = 16.49, p < 0.001$). Bobcats and coyotes did not differ in their average annual vehicle mortality rate ($\chi^2_1 = 0.193, p = 0.661$).

Activity and Urban Association

Coyotes as a group were more active at night (66% of points active) than during the day (51% of points active). For bobcats there was little difference between day and night in the percentage of points active (night, 64% active; day, 60% active).

Based on the analysis of all radiolocations for each species, both coyotes and bobcats shifted their use of altered open areas, and particularly of developed areas, to the night. Based on only bobcat locations recorded as active, 75% of developed-area locations, 47% of altered-open-area locations, and 27% of natural-area locations occurred at night (average percentages across 40 bobcats). For inactive locations, on average 77% of developed-area locations, 58% of altered-open-area locations, and 21% of natural-area locations occurred at night. On average overall, 25% of all locations, 28% of active locations, and 26% of inactive locations were recorded at night.

Coyotes exhibited the same pattern. Of coyote radiolocations recorded as active, on average 80% of developed-area locations, 60% of altered-open-area locations, and 29% of natural-area locations occurred at night (averages across 66 coyotes). For inactive locations, on average 66% of developed-area locations, 80% of altered-open-area locations, and 23% of natural-area locations occurred at night. On average overall, 25% of all locations, 32% of active locations, and 25% of inactive locations were recorded at night.

Table 3. Average annual cause-specific mortality rates for bobcats and coyotes in urban southern California relative to urban association,[a] 1996–2000.[b]

	Urban association (%)	*Radio days*	*Survival rate*	*Vehicle mortality rate (no. deaths)*	*Predation mortality rate (no. deaths)*	*Toxin mortality rate (no. deaths)[c]*	*Gunshot mortality rate (no. deaths)[c]*	*Unknown/ miscellaneous mortality rate (no. deaths)*
Bobcats								
group 1	0	4479	0.704	0.141 (3)	0.098 (2)	na	na	0.078 (2)
group 2	3–16	12104	0.825	0.042 (2)	0.024 (1)	na	na	0.024 (1)
group 3	>22	8890	0.904	0.000 (0)	0.023 (1)	na	na	0.059 (2)
Coyotes								
group 1	0	5013	0.744	0.027 (1)	0.232 (4)	0.053 (2)	0.000 (0)	0.000 (0)
group 2	1–19	13037	0.850	0.057 (3)	0.021 (1)	0.045 (3)	0.021 (1)	0.038 (2)
group 3	20–37	8712	0.823	0.061 (2)	0.027 (1)	0.000 (0)	0.000 (0)	0.066 (3)
group 4	>46	4515	0.836	0.046 (1)	0.000 (0)	0.135 (3)	0.000 (0)	0.000 (0)

[a] *Urban association is based on the percentage of radiolocations in developed and altered open areas.*
[b] *Survival and mortality rates are for the 66 coyotes and 40 bobcats with fewer than five locations.*
[c] *The na indicates that no bobcats ever died of this cause, so we did not compute mortality rates for bobcats for these causes.*

At the individual animal level there was a relationship between urban association and night activity. For adult female bobcats ($n = 11$), level of night activity increased with percent range non-natural ($r_s = 0.454$, $0.10 > p > 0.05$) but not with percent range developed ($r_s = 0.345$, $0.25 > p > 0.10$). The percentage of night points active increased with urban association for adult male bobcats ($n = 13$) for percent range non-natural ($r_s = 0.643$, $0.01 > p > 0.005$), although not for percent range developed ($r_s = 0.308$, $0.25 > p > 0.10$). For young female bobcats ($n = 8$), neither relationship was significant, although both were positive.

For coyotes there were strong relationships between urban association and night activity. The relationship was significant for both urban-association measures for all coyotes ($n = 39$) (range developed: $r_s = 0.306$, $0.05 > p > 0.025$; range non-natural: $r_s = 0.286$, $0.05 > p > 0.025$) and for adult male coyotes ($n = 22$; range developed: $r_s = 0.453$, $0.05 > p > 0.025$; range non-natural: $r_s = 0.444$, $0.10 > p > 0.05$). For adult female coyotes ($n = 17$) there was a significant relationship between percentage of night points active and percent range developed ($r_s = 0.450$, $0.10 > p > 0.05$) but not for percent range non-natural ($r_s = 0.375$, $0.25 > p > 0.10$).

Discussion

Even though these carnivores utilized developed areas, all groups including coyotes and adult male bobcats were predominantly associated with natural areas (Table 1). Natural area was also the largest component of home ranges of coyotes in Tucson (Grinder & Krausman 2001*a*), and coyotes in Seattle preferred the least-disturbed habitats, even when they were scarce within the animal's home range (Quinn 1997*a*). Although coyotes are omnivorous and can take advantage of human-related food items, including ornamental fruit, garbage, pet food, and pets (McClure et al. 1995; Quinn 1997*b*; Fedriani et al. 2001), even in the most "humanized" part of their study area. Fedriani et al. (2001) found that at most 25% of the coyote diet consisted of anthropogenic food. Coyotes are opportunistic animals that find available resources in a disturbed landscape, but they still largely inhabit natural areas and subsist on natural foods.

For bobcats, age and sex affected sensitivity to urbanization. Similar sex differences were also found when individual bobcats were intensively monitored in the study area (Tigas et al. 2002). The low level of urban association of adult female bobcats may be related to the species' polygynous social system, in which females care for the young. Areas frequented or modified by humans may be perceived by female bobcats as unsafe for raising young. In Golden Gate National Recreation Area in northern California, female bobcats also appear to be more sensitive to urbanization because they maintain home ranges only in the interior of the park, whereas males range out to the park edge (Riley 1999). Our findings that young female bobcats were more urban-associated than adult females whereas young male bobcats were less urban-associated than adult males, although currently based on a small sample of animals, is in accordance with bobcat social behavior. Female bobcats are generally territorial by prior rights land tenure (Bailey 1974; Anderson 1987), and in high-density populations young females searching for a territory may be willing to utilize marginal habitats. Dispersing Iberian lynx (*Lynx pardinus*) use lower-quality habitat than residents (Palomares et al. 2000). Adult male bobcats have larger home ranges that generally increase in size over time in order to encompass more females (Connor et al. 1999), and their greater willingness to move through developed areas may allow more mating opportunities.

For some predators such as red foxes (Harris 1981), raccoons (Riley et al. 1998), and Cooper's Hawks (*Accipiter cooperii*; Mannan & Boal 2000), density increases and home range size decreases in urban areas, presumably because of high-density food supplies and sufficient habitat requirements. Fedriani et al. (2001) suggest that coyote density may be enhanced by human-related food items in this study area, and, in comparison with other populations, the home ranges of bobcats and coyotes in our study were small. The high productivity of environments in coastal California may allow bobcats and coyotes to meet metabolic requirements with small home ranges, but the constraints of urban habitat fragmentation may also restrict home range size. Of the three bobcat studies that have reported home ranges of a similar size (Lembeck & Gould 1979; Miller & Speake 1979), one was also in an urban area (Riley 1999), and female home ranges were significantly smaller there than in a nearby rural area. Coyote home ranges can also be small in urban areas (Atkinson & Shackleton 1991; but see Bounds & Shaw 1997).

Although developed and altered open areas may offer increased food resources, we observed a positive relationship between home range size and urban association. This suggests that non-natural areas are less suitable than natural areas in some important aspect. Secure resting and denning locations may be more dispersed in developed areas, and although coyotes, adult male bobcats, and young female bobcats may forage in the neighborhoods, they may be less willing to rest there. For adult male bobcats, the significant relationship with percentage range developed but not with percentage range non-natural may indicate that the altered open areas are more equivalent to natural areas. In general, bobcats had consistently higher association with altered open areas than with developed areas (Table 1).

A decreased sense of security around humans would also explain the shift toward nocturnal use of more-developed areas in both bobcats and coyotes. Urban coyotes in Seattle move through developed habitats more at night than during the day (Quinn 1997*a*), and coyotes in a suburban area in Wyoming have also shifted to less diurnal activity than animals in nearby Grand Teton National Park (McClennen et al. 2001). Coyotes in southeastern Colorado are more active during the day since population exploitation and harassment have ceased (Kitchen et al. 2000).

The survival rates for bobcats and coyotes in our study were similar to those reported in other unexploited populations (Gese et al. 1989; Fuller et al. 1995; Chamberlain et al. 1999; Grinder & Krausman 2001*b*) and higher than those in harvested populations (Davison 1980; Fuller et al. 1985; Windberg et al. 1985). Contrary to our expectations, there were no differences in survival rate relative to urban association. Although our sample of animals for which we could determine home ranges may have been biased toward higher survival, we found no more of a relationship between survival rate and urban association with animals found at ≥5 locations. We followed mostly full-grown animals that were at least 6–9 months old, so differences in survival rate could be more evident in young animals. Perhaps when bobcats and coyotes have negotiated their first few months in the urban landscape, the lack of human exploitation or larger carnivores produces high survivorship.

Still, if there were mortality sources associated with urbanization and fragmentation, such as vehicle collisions, nuisance animal trapping, or contaminant build-up, animals with more contact with developed areas should have lower survivorship. In Tucson, humans—specifically, their vehicles—accounted for most coyote mortality (Grinder & Krausman 2001*b*). In our study area almost every animal lives in a fragmented and urbanized landscape: only 4 of 40 coyotes and 2 of 35 bobcats had home ranges consisting entirely of natural area. Consequently, nearly every bobcat and coyote was potentially affected by human-associated mortality sources.

Similarly, mortality rates from human-related causes were not positively related to urban association. For bobcats, the vehicle death rate was highest in animals with the least urban association. In this landscape roads are omnipresent, and even if they are denser in urban zones, those traversing open space can be particularly dangerous, especially if used by many vehicles traveling at high speed. Animals most exposed to urban areas may also gain familiarity with roads and develop the ability to safely navigate them. Las Virgenes Road, a throughway between the 101 freeway and the town of Malibu, bisects significant natural area. Radiocollared animals in this area had low or no urban association, but a number of collared and uncollared animals were killed on this road. Four female bobcats were radiotracked in the vicinity of Las Virgenes road. Two that never crossed the road each survived for over 5 years. The two that were located on both sides of the road were each struck and killed by vehicles <15 months after capture (Fig. 3).

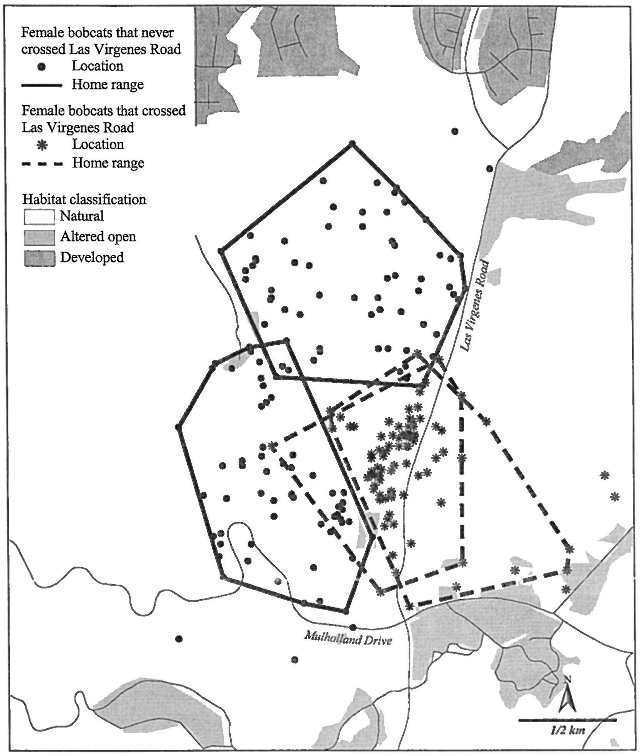

Figure 3. Home ranges (95% minimum convex polygons) of four female bobcats along Las Virgenes Road, Los Angeles County. Risk of vehicle mortality was not related to urban association, as illustrated by these four female bobcats with low urban association (<4% for each). The two bobcats that crossed the road (dashed lines) were killed by vehicles, whereas the other two were not.

The coyote mortality rate from anticoagulant poisoning was also not related to urban-association. Anticoagulant poisoning deaths were generally caused by brodifocoum, a chemical designed and designated as an indoor rodent poison (Hosea 2000). Although the highest mortality rate was among coyotes with the highest urban association, animals with the lowest urban association also died from anticoagulant poisoning. Although coyotes may have been exposed to poisons in residential areas or on golf courses, even animals in large natural zones may consume prey that have ingested poisons.

Woodroffe and Ginsburg (1998) suggest that minimizing carnivore mortality at the boundaries of nature reserves may be more important for conserving carnivores than the size of the reserve. Our results further indicate that in fragmented urban landscapes, human-caused mortality may affect all animals. Carnivore conservation efforts in these landscapes must account for the pervasive effects of humans and development, even within reserves.

Bobcats are more sensitive to urbanization than omnivorous canids such as coyotes and gray foxes (Riley 1999; Crooks 2002; Tigas et al. 2002; this study). The higher sensitivity of adult female bobcats in particular is important for bobcat population viability because lands that are inhospitable to females cannot produce new animals. The most marginal areas used by bobcats may be a population sink (sensu Pulliam 1988) if dispersing bobcats reach these areas from nearby source populations but do not reproduce there. Source-sink dynamics can have critical implications for the long-term prospects of felid populations (Gaona et al. 1998). An important management issue then becomes the minimum requirements for adult female bobcats to survive and successfully reproduce. Adult female home ranges averaged 1.7 km^2, and we know that fragments of 3.15 and 4.45 km^2 supported at least three female bobcats. The habitat quality of a particular patch is important, however, and intensive human alteration will limit its value. We do not know the reproductive success of bobcats in habitat fragments or how it compares with that in nearby wildlands. We also know from concurrent scat, track, and camera surveys (Tigas 2000) that bobcats utilize fragments as small as 0.4 km^2. But whether only males use these smallest patches, whether and how bobcats move between these patches, and finally whether reproduction occurs in them are open questions.

Even the highly adaptable coyote utilizes natural areas more than developed areas, expands its home range in increasingly urbanized areas, shifts its use of developed areas to periods of decreased human presence, and is vulnerable to vehicle collisions and poison. Ultimately, we must not only learn the requirements of carnivore species in developing landscapes, we must also educate people to value carnivores and promote their conservation by preserving open space, using rodenticides sparingly and correctly, providing usable crossing points under freeways and major roads, driving slower where carnivores cross roads, and living with rabbits in the yard and in the park.

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