Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation

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Abstract: *I examined the effects of habitat fragmentation on the distribution and abundance of mammalian carnivores in coastal southern California and tested the prediction that responses to fragmentation varied with the body size of carnivore species. I conducted track surveys for nine native and two exotic carnivore species in 29 urban habitat fragments and 10 control sites. Fragment area and isolation were the two strongest landscape descriptors of predator distribution and abundance. Six species were sensitive to fragmentation, generally disappearing as habitat patches became smaller and more isolated; three species were enhanced by fragmentation, with increased abundance in highly fragmented sites; and two species were tolerant of fragmentation, with little to no effect of landscape variables on their distribution and abundance. Within urban habitat fragments, the carnivore visitation rate increased at sites with more exotic cover and closer to the urban edge, a pattern driven largely by the increased abundance of fragmentation-enhanced carnivores at edge sites. Finally, body size, in conjunction with other ecological characteristics, partially accounted for the heterogeneity in responses to fragmentation among carnivore species. These differential sensitivities are useful criteria for choosing appropriate focal species for ecological research and conservation planning, a choice that depends on the scale of fragmentation in a region and the commensurate responses of carnivore populations at that scale.*

Sensibilidad Relativa a la Fragmentación del Hábitat de Mamíferos Carnívoros

Resumen: *Examiné los efectos de la fragmentación del hábitat sobre la distribución y abundancia de mamíferos carnívoros en la costa del sur de California y evalué la predicción de que las respuestas a la fragmentación variaban con el tamaño corporal de carnívoros. Se realizaron muestreos de huellas para nueve especies nativas y dos exóticas en 29 fragmentos de hábitat urbano y 10 sitios control. El área fragmentada y su aislamiento fueron los dos principales descriptores de la distribución y abundancia de depredadores. Seis especies fueron sensibles a la fragmentación, generalmente las especies desaparecían conforme los fragmentos eran más pequeños y aislados, tres especies fueron favorecidas por la fragmentación, con incremento en su abundancia en sitios altamente fragmentados, y dos especies fueron tolerantes a la fragmentación con poco o ningún efecto de las variables del paisaje sobre su distribución y abundancia. Dentro de los fragmentos de hábitat urbano, las tasas de presencia de carnívoros incrementaron en sitios con mayor cobertura exótica y cercanos al borde urbano, un patrón dirigido principalmente por el incremento en la abundancia de carnívoros favorecidos por la fragmentación en el borde de los sitios. Finalmente, el tamaño corporal, conjuntamente con otras características ecológicas, fueron parcialmente responsables de la heterogeneidad en respuestas a la fragmentación entre especies de carnívoros. Estas sensibilidades diferenciales son un criterio útil para seleccionar especies focales apropiadas para investigaciones ecológicas y la planeación de la conservación, una selección que depende de la escala de fragmentación en una región y de las respuestas apropiadas de las poblaciones de carnívoros a esa escala.*

Introduction

The destruction of habitat has been targeted as one of the most serious threats to biological diversity world-

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wide (Wilcove et al. 1998), and in areas with increasing urbanization, the loss and fragmentation of habitat is virtually inevitable. Mediterranean scrub habitats in coastal southern California are particularly threatened. Intensive development in the region over the past century has destroyed all but 10% of the native coastal sage scrub habitat (McCaull 1994). This habitat loss has created a "hotspot" of endangerment and extinction for the highly endemic biota in the region (Dobson et al. 1997). Mammalian carnivores are thought to be particularly vulnerable to local extinction in fragmented landscapes because of their relatively large ranges, low numbers, and direct persecution by humans (Noss et al. 1996; Woodroffe & Ginsberg 1998). The decline and extirpation of top predators from fragmented systems may generate trophic cascades that alter the structure of ecological communities (Crooks & Soulé 1999). Indeed, the persistence of these environmentally sensitive and ecologically pivotal species may be indicative of the integrity of entire ecosystems (Noss et al 1996). As such, mammalian carnivores can serve as useful tools for the study of ecological disturbances or for conservation planning and reserve design (Soulé & Terborgh 1999).

Mammalian predators are difficult to study, however, because of their low densities, nocturnal and secretive habits, and wariness of humans (Sargeant et al. 1998). As a result, the ecology of many carnivore species and their responses to ecological disturbances such as fragmentation are often poorly understood. Although considered members of the same ecological guild, carnivores may vary in their responses to fragmentation. In particular, differences in body size among carnivore species have been proposed as an important determinant of extinction probability (Brown 1986; Belovsky 1987). The relationship between body size and extinction risk in animals is complex, however, and has been the subject of considerable debate, with studies predicting and reporting positive, negative, or no relation of body size to extinction probability (reviewed by Johst & Brandl 1997). Few studies have evaluated if, how, or why carnivore species differ in their relative sensitivities to fragmentation effects.

My goal was to analyze the effects of the loss and fragmentation of habitat on mammalian carnivores in the urbanizing landscape of coastal southern California. Habitat fragmentation must be viewed as a multiscale problem, with fragmentation effects depending on the scale of fragmentation and the movement patterns of target species (Andren 1994). I therefore surveyed a suite of carnivore species that occur across a range of fragmentation levels and evaluated their responses to fragmentation at two spatial scales: (1) landscape-level heterogeneity among fragments and (2) local heterogeneity at sites within fragments. To allow for a more comprehensive assessment of relative sensitivities to fragmentation, I not only documented the presence or absence of

each carnivore species, but also measured their relative abundance at each site. Finally, I tested the prediction that responses to fragmentation vary with body size in carnivore species, explored other ecological traits of these predators that may contribute to extinction risk, and used these differential sensitivities to evaluate the utility of mammalian carnivores as focal species with which to assess the degree of functional landscape connectivity.

Methods

Study Areas

I conducted carnivore surveys in 29 urban habitat fragments in coastal San Diego County from Fall 1995 through Summer 1997. Twenty-eight of these fragments were originally studied by Soulé et al. (1988). The fragments, completely surrounded by human-modified landscapes, are typically dendritic canyons dissecting coastal mesas, although a few also contain mesa-top habitat. The fragments support a mosaic of shrub habitat, including mixed chaparral, chamise chaparral, maritime succulent shrub, and coastal sage scrub, the dominant assemblage in most sites. Disturbed areas within fragments were typically dominated by ruderal weed species, ornamental plants invading from surrounding residences, fire-retardant ground cover such as South African iceplant (*Carpobrotus edulis*), and non-native trees (e.g., palms and species of *Eucalyptus* and *Acacia*) (Alberts et al. 1993).

From Fall 1995 through Summer 2000, I conducted carnivore surveys in less disturbed areas in coastal southern California to act as controls to the small, urban habitat remnants. These control areas varied in size and degree of isolation (Table 1), ranging from relatively small reserves isolated within urban developments (e.g., Point Loma Ecological Reserve) to large blocks of habitat relatively continuous with larger natural areas (e.g., Miramar Marine Corps Air Station).

Carnivore Surveys

I assessed the distribution and relative abundance of nine native and two non-native predator species through track surveys. Native species were the mountain lion (*Felis concolor*), bobcat (*Felis rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), western spotted skunk (*Spilogale gracilis*), and long-tailed weasel (*Mustela frenata*). Non-native target species were the domestic cat (*Felis catus*) and Virginia opossum (*Didelphis virginiana*), a marsupial introduced to California around 1910 (Jameson & Peeters 1988).

Table 1. Landscape variables and distributions of 11 mammalian carnivore species for 10 control sites and 29 urban habitat fragments in coastal southern California (1, present; 0, absent).

	Area (ha)	Age (yrs)	Distance Y (m)	Distance Z (m)	Long-tailed weasel	Spotted skunk	Badger	Mountain lion	Bobcat	Coyote	Gray fox	Striped skunk	Raccoon	Opossum	Domestic cat
Control sites															
Miramar Marine Corps Air Station	5806	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Chino Hills State Park	4452	0	200	200	1	0	1	1	1	1	1	1	1	1	0
Limestone Canyon/Whiting Ranch	4450	0	15	15	0	0	1	1	1	1	1	1	1	1	0
San Joaquin Hills	4219	22	5353	2930	0	1	0	0	1	1	1	1	1	1	0
Weir Canyon	1923	0	69	69	0	0	0	1	1	1	1	1	0	1	0
Santa Margarita Ecological Reserve	1763	0	30	30	0	0	0	1	1	1	1	0	1	0	0
Starr Ranch	1548	0	0	0	0	1	0	1	1	1	1	1	1	1	0
Tenaja	1191	0	0	0	1	0	1	1	1	1	1	1	1	1	0
Torrey Pines State Reserve	428	0	68	68	0	0	0	0	1	1	1	1	1	1	0
Point Loma Ecological Reserve	264	45	5700	5700	0	0	0	0	0	1	1	1	1	0	1
Urban fragments															
Florida	102	59	2100	233	0	0	0	0	0	1	1	0	0	0	0
Torrey Pines Extenstion	74	20	91	91	0	0	0	0	1	1	1	1	0	1	1
Balboa Terrace	56	43	121	117	0	0	0	0	0	1	1	1	1	1	1
Alta La Jolla	34	23	121	93	0	0	0	0	0	1	1	1	1	1	1
Kate Sessions	31	25	121	93	0	0	0	0	0	1	1	1	1	1	1
Zena	15	45	2865	467	0	0	0	0	0	1	1	1	1	1	1
Canon	12	67	1219	1167	0	0	0	0	0	0	1	1	0	1	1
Laurel	10	88	1554	350	0	0	0	0	0	1	1	1	1	1	1
32nd Street South	10	65	304	233	0	0	0	0	0	1	1	0	0	0	1
Pottery	10	23	45	70	0	0	0	0	0	1	0	1	1	1	0
Washington	9	83	365	187	0	0	0	0	0	1	1	1	1	1	1
Syracuse	9	27	40	70	0	0	0	0	0	1	1	1	0	1	1
Baja	8	40	670	70	0	0	0	0	0	1	1	1	1	1	1
Raffee	8	28	61	163	0	0	0	0	0	1	1	1	1	1	1
Solana	8	20	550	187	0	0	0	0	0	1	1	0	0	1	0
Acuna	7	31	110	47	0	0	0	0	0	1	1	1	1	1	1
Juan	7	32	228	70	0	0	0	0	0	1	0	0	0	1	1
Chollas	6	45	1005	467	0	0	0	0	1	1	1	1	1	1	1
Mil Cumbres	6	20	550	23	0	0	0	0	0	1	1	0	0	1	1
Chateau	6	29	110	47	0	0	0	0	0	1	1	0	0	1	1
Oak Crest	6	15	400	140	0	0	0	0	0	1	0	0	1	1	1
54th	4	29	609	187	0	0	0	0	0	1	0	1	0	1	1
60th	4	46	335	350	0	0	0	0	0	1	0	1	0	0	1
Spruce	4	95	1767	93	0	0	0	0	0	1	1	1	1	1	1
Titus	3	86	280	163	0	0	0	0	0	1	1	1	1	1	1
Montanosa	3	11	91	93	0	0	0	0	0	1	0	0	0	1	1
El Mac	2	41	883	163	0	0	0	0	0	1	1	1	1	0	1
Poinsettia	2	59	350	350	0	0	0	0	0	0	1	0	1	1	1
Talbot	2	64	1219	933	0	0	0	0	0	0	1	1	1	1	1
Urban fragment occupancy					0	0	0	0	2	26	25	21	19	26	25
Total occupancy					2	2	3	7	11	36	34	30	28	34	26

I established a series of track-detection stations at approximately 250-m intervals along dirt roads or trails (human and/or wildlife) along the main axis of each study area (Linhart & Knowlton 1975; Conner et al. 1983; Sargeant et al. 1998). Each track station consisted of a 1-m-diameter, 1-cm-deep, circle of freshly sifted gypsum baited with a liquid carnivore scent lure (Russ Carman's Pro-Choice and Canine Call, Sterling Fur & Tool, Sterling, Ohio) every other day. Track transects were checked and reset daily for 5 consecutive days. Tracks on each station were measured and identified to species; tracks with ambiguous identifications were omitted from analyses. Track surveys were conducted once each sampling quarter: fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Each site was sampled for 1–2 years.

The track index of each carnivore species in each quarterly sampling session was expressed as the total number of visits recorded for a species, divided by the total sampling effort. I defined a visit as at least one track of a species on a track station (Conner et al. 1983). Mathematically, the track index (I) was calculated as

$$I = \ln[\{v_j/(s_j n_j)\} + 1],$$

where v_j is the number of stations visited by a species in transect j, s_j is the number of stations in transect j, and n_j is the number of nights that stations were operative in transect j. Thus, I for each species represents the visitation rate per track station per night in each study area. Although this index cannot be directly translated into numbers of individuals and hence does not measure absolute densities, it does provide an index of the relative abundance of a species at each sampling point (Conner et al. 1983; Sargeant et al. 1998). For each species, I averaged track indices across quarterly sampling sessions to derive a mean index at each study area for the duration of the study. Indices were log-transformed to meet normality assumptions in the statistical analyses. Overall, track surveys totaled 6540 station-nights ($s_j n_j$) among all study sites.

Landscape Variables

I used area, age, and isolation to assess the effects of landscape-level fragmentation on carnivore populations (Table 1). I measured the total area of each fragment based on digitized images of scaled aerial photographs taken in 1995. Total area of each control site was defined as the reserve boundaries within which the surveys were conducted. Because control sites were often adjacent to unfragmented habitat, area approximations represent minimum estimates.

Fragment age, defined as the number of years since isolation of the habitat fragment by urban development, was based on dated aerial photographs and building permit records (Soulé et al. 1988). Because fragment age is

highly negatively correlated to the proportion of native shrub cover within fragments (Suarez et al. 1998; Crooks et al. 2001), I used age to measure a time effect per se in the fragments and to represent the cumulative loss of native habitat in the entire fragment since isolation. Age was scored as zero for control sites that were directly adjacent to larger natural areas (Miramar Marine Corps Air Station, Starr Ranch Audubon Sanctuary, Tenaja Corridor) or that were separated from such areas by only a roadway and not by urban development (Chino Hills State Parks, Limestone Canyon/Whiting Ranch, Santa Margarita Ecological Reserve, Torrey Pines State Reserve, Weir Canyon).

Two variables were calculated to characterize the degree of isolation of each site: distance Y, the distance to the closest habitat patch (measured from patch edge to patch edge) of equal or larger size (Soulé et al. 1988), and distance Z, the shortest distance to any other habitat fragment, reserve, or possible movement linkage to such sites (e.g., riparian channels, power line easements, golf courses). Isolation was scored as zero for control sites directly adjacent to a larger natural area and as the width of the roadway for control sites isolated from larger habitat blocks by a roadway.

All landscape variables were log-transformed to meet normality assumptions in the statistical analyses. When only the urban habitat fragments were considered, fragment age was positively related to distance Y ($r = 0.564$, $p = 0.001$) and distance Z ($r = 0.526$, $p = 0.003$), and distance Y was positively related to distance Z ($r = 0.362$, $p = 0.053$). When both habitat fragments and control areas were included, area was negatively related to age ($r = -0.813$, $p < 0.001$), distance Y ($r = -0.467$, $p = 0.003$), and distance Z ($r = -0.299$, $p = 0.065$); age was positively related to distance Y ($r = 0.741$, $p < 0.001$) and distance Z ($r = 0.597$, $p < 0.001$); and distance Y was positively related to distance Z ($r = 0.761$, $p < 0.001$).

SPECIES RICHNESS AND DISTRIBUTION

Island biogeography theory predicts that landscape variables such as size and isolation should help determine the number of species on islands (MacArthur & Wilson 1967). To test this prediction, I calculated two measures of carnivore species richness for each study area: (1) the number of carnivore species detected at the site during the course of the study and (2) the number of native carnivore species detected, excluding the non-native opossum and domestic cat. A species was present in a study area if it was detected on track stations within the site at least once during the course of the study. Presence was verified with a combination of remotely triggered cameras, scat surveys, and opportunistic visual sightings. Presence of a species does not necessarily imply that the site can support resident animals or populations. Like-

wise, failure to detect a species at a site does not indicate that the species has never visited the area, but rather that it was not recorded during sampling sessions.

I used backward-elimination multiple regression to identify which landscape variables (size, age, and isolation) were the best predictors of carnivore species richness in a study site. Independent variables with $p < 0.15$ were included in all regression models to minimize exclusion of important predictors from the model, and tolerance values were set at 0.10 throughout to control for multicollinearity (Tabachnick & Fidell 1996). Comparison-wide error rates were examined in all statistical analyses (Mead 1988; Stuart-Oaten 1995) ($p < 0.05$, statistically significant; $0.05 < p < 0.10$, marginally significant). I first conducted the multiple-regression analyses including only the 29 urban habitat fragments and then including all 39 study sites.

I used logistic-regression analyses to evaluate the effect of landscape variables on the distribution of individual carnivore species. First, I constructed bivariate logistic-regression models to evaluate the separate effects of area and isolation (distance Z) on the probability of occurrence for each species across all 39 study sites. Area and distance Z were chosen because preliminary analyses indicated that they were the two strongest predictors of carnivore distribution. For species with significant area and isolation effects, I plotted logistic-regression curves of the probability of occurrence of each species as a function of area, holding isolation constant by substituting its median value into a two-way (area $\times$ isolation) logistic model. Likewise, I constructed isolation curves after holding area constant by substituting its median value into the two-way logistic model. From these curves, I calculated the area and isolation at which the probability of occurrence of the species equaled 50% and used these estimates to represent the relative area and isolation requirements for each species (following Crooks et al. 2001). Finally, I used multiple-logistic-regression models to graphically evaluate the combined effect of area and isolation on probability of occurrence for each species.

Logistic-regression estimates of probability of occurrences and relative area and isolation requirements are not intended, however, to represent the actual fragment size or isolation necessary to ensure the long-term persistence of a population (Hinsley et al. 1996). Rather, probability of occurrence measures the probability of an individual visiting the study area at least once during the course of the study, and the area and isolation estimates generated are intended to function only as relative indices of sensitivity to fragmentation. Area and isolation estimates are likely to be more accurate for those species with the most detections.

RELATIVE ABUNDANCE

I used backward-elimination regression models to identify which landscape variables were the best predictors

of the track indices of each species in each study area. The analyses were first conducted including only the 29 urban habitat fragments. Mountain lions, spotted skunks, badgers, and long-tailed weasels were omitted from these analyses because they were not detected in any urban habitat fragments. Bobcats, detected in only two fragments, were also omitted.

I repeated the multiple-regression analyses across all 39 fragments and control sites, including mountain lions and bobcats in the analyses. Spotted skunks, badgers, and long-tailed weasels were again omitted due to low detection rates. Because the track indices for mountain lions and bobcats were zero for many sites, the results of these regressions must be interpreted with caution. The final regression models were determined largely by the patterns of species' presence or absence across sites and not by variation in relative abundance among sites where they occurred. Nevertheless, I report regression models for mountain lions and bobcats to allow for further evaluation of the effects of landscape variables on these species and for further comparisons of their fragmentation sensitivities to those of other carnivore species.

Local Variables

Habitat heterogeneity within these urban habitat fragments is an important determinant of the persistence of native scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000), all potential prey for carnivore species. I measured three variables to investigate the effect of habitat heterogeneity on carnivore populations: distance to the urban edge, percent cover of native shrubs, and percent cover of exotic vegetation. I estimated the distance of each track station to the nearest urban edge (the backyards of the houses bordering the fragment) and log-transformed these values to meet normality assumptions in the statistical analyses. I used a Braun-Blanquet categorical scale (Kent & Coker 1992) to estimate the percent cover of native shrubs and of total exotic cover within a 20-m radius around each track station. The cover scale was 0 (<1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), and 5 (76–100%). Distance to edge was positively related to shrub cover ($r = 0.281$, $p = 0.007$) and negatively related to exotic cover ($r = -0.341$, $p = 0.001$), and shrub cover was negatively related to exotic cover ($r = -0.694$, $p < 0.001$).

SPECIES RICHNESS AND RELATIVE ABUNDANCE

I calculated the total number of carnivore species and the number of native carnivore species detected at each track station in the 29 urban habitat fragments during the course of the study; two exotic species (opossum and domestic cat) and five native species (bobcat, coyote, gray fox, striped skunk, and raccoon) were detected

in the urban fragments and were hence included in the analyses. I then used backward-elimination multiple regression to identify which local variables were the best predictors of carnivore species richness at each station.

I calculated the mean track index for each species at each track station in the 29 urban habitat fragments to generate relative abundance indices. Again, mountain lions, spotted skunks, long-tailed weasels, badgers, and bobcats were omitted from these analyses due to low detection rates within fragments. I then used backward-elimination multiple regression to identify which local variables were the best predictors of the relative abundance of each species at a station. Some species were absent from some fragments, however, an absence driven in part by landscape variables such as area, age, and isolation. I therefore conducted the regressions for each species after excluding from the analyses all fragments where that species was never detected. By excluding these fragments I could account for the effects of landscape-level fragmentation on the presence or absence of a species and therefore more fully analyze the effects of local variables within fragments where that species occurred.

To further evaluate the effect of the urban edge on carnivores within fragments, for each species I graphed the mean track index at each station as a function of the distance of that station from the urban edge. Edge distances were classified into five categories: 0–24 m ($n = $ 14 stations), 25–49 m ($n = 35$), 50–99 m ($n = 16$), 100–199 ($n = 19$), and >200 m ($n = 7$). Direct comparisons of track indices between species can be misleading, because the response of species to track stations may differ (Conner et al. 1983; Sargeant et al. 1998). To allow for more meaningful comparisons of track indices, I standardized the index for each species by dividing each value by the maximum track index recorded for that species. Therefore, these standardized track indices for each species ranged on a scale of 0 to 1.

Body Size and Fragmentation Sensitivity

I evaluated the relationship between body mass and sensitivity to fragmentation among carnivore species through linear-regression analysis. As an index of sensitivity to fragmentation, I calculated the average area of study sites occupied by each species, multiplying the area of each study site by the standardized track index (scale 0 to 1) of that species at that site. With area weighted by relative abundance per sampling point, the indices accounted not just for occupancy but also for differences in the relative abundance of a species among study sites. For example, for a given species, some study sites supported resident populations, whereas other study sites were only visited temporarily during the course of the study. Average area weighted by relative abundance accounted for such differences. In addition, I also compared body mass to typical home-range sizes and population densities reported in the literature for these species.

Results

Landscape Heterogeneity: Comparisons among Fragments

SPECIES RICHNESS AND DISTRIBUTION

The distribution of carnivore species varied across study sites (Table 1). Coyotes, opossums, gray foxes, domestic cats, striped skunks, and raccoons were detected in most urban fragments. Bobcats were detected in 9 of the 10 control sites but in only 2 urban habitat fragments, and mountain lions were detected in only 7 control sites and no urban fragments. I recorded few to no visits of mountain lions and bobcats in the habitat fragments, despite higher sampling intensity per unit area (station-nights/total area of site) in the 29 fragments (mean = 8.30 station-nights/ha, SE = 0.910) than in the 10 control sites (mean = 0.43 station-nights/ha, SE = 0.158) ($t = 4.58$, $p < 0.001$). Detections of spotted skunks, long-tailed weasels, and badgers were rare and occurred only in the larger habitat blocks.

Among the 29 urban habitat fragments, no landscape variables were retained as predictors of the total number of carnivore species in backward-elimination regression models (Table 2). When the opossum and domestic cat were excluded, however, the species richness of native carnivores exhibited a weak negative trend with fragment isolation (distance Z) and a weak positive trend with fragment age. When control sites were included in the analyses, both total carnivore species richness and native carnivore species richness increased with the area of the study site.

Logistic-regression models for each species indicated that the probability of occurrence across all sites was positively related to fragment area for coyotes ($\chi^2 = 5.57$, $p = 0.018$), bobcats ($\chi^2 = 29.85$, $p < 0.001$), mountain lions ($\chi^2 = 27.35$, $p < 0.001$), spotted skunks ($\chi^2 = 5.85$, $p = 0.016$), long-tailed weasels ($\chi^2 = 5.37$, $p = 0.021$), and badgers ($\chi^2 = 9.73$, $p = 0.002$). In contrast to these native carnivores, the probability of occurrence of domestic cats was higher in smaller fragments ($\chi^2 = 22.63$, $p < 0.001$). Area was not a significant predictor of probability of occurrence for gray foxes ($\chi^2 = 0.24$, $p = 0.627$), striped skunks ($\chi^2 = 1.81$, $p = 0.178$), raccoons ($\chi^2 = 2.02$, $p = 0.155$), or opossums ($\chi^2 = 0.357$, $p = 0.550$).

Logistic-regression models indicated that probability of occurrence across all sites decreased with fragment isolation (distance Z) for coyotes ($\chi^2 = 6.92$, $p = 0.008$), bobcats ($\chi^2 = 11.57$, $p < 0.001$), and mountain lions ($\chi^2 = 11.88$, $p < 0.001$). In contrast, probability of oc-

Table 2.   Backward-elimination regression models of the effects of landscape variables on carnivore species richness and relative abundance among 29 urban habitat fragments and 10 control sites in coastal southern California.[a]

Variables	R^2	Whole-model p	Coefficient	p
Urban habitat fragments				
total species richness				
n.s.[b]				
native species richness	0.146	0.129		
distance Z			−0.408	0.067
age			+0.374	0.091
coyote	0.133	0.052		
area			+0.365	0.052
gray fox	0.114	0.074		
area			−0.336	0.074
domestic cat	0.393	0.002		
area			−0.550	0.001
distance Z			+0.246	0.122
opossum	0.164	0.029		
area			−0.405	0.029
striped skunk				
n.s.				
raccoon				
n.s.				
All sites				
total species richness	0.194	<0.001		
area			+0.440	<0.001
native species richness	0.372	<0.001		
area			+0.610	<0.001
coyote	0.15	0.015		
area			+0.388	0.015
bobcat	0.595	<0.001		
age			−0.921	<0.001
distance Y			+0.607	0.004
distance Z			−0.376	0.030
mountain lion	0.277	<0.001		
age			−0.526	<0.001
gray fox	0.197	0.005		
area			−0.444	0.005
raccoon	0.081	0.081		
area			−0.284	0.081
domestic cat	0.335	<0.001		
area			−0.579	0.001
opossum	0.241	0.002		
area			−0.491	0.002
striped skunk				
n.s.				

[a]*Independent variables are fragment area, age, and isolation (distance* Y *and distance* Z). *Independent variables with* p < 0.15 *were included in the final regression models.*
[b]*No independent variables were retained in the regression model (*p > 0.15); n.s., not significant.*

currence was higher in more isolated fragments for domestic cats ($\chi^2 = 4.25$, $p = 0.039$). Isolation was not a significant predictor of probability of occurrence for gray foxes ($\chi^2 = 0.35$, $p = 0.553$), opossums ($\chi^2 = 1.88$, $p = 0.171$), spotted skunks ($\chi^2 = 0.18$, $p = 0.671$), striped skunks ($\chi^2 = 0.69$, $p = 0.407$), raccoons ($\chi^2 = 0.06$, $p = 0.811$), long-tailed weasels ($\chi^2 = 1.74$, $p = 0.187$), or badgers ($\chi^2 = 2.62$, $p = 0.106$).

After I controlled for isolation effects, the estimated area at which probability of occurrence was 50% was 1 ha for coyotes, 1.8 km² for bobcats, and 23 km² for mountain lions (Fig. 1a). The probability of occurrence

for domestic cats dropped below 50% in fragments larger than 1.4 km²; cats were never detected in the interior of control sites, and few if any feral cats occurred in these sites.

After I controlled for area effects, the estimated fragment isolation (distance Z) at which probability of occurrence was 50% was 883 m for coyotes and 6 m for bobcats (Fig. 1b). The probability of occurrence for mountain lions was <50% across the entire isolation range of fragments. In contrast, the probability of occurrence for domestic cats was >50% across the entire range of fragment isolation.
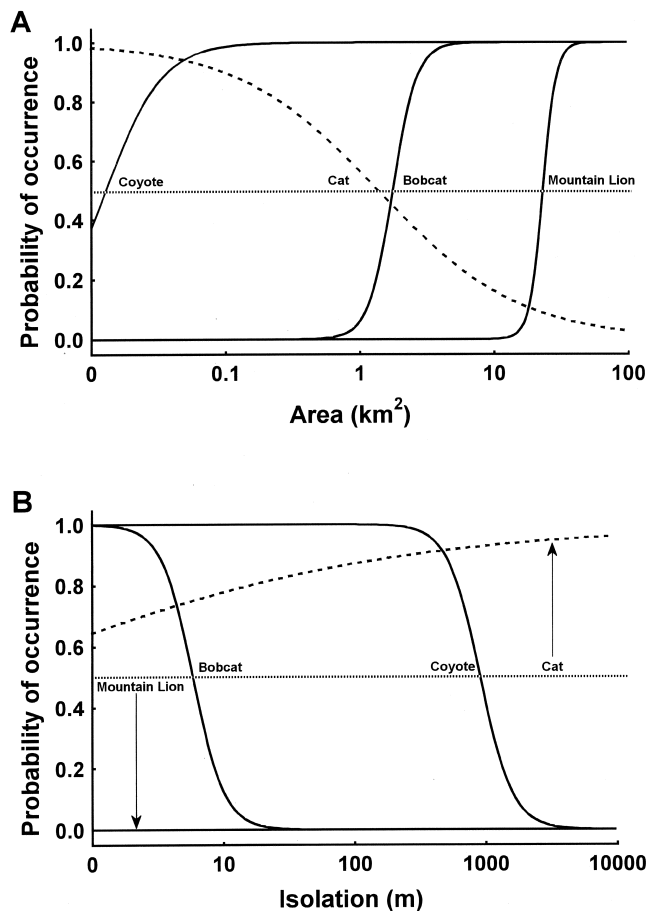
Figure 1. Logistic-regression models of the probability of occurrence of native (solid lines) and exotic (dashed line) carnivores as a function of (a) fragment area and (b) isolation. Area and isolation curves were constructed after the other independent variable was held constant by substituting its median values into a two-way (area × isolation) logistic-regression model. Only species with significant area and isolation effects are presented. Dotted line represents 50% probability of occurrence.

Multiple logistic-regression models of the combined effect of area and isolation on mountain lions, bobcats, and coyotes generated "extinction surfaces" that consisted of plateaus of occupancy at larger and less isolated sites that declined to basins of local extinctions at small and isolated fragments (Fig. 2). The effect of the area-isolation interaction, and hence the contour of the extinction surfaces, varied among species. The plateau for mountain lions was small and occurred only in the largest unfragmented sites, with large basins across all other study areas. The plateau for bobcats spanned a wider range of sites, but probability of occurrence dropped to zero in sites that were both small and isolated. Bobcats occurred in relatively small sites, but only those with little to no isolation. The plateau of coyotes was large, with

a low probability of occurrence in only the smallest, most isolated urban fragments. Domestic cats exhibited a surface that was the inverse of these native predators. Their probability of occurrence was high in small and isolated fragments but lower in larger, less fragmented sites.

It should be emphasized, however, that the probability of residency or long-term viability of populations is undoubtedly lower than these probabilities of occurrence, particularly in smaller and isolated sites. For example, coyotes visited some fragments only temporarily during the course of the study. In some quarterly sampling sessions they were detected and in others they were not. Although the plateau of occupancy for coyotes encompassed most combinations of area and isolation, residency declined with fragment area. The average area of the 13 fragments in which coyotes came and went (mean = 0.75 [5.6 ha back-transformed], SD = 0.20) was smaller ($t = 3.01$, $p = 0.006$) than the average area of the 13 fragments in which coyotes were detected in every quarterly sampling session (mean = 1.19 [15.6 ha back-transformed], SD = 0.95).

RELATIVE ABUNDANCE

When only the 29 urban habitat fragments were included in the analyses, the relative abundance of coyotes at each sampling point was higher in larger fragments, whereas track indices of gray foxes, domestic cats, and opossums were higher in smaller fragments (Table 2). No variables were retained in the final model for raccoons and striped skunks ($p > 0.15$).

When control sites were also included in the regressions, coyote track indices at each sampling point again tended to be higher in larger sites. In contrast, the track indices of gray foxes, domestic cats, opossums, and raccoons were higher in smaller sites (Table 2). No landscape variables were retained in the models for the relative abundance of striped skunks.

When control sites were included in the regression models, fragment age was retained as the most significant predictor of the relative abundance of mountain lions and bobcats (Table 2); both species were less abundant in older sites. Mountain lions and bobcats were detected in relatively few sites, most of which were control areas not isolated by urban development (age = 0) and, for bobcats, a couple of recently isolated fragments (Table 1). This pattern generated the significant, negative slope between relative abundance and age for the two species.

The relative abundance of bobcats decreased with distance to the nearest movement linkage or natural area (distance Z) but, paradoxically, increased with distance to the nearest habitat patch of equal or larger size (distance Y). Bobcats were detected at sites that were relatively distant from larger natural areas (high values of

Bobcat

Domestic Cat
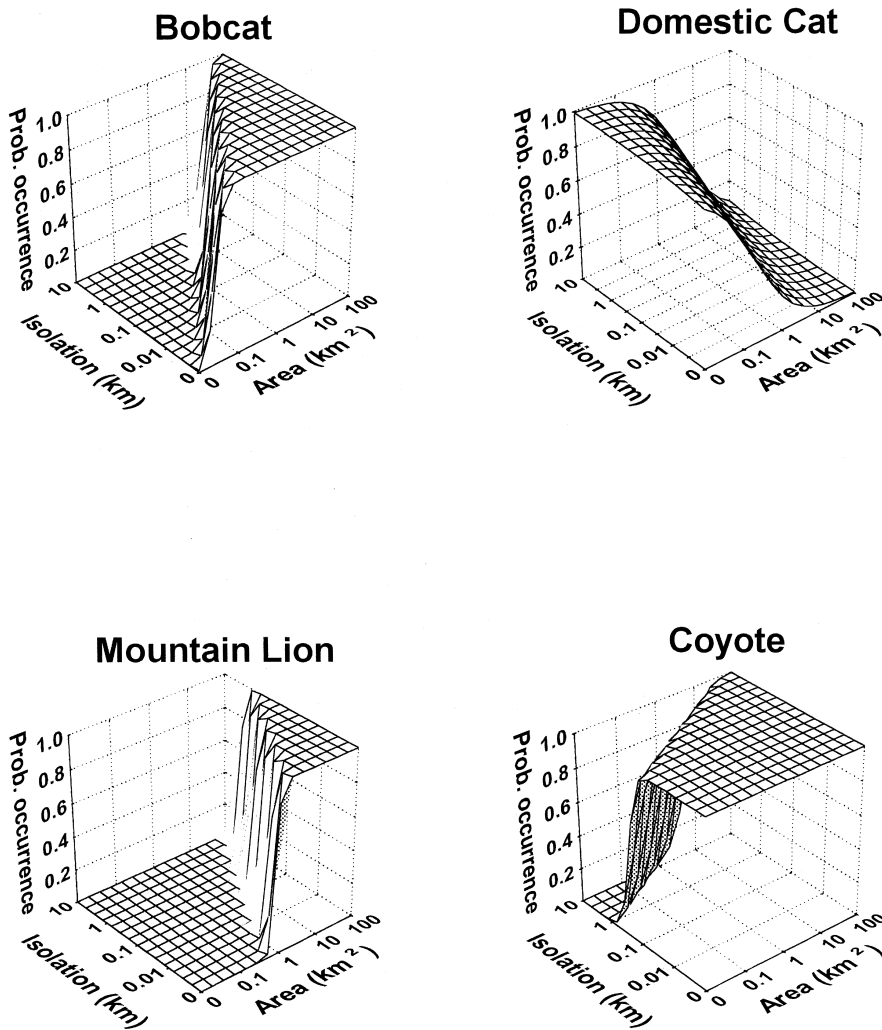
Mountain Lion

Coyote

Figure 2. Multiple logistic-regression models of the probability of occurrence of mountain lions, bobcats, coyotes, and domestic cats as a function of fragment area and isolation. Only species with significant area and isolation effects are presented.

distance Y), but only if they were large or were near movement linkages to larger habitat blocks (low value of distance Z). For example, bobcats have persisted in the San Joaquin Hills, an isolated (distance Y = 5353 m) but large (4219 ha) habitat block. Bobcats were also detected in Mil Cumbres, a small (6 ha) urban fragment that was isolated from larger natural areas (distance Y = 550 m) but that was near a golf course (distance Z = 23 m), which likely served as a movement linkage to natural areas to the east.

Local Heterogeneity: Comparisons within Fragments

SPECIES RICHNESS AND RELATIVE ABUNDANCE

The number of carnivore species detected was greater at track stations closer to the urban edge (Table 3). This pattern was largely determined by non-native species. When exotic predators (domestic cats, opossums) were excluded from the analyses, the number of native species detected at each station did not vary significantly with any local variables.

The relative abundance of gray foxes and opossums was higher at track stations near the urban edge within fragments where each species occurred (Table 3). The abundance of domestic cat exhibited a weak negative trend with distance to urban edge. The relative abundance of striped skunks tended to be higher at greater distances from the urban edge. Domestic cats and raccoons tended to be more abundant at stations with more exotic cover. No local variables entered the model for the relative abundance of coyotes.

A graphical analysis revealed that the coyote rate of visitation to track stations was high both near the urban edge and into the interior of the urban habitat fragments (Fig. 3). The abundance of striped skunks also was relatively high in the interior of fragments. In contrast, the abundance of opossums, gray foxes, domestic cats, and raccoons was relatively high within 50 m from urban development, but then tended to decline into the interior of the habitat fragment.

Body Size and Fragmentation Sensitivity

When all species were included in the regression, the relationship between body mass (Table 4) and the average

Table 3. Backward-elimination regression models of the effects of local habitat variables on carnivore species richness and relative abundance at 92 track stations within 29 urban habitat fragments in southern California.[a]

Variables	R^2	*Whole-model* p	*Coefficient*	p
Total species richness	0.049	0.036		
edge			−0.222	0.036
Native species richness				
n.s.[b]				
Coyote (87 stations)				
n.s.				
Gray fox (85)	0.146	<0.001		
edge			−0.382	<0.001
Striped skunk (69)	0.042	0.095		
edge			0.205	0.095
Raccoon (62)	0.056	0.066		
exotic			0.237	0.066
Domestic cat (73)	0.143	0.005		
exotic			0.242	0.057
edge			−0.205	0.105
Opossum (79)	0.079	0.013		
edge			−0.281	0.013

[a]*Independent variables are distance to urban edge, native shrub cover, and total exotic cover. Independent variables with p < 0.15 were included in the final regression models. For each species, stations were included only in analyses for those fragments where the species was detected.*
[b]*No independent variables were retained in the regression model (p > 0.15); n.s., not significant.*

area of study sites occupied by each carnivore species, weighted by the standardized track index of each species at each site, was not significant ($r = -0.392$, $p = 0.233$) (Fig. 4a). Spotted skunks, long-tailed weasels, and badgers, however, appeared to be outliers to an otherwise positive relationship between body size and average area of sites occupied. When these three species were excluded from the regression, the positive relationship was significant ($r = 0.725$, $p = 0.042$). Body mass was also positively related to typical home-range sizes (Fig. 4b: $r = 0.720$, $p = 0.012$) and negatively related to typical population densities (Fig. 4c: $r = -0.705$, $p = 0.015$) recorded for these species (Table 4).

Discussion

Landscape Heterogeneity and Carnivore Populations

Fragment area and isolation were the two strongest landscape predictors of predator distribution and abundance. Badgers, long-tailed weasels, spotted skunks, mountain lions, bobcats, and coyotes appear to be the species most sensitive to fragmentation, with a lower probability of occurrence and relative abundance per unit area in smaller and more isolated habitat patches. In contrast, the probability of occurrence and relative abundance of domestic cats, gray foxes, and opossums tended to decrease with fragment area and increase with fragment isolation. Landscape descriptors had relatively little effect on the distribution and abundance of raccoons and striped skunks. Because some carnivores

were fragmentation-sensitive, some fragmentation-enhanced, and some fragmentation-tolerant, landscape variables appear to affect species composition more than species richness.

The probability of occurrence of mountain lions, bobcats, and coyotes declined in sequence as habitat patches became smaller and more isolated (Fig. 1). Because mountain lions, bobcats, and coyotes generally occurred in fragments above some threshold of size and isolation, local extinctions of their populations in a fragmenting landscape appear deterministic and predictable (Brown 1986). Such thresholds also suggest that, depending on the species and the degree of fragmentation, a single large reserve would have a higher probability of supporting populations of these predators than archipelagos of similar but smaller isolates (Soulé & Simberloff 1986). For example, our models predict that the probability of occurrence of bobcats will be low in 10 1-km^2 isolates but higher in a 10-km^2 reserve, and that the probability of occurrence of mountain lions will be low in 10 10-km^2 isolates but higher in a 100-km^2 reserve (Fig. 1).

Unlike true islands, habitat patches are part of a landscape mosaic, and the presence of a given species in a patch may be a function not only of patch size and isolation, but also of how the species perceives the intervening matrix (Andren 1994; Rosenblatt et al. 1999). In previous studies in this system, fragment age and area were the most important landscape predictors of the distribution and abundance of native plants (Alberts et al. 1993), scrub-breeding birds (Soulé et al. 1988; Crooks et al. 2001), rodents (Bolger et al. 1997), and invertebrates
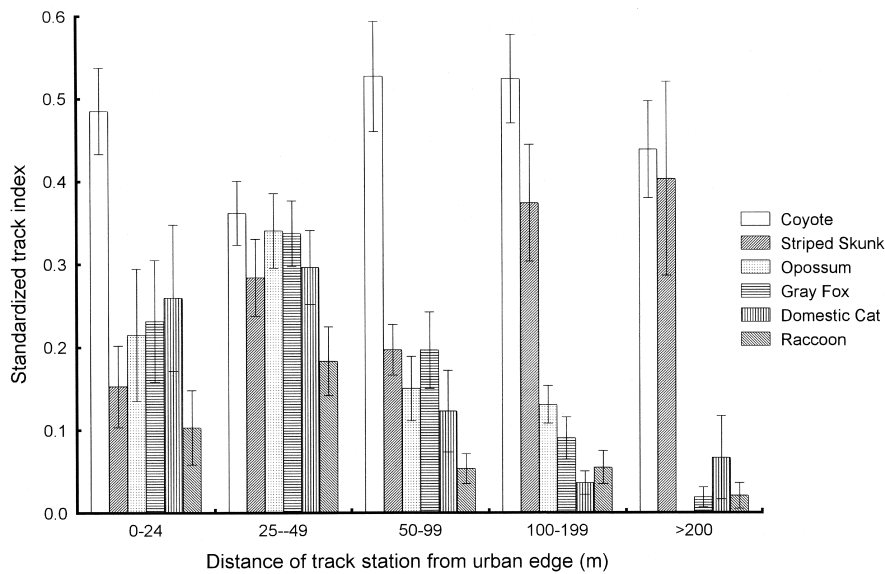
Figure 3. Track indices of carnivore species within urban habitat fragments as a function of the distance of the station from the urban edge. Track indices are standardized for each species.

(Suarez et al. 1998; Bolger et al. 2000). With limited exceptions, isolation effects were absent for these species, likely due to their strict habitat requirements and low dispersal capabilities (Soulé et al. 1992). For these taxa, little to no dispersal across developed areas resulted in complete isolation once fragmentation had occurred, with the fragments operating as true islands immersed within a relatively inhospitable matrix. My results also indicate that fragment isolation was not a strong predictor of the distribution and abundance of human-tolerant mesopredators, although the causal mechanisms differed. Unlike many native scrub-breeding birds, rodents, and invertebrates, mesopredator species such as raccoons, striped skunks, opossums, and domestic cats move through and reside within developed areas and thus perceive the urban matrix as somewhat permeable. High rates of movement through the matrix within

which fragments are embedded should also minimize the effects of fragment isolation.

Local Heterogeneity and Carnivore Populations

Within the urban fragments, exotic cover and distance to the urban edge were the strongest local predictors of carnivore distribution and abundance. These two variables were correlated, with more exotic cover and less native shrub cover closer to the urban edge. Previous studies have found that scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000) require native vegetation to persist in these fragments. Unlike many of these species, however, the mammalian carnivores detected in the habitat fragments are resource generalists that likely benefit from the supplemental food resources

Table 4.   Ecological characteristics of mammalian carnivores detected in coastal southern California.[a]

Species	Weight (kg)	Home range (km²)	Density (km²)	Reference
Mountain lion	69.5 (36.0–103.0)	492 (112–829)	0.027 (0.005–0.048)	Beier & Barrett 1993; Nowak 1999
Coyote	13.5 (7.0–20.0)	5.69 (0.66–11.96)	0.3 (0.2–0.4)	Nowak 1999; Sauvajot et al. 2000
Bobcat	9.7 (4.1–15.3)	2.94 (0.24–5.63)	1.34 (1.15–1.53)	Lembeck 1986; Nowak 1999
Badger	8.0 (4–12)	2.0 (1.6–2.4)	2.70 (0.39–5.0)	Messick 1987; Nowak 1999
Raccoon	7.0 (2.0–12.0)	0.52 (0.39–0.65)	11.2 (2.3–20.0)	Nowak 1999
Gray fox	4.4 (1.8–7.0)	0.69 (0.22–1.87)	5.2 (0.4–10.0)	Nowak 1999; Riley 1999
Domestic cat[b]	3.9 (3.3–4.5)	0.40 (0.001–3.80)	150 (2–500)	Barratt 1997; Nowak 1999
Opossum	3.8 (2.0–5.5)	0.20 (0.05–2.54)	26 (2–116)	Nowak 1999
Striped skunk	1.6 (0.7–2.5)	0.21 (0.11–0.37)	3.3 (1.8–4.8)	Nowak 1999
Spotted skunk	0.6 (0.2–1.0)	0.49 (0.34–0.65)	24.4 (8.8–40)	Crooks & Van Vuren 1995; Kinlaw 1995; Nowak 1999
Long-tailed weasel	0.2 (0.09–0.34)	0.62 (0.04–1.20)	19.4 (0.38–38)	Nowak 1999

[a]*Estimates of body size, home range, and population density vary considerably (Nowak 1999). Values are typical averages and ranges (in parentheses). If no average estimate was provided, median values, calculated from the ranges, are presented. Body-mass estimates were taken from Nowak (1999). Where available, home ranges and population densities were taken from studies conducted in California.*
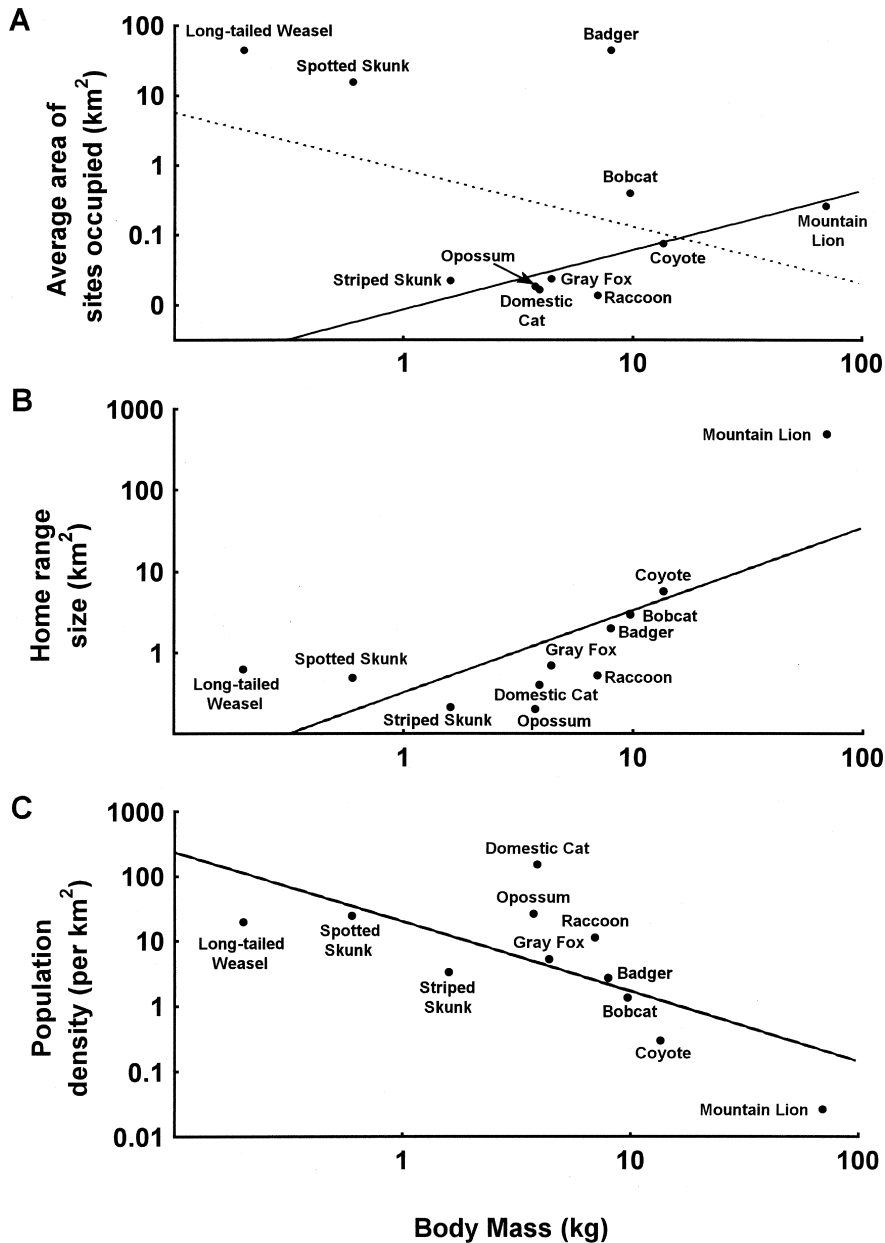[b]*Estimates include studies from suburban, urban, rural, and island cat populations.*

Figure 4. Relationship between log body mass and (a) log average area of sites occupied by mammalian carnivores, weighted by the relative abundance of each species at each site, (b) log home-range size (r = 0.720, p = 0.012; see Table 4 for values), and (c) log population density (r = −0.705, p = 0.015; see Table 4 for values). Dotted line in (a) is the least-squares regression fit including all species in the analysis (r = −0.392, p = 0.233), and the solid line in (a) is the regression excluding spotted skunks, long-tailed weasels, and badgers (r = 0.725, p = 0.042).

(e.g., garden fruits and vegetables, garbage, direct feeding by humans) associated with residential developments. As a result, the carnivore visitation rate actually increased at sites with more exotic cover and closer to the urban edge, a pattern determined largely by the increased abundance of fragmentation-enhanced mesopredators (gray foxes, opossums, and domestic cats) at edge sites within habitat fragments. Although some carnivores within the habitat fragments seem tolerant of disturbance, these fragments have already lost an entire suite of predator species, including mountain lions, bobcats, spotted skunks, long-tailed weasels, and badgers. Furthermore, the habitat fragments are relatively small (<100 ha), so the most "interior" sites within the fragments are still relatively near (<250 m) urban edges.

Unlike true islands, "edge effects" that emanate from the human-dominated matrix can increase the extinction probability of isolated populations (Murcia 1995; Woodroffe & Ginsberg 1998). Human-tolerant mesopredators in southern California represent such an edge effect. They occur within the developed matrix, are more abundant along the edges of habitat fragments, and are effective predators on birds, bird nests, and other vertebrates in this system and elsewhere (Crooks & Soulé 1999). Several factors likely account for increased numbers and activity of mesopredators in disturbed landscapes. Residential developments represent suitable habitat for some mesopredator species whose distributions are closely associated with human-dominated landscapes (Donovan et al. 1997). In addition to

habitat suitability, however, dominance interactions between carnivores affect mesopredator populations. When large, dominant predators disappear in fragmented systems, smaller, subordinant predators can subsequently undergo an ecological release, a pattern termed mesopredator release (Soulé et al. 1988; Crooks & Soulé 1999). In the San Diego habitat fragments, Crooks and Soulé (1999) found that lower visitation rates of coyotes in small, isolated remnants resulted in elevated numbers and activity of urban mesopredators, even after statistically controlling for potential confounding variables such as fragment area, age, and isolation. Mesopredator species therefore appear to be ecologically released by fragmentation not only because they can adapt well to urban environments, but also because such sites may provide refugia from dominant predators.

All Carnivores Are Not Created Equal

Although they are generally considered part of the same ecological guild, I found that carnivores were heterogeneous in their sensitivities to landscape and local fragmentation variables. As predicted, body-size differences partially accounted for this heterogeneity in response. Body mass was positively related to typical home-range sizes (Fig. 4b) and negatively related to typical population densities (Fig. 4c) recorded for these species, patterns consistent with those observed among mammals (Lindstedt et al. 1986). Due to their wide ranges and low densities, larger-bodied carnivores generally required larger areas (Fig. 4a), eventually disappearing in habitat fragments that were not connected by movement corridors. Obvious exceptions to the allometry of body size and fragmentation sensitivity, however, were spotted skunks, long-tailed weasels, and badgers, small- to medium-bodied species that exhibit relatively small home ranges and high population densities but that were detected only in the largest habitat blocks. Unlike the generalist urban mesopredators, these relatively specialized mustelids tend to be primarily carnivorous and somewhat restricted in their habitat preferences (Nowak 1999). Such specializations likely contribute to their patchy distribution in coastal southern California and increase their vulnerability to environmental disturbances. Clearly, in addition to body size, other ecological traits such as diet, resource specialization, social structure, and behavior contribute to species-specific responses to fragmentation effects.

Differential sensitivities to fragmentation can be useful criteria when focal species are chosen for ecological research and conservation planning. Mammalian carnivores can be excellent focal organisms with which to evaluate the degree of functional landscape-level connectivity, because they are area-dependent species that require movement corridors for persistence (Beier 1993;

Noss et al. 1996; Soulé & Terborgh 1999). The choice of appropriate carnivore focal species, however, depends on the scale or intensity of fragmentation in an area and the corresponding responses of carnivore populations to fragmentation effects at that scale. As Figs. 1 and 2 make evident, the scale of landscape-level connectivity in southern California varies widely, ranging from small, isolated urban remnants to large, intact habitat blocks.

At one extreme of the connectivity scale are the highly fragmented landscapes of urban coastal southern California (e.g., patch size <1 km²; Fig. 1a). Coyotes and urban mesopredators can be useful focal species with which to understand the effects of fragmentation at this scale. Fragmentation-enhanced predators such as opossums and domestic cats can function as direct, positive indicators of environmental disturbances associated with urban development, edge effects, and the invasion of exotic predators and competitors into natural systems. Coyotes have also persisted in developed areas in southern California. The remarkable behavioral plasticity of coyotes and their ability to succeed in disturbed areas limits their utility as an indicator of connectivity across much of coastal southern California. Nevertheless, coyote occupancy, residency, and relative abundance declined with fragment area and isolation, to the point of local extinctions of coyote populations in the smallest, most isolated urban remnants. Coyotes can therefore serve as useful indicators of functional connectivity in highly fragmented areas, particularly those sites that have already lost more vulnerable predators such as bobcats and mountain lions (Figs. 1 & 2). Furthermore, the ecologically pivotal role of coyotes (Crooks & Soulé 1999) warrants their inclusion in research and conservation plans, particularly in regions with active predator-control programs.

Mountain lions are situated at the opposite end of the connectivity scale (e.g., patch size >100 km²; Fig. 1a) and appear extremely sensitive to the loss and fragmentation of habitat. The large body size and solitary behavior of mountain lions translate to large home ranges and low population densities (Table 4). Therefore, many of the isolated habitat remnants in urban southern California are likely too small and too isolated to permanently support any resident lion populations (Figs. 1 & 2) (see also Beier 1993). Consequently, mountain lions or other large, apex predators may not be the most effective indicator species with which to evaluate the degree of functional landscape-level connectivity in moderately to highly fragmented landscapes. The mountain lion's requirement for a large home range and its sensitivity to environmental perturbations, however, can make it a valuable focal species in larger, more intact habitat blocks (Beier 1993).

Finally, bobcats were intermediate in their sensitivity to fragmentation, a degree of sensitivity commensurate to the scale of fragmentation across much of coastal

southern California (e.g., 1 km^2 <patch size < 100 km^2; Fig. 1a). Bobcats were less sensitive to disturbance than mountain lions, which seldom occurred in fragmented areas, yet were more sensitive than coyotes and meso-predators, which were detected in even small urban habitat fragments. Bobcats are generally solitary and are strictly carnivorous (Nowak 1999), resulting in low densities and in resource specializations that likely increase their probability of local extinction. Landscape connectivity appears to be the key to the persistence of bobcat populations in developing landscapes. They can persist in fragmented habitats, but, as my results suggest, only in those landscapes with adequate movement linkages to larger natural areas. The status of bobcat populations is therefore a valuable indicator of the degree of functional, landscape-level connectivity across much of the fragmented landscapes of coastal southern California. In other systems, the choice of indicator species will require information on the level of fragmentation and connectivity in that region and how species respond to fragmentation effects at that scale.

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